Modelling height, height growth and site index from national forest inventory data in Norway

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Department of Ecology and Natural Resource Management
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Preface

This thesis has been submitted to the Department of Ecology and Natural Resource Management (INA), Norwegian University of Life Sciences as a part of my PhD studies. Approval of thesis, academic training, trial lecture, and public defense are four main components for completion of PhD degree. The Norwegian State Educational Loan Fund supported my PhD studies.

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Ram P. Sharma,
August 2013, Ås

Contents

Abstract

The present study aimed to develop dominant height growth models, site index prediction models, individual tree height growth models, and height-diameter models using Norwegian national forest inventory (NFI) data. Data from other sources such as long-term experiment (LTE), stem analysis and meteorological stations were used as supplementary data. Data from Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.) and downy birch (*Betula pubescens* (Ehrh.)) were used. Since primarily designed for other objectives, NFI data have various weaknesses (measurement errors, small sample plot size, few height sample trees, and short time series) that were challenging modelling in the present study. Despite these challenges, various forest models were developed. The thesis contains four individual papers addressing the individual objectives as pointed out above.

Paper I presents dominant height growth models that were developed using the generalized algebraic difference approach. Model parameters were estimated using nested regression techniques. NFI data models showed significant bias for young stands and higher site index classes when compared with LTE data. Therefore, NFI data and LTE data were pooled to develop combined data models. These models showed no significant bias for any ages and site index classes for both NFI and LTE data. The combined data models showed no significant bias when tested on independent stem analysis data and on region-specific model fitting data for Norway spruce and Scots pine.

Paper II presents site index prediction models that were developed using the site index as a function of site and climate variables. Significant time trends in observed site indices were included in the site index prediction models. Among various models developed, a model including year of stand origin, temperature sum, understory vegetation type, soil depth, aspect, slope, and latitude described the largest proportion of the total variation in site indices for both Norway spruce and Scots pine. Analyses showed that site index increased after about 1940, which might be due to increased temperature and precipitation, and various other reasons.

Paper III presents both spatially explicit and spatially non-explicit individual tree height growth models developed using a potential modifier function that reduces the potential height growth (Paper I) to the expected height growth of individual trees. Parameters in competition indices and parameters in the potential modifier models were estimated simultaneously from the data.

Under strong competition, height growth was substantially reduced for both Norway spruce and Scots pine. For Scots pine, height growth was also reduced under very low competition.

Paper IV presents height-diameter models, which were developed incorporating stand variables that are independent of thinning as covariates and sample plot-level variations as random effects. For all three species, generalized mixed effects models predicted heights without substantial bias when the random effects were predicted using all measured heights of the focused species (species used to develop species-specific model) per sample plot.

The present study successfully developed methods to fit models to the NFI data that were not collected for growth modelling proposes. The models substantially improved the current models, which have been applied in an individual tree based forest simulator-T. Therefore, all models presented in the thesis may be used in future Norwegian forest simulators.

List of papers

Paper I

Sharma, R.P., Brunner, A., Eid, T. and Øyen, B.-H., 2011. Modelling dominant height growth from national forest inventory individual tree data with short time series and large age errors. *Forest Ecology and Management*, 262(12): 2162-2175.

Paper II

Sharma, R.P., Brunner, A. and Eid, T., 2012. Site index prediction from site and climate variables for Norway spruce and Scots pine in Norway. *Scandinavian Journal of Forest Research*, 27(7): 619-636.

Paper III

Sharma, R.P. and Brunner, A. Modelling individual tree height growth of Norway spruce and Scots pine from national forest inventory data in Norway (in review).

Paper IV

Sharma, R.P., and Breidenbach, J. Modelling height-diameter relationships for Norway spruce, Scots pine, and downy birch using Norwegian national forest inventory data (submitted).

1. Introduction

Forest site productivity may be assessed in different ways, but commonly used methods are site index models (dominant height growth models) and site index prediction models (site index prediction from site variables). Such models are fundamental components of growth and yield models, and therefore need to be precise over the entire range of forest growth conditions. A challenge with the existing and most frequently applied Norwegian site index models (Tveite, 1977; Tveite and Braastad, 1981) and site index prediction models (Nilsen and Larsson, 1992) is that they do not properly represent the entire range of forest growth conditions in Norway. The site index models are lacking data from the western and northern parts of Norway, and are therefore likely to be biased for these regions (Blingsmo, 1985; Øyen and Nes, 1997; Tveite, 1994; Orlund, 2001). Site index models are also dominant height growth models, and may therefore be used to predict maximum possible (potential) height growth in individual tree based growth models (e.g. Pretzsch et al., 2002). However, the presently applied Norwegian site index models (Tveite, 1977; Tveite and Braastad, 1981) cannot be used for the purpose, because the potential height growth derived from them is inconsistent and unrealistic, i.e., height growth culminates at unrealistic ages. Also, the site index prediction models developed by Nilsen and Larsson (1992) are lacking data from large parts of the Norwegian forests. Another challenge is that significant age trends in the residuals of these models were observed, but age was not included in the models. Bøhler and Øyen (2011) tested the models for samples of Norway spruce and found biased site index predictions.

A large part of the Norwegian productive forests is uneven-aged, a mixture of species, or of heterogeneous structure (NIJOS, 2000). For a description of the dynamics of such forests regarding radial (diameter or basal area) growth, individual tree diameter and basal area growth models have been developed (Andreassen and Tomter, 2003; Bollandsås et al., 2008; Bollandsås and Næsset, 2009). However, individual tree height growth models are still lacking for Norway to describe forest dynamics.

Heights for individual trees on sample plots are often needed for estimation of volume, biomass and carbon. Because of high inventory costs, measuring heights for all trees is not possible, and therefore only a sample of trees is usually measured for heights. This means that the missing height measurements need to be predicted. This can be done, for example, with height-diameter models. A requirement for such models is that they are able to predict height with an appropriate accuracy. By applying a mixed effects modelling approach, which takes the sample plot-level random variations into account, accuracy of the predictions can be improved. A weakness of the presently applied height-diameter models in Norway (Øyen and Andreassen, 2002; Bollandsås, 2007) is that sample plot-level random effects were not included when they were developed. Another weakness is that they did not include height of dominant tree as covariate, which represents the stand development stage over time (e.g. Adame et al., 2008; Crecente-Campo et al., 2010).

Individual tree based forest simulators have been developed in various countries such as BWIN (Nagel, 1997) and SILVA in Germany (Pretzsch et al., 2002), MOSES (Hasenauer et al., 2006) and PROGNAUS (Monserud and Sterba, 1996; Sterba and Monserud, 1996) in Austria, HEUREKA in Sweden (Lämås and Eriksson 2003), and MOTTI in Finland (Hynynen et al., 2005) as decision-making tools for practical forest management planning. Together with several other models, these simulators comprise spatially explicit or spatially non-explicit individual tree height growth models. In Norway, the individual tree based forest simulator -T (Gobakken et al., 2008) has been developed. This simulator comprises of various models such as diameter and height growth models, mortality models, recruitment models, height-diameter models and volume functions. To predict heights, the simulator currently applies height-diameter models (Bollandsås, 2007) for old even-aged and uneven-aged stands and dominant height growth models (Tveite, 1977; Tveite and Braastad, 1981) for young even-aged stands. These models may be replaced with more accurate mixed effects height-diameter models for prediction of heights. Alternatively, height growth predictions accuracy could also be improved by implementing individual tree height growth models in the simulator

The present study used national forest inventory (NFI) data as main data source while data from other sources (long-term experimental plots, stem analysis, meteorological stations) were used as supplementary data. In recent years, NFIs have started to supply permanent sample plot data in various European countries including Norway. These data are useful for growth modellers because individual trees are repeatedly measured on the permanent sample plots. The repeatedly measured individual tree data allow deriving the increments that may be used to model growth at the individual tree-level. In addition, tree positions are in most countries also recorded in the NFIs and this allows developing spatially explicit individual tree based growth models. The NFI data cover a wide range of tree sizes, ages, growth conditions, and management practices across the country. Since NFI data are not collected for growth modelling, they often contain measurement errors that are acceptable for the main purpose (large scale resource assessments), but are very large for growth modelling. In addition, NFI data still represent short time periods, which may cause challenges in growth modelling. Despite these challenges, NFI data have frequently been used to develop various forest models such as dominant height growth models (e.g. Huuskonen and Miina, 2007), individual tree radial growth models (e.g. Monserud and Sterba, 1996; Sterba and Monserud, 1997; Adame et al., 2008; Condés and Sterba, 2008), individual tree height growth models (Hasenauer and Monserud, 1997; Condés and Sterba, 2008), individual tree mortality models (e.g. Monserud and Sterba, 1999), and height-diameter models (Mehtatalo, 2004, 2005; Nanos et al., 2004; Adame et al., 2008; Crecente-Campo et al., 2010). In Norway, stand basal area and volume growth models (Gizachew and Brunner, 2011), individual tree radial growth models (Andreassen and Tomter, 2003; Bollandsås and Næsset, 2009), individual tree mortality models (Eid and Tuhus, 2001; Bollandsås, 2007), and height-diameter models (Bollandsås, 2007) have been developed from NFI data.

Norwegian forests are mainly dominated by Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), both in area coverage and standing volume (Larsson and Hylen, 2007), and these two species were therefore in the focus of this thesis. The main objective of the thesis was to develop dominant height growth models, site index prediction models, individual tree height growth models and mixed effects height-diameter models using NFI data. All these models may be used in the present Norwegian individual tree based forest simulator - T (Gobakken et al., 2008) or in any other simulator that may be developed in the future.

The thesis is divided into four different papers to cover the main objective, each of them corresponding to the following sub-objectives:

1. To develop dominant height growth models for Norway spruce and Scots pine in Norway (Paper I)

2. To develop site index prediction models from site and climate variables for Norway spruce and Scots pine in Norway (Paper II)

3. To develop individual tree based height growth models for Norway spruce and Scots pine in Norway (Paper III)

4. To develop height-diameter models for Norway spruce, Scots pine, and Downy birch in Norway (Paper IV)

2. Background

2.1. Site productivity

The terms “site quality” and “site productivity” are often used interchangeably. The Society of American Foresters (1971) defined “site” as “an area considered in terms of its environment that determines the type and quality of plants the area can carry”. Site is collectively characterized as an interaction of the environmental factors that exist in a given area, whereas site quality refers to the productivity potential of a given site. Site productivity is therefore a quantitative measure of site quality. The definitions of the terms “site”, “site quality”, and “site productivity” and descriptions of methods of site productivity assessment have been elaborated by many authors (Carmean, 1975; Vanclay, 1994; Skovsgaard and Vanclay, 2008; Pokharel and Dech, 2011).

Assessment of site productivity started 200 - 300 years ago with the introduction of scientific methods in forestry in Europe (Skovsgaard and Vanclay, 2008). Assessments of site productivity were carried out in Sweden and Finland in the early 1900s (Cajander, 1909; Jonsson, 1914; Cajander, 1921) and some years later in Norway (Landsskogtakseringen, 1938; Eide and Langsæter, 1941). Further improvements in assessment of site productivity for major tree species were made with the development of a series of site index models in these countries, i.e., in Sweden (Fries, 1969; Hägglund, 1972, 1973, 1974; Johansson, 1996; Elfving and Kiviste, 1997), in Finland (Gustavsen, 1980; Vuokila and Väliaho, 1980; Gustavsen, 1996; Karlsson, 2000), and in Norway (Brantseg, 1969; Tveite, 1969, 1977, 1981; Tveite and Braastad, 1981).

Different methods may be used to assess site productivity (Vanclay, 1992, 1994; Skovsgaard and Vanclay, 2008; Pokharel and Dech, 2011). A commonly applied method is based on dominant height (mean height of 100 largest trees per hectare) at given base age (site index). Dominant height of a stand reflects the productivity of a fully stocked even-aged stand because height growth is independent of stand density over a wide range of densities (Skovsgaard and Vanclay, 2008). Dominant height at a given base age (e.g. Monserud, 1984; Garciá and Batho, 2005; Martin-Benito et al., 2008; Nord-Larsen et al., 2009; Perin et al., 2013) may therefore be used as a measure of site productivity.

Two approaches may be used to develop site index models, i.e., the traditional base-age specific approach (e.g. Payandeh, 1974) and the more recent base-age invariant approach (e.g. Elfving and Kiviste, 1997). The presently applied Norwegian site index models (Tveite, 1977; Tveite and Braastad, 1981) are base-age specific models. Base-age specific models are developed from height data with a common base age. Development of such models may therefore require inter- or extrapolation to determine height at the base age if height is not measured at that age. Thus, stem analysis data are most suitable for base-age specific models. The base-age invariant approach, on the other hand, is applicable even if height data with no common base age is available. This avoids the need of inter- or extrapolation to determine height at base age if height is not measured at that age (Cieszewski, 2001; Nord-Larsen, 2006a). Thus, base-age invariant models are most suitable for permanent sample data.

Algebraic difference models are base-age invariant and formulated with the algebraic difference approach (ADA) (Bailey and Clutter, 1974). The ADA allows only one parameter of a base function to be site-specific, and the models derived with this approach may produce anamorphic curves or curves with a single asymptote (Cieszewski and Bailey, 2000; Cieszewski, 2001, 2002, 2003; Krumland and Eng, 2005). Cieszewski and Bailey (2000) developed base-age invariant site index models by using the generalized algebraic difference approach (GADA), which allows more than one parameter of a base function to be site-specific. GADA models can generate polymorphic curves with multiple asymptotes (Cieszewski, 2001, 2003; Cieszewski et al., 2007). Both GADA and ADA models may be used to fit short time series of height-age data, even if no common base age is available in the series (e.g. García, 2005; De los Santos-Posadas et al., 2006; Tiwari and Singh, 2009). In recent years, GADA has become a standard approach for developing dominant height growth models (Diéguez-Aranda et al., 2005; Diéguez-Aranda et al., 2006; Cieszewski et al., 2007; Martin-Benito et al., 2008; Bravo-Oviedo et al., 2008; Nord-Larsen et al., 2009).

Site index models may be applied for fully stocked even-aged stands with closed canopies that are dominated by one tree species for which site productivity should be assessed. However, site index models may fail if dominant trees are not present or not possible to identify (Dahms, 1963). Site index models cannot be applied to mixed and uneven-aged stands, or to stands stocked with another tree species. For unstocked sites where harvests or natural disturbances have taken place, site index models cannot be used. Furthermore, for very young stands, a small error in measurement of dominant height or age may lead to substantial errors in estimated site indices (Kwiaton et al., 2011).

Alternatively, site productivity may be assessed with site index prediction models developed from site variables describing location, topography, soil, understory vegetation or climate (e.g. Carmean 1975; Hägglund 1981; Pokharel and Dech, 2011). Many site variables can easily be measured in the field or extracted from maps or databases, and therefore site index prediction models can be developed from such variables (e.g. Hägglund and Lundmark, 1977; Nilsen and Larsson, 1992; Seynave et al., 2005; Socha, 2008; Farrelly et al., 2011). Most of the previously developed site index prediction models are based on small data sets, however, and only a few studies have used extensive data from NFIs or other sources (e.g. Hägglund and Lundmark, 1977; Tegnhammer, 1992; Elfving, 1994; Schadauer, 1999; Chen et al., 2002; Seynave et al., 2005; Beaulieu et al., 2011).

Site index for a given site may change over the year of stand origin. Such variations have been reported in Norway (Nilsen and Larsson, 1992; Bøhler and Øyen, 2011), in Sweden (Hägglund and Lundmark, 1977; Elfving, 1994; Elfving and Nyström, 1996a, b; Elfving and Tegnhammar, 1996; Elfving et al., 1996), in Finland (Tamminen, 1993; Mielikäinen and Timonen, 1996), and other European countries (Hassall et al., 1994; Spiecker et al., 1996; Schadauer, 1999; Kiviste, 1999; Socha, 2008; Bontemps et al., 2009). These studies showed higher site indices for younger stands than for older stands under similar site conditions. Significant trends (hereafter termed as site index trend) were found in observed site indices over the year of stand origin. Site index trends may be caused by several factors, but the role of individual factors has rarely been quantified (Tegnhammar, 1992). Factors that may cause site index trends are changes of growing conditions and improved forest management practices over time. Even if real changes in growing condition over time would not exist, site index trends can be found in forest inventory data. In forest inventory data, site indices are strongly correlated with stand age due to shorter rotations for stands on better sites and longer rotations for stands on poorer sites (Tegnhammar, 1992).

Several site index prediction models have been developed by including stand age in order to correct for site index trends. Site index prediction models developed with Swedish NFI data also showed site index trends. Therefore, Tegnhammar (1992) developed a correction function for site index, which is based on stand age and varying with latitudes. Elfving and Nyström (1996b) found site index trends while applying this correction function to the independent data of Norway spruce in northern Sweden. Elfving (1994) also introduced stand age as independent variable in the Swedish site index prediction models (Hägglund and Lundmark, 1977). Similarly, a site index trend was found for Norway spruce in the Austrian NFI data and age was therefore included as an additional explanatory variable in the site index prediction models (Schadauer 1999). A significant interaction of the site index trend with the temperature sum in these models also indicated a regional variation in the site index trends. Schadauer (1999) suggests that site index trends are more likely caused by a real shift in growing conditions over time than by inappropriate time trends implicit in site index models. Albert and Schmidt (2010) also described strong trends in site indices after 1970 for Norway spruce and common beech in Germany.

The presently applied Norwegian site index models for Norway spruce and Scots pine (Tveite, 1977; Tveite and Braastad, 1981) are based on data from experimental permanent sample plots located in eastern and middle Norway, while western and northern regions are not represented. The data used for these models also inadequately represent poorer sites and data were completely lacking from higher altitudes. Significant deviations of dominant height developments based on these models have been reported for western Norway (Blingsmo, 1985; Øyen and Nes, 1997; Orlund, 2001) and northern Norway (Tveite, 1994).

2.2. Forest growth models

Modelling growth and yield has been an intrinsic part of forestry research for many years, but still remains an area of important and active research (e.g. Porte and Bartelink, 2002; Vanclay, 1994). Growth models are useful tools for forest managers for various purposes such as inventory updating, evaluation of silvicultural alternatives, harvest scheduling, and management planning in general (Garciá, 1994; Amaro et al., 2003). Based on the management objectives, access to the computational facilities and input data, growth models may operate either at stand level or at individual tree level.

2.2.1. Stand-level growth models

Stand growth is commonly measured in terms of stand basal area growth, stand height growth or stand volume growth. Stand growth can be modelled as a function of stand variables such as site index, stand age, stand diameter (e.g. quadratic mean diameter), stand basal area, stand density index, and number of stems (e.g. Pienaar and Rheney, 1995; Huuskonen and Miina, 2007; Gizachew and Brunner, 2011). Stand growth models do not describe growth dynamics of individual trees and are usually applicable only for even-aged and homogenous stands.

Various stand-level growth models for Norway spruce and Scots pine have been developed as basis for decision-making tools for forest management planning in Norway. Most of these models are based on data from long-term experimental plots and on supplementary data from temporary sample plots administered by the Norwegian Forest and Landscape Institute (Andreassen et al., 2008). The models are either basal area growth models (Eide and Langsæter, 1941; Brantseg, 1969; Nilsen and Haveraaen, 1982; Andreassen et al., 2008), diameter growth models (Braathe, 1955; Braastad, 1974; Blingsmo, 1984; Andreassen and Øyen, 2002; Gobakken and Næsset, 2002), or volume growth models (Braastad, 1975; Blingsmo, 1988). Stand-level mortality and recruitment models have also been developed using NFI data (Eid and Øyen, 2003; Lexerød and Eid, 2005). Many of the above-mentioned models have been used in Norwegian stand-level simulators for forest management planning such as BESTPROG (Blingsmo and Veidahl, 1994), AVVIRK2000 (Eid and Hobbelstad, 2000; Eid and Hobbelstad, 2005), and GAYA (Hoen and Eid, 1990).

2.2.2. Individual tree based growth models

As opposed to stand-level growth models, individual tree based growth models describe growth of individual trees in a stand. The growth of an individual tree, i.e., the subject tree (also called a focal tree or target tree), within a stand largely varies due to competition from other trees. Competition varies with competitor species, number, size, distance, and direction. Individual tree based growth models are usually developed to describe growth dynamics for structurally complex and heterogeneous stands (Wykoff, 1990; Pretzsch et al., 2002; Uzoh and Oliver, 2006; Bollandsås and Næsset, 2009). In these models, the potential growth of individual trees is reduced by competition indices, which may be either spatially explicit (also called distance dependent) (Bella, 1971; Biging and Dobbertin, 1992; Ledermann and Stage, 2001; Rivas et al., 2005) or spatially non-explicit (also called distance independent) (Wykoff, 1990; Uzoh and Oliver, 2006; Bollandsås and Næsset, 2009). Only spatially explicit individual tree based growth models are sensitive to differences in the spatial arrangement of the trees.

Most individual tree based growth models describe radial growth at breast height. Radial growth of a tree is more affected by competition than height growth. Consequently, few individual tree height growth models have been developed (Hasenauer and Monserud, 1997; Pretzsch et al., 2002; Fahlvik and Nyström, 2006; Nord-Larsen, 2006b; Uzoh and Oliver, 2006; Ritchie and Hamann, 2008; Vaughn et al., 2010). Except for a few (e.g. Hasenauer and Monserud, 1997; Pretzsch et al., 2002), all these models are based on limited data regarding quantity and representativeness. In recent years, data from NFIs supply repeatedly measured heights of individual trees. A weakness of such data, however, is that large measurement errors are involved. Alternatively, stem analysis data free from these errors could be used for modelling. However, stem analysis data suffer from missing descriptions of the competitive situation over time and seldom represent larger areas.

All existing individual tree based growth models in Norway are diameter growth models (Bollandsås, 2007; Bollandsås and Næsset, 2009) or basal area growth models (Andreassen and Tomter, 2003). Also mortality models for individual trees have been developed (Eid and Tuhus, 2001; Bollandsås, 2007). All these models are based on NFI data. Individual tree height growth models for Norway are lacking. The individual tree based forest simulator - T (Gobakken et al., 2008) developed for Norway comprises various modules (growth models, mortality models, recruitment models, height-diameter models, volume functions). The diameter growth models (Bollandsås, 2007) are driving the simulation processes. Dominant height growth models (Tveite, 1977; Tveite and Braastad, 1981) are used to predict height for individual trees in young stands, assuming all trees of a certain age and site index to attain the same height. For older stands, height-diameter models (Bollandsås, 2007) are used to predict heights. Since the presently applied height-diameter models (Bollandsås, 2007) lack sample plot-level random effects and dominant height as a covariate, the models are likely to be biased.

Many individual tree based forest simulators have been developed for forest management planning in other European countries. Examples of such simulators are BWIN (Nagel, 1997) and SILVA (Pretzsch et al., 2002) for Germany, MOSES (Hasenauer et al., 2006) and PROGNAUS (Monserud and Sterba, 1996; Sterba and Monserud, 1996) for Austria, HEUREKA (Lämås and Eriksson, 2003) for Sweden, and MOTTI (Hynynen et al., 2005) for Finland. SILVA and MOSES are spatially explicit and comprise many different models with different purposes (growth, crown expansion, mortality). PROGNAUS is a spatially non-explicit simulator and comprises various models (growth models, mortality, dynamic crown ratio, harvesting). HEUREKA and MOTTI are spatially non-explicit simulators. HEUREKA comprises production modules (growth models, volume functions, mortality models, and recruitment models), a treatment module (silvicultural and harvest operations), and an optimization module. In HEUREKA, simulations are also possible for different climate scenarios.

A number of challenges are still associated with all these simulators. In addition to growth, the simulators should be able to precisely simulate regeneration and recruitment, probabilities of survival or mortality, and wood quality (e.g. annual ring width, wood density, knot width), as well as growth and other processes under changing site and climate conditions. Climate sensitive forest models (e.g. Mäkelä et al., 2006; Albert and Schmidt, 2010; Schmidt, 2010; Schmidt et al., 2011) may be implemented in the simulators. Process-based growth models accurately predicting wood quality (e.g. Mäkelä and Mäkinen, 2003; Kantola et al., 2007) may also be used as growth modules in the simulators. Another challenge related to forest simulators is the availability of regional data for region-specific models and predictions. Getting appropriate individual tree information as required for different simulators may also be difficult. For such cases, missing input data may be generated with algorithms (e.g. STRUGEN developed by Pretzsch (1997)).

Tree growth is determined by the availability of growth resources such as moisture, nutrients, light, and temperature. The radial growth of a tree is more affected by competition than height growth. The radial growth response to competition is nearly linear. Height growth of dominant trees, however, is often not affected by competition, although height growth of suppressed trees may be significantly reduced when competition increases above a certain level (Brunner and Nigh, 2000). Thus, height growth has an asymptotic response to competition. In order to model individual tree growth, expected height growth of individual trees may be obtained through the potential growth reduction approach. Potential height growth is either estimated simultaneously with a modifier for competition (Courbaud et al., 1993; Hasenauer and Monserud, 1997; Huang and Titus, 1999; Uzoh and Oliver, 2006; Vaughn et al., 2010) or it is estimated separately (Biging and Dobbertin, 1992, 1995; Pretzsch et al., 2002).

Earlier individual tree based growth models assumed certain effects of distance (e.g. Pukkala 1989) and size ratio (e.g. Hegyi 1974) in competition indices, but recent models estimate distance effects and size ratio effects from the data (Miina and Pukkala 2000; Canham et al. 2004; Boyden et al. 2008; Bøhler et al., 2008; Richards et al., 2008; Peltoniemi and Makipaa 2011; Pommerening et al. 2011; Sabatia and Burkhart 2012). For models describing individual tree height growth, the effects of distance and size ratio have rarely been estimated from the data.

2.3. Height-diameter models

Height measurements are needed for estimation of tree volume, site index, growth and yield, biomass, and carbon. Diameter is easily measured for all standing trees, but measuring height is more difficult, time consuming, and costly. Thus, height measurement for all trees on sample plots located across an extensive area is not practically feasible. Height-diameter models developed from sample plot data are commonly used to predict missing heights on the same sample plot (e.g. Nord-Larsen, 2006a; Gizachew and Brunner, 2011). However, this may not always be possible if there are few observations available per sample plot. Species-specific height-diameter models are thus needed to predict missing heights. The height-diameter relationship differs from one sample plot to another due to differences in site quality, age, and silvicultural treatments (Calama and Montero, 2004; Sharma and Parton, 2007; Schmidt et al., 2011). The height-diameter relationship is therefore highly site- and stand density-specific, and is not constant over time (Curtis, 1967; Zeide and Curtis, 2002; Pretzsch, 2009). Thus, more accurate height-diameter models may be developed by integrating stand variables as covariates (Sharma and Zhang, 2004; Temesgen and Gadow, 2004; Newton and Amponsah, 2007; Bollandsås, 2007; Lei et al., 2009). Height prediction accuracy of the models can further be improved through inclusion of sample plot-specific random effects (Mehtatalo, 2004, 2005; Castedo-Dorado et al., 2006; Adame et al., 2008; Crecente-Campo et al., 2010; Schmidt et al., 2011).

NFI data have frequently been used to develop height-diameter models such as in Spain (e.g. Nanos et al., 2004; Adame et al., 2008; Crecente-Campo et al., 2010), Finland (e.g. Mehtatalo, 2004, 2005), and Norway (Bollandsås, 2007). Except models by Bollandsås (2007), other models have included stand variables as covariates and plot-level or measurement occasion-level random effects. Height-diameter models have also been developed as dynamic models with a large amount of data in Germany (e.g. Albert and Schmidt, 2010; Schmidt, 2010) and in Estonia (Schmidt et al., 2011) to be used as growth models that are sensitive to climate change.

The database from the Norwegian NFI contains height measurements for only few sample trees on each plot, while diameter at breast height (dbh) is available for all trees on the sample plot. Missing height measurements therefore need to be predicted. Mixed effects height-diameter models may be more appropriate than ordinary least square models to achieve this (e.g. Robinson and Wykoff, 2004; Sharma and Parton, 2007; Crecente-Campo et al., 2010).

2.4. Data sources for developing growth models

Forest growth models may be developed using data originating from different sources such as permanent NFI sample plots, long-term experiment (LTE) plots, and stem analysis. Many European countries have been carrying out NFI programs for several years. In some countries (e.g. Norway, Austria), the NFI supplies individual tree positions, which are necessary for spatially explicit individual tree growth models. As compared to data from LTE, NFI data often contain large measurement errors, short times series, few height sample trees, and the sample plot size is often small. In order to prepare NFI data for growth modelling, modellers need to develop new methods of data preparation or apply different types of models than for data from other sources.

Dominant height growth models are often developed from stem analysis data (Martin-Benito et al., 2008). Dominant height growth models developed with NFI data are very rare

(Huuskonen and Miina, 2007). LTE data from permanent sample plots are also often used to develop dominant height growth models (e.g. Elving and Kiviste, 1997; Nord-Larsen 2006a, Nord-Larsen et al., 2009). The accuracy of the height growth data (relative to real height growth) varies, but is usually higher for stem analysis data than for permanent sample plot data (García, 2005). However, stem analysis data may be biased if changes in tree dominancy over time go undetected (Dahms, 1963; Zeide and Zakrzewski, 1993; Cherubini et al., 1998). When developing dominant height growth models, stand age may be replaced with climate variables such as solar radiation or temperature (e.g. Mason et al., 2011). This means that the models become climate sensitive. Data for individual tree based growth models usually originate from repeatedly measured individual trees on permanent sample plots. Stem analysis data are costly and this is the reason why few growth models are based on such data.

3. The Norwegian National Forest Inventory

All models presented in the thesis were developed using NFI data as per the objective. The Norwegian Forest and Landscape Institute conducts the NFI in Norway. The NFI is a permanent and rotating systematic sample plot inventory. The circular sample plots are located in a 3 × 3 km grid covering the whole country except above 70° N Latitude (Landsskogtakseringen, 2007). Circular sample plots with an area of 100 m^2 were established during the period between 1986 and 1993, but trees with a dbh >20 cm were measured inside a circle of 250 m^2. The sample plot size was extended to 250 m^2 during the period between 1994 and 1998. Since 1994 each sample plots has been inventoried every fifth year. Out of 16000, approximately 66% sample plots are located in productive forests (minimum production of 1 m^3 ha^{-1} yr^{-1}) (Tomter, 2000). The NFI data represents all forest types, stand ages, management practices, and growth conditions of forests in Norway. The main purpose of the NFI is to estimate forest resources and document resource changes over time.

Data from the NFI database were selected according to criteria specified in the respective papers. In general, however, only data from undivided sample plots (not intercepted by roads, water bodies, and agricultural fields) located on productive forests were used. Diameters are measured for all trees with a dbh >5 cm, but height above stump (stump height is defined as 1% of the total height) is measured for a subsample selected using relascope sampling (i.e., probability proportional to basal area). Height sample trees were selected based on an angle gauge factor of 6 m^2 ha^{-1}during earlier inventories, whereas a flexible factor was used during later inventories to guarantee a larger number of sample tree per plot. Using site index models (Tveite, 1977; Tveite and Braastad, 1981), site index for each NFI sample plot was estimated from height and age of one dominant tree outside the 250 m^2 plot, but inside a 1000 m^2 concentric plot. Except for paper IV that used data from inventory period between 1986 and 2011, NFI data in the period between 1986 and 2008 were used. Height measurements for one to six trees were available for most of the sample plots in the period between 1986 and 2003 and ten or more trees after 2003. Given the low precision of height measurements made with hand-held instruments relative to a five-year's height growth, large measurement errors can be expected for individual height increments.

4. Main results

4.1. Dominant height growth models (paper I)

Data used in this paper were obtained from the Norwegian NFI, long-term experiments (LTE), stem analysis, and from weather stations of the Norwegian Meteorological Institute. Dominant trees were selected based on the combined ranks of height and dbh from all sample trees. Between one and three trees per plot and measurement occasion were identified as dominant trees. Only Norway spruce or Scots pine dominated (>70% species-specific standing volume) sample plots were used for the analyses. Figure 1 shows the location of NFI sample plots selected. About one third of the total NFI sample plots were used. The selected data represent all growing conditions and stand ages in the country, were based on three re-measurements, and cover a period of 22 years (1986 - 2008). A number of the time series had negative increments due to large height measurement errors. The NFI inventory procedure was based on an age recorded from an increment core taken at breast height of one site index tree, and based on this a basal area-weighted mean age was estimated for the plots. Thus, ages might have large errors.

The Norwegian Forest and Landscape Institute has established a series of permanent sample plots located in a number of sites across the country. These sample plots are part of long-term experiments, and they were often established for testing thinning methods and other treatments. The sample plots have been remeasured regularly, creating time series for dominant height data with a length of 10 - 80 years. Most of dominant height data originated from younger stands on better sites.

Stem analysis data were collected from Telemark, Buskerud, Oppland, and Hedmark counties in southeastern Norway. By means of forest management plans, 31 stands with ages varying from 50 to 180 years covering all existing site index classes in the region were identified. Trees were then harvested, stem discs prepared, and height-age series constructed.

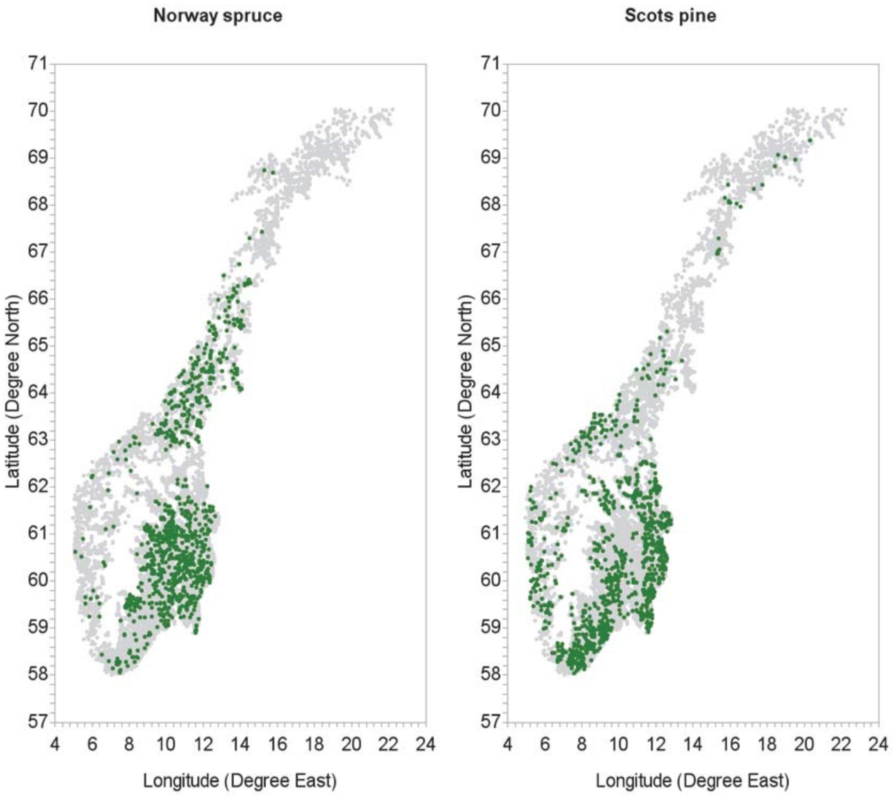

Figure 1. Location of NFI sample plots (green dots used represent sample plots in paper I; grey dots represent sample plots of productive forests not used in paper I).

The generalized algebraic difference approach (Cieszewski and Bailey, 2000) was used to develop dominant height growth models. The models were derived from eight base functions of either fractional or exponential form. Since the site-specific parameters describing site index for individual sample plots were not known, nested regression techniques were applied (Cieszewski et al., 2000; Krumland and Eng, 2005). Correlated errors in the height growth time series were accounted for by incorporating an autoregressive error structure into the models. In order to avoid biased parameter estimates caused by errors in the independent age variable, a method described by Kangas (1998) was applied to the best model.

The dominant height growth models were first developed with NFI data and then tested against LTE data. Combined data models were also developed with NFI data and LTE data pooled together, and then tested against independent stem analysis data. The models were evaluated using fit statistics, prediction statistics, and graphical analysis.

Despite short time series and large age errors, the NFI data models appropriately described dominant heights of the LTE data for most of the site index and age range covered by the NFI data. A significant bias was only detected for very young stands on better site index classes. However, this bias was substantially reduced when the combined data models were developed. Since the NFI data and LTE data supplemented each other well to cover the whole range of site indices and ages, the combined data models adequately described both NFI data and LTE data. The combined data models also adequately described the stem analysis data for all ages and site index classes. Furthermore, the combined data models adequately described the region-specific data from both NFI and LTE for all ages and site index classes. Height curves of the presently applied Norwegian dominant height growth models (Tveite, 1977 and Tveite and Braastad, 1981) significantly deviate from those presented in this paper (Figure 2). The dominant height growth of Norway spruce derived from the models also only has a single culmination as opposed to Tveite’s model. Identical height growth occurs in the old site index model for Scots pine (Tveite and Braastad, 1981) for all site index classes after about 100 years of stand age, which is a consequence of extrapolation in this range and does not reflect dominant height growth. Dominant height growth models presented in the thesis can be used as potential height growth models to develop individual tree height growth models (paper III).

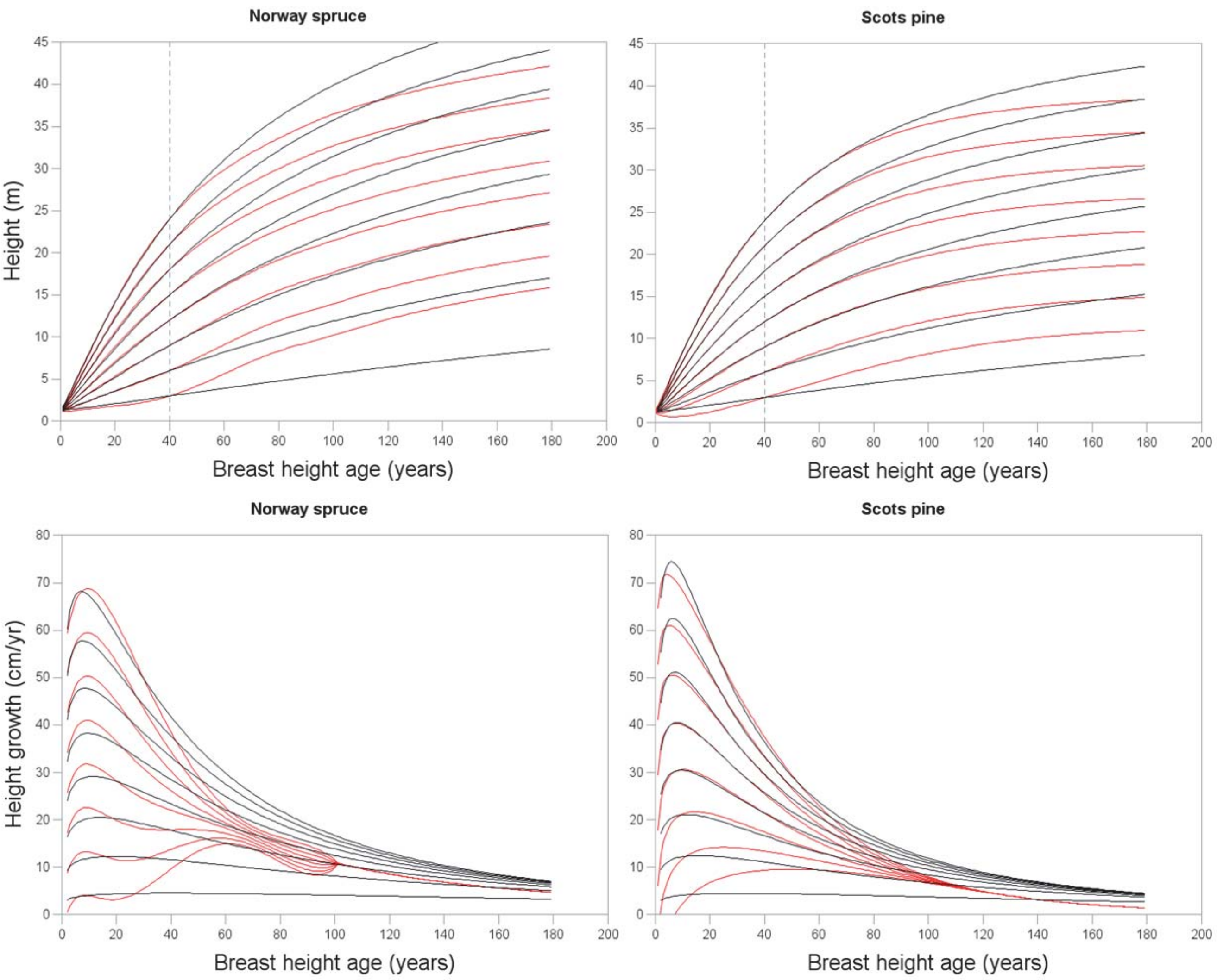

Figure 2. Presently applied Norwegian site index models (Tveite 1977; Tveite and Braastad, 1981) (red) and new site index models (paper I) (black) for a site index class interval of 3m.

4.2. Site index prediction models (paper II)

To develop site index prediction models, data describing site and climate from the Norwegian NFI and the Norwegian Meteorological Institute, respectively, were used. Except for a few sample plots (27 for Norway spruce, 34 for Scots pine) that were excluded due to missing site variables, the same NFI sample plots as described for paper I were used (Figure 1). Site indices for the sample plots were first estimated by using the dominant height growth models developed in paper I. Subsequently they were used as observed site index (response variable) in the site index prediction models. Only variables that can be measured in the field or recorded easily from other sources at low cost were used as explanatory variables, i.e., altitude, latitude, slope, aspect, soil depth, and understory vegetation type. Mean growing season temperature and precipitation sums were used to describe the long-term climate conditions. Since trends in observed site indices (Figure 3) could not be described by the site and climate variables alone, year of stand origin was used as an additional explanatory variable.

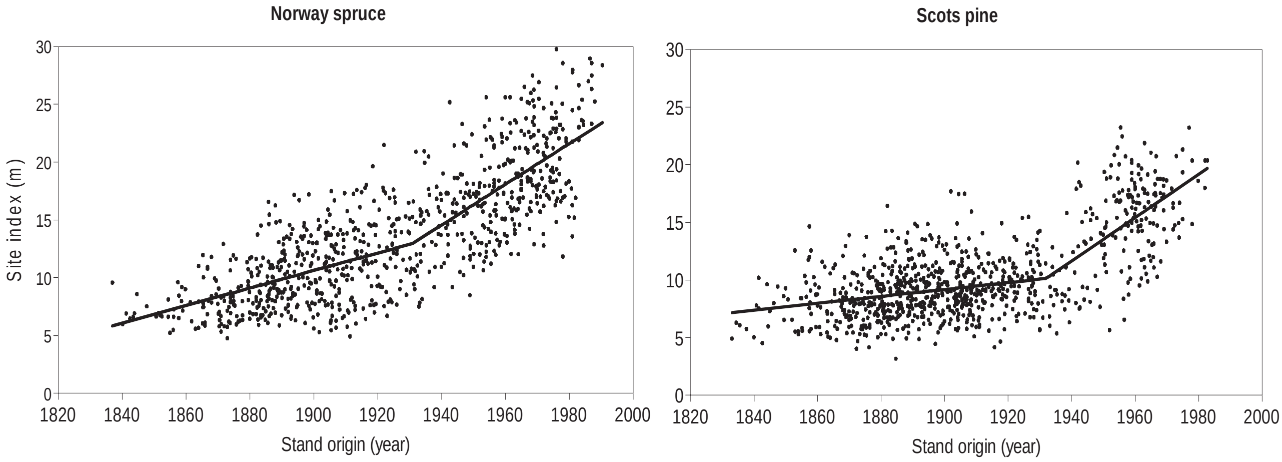

Figure 3. Observed site index over the year of stand origin for Norway spruce and Scots pine. A segmented linear model describes the trend of observed site indices against year of stand origin data (basic model).

For each species, ten different site index prediction models were developed. A basic model was developed using only year of stand origin as explanatory variable while other models used different combinations of explanatory variables to facilitate applications of the models to a range of situations with different access to explanatory variables. Since there were two distinct trend segments in the observed site indices over the year of stand origin (Figure 3), a segmented linear regression method was applied. The site index prediction models were evaluated using fit statistics and graphical analysis.

Among the ten different site index prediction models, a model including year of stand origin, temperature sum, understory vegetation type, soil depth, aspect, slope, and latitude described the largest proportion of the total variation in site indices for both Norway spruce and Scots pine. However, the other models were only marginally inferior to this model. All models showed a strong nonlinear effect of the year of stand origin on the observed site indices, which also varied with temperature sum. For both species, site indices increased with increasing year of stand origin, and the site index trend was significantly steeper for stands originating after about 1940 than for the stands originating before this year (Figure 3).

4.3. Individual tree height growth models (paper III)

Height increment data from trees sampled on Norwegian NFI sample plots were used to model individual tree height growth. The models applied the potential modifier concept (e.g. Pretzsch et al., 2002). The site index models describing the development of dominant height (paper I) were used to define potential height growth of individual trees. A large number of trees with negative height increments or large positive errors exist in the data, and consequently relative height growth (ratio of height growth of an individual tree to potential height growth) exceeded the theoretical range (0 - 1) for many trees. Figure 4 shows the location of all sample plots used in this paper.

The potential modifier models describe relative height growth as a function of a competition index. Three spatially explicit indices and two spatially non-explicit indices were tested. All indices are based on dbh because tree height and crown data were available only for a few trees per sample plot. The distance effect of competitors was estimated from the data and therefore a search radius for competitors was not applied. A correction for the plot edge bias was done by applying the linear expansion method (Martin et al., 1977; Pretzsch, 2009). The estimated indices were scaled to the range between 0 and 1. Parameters of the potential modifier models and parameters of the competition indices were estimated simultaneously from the data rather than using assumed values as usually done in conventional spatially explicit indices (e.g. Hegyi, 1974; Pukkala, 1989). Correlated errors in the height growth time series were accounted for by incorporating an autoregressive error structure into the potential modifier models. The fitted models were evaluated using fit statistics and graphical analysis.

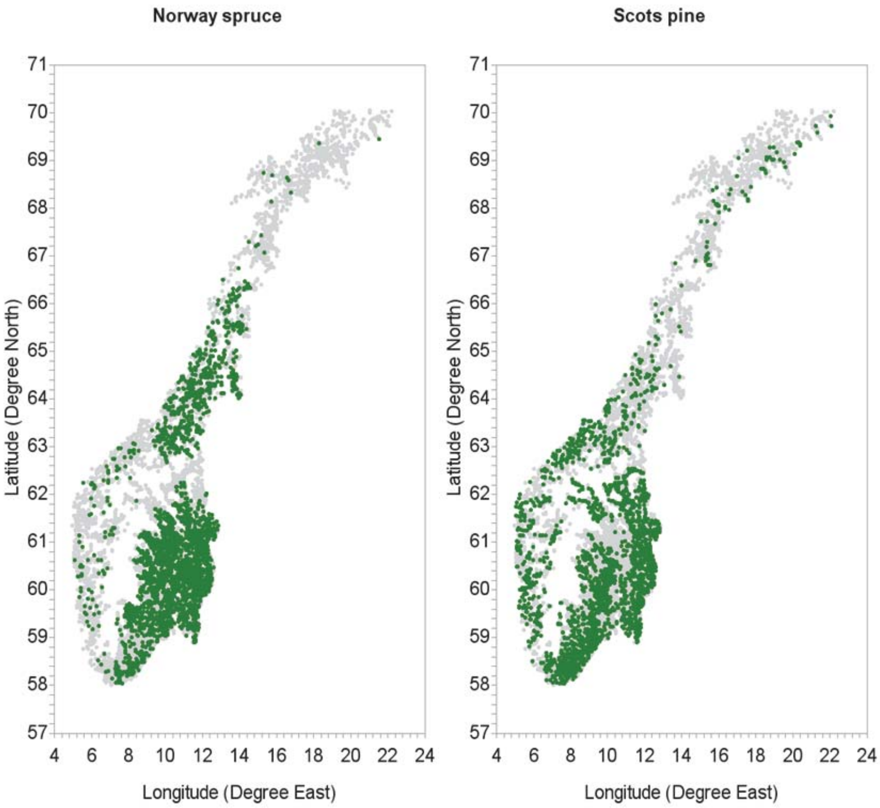

Figure 4. Location of NFI sample plots (green dots represent sample plots used in paper III, grey dots represent sample plots of productive forests not used in paper III).

The results showed that the potential modifier models only described a small part of the total variation in relative height growth for both Norway spruce and Scots pine. Height measurement errors caused large residual variation of the models. All five indices resulted in similar fit statistics. The potential modifier models showed that the height growth of dominant trees was unaffected by competition. Under strong competition height growth of both species was gradually reduced (Figure 5). However, as compared to moderate levels of competition, none or very low levels of competition also reduced height growth of Scots pine. This may be due to higher sensitivity of shade-intolerant species to competition compared to shade-tolerant species (e.g. Norway spruce). The models showed significantly decreased competition with increasing distance from the competitor. However, competitors at larger distances influenced height growth for Scots pine as well. Spatially explicit indices resulted in only marginally improved fit statistics compared to the spatially non-explicit indices. This could be due to the small sample plot size that reduces the spatial explicitness as a large part of estimated indices comes from the off-plot trees through edge expansion. At the same time, the small sample plot size also makes spatially non-explicit competition indices more spatially explicit by only using neighbors close to the subject trees. Both spatially explicit and spatially non-explicit models are therefore likely to be more precise for trees located towards the plot center than trees located towards to the plot edge.

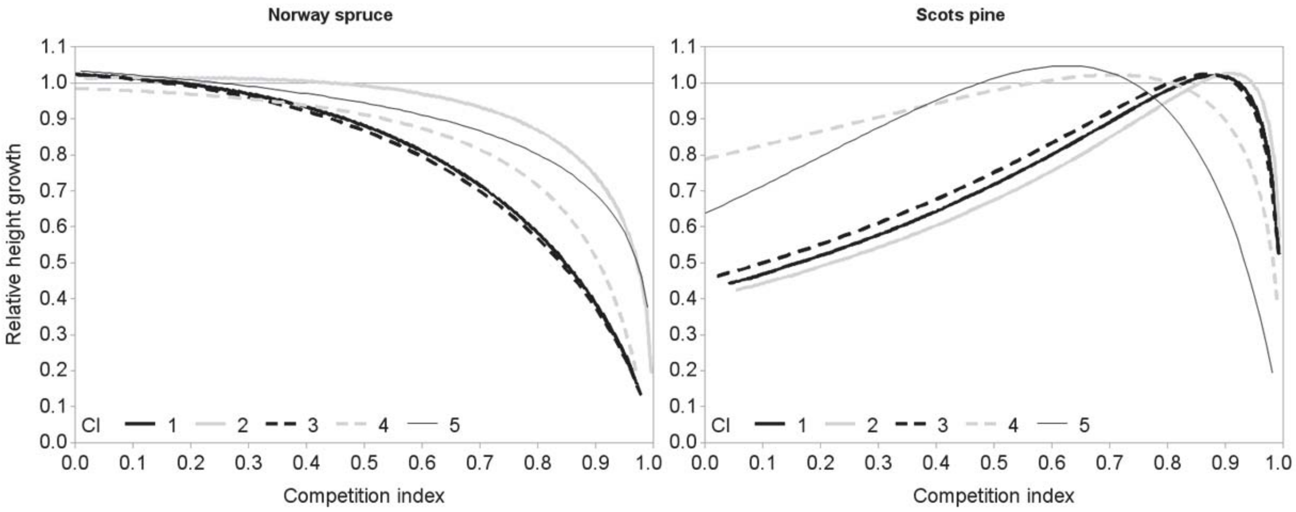

Figure 5. Potential modifier models for individual tree height growth of Norway spruce and Scots pine for five different competition indices (CI: 1 = modified version of view angle based competition index; 2 = modified version of Hegyi's competition index; 3 = competition index based on negative exponential to describe distance function; 4 = basal area sum of larger trees; 5 = ratio between subject tree's dbh and quadratic mean diameter).

4.4. Height-diameter models (paper IV)

Norway spruce, Scots pine and downy birch were considered. Repeatedly measured heights and diameters over a period of 25 years (1986 - 2011) were used. Sample plots with at least four height sample trees measured in at least two consecutive measurement occasions were selected for fitting height-diameter models. Data from the inventory period between 1986 and 1993 were used for validation while data from the four inventories in the period between 1994 and 2011 were used for model development. Figure 6 shows the location of sample plots selected for the modelling.

In addition to dbh, various stand variables were tested as explanatory variables (also called covariates) to better describe height-diameter relationships. Based on the relationships between stand variables and estimated values of parameters of the base model fitted to the species-specific data for each sample plot and measurement occasion individually, appropriate stand variables were chosen. Scatter plots of each stand variable against estimated values of parameters of the base model were used to identify significant effects. Height and dbh of the tallest tree per plot and measurement occasion showed strong effects and the base model was expanded by including these two variables. Mixed effects models were constructed by including sample plot-level variations as random effects. The final mixed effects models presented in this paper are: 1) a model without covariates (basic mixed effects model), and 2) a model with covariates (generalized mixed effects model).

Using validation data, sample plot-level random effects were predicted from measured heights using the empirical best linear unbiased prediction (EBLUP) method (Pinheiro and Bates, 2000; Calama and Montero, 2004) and used to calibrate sample plot-specific height-diameter models. In this calibration, various alternative numbers of height trees were used and resulting height prediction accuracies were compared.

The results showed that the generalized height-diameter model described a larger part of the total variation in heights than the basic model. The height prediction accuracy increased with increasing number of height trees used in calibration of sample plot-specific height-diameter models. For all three species, the generalized mixed effects model with random effects predicted from all measured heights of the focused species (species used for species-specific model) provided the highest prediction accuracy across all diameter classes. For mixed species stands, where measured height of the focused species was not available for calibration of sample plot-specific models, the generalized ordinary least square height-diameter model showed smaller bias than its mixed effects version.

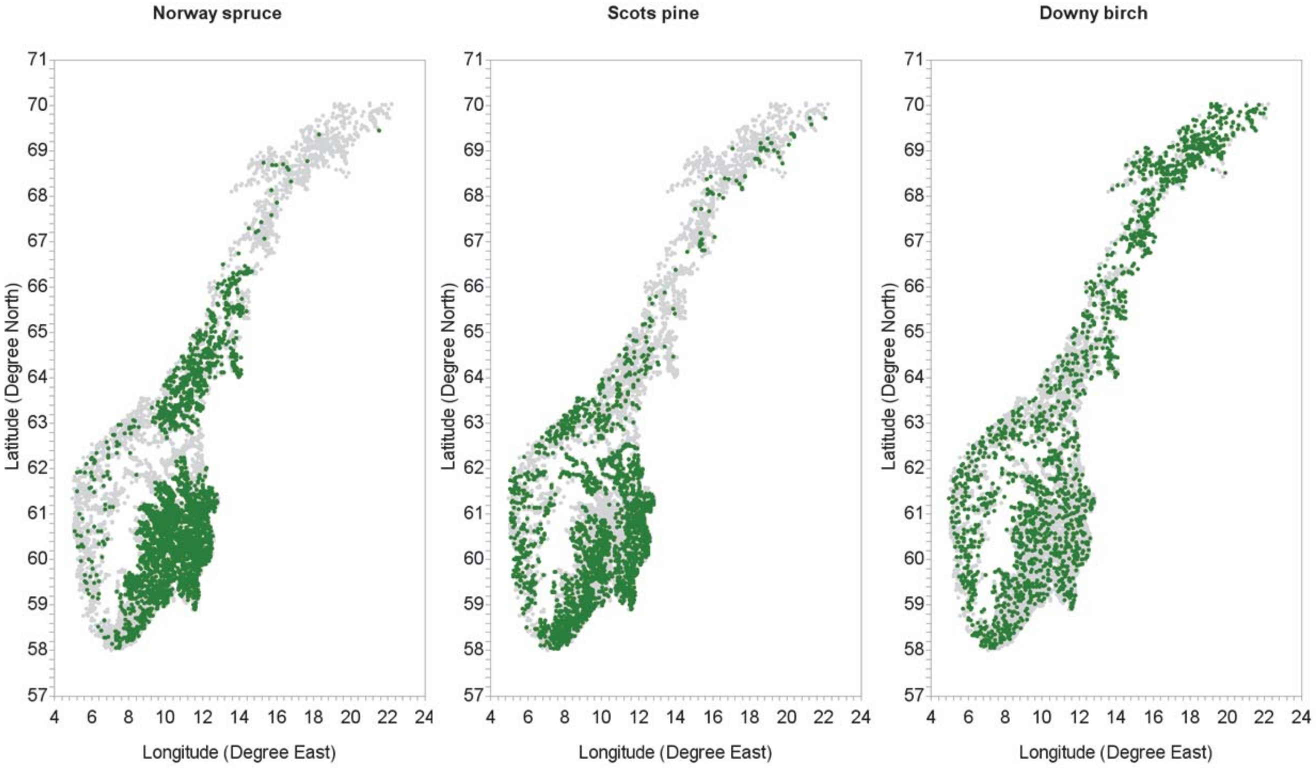

Figure 6. Location of NFI sample plots (green dots represent sample plots used in paper IV, grey dots represent sample plots of productive forests not used in paper IV).

5. Discussion

The main data source of the thesis was NFI data. Since NFIs are designed for a different objective than growth modelling, some errors and inconsistencies in the NFI data are inevitable. In the same way as for the dominant height growth models developed in the present study (paper I), the dominant height growth model presented by Huuskonen and Miina (2007) for young even-aged stand of Scots pine in Finland was also based on NFI data. Sample plot-level random effects were included in this model by applying the mixed effects modelling approach. However, due to fewer replications per sample plot, application of mixed effects modelling was not possible in paper I. To directly compare predictions between different dominant height growth models at different stand development stages and for countries is difficult. The fit statistics of the Finnish model and the one presented in paper I, however, indicate that dominant height growth models developed from the NFI data in the countries were of the similar quality.

In the individual tree height growth model developed from Spanish NFI data (Condés and Sterba, 2008), 0.5 m was added to the annual height increment to reduce the problems of negative or zero increments while transforming to the logarithmic scale. The individual tree height growth models developed with Austrian NFI data (Hasenauer and Monserud, 1997) showed that models fitted to height increment data predicted using height-diameter models have substantially improved fit statistics compared to models fitted to original inventory data. The fit statistics of models fitted to the original inventory data, however, were very similar to those in the models presented by Condés and Sterba (2008). Unlike in this study (paper III), which estimated potential height growth of individual trees separately, the individual tree height growth models for Spain and Austria were developed using a potential height growth of individual trees that was estimated simultaneously with the modifier function. As in the present study, measurement errors in the NFI data of Spain and Austria also caused large residual variations of the individual tree height growth models.

As NFI data in other countries, Norwegian NFI data contain large errors in the measured heights and recorded ages, which are a major weakness for growth modelling. Short time series, few height sample trees (only in earlier inventories), and small sample plot sizes were also challenging in the present study. In spite of these weaknesses, it was possible to develop dominant height growth models, site index prediction models, individual tree height growth models, and height-diameter models that seem to work reasonably well. The dominant height growth models (paper I), for example, were little affected by problems of height measurement errors, short-time series, large age errors, and small sample plot size as indicated by tests of NFI data models against LTE data.

Height measurement errors and small sample plot size appeared to be more challenging for the individual tree height growth models (paper III) than the dominant height growth models (paper I). Combined errors from height measurement and errors from other sources (e.g. site index estimation, dominant height growth models, and periodic growth variation) resulted in weak relationships between relative height growth and the competition indices. The errors in the spatially explicit competition indices may be caused by the small sample plot size because some true competitors may be excluded from the index estimation since it is partly based on off-plot competitors estimated by the linear expansion method. The linear expansion method assumes similar stand conditions outside and inside the sample plot, but this may not hold. With larger sample plot size, on the other hand, some extra competitors may be included in the competition index estimation. In both cases, some errors might involve in the estimated competition indices, but error analysis involves a very complex process (e.g. Hynynen Ojansuu, 2003; Lappi, 2005). Errors in the estimated competition indices might bias the estimated parameters of the potential modifier models. In order to reduce biased parameter estimates due to errors in the independent variable (i.e., competition index), a method described by Kangas (1998) needs to be applied. However, the present study did not apply it because the error variance was unknown.

As compared to radial growth, competition effects on height growth are low. However, effects of competition on height growth could be estimated from the data (paper III). Parameters in the potential modifier models and parameters in the competition indices were estimated simultaneously from the data. This means that effects of distance and size ratio in competition indices were estimated from data, rather than based on assumptions, as usually done in the conventional competition indices (Hegyi, 1974; Pukkala, 1989).

NFI data have previously also frequently been used to develop height-diameter models (see Mehtatalo, 2004, 2005 in Finland, Nanos et al., 2004; Adame et al., 2008; Crecente-Campo et al., 2010 in Spain, and Bollandsås, 2007 in Norway). Except Norwegian models, other models included either sample plot-level random effects only (Adame et al., 2008; Crecente-Campo et al., 2010) or both sample plot-level random effects and measurement occasion-level variations as random effects (Mehtatalo, 2004, 2005). All these mixed effects models and those presented in the present study precisely predicted heights when appropriate numbers of height trees were used to calibrate subject-specific (sample plot- or measurement occasion-specific) height-diameter models. Tests of the height-diameter models based on Spanish NFI data did not show substantial bias for research sample plot data (Adame et al., 2008; Crecente-Campo et al., 2010). As for other NFI-based forest models, studies on height-diameter models also reported that NFI data have caused some problems due to height measurement errors. To reduce residual variations of the models as much as possible, a considerable number of observations (extreme outliers) needed to be excluded because of such errors (e.g. Crecente-Campo et al., 2010). However, the present study did not exclude observations due to height measurement errors.

Like in the present study, significant trends in observed site indices or increased growths have been reported in previous studies such as in Norway (Nilsen and Larsson, 1992; Bøhler and Øyen, 2011), Sweden (Elfving, 1994; Elfving and Nyström, 1996a, b; Elfving and Tegnhammar, 1996; Elfving et al., 1996), Finland (Tamminen, 1993; Mielikäinen and Timonen, 1996), and other European countries (Hassall et al., 1994; Spiecker et al., 1996; Schadauer, 1999; Kiviste, 1999; Bontemps et al., 2009). To reduce prediction bias due to such trends, site index prediction models have therefore frequently included stand age as an additional explanatory variable (Nilsen and Larsson, 1992; Tegnhammar, 1992; Elfving, 1994; Elfving and Nyström, 1996a; Schadauer, 1999). The strong trend in site indices on similar sites is due to various factors like increased temperature and precipitation, elevated atmospheric CO_2 concentration and nitrogen deposition, and improved forest management practices. It is, however, difficult to identify the specific factors and quantify their contribution to the trends. A number of changes in growing conditions and management practices during the last century have been discussed as main causes for site index trends or increased growth (e.g. Tegnhammar, 1992; Elfving and Tegnhammar, 1996; Spiecker et al., 1996; Spiecker, 1999; Kahle et al., 2008a; Kahle et al., 2008b; Solberg et al., 2009). Site index trends may significantly vary from region to region (e.g. Schadauer, 1999) due to variations in temperature and precipitation or other factors affecting growth. These trends may be stronger in warmer region than colder regions. Studies on changes of site indices over time are very important for forest management planning because they will allow for better predictions of future growth in a changing climate.

All models developed in the present study may be used in a Norwegian individual tree based simulator in the future. The dominant height growth models (paper I) can be implemented as site index models, replacing the presently applied ones (Tveite, 1977; Tveite and Braastad, 1981). Alternatively, site index prediction models (paper II) can be implemented. Site index prediction models that include corrections for site index trends may account for better predictions of future growth.

Also the individual tree height growth models (paper III) may be implemented in a forest simulator. Spatially explicit individual tree height growth models are the best option for such a simulator because this will allow better simulations for heterogeneous and mixed species stands than if they were non-spatially explicit. To apply spatially explicit individual tree height growth models for practical management planning is a challenge, because the required input data is associated with high inventory costs. In the future, however, the tree data and positions required for such models may be available from airborne laser scanning (e.g. Hyyppa et al., 2012). The required data may also be generated based on empirical spatial distribution patterns (e.g. Pretzsch, 1997).

The main aim of developing height-diameter models was to apply them in inventories where height data is missing for many trees on a sample plot. However, instead of using individual tree height growth models, it is also possible to use height-diameter models together with individual tree diameter growth models in a forest simulator in order to predict height development. Height-diameter models (Bollandsås, 2007) are presently applied in the Norwegian forest simulator - T. These height-diameter models, however, may now be replaced with the height-diameter models presented in the present study (paper IV). These models include sample plot-level variations as random effects and are therefore probably more suitable for this purpose than the previous ones. To implement height-diameter models in a forest simulator may also prevent problems that may come up with independent use of individual tree diameter growth and height growth models in a simulator. The parameters of diameter and height growth models are usually not estimated simultaneously and therefore model predictions may result in unreasonable height-diameter ratios for individual trees. (e.g.

Hasenauer et al., 1998). This incompatibility could be avoided if the height-diameter models presented are used together with individual tree diameter models in the simulator. However, none of the models was tested for such a possibility in the present study.

6. Conclusions

Despite several challenges inherent to NFI data, dominant height growth models, site index prediction models, spatially explicit and spatially non-explicit individual tree height growth models, and mixed effects height-diameter models were developed in the present study. Most statistical tests of models presented showed adequate prediction accuracies, but also revealed that the challenges related to the NFI data had little effect on the dominant height growth models as compared to individual tree height growth models. However, it was possible to estimate the parameters of competition indices and the parameters of potential modifier models simultaneously. The significant trends in observed site indices were included in the developed site index prediction models. Height-diameter models were developed by including stand variables that are independent of thinning as covariates and sample plot-level variations as random effects. All models presented in the thesis will be used in Norwegian individual tree based simulator in the future.

7. References

Adame, P., del Río, M. and Cañellas, I., 2008. A mixed nonlinear height-diameter model for pyrenean oak (*Quercus pyrenaica* Willd.). Forest Ecology and Management, 256(1-2): 88-98.

Adame, P., Hynynen, J., Cañellas, I. and del Río, M., 2008. Individual-tree diameter growth model for rebollo oak (*Quercus pyrenaica* Willd.) coppices. Forest Ecology and Management, 255(3-4): 1011-1022.

Albert, M. and Schmidt, M., 2010. Climate-sensitive modelling of site-productivity relationships for Norway spruce (*Picea abies* (L.) Karst.) and common beech (*Fagus sylvatica* L.). Forest Ecology and Management, 259(4): 739-749.

Amaro, A., Reed, D. and Soares, P., 2003. Modelling forest systems. CABI Publishing, Wallingford, Oxon, OX108DE, UK, first edition, 432 p.

Andreassen, K. and Øyen, B.-H., 2002. Nye tilvekstmodeller for granskog behandlet med bledningshogst (New growth models for selection stands of Norway spruce forest). Aktuelt fra skogforskningen 6/02: 10 -12 [In Norwegian].

Andreassen, K. and Tomter, S.M., 2003. Basal area growth models for individual trees of Norway spruce, Scots pine, birch and other broadleaves in Norway. Forest Ecology and Management, 180(1-3): 11-24.

Andreassen, K., Eid, T. and Tomter, S.M., 2008. Growth models for stands in ordinary even-aged forest in Norway. Forskning fra Skog og Landskap, 6/08: 19 [In Norwegian with English summary].

Bailey, R.L. and Clutter, J.L., 1974. Base-age invariant polymorphic site curves. Forest Science, 20(2): 155-159.

Beaulieu, J., Raulier, F., Prégent, G. and Bousquet, J., 2011. Predicting site index from climatic, edaphic, and stand structural properties for seven plantation-grown conifer species in Quebec. Canadian Journal of Forest Research, 41(4): 682-693.

Bella, I.E., 1971. New competition model for individual trees. Forest Science, 17(3): 364-372.

Biging, G.S. and Dobbertin, M., 1992. Comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. Forest Science, 38(3): 695-720.

Biging, G.S. and Dobbertin, M., 1995. Evaluation of competition indices in individual tree-growth models. Forest Science, 41(2): 360-377.

Blingsmo, K., 1984. Diameter increment functions for stands of birch, Scots pine and Norway spruce. Norwegian Forest Research Institute, Ås Research Paper No. 7, 22 p. [In Norwegian with English summary].

Blingsmo, K., 1985. Overhøydeutviklingen i granbestand på Vestlandet (Top height development of Norway spruce in Western Norway). Norwegian Forest Research Institute. Research paper, 1/85: 1-8 [In Norwegian with English summary].

Blingsmo, K., 1988. Volumtilvekst for bjørk, gran og furu bestand (Volume growth in birch, Norway spruce and Scots pine stands). Research paper from Norwegian Forest Research Institute, Ås, 2 p. [In Norwegian].

Blingsmo, K. and Veidahl, A., 1994. Bestprog. Et beslutningsstøtteverktøy for bestand behandling (Bestprog: a decision support tool for forest management). Institute for skogfag. NLH, Ås, p. 1-35 [In Norwegian].

Bøhler, F., Brunner, A. and Øyen, B.-H., 2008. Toppkapping i ungskogpleie av gran: Vekstreaksjoner på toppkappede trær. Forskning fra Skog og landskap, Vol 4/08. Skog og Landskap, Ås [In Norwegian with English summary].

Bøhler, F. and Øyen, B.-H., 2011. Estimation of site index in old, semi-natural stands of Norway spruce at high altitude. Forskning fra Skog og Landskap 1/11, p. 17 [In Norwegian with English summary].

Bollandsås, O.M., 2007. Uneven-age forestry in Norway: inventory and management models, PhD thesis, Norwegian University of Life Sciences, Ås, Norway.

Bollandsås, O.M., Buongiorno, J. and Gobakken, T., 2008. Predicting the growth of stands of trees of mixed species and size: A matrix model for Norway. Scandinavian Journal of Forest Research, 23(2): 167-178.

Bollandsås, O.M. and Næsset, E., 2009. Weibull models for single-tree increment of Norway spruce, Scots pine, birch and other broadleaves in Norway. Scandinavian Journal of Forest Research, 24(1): 54-66.

Bontemps, J.D., Herve, J.C. and Dhote, J.F., 2009. Long-term changes in forest productivity: A consistent assessment in even-aged stands. Forest Science, 55(6): 549-564.

Boyden, S., Binkley, D. and Stape, J.L., 2008. Competition among *Eucalyptus* trees depends on genetic variation and resource supply. Ecology, 89(10): 2850-2859.

Braastad, H., 1974. Diameter increment functions for *Picea abies*. Reports of the Norwegian Research Institute, 31: 1-74 [In Norwegian with English summary].

Braastad, H., 1975. Yield tables and growth models for *Picea abies*. Reports of the Norwegian Research Institute, 31: 357 - 537 [In Norwegian with English summary].

Braathe, P., 1955. Forholdet treantall-høyde som tetthetsangiver (The relatiionship between stem numbers and height as density indicator). Tidsskrift for Skogbruk, 64: 231-238 [In Norwegian].

Brantseg, A., 1969. Furu sønnafjells: produksjonstabeller. Meddelelser fra Det norske Skogforsøksvesen 26: 1-291.

Bravo-Oviedo, A., Tomé, M., Bravo, F., Montero, G. and del Rio, M., 2008. Dominant height growth equations including site attributes in the generalized algebraic difference approach. Canadian Journal of Forest Research, 38(9): 2348-2358.

Brunner, A. and Nigh, G., 2000. Light absorption and bole volume growth of individual Douglas-fir trees. Tree Physiology, 20(5-6): 323-332.

Cajander, A.K., 1909. Ueber waldtypen I. Acta Forestalia Fennica, 1: 1-175.

Cajander, A.K., 1921. Ueber waldtypen in aøgemeinen. Acta Forestalia Fennica, 20(1): 1-77.

Calama, R. and Montero, G., 2004. Interregional nonlinear height-diameter model with random coefficients for stone pine in Spain. Canadian Journal of Forest Research, 34(1): 150-163.

Canham, C.D., LePage, P.T. and Coates, K.D., 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Canadian Journal of Forest Research, 34(4): 778-787.

Carmean, W.H., 1975. Forest site quality evaluation in the United States. Advanced Agronomy, 27: 209-269.

Castedo-Dorado, F., Diéguez-Aranda, U., Anta, M.B., Rodríguez, M.S. and von Gadow, K., 2006. A generalized height-diameter model including random components for radiata pine plantations in northwestern Spain. Forest Ecology and Management, 229(1-3): 202-213.

Chen, H.Y.H., Krestov, P.V. and Klinka, K., 2002. Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. Canadian Journal of Forest Research, 32(1): 112-119.

Cherubini, P., Dobbertin, M., and Innes, J.L., 1998. Potential sampling bias in long-term forest growth trends reconstructed from tree rings: A case study from the Italian Alps. Forest Ecology and Management, 109: 103-118.

Cieszewski, C. and Bailey, R.L., 2000. Generalized algebraic difference approach: Theory based derivation of dynamic site equations with polymorphism and variable asymptotes. Forest Science, 46(1): 116-126.

Cieszewski, C.J., Harrison, M. and Martin, S.W., 2000. Practical methods for estimating non-biased parameters in self-referencing growth and yield models. Daniel B. Warnell School of Forest Resources, University of Georgia Athens, Georgia. Plantation Management Research Cooperative (PMRC) Technical Report 2000-7, 11 p.

Cieszewski, C.J., 2001. Three methods of deriving advanced dynamic site equations demonstrated on inland Douglas-fir site curves. Canadian Journal of Forest Research, 31(1): 165-173.

Cieszewski, C.J., 2002. Comparing fixed- and variable-base-age site equations having single versus multiple asymptotes. Forest Science, 48(1): 7-23.

Cieszewski, C.J., 2003. Developing a well-behaved dynamic site equation using a modified Hossfeld IV function $Y^3 = (ax^m)/(c + x^{m-1})$, a simplified mixed-model and scant subalpine fir data. Forest Science, 49(4): 539-554.

Cieszewski, C.J., Strub, M. and Zasada, M., 2007. New dynamic site equation that fits best the Schwappach data for Scots pine (*Pinus sylvestris* L.) in Central Europe. Forest Ecology and Management, 243(1): 83-93.

Condés, S. and Sterba, H., 2008. Comparing an individual tree growth model for *Pinus halepensis* Mill. in the Spanish region of Murcia with yield tables gained from the same area. European Journal of Forest Research, 127(3): 253-261.

Courbaud, B., Houllier, F. and Rupe, C., 1993. A model for height growth of trees in uneven-aged spruce mountain forest. Annals of Forest Science, 50(4): 337-351.

Crecente-Campo, F., Tomé, M., Soares, P. and Diéguez-Aranda, U., 2010. A generalized nonlinear mixed-effects height-diameter model for *Eucalyptus globulus* L. in northwestern Spain. Forest Ecology and Management, 259(5): 943-952.

Curtis, R.O.,1967. Height-diameter and height-diameter-age equations for second growth Douglas fir. Forest Science, 13 (4): 365-375.

Dahms, W.G., 1963. Correction for possible bias in developing site index curves from sectioned tree data. Journal of Forestry 61: 25-27.

De los Santos-Posadas, H.M., Montero-Mata, M. and Kanninen, M., 2006. Dynamic dominant height growth curves for *Terminalia amazonia* (Gmel.) Excell in Costa Rica. Agrociencia, 40(4): 521-532.

Diéguez-Aranda, U., Burkhart, H.E. and Rodriguez-Soalleiro, R., 2005. Modeling dominant height growth of radiata pine (*Pinus radiata* D. Don) plantations in north-western Spain. Forest Ecology and Management, 215(1-3): 271-284.

Diéguez-Aranda, U., Burkhart, H.E. and Amateis, R.L., 2006. Dynamic site model for loblolly pine (*Pinus taeda* L.) plantations in the United States. Forest Science, 52(3): 262-272.

Eid, T. and Hobbelstad, K., 2000. AVVIRK-2000: A large-scale forestry scenario model for long-term investment, income and harvest analyses. Scandinavian Journal of Forest Research, 15(4): 472-482.

Eid, T. and Tuhus, E., 2001. Models for individual tree mortality in Norway. Forest Ecology and Management, 154(1-2): 69-84.

Eid, T. and Øyen, B.H., 2003. Models for prediction of mortality in even-aged forest. Scandinavian Journal of Forest Research, 18(1): 64-77.

Eid, T. and Hobbelstad, K., 2005. Langsiktige investerings-avvirknings- og inntektsanalyser for skog med Avvirk-2000 (Long term analyses of investment, harvesting and incomes in forest with Avvirk-2000 simulator). Research paper from Norwegian Forest and Landscape Institute, 2/05, 29 p. [In Norwegian].

Eide, E. and Langsæter, A.E., 1941. Produksjonsundersøkeler i granskog (Forest production investigations in Norway spruce forest). Meddr norske Skogfors Ves, 7: 355 -500 [In Norwegian with German summary].

Elfving, B., 1994. Analyser av bonitering med ståndortsfaktorer, grundade på rikstax-data från 1983-1986 (Analysis of site classification from site variables based on national forest inventory data from 1983 -1986). Institutionen för skogsskötsel, Arbetsrapporter Nr. 75 [In Swedish].

Elfving, B. and Nyström, K., 1996a. Stability of site index in Scots pine (*Pinus sylvestris*, L.) plantations over year of planting in the period 1900-1977 in Sweden. **In**: H. Spiecker, K. Mielikäinen, M. köhl and J.P. Skovsgaard (Eds.), Growth trends in European forests. European Forest Research Report 5. European Forest Institute, Leiden, Boston, pp. 71-77.

Elfving, B. and Nyström, K., 1996b. Yield capacity of planted *Picea abies* in Northern Sweden. Scandinavian Journal of Forest Research, 11: 38-49.

Elfving, B., Tegnhammar, L. and Tveite, B., 1996. Studies on growth trends of forests in Sweden and Norway. **In**: H. Spiecker, K., Mielikäinen, M. Köhl and J. P. Skovsgaard (Eds.), Growth trends in European forests. European Forest Research Report 5, European Forest Institute, Leiden, Boston, pp. 61-70.

Elfving, B. and Tegnhammar, L., 1996. Trends of tree growth in Swedish forests 1953-1952: An analysis based on sample trees from the national forest inventory. Scandinavian Journal of Forest Research, 11: 26-37.

Elfving, B. and Kiviste, A., 1997. Construction of site index equations for *Pinus sylvestris* L. using permanent plot data in Sweden. Forest Ecology and Management, 98(2): 125-134.

Fahlvik, N. and Nyström, K., 2006. Models for predicting individual tree height increment and tree diameter in young stands in southern Sweden. Scandinavian Journal of Forest Research, 21: 16-28.

Farrelly, N., Dhubháin, Á.N. and Nieuwenhuis, M., 2011. Site index of Sitka spruce (*Picea sitchensis*) in relation to different measures of site quality in Ireland. Canadian Journal of Forest Research, 41(2): 265-278.

Fries, J., 1969. Boniteringskurvor för tall och gran (Site index curves for pine and spruce). Skogen, 56: 1-20 [In Norwegian with English Summary].

Fox, J.C., Ades, P.K. and Bi, H., 2001. Stochastic structure and individual-tree growth models. Forest Ecology and Management, 154(1-2): 261-276.

García, O., 1994. The state-space approach in growth modeling Canadian Journal of Forest Research, 24(9): 1894-1903.

García, O., 2005. Comparing and combining stem analysis and permanent sample plot data in site index models. Forest Science 51: 277-283.

García, O. and Batho, A., 2005. Top height estimation in lodgepole pine sample plots. Western Journal of Applied Forestry, 20(1): 64-68.

Gizachew, B. and Brunner, A., 2011. Density-growth relationships in thinned and unthinned Norway spruce and Scots pine stands in Norway. Scandinavian Journal of Forest Research, 26(6): 543-554.

Gobakken, T. and Næsset, E., 2002. Spruce diameter growth in young mixed stands of Norway spruce (*Picea abies* (L.) Karst.) and birch (*Betula pendula* Roth *B. pubescens* Ehrh.). Forest Ecology and Management, 171(3): 297-308.

Gobakken, T., Lexerod, N.L. and Eid, T., 2008. T: A forest simulator for bioeconomic analyses based on models for individual trees. Scandinavian Journal of Forest Research, 23(3): 250-265.

Gustavsen, H., 1980. Talousmetsein kasvupaikkaluokittelu valtapituuden avulla (Site index curves for Finland). Folia Forestalia, 45(4): 1-31.

Gustavsen, H., 1996. Site index model approach for drained peat land forest stands. Suo 47: 37-46.

Hägglund, B., 1972. Om övre höjdens utveckling för gran i norra Sverige (Site index curves for Norway Spruce in northern Sweden). Royal College of Forestry, Department of Forest Yield Research. Report 21, 298 p.

Hägglund, B., 1973. Om övre höjdens utvekling för gran i södra Sverige (Site index curves for Norway spruce in southern Sweden). Royal College of Forestry, Department of Forest Yield Research. Report 24, 49 p.

Hägglund, B., 1974. Övre höjdens utveckling i tallbestånd (Site index curves for Scots pine in Sweden). Royal College of Forestry, Department of Forest Yield Research. Report 31, 54 p.

Hägglund, B. and Lundmark, J.E., 1977. Site estimation by means of site properties: Scots pine and Norway spruce in Sweden. Studia Forestalia Suecica, 138: 1-38.

Hägglund, B., 1981. Evaluation of forest site productivity. Forestry Abstract, 42: 515-527.

Hasenauer, H. and Monserud, R.A., 1997. Biased predictions for tree height increment models developed from smoothed 'data'. Ecological Modelling, 98(1): 13-22.

Hasenauer, H., Monserud, R.A. and Gregoire, T.G., 1998. Using simultaneous regression techniques with individual-tree growth models. Forest Science, 44(1): 87-95.

Hasenauer, H., Kindermann, G. and Steinmetz, P., 2006. The tree growth model MOSES 3.0. **In**: H. Hasenauer (Ed.), Sustainable forest management, Growth models for Europe. Springer-Verlag Berlin Heidelberg, 388 p.

Hassall, R.B., Macmillan, D.C. and Miller, H.G., 1994. Predicting Sitka spruce yields in the Buchan area of north-east Scotland. Forestry, 67(3): 219-235.

Hegyi, F., 1974. A simulation model for managing jack-pine stands. **In**: J. Fries (Ed.), Growth models for tree and stand simulation. Royal College of Forestry, Stockholm, Sweden. Research Note 30, pp. 74-90.

Hoen, H.F. and Eid, T., 1990. En modell for analyse av behandlingsstrategier for en skog ved bestandssimulering og lineær programmering (A model for analysis of forest management alternatives using stand simulation and linear programming). Rapport fra Norsk instttutt for skogforskning, 9: 1-35 [In Norwegian].

Huang, S.M. and Titus, S.J., 1999. An individual tree height increment model for mixed white spruce-aspen stands in Alberta, Canada. Forest Ecology and Management, 123(1): 41-53.

Huuskonen, S. and Miina, J., 2007. Stand-level growth models for young Scots pine stands in Finland. Forest Ecology and Management, 241(1-3): 49-61.

Hynynen, J., and Ojansuu, R., 2003. Impact of plot size on individual-tree competition measures for growth and yield simulators. Canadian Journal of Forest Research 33 (3): 455-465.

Hyyppa, J., Holopainen, M. and Olsson, H., 2012. Laser scanning in forests. Remote Sensing, 4(10): 2919-2922.

Hynynen, J., Ahtikoski, A., Siitonen, J., Sievänen, R. and Liski, J., 2005. Applying the MOTTI simulator to analyse the effects of alternative management schedules on timber and non-timber production. Forest Ecology and Management, 207(1-2): 5-18.

Johansson, T., 1996. Site index curves for Norway spruce (*Picea abie*s (L.) Karst.) planted on abandoned farmland. New Forests, 11(1): 9-29.

Jonsson, T., 1914. Om bonitering av skogmark (About site index estimation of forest fields). Journal of the Swedish Forestry Society, 2(5): 369-392 [In Swedish].

Kahle, H.-P., Karjalainen, T., Schuck, A., Ågren, G. I., Kellomäki, S., Mellert, K., et al. (Eds.). (2008a). Causes and consequences of forest growth trends in Europe. European Forest Research Report 21, European Forest Institute, Leiden, Boston, 261 p.

Kahle, H.-P., Spiecker, H., Unseld, R., Pérez-Martínez, P.-J., Prietzel, J., Mellert, K.-H., et al. (2008b). Temporal trends and spatial patterns of height growth in relation to changes in air temperature and precipitation, and in relation to levels of foliar nitrogen and nitrogen deposition. **In**: H.-P. Kahle, T. Karjalainen, A. Schuck, G. I. Ågren, S. Kellomäki, K. Mellert, J. Prietzel, K.-E. Rehfuess and H. Spiecker (Eds.), Causes and consequences of forest growth trends in Europe. European Forest Research Report 21, European Forest Institute, Leiden, Boston, pp. 127-168.

Kangas, A.S., 1998. Effect of errors-in-variables on coefficients of a growth model and on prediction of growth. Forest Ecology and Management, 102(2-3): 203-212.

Kantola, A., Mäkinen, H. and Mäkelä, A., 2007. Stem form and branchiness of Norway spruce as a sawn timber- predicted by a process based model. Forest Ecology and Management, 241(1-3): 209-222.

Karlsson, K., 2000. Height growth patterns of Scots pine and Norway spruce in the coastal areas of western Finland. Forest Ecology and Management, 135(1-3): 205-216.

Kiviste, A., 1999. Site index change in the 1950s - 1990s according to Estonian forest inventory data. **In:** T. Karjalainen, H. Spiecker, and O. Laroussinie (Eds.), Causes and consequences of accelerating tree growth in Europe. European Forest Institute proceedings 27: 85-100.

Krumland, B. and Eng, H., 2005. Site index systems for major young-growth forest and woodland species in northern California. California Department of Forest and Fire Protection, Sacramento, CA. Forestry Report 4: 1-219.

Kwiaton, M.M., Wang, J.R. and Reid, D.E.B., 2011. A height growth model and associated growth intercept models for estimating site index in black spruce (*Picea mariana* Mill. B.S.P.) plantations in northern Ontario, Canada. Northern Journal of Applied Forestry, 28(3): 129-137.

Landsskogtakseringen, 1938. Taksering av Norges skoger. Østfold fylke. Revisjonsteksering 1937 [In Norwegian].

Landsskogtakseringen, 2007. Landsskogtakseringens feltinstruks 2007 (Field manual of the national forest inventory 2007), Håndbok fra Skog og landskap, 06/2007, 116 p. + appendix [In Norwegian].

Lappi, J., 2005. Plot size related measurement error bias in tree growth models. Canadian Journal of Forest Research, 35: 1031-1040.

Larsson, J.Y. and Hylen, G., 2007. Statistics of forest conditions and forest resources in Norway recorded during 2000-2004. Viten fra Skog og Landskap, 1: 1-91 [In Norwegian with English Summary].

Ledermann, T. and Stage, A.R., 2001. Effects of competitor spacing in individual-tree indices of competition. Canadian Journal of Forest Research, 31(12): 2143-2150.

Lexerød, N. and Eid, T., 2005. Recruitment models for Norway spruce, Scots pine, birch and other broadleaves in young growth forests in Norway. Silva Fennica, 39(3): 391-406.

Lei, X., Peng, C., Wang, H. and Zhou, X., 2009. Individual height–diameter models for young black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) plantations in New Brunswick, Canada. The Forestry Chronicle, 85(1): 43-56.

Lämås, T. and Eriksson, L.O., 2003. Analysis and planning systems for multiresource, sustainable forestry: the Heureka research programme at SLU. Canadian Journal of Forest Research, 33(3): 500-508.

Mäkelä, A., Kolari, P., Karimäki, J., Nikinmaa, E., Perämäki, M., and Hari, P., 2006. Modelling five years of weather-driven variation of GPP in a boreal forest. Agricultural and Forest Meteorology, 139(3-4): 382-398.

Martin-Benito, D., Gea-Izquierdo, G., del Rio, M. and Canellas, I., 2008. Long-term trends in dominant-height growth of black pine using dynamic models. Forest Ecology and Management, 256(5): 1230-1238.

Martin, G.L., Ek, A.R. and Monserud, R.A., 1977. Control of plot edge bias in forest stand growth simulation models. Canadian Journal of Forest Research, 7(1): 100-105.

Mason, E.G. Methol, R. and Cochrane, C., 2011. Hybrid mensurational and physiological modelling of growth and yield of *Pinus radiata* D.Don using potentially useable radiation sums. Forestry, 84(2): 99-108.

Mehtatalo, L., 2004. A longitudinal height-diameter model for Norway spruce in Finland. Canadian Journal of Forest Research, 34(1): 131-140.

Mehtatalo, L., 2005. Height-diameter models for Scots pine and birch in Finland. Silva Fennica, 39(1): 55-66.

Mileikäinen, K. and Timonen, M., 1996. Growth trends of Scots pine (*Pinus sylvestris*, L.) in unmanaged and regularly managed stands in southern and central Finland. **In**: H. Spiecker, K. Mielikäinen, M. köhl and J. P. Skovsgaard (Eds.), Growth trends in European forests. European Forest Research Report 5, pp. 41-59.

Miina, J. and Pukkala, T., 2000. Using numerical optimization for specifying individual-tree competition models. Forest Science, 46(2): 277-283.

Mitchell, K.J., 1975. Dynamics and simulated yield of Douglas-fir. Forest Science Monograph 17: 1-39.

Monserud, R.A., 1984. Height growth and site index curves for inland Douglas-fir based on stem analysis data and forest habitat type. Forest Science, 30(4): 943-965.

Monserud, R.A. and Sterba, H., 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. Forest Ecology and Management, 80(1-3): 57-80.

Monserud, R.A. and Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. Forest Ecology and Management, 113(2-3): 109-123.

Nagel, J., 1997: BWIN- program for standard analysis and prognosis. User's manual for version 3.0. Niedersächsische Forstliche Versuchsanstalt Göttingen.

Nanos, N., Calama, R., Montero, G. and Gil, L., 2004. Geostatistical prediction of height/diameter models. Forest Ecology and Management, 195(1-2): 221-235.

Newton, R.F. and Amponsah, I.G., 2007. Comparative evaluation of five height-diameter models developed for black spruce and jack pine stand-types in terms of goodness-of-fit, lack-of-fit and predictive ability. Forest Ecology and Management, 247(1-3): 149-166.

NIJOS, 2000. Skog 2000. Statistics of forest conditions and resources in Norway. Norwegian Institute of Land Inventory, Ås, Vol. 7.

Nilsen, P. and Haveraaen, O., 1982. En analyse av tilvekst i gammel granbestand. Rapport fra Norsk institutt for skogforskning, 82/13: 38.

Nilsen, P. and Larsson, J., 1992. Site index estimation from vegetation type and site properties. Rapport fra Skogforsk, 22/92: 1-43 [In Norwegian with English summary].

Nord-Larsen, T., 2006a. Developing dynamic site index curves for European beech (*Fagus sylvatica* L.) in Denmark. Forest Science, 52(2): 173-181.

Nord-Larsen, T., 2006b. Modeling individual-tree growth from data with highly irregular measurement intervals. Forest Science, 52(2): 198-208.

Nord-Larsen, T., Meilby, H. and Skovsgaard, J.P., 2009. Site-specific height growth models for six common tree species in Denmark. Scandinavian Journal of Forest Research, 24(3): 194-204.

Orlund, A., 2001. Bonitering av plantet gran (*Picea abies* L. Karst) og sitkagran (*Picea sitchensis* Bong. Carr.) på vestlandet (Site quality classification of planted Norway spruce and Sitka spruce in west coast of Norway). Skogforsk 2/01: 1-17 [In Norwegian with English summary].

Payandeh, B., 1974. Formulated site index curves for major timber species in Ontario. Forest Science, 20(2): 143-144.

Peltoniemi, M. and Makipaa, R., 2011. Quantifying distance-independent tree competition for predicting Norway spruce mortality in unmanaged forests. Forest Ecology and Management, 261(1): 30-42.

Perin, J., Hébert, J., Brostaux, Y., Lejeune, P. and Claessens, H., 2013. Modelling the top-height growth and site index of Norway spruce in Southern Belgium. Forest Ecology and Management, 298(0): 62-70.

Pienaar, L.V. and Rheney, J.W., 1995. Modeling stand level growth and yield response to silvicultural treatments. Forest Science, 41(3): 629-638.

Pinheiro, J.C. and Bates, D.M., 2000. Mixed-effects models in S and S-PLUS. New York: Springer, 528 p.

Pokharel, B. and Dech, J.P., 2011. An ecological land classification approach to modeling the production of forest biomass. Forestry Chronicle, 87(1): 23-32.

Pommerening, A., Lemay, V. and Stoyan, D., 2011. Model-based analysis of the influence of ecological processes on forest point pattern formation - A case study. Ecological Modelling, 222(3): 666-678.

Porte, A. and Bartelink, H.H., 2002. Modelling mixed forest growth: a review of models for forest management. Ecological Modelling, 150(1-2): 141-188.

Pretzsch, H., 1997. Analysis and modeling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in Lower Saxony. Forest Ecology and Management, 97(3): 237-253.

Pretzsch, H., Biber, P. and Dursky, J., 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. Forest Ecology and Management, 162(1): 3-21.

Pretzsch, H., 2009. Forest dynamics, growth and yield: from measurement to model. Springer Verlag, Berlin, Germany, 664 p.

Pukkala, T., 1989. Methods to describe the competition process in a tree stand. Scandinavian Journal of Forest Research, 4: 187-200.

Richards, M., McDonald, A.J.S. and Aitkenhead, M.J., 2008. Optimisation of competition indices using simulated annealing and artificial neural networks. Ecological Modelling, 214(2-4): 375-384.

Ritchie, M.W. and Hamann, J.D., 2008. Individual-tree height-, diameter- and crown-width increment equations for young Douglas-fir plantations. New Forests, 35(2): 173-186.

Rivas, J.J.C., Gonzalez, J.G.A., Aguirre, O. and Hernandez, F., 2005. The effect of competition on individual tree basal area growth in mature stands of *Pinus cooperi* Blanco in Durango (Mexico). European Journal of Forest Research, 124(2): 133-142.

Robinson, A.P. and Wykoff, W.R., 2004. Imputing missing height measures using a mixed-effects modeling strategy. Canadian Journal of Forest Research, 34(12): 2492-2500.

Sabatia, C.O. and Burkhart, H.E., 2012. Competition among loblolly pine trees: Does genetic variability of the trees in a stand matter? Forest Ecology and Management, 263(0): 122-130.

Schadauer, K., 1999. Site index and site characteristics of Norway spruce according to data of the Austrian Forest Inventory. Mitteilungen der Forstlichen Bundesversuchsantalt Wien. Report 171, 38 p. [In German with English summary].

Schmidt, M., 2010. Ein standortsensitives, longitudinales Höhen-Durchmesser-Modell als eine Lösung für dasStandort-Leistungs-Problem in Deutschland. DVFFA - Sektion Ertragskunde, Jahrestagung, pp. 131-152 [In German with English summary].

Schmidt, M., Kiviste, A. and von Gadow, K., 2011. A spatially explicit height-diameter model for Scots pine in Estonia. European Journal of Forest Research, 130(2): 303-315.

Seynave, I., Gegout, J. C., Herve, J. C., Dhote, J. F., Drapier, J., Bruno, E., and Dume, G. 2005. *Picea abies* site index prediction by environmental factors and understory vegetation: a two-scale approach based on survey databases. Canadian Journal of Forest Research, *35*(7): 1669-1678.

Sharma, M. and Zhang, S.Y. 2004. Height-diameter models using stand characteristics for *Pinus banksiana* and *Picea mariana*. Scandinavian Journal of Forest Research, 19(5): 442-451.

Sharma, M. and Parton, J., 2007. Height-diameter equations for boreal tree species in Ontario using a mixed-effects modeling approach. Forest Ecology and Management, 249(3): 187-198.

Skovsgaard, J.P. and Vanclay, J.K., 2008. Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. Forestry, 81(1): 12-31.

Socha, J., 2008. Effect of topography and geology on the site index of *Picea abies* in the west Capthian, Poland. Scandinavian Journal of Forest Research, 23(3): 203-213.

Solberg, S., Dobbertin, M., Reinds, G. J., Lange, H., Andreassen, K., Fernandez, P. G., et al., 2009. Analyses of the impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: A stand growth approach. Forest Ecology and Management, *258*(8): 1735-1750.

Spiecker, H., Mielikäinen, K., Köhl, M. and Skovsgaard, J.P. (Eds.), 1996. Growth trends in European forests. European Forest Research Report 5. European Forest Institute. Springer-Verlag, Berlin, 372 p.

Spiecker, H., 1999. Overview of recent growth trends in European forests. Water, Air, and Soil Pollution 116 (1-2): 33-46.

Sterba, H. and Monserud, R., 1996. Validation of the single tree stand growth simulator PROGNAUS with permanent plot data. Proceeding of IUFRO 20th World Congress, 6 -12 August, 1995, Tempere, Finland, pp. 36-49.

Sterba, H. and Monserud, R.A., 1997. Applicability of the forest stand growth simulator PROGNAUS for the Austrian part of the Bohemian Massif. Ecological Modelling, 98(1): 23-34.

Tamminen, P., 1993. Estimation of site index for Scots pine and Norway spruce stands in South Finland using site properties. Folia Forestalia, 819: 1-26 [In Finish with English summary].

Tegnhammar, L., 1992. On the estimation of site index for Norway spruce. Department of Forest Survey, Swedish University of Agricultural Sciences. Report 53, 259 p. [In Swedish with English summary].

Temesgen, H. and Gadow, K.V. 2004. Generalized height-diameter models: an application for major tree species in complex stands of interior British Columbia. European Journal of Forest Research, 123: 45-51.

Tiwari, V.P. and Singh, B., 2009. Site index model for *Tecomella undulata* (Sm.) Seem. (*Bignoniaceae)* plantations in a hot arid region of India. Journal of Arid Environment, 43: 490-493.

Tomter, S.M., 2000. Skog 2000. Statistikk over skogforhold og -ressurser i Norge (Statistics of forest conditions and resources in Norway). Norwegian Forest and Landscape Institute, Ås, 84 pp. [In Norwegian].

Tveite, B., 1969. A method of construction of site index curves. Meddr norske Skogfors Ves 27: 131-160.

Tveite, B., 1977. Site index curves for Norway spruce (*Picea abies* (L.) Karst.). Report of Norwegian Forest Research Institute, 33(1): 1-84 [In Norwegian with English summary].

Tveite, B., 1981. Bonitering for gran, furu og bjørk. Norsk Skogbruk, 27(4): 17-22.

Tveite, B. and Braastad, H., 1981. Bonitering for gran, furu og bjørk (Site index for Norway spruce, Scots pine and birch). Norsk Skogbruk, 27(4): 17-22.

Tveite, B., 1994. Høgdeutvikling og volumproduksjon i gran- og furuskog nord for Saltfjellet (Height development and volume production in spruce and pine forests north for Saltfjellet), pp. 92-99. **In**: J. Bergan (Ed.), Faglige emner innen primærproduksjonen i skogbruket i Nord-Norge. Norwegian Forest Research Institute, Ås [In Norwegian].

Tveite, B., 2004. Produksjon i norsk eikeskog.Skogforsk, Ås, 13 p.

Uzoh, F.C.C. and Oliver, W.W., 2006. Individual tree height increment model for managed even-aged stands of ponderosa pine throughout the western United States using linear mixed effects models. Forest Ecology and Management, 221(1-3): 147-154.

Vanclay, J.K., 1992. Assesing site productivity in tropical moist forests - a review. Forest Ecology and Management, 54(1-4): 257-287.

Vanclay, J.K., 1994. Modelling forest growth and yield. Applications to mixed tropical forests. CAB International, Oxon, U.K., 312 p.

Vaughn, N.R., Turnblom, E.C. and Ritchie, M.W., 2010. Bootstrap evaluation of a young Douglas-fir height growth model for the Pacific Northwest. Forest Science, 56(6): 592-602.

Vuokila, Y. and Väliaho, H., 1980. Growth and yield models for conifer cultures in Finland. Communicationes Instituti Forestalis Fenniae, 99(2): 1-271.

Wykoff, W.R., 1990. A basal area increment model for individual conifers in the Northern Rocky Mountain. Forest Science, 36(4): 1077-1104.

Zeide, B., and Zakrzewski, W.T., 1993. Selection of site trees- the combined method and its application. Canadian Journal of Forest Research, 23: 1019-1025.

Zeide, B. and Curtis, V. 2002. The effect of density on the height-diameter relationship. **In**: General Technical Report, SRS-48. Asheville, NC: USDA, Forest Service, Southern Research Station, pp. 463-466.

Øyen, B.-H. and Nes, K., 1997. Growth patterns of Scots pine (*Pinus sylvestris* L.) in western Norway. Meddelelser fra Skogforsk, 47.18: 24.

Øyen, B.-H. and Andreassen, K., 2002. Modeller for å estimere trehøyde ved hjelp av diameter og bestandsdata. Norwegian Forest Research Institute. Aktuelt, 6: 13-14 [In Norwegian].

PAPER I

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Modelling dominant height growth from national forest inventory individual tree data with short time series and large age errors

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ABSTRACT

We developed dominant height growth models for Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) in Norway using national forest inventory (NFI) data. The data were collected for a different purpose which potentially causes problems for dominant height growth modelling due to short time series and large age errors. We used the generalized algebraic difference approach and fitted 15 different models using nested regression techniques. Despite the potential problems of NFI data the models fitted to these data were unbiased for most of the age and site index range covered by the NFI data when tested against independent data from long-term experiments (LTE). Biased predictions for young stands and better site indices that are better represented in the LTE data, led us to fit models to a combined data set for unbiased predictions across the total data range. The models fitted to the combined data that were unbiased with little residual variation when tested against an independent data set based on stem analysis of 73 sample trees from southeastern Norway. No indications of regional differences in dominant height growth across Norway were detected. We tested whether the better growing conditions during the short time series (22 years) of the NFI data had affected our dominant height growth models relative to long-term growing conditions, but found only minor bias. The combination with LTE data that have been collected during a longer period (91 years) reduced this potential bias. The dominant height growth models presented here can be used as potential height growth models in individual tree-based forest growth models or as site index models.

1. Introduction

Dominant height of a stand reflects the productivity of a fully stocked even-aged stand because it is independent of density over a wide range of densities (Skovsgaard and Vanclay, 2008), and therefore dominant height at a given reference age is used as a measure of site productivity (Spurr, 1952; Monserud, 1984). Site index models are also dominant height growth models and are therefore used to predict maximum possible (potential) height growth in individual tree based growth models (Pretzsch et al., 2002; Reed et al., 2003; Hasenauer et al., 2006). Norwegian dominant height growth models for Norway spruce and Scots pine (Tveite, 1977; Tveite and Braastad, 1981) were intended to be used to predict site index only and the derived potential height growth shows unrealistic culmination of height growth. Dominant height growth models for Norway spruce and Scots pine have also been developed in Sweden (e.g. Fries, 1969; Hägglund, 1972, 1973, 1974; Johansson, 1996; Elfving and Kiviste, 1997) and Finland (e.g. Gustavsen, 1980; Vuokila and Väliaho, 1980; Karlsson, 2000). Data sources were mostly stem analysis and permanent sample plots. Except for a few examples (Elfving and Kiviste, 1997; Eriksson et al., 1997), previous fennoscandian dominant height growth models have been developed with simple methods, e.g. involving guide curves, resulting in base-age specific models, which assume an error-free observation of height at the base age and are limited to certain types of observations and predictions.

Today, dominant height growth models are mostly developed using base-age invariant approaches (Anta and Dieguez-Aranda, 2005; Krumland and Eng, 2005; Nord-Larsen, 2006a; Cieszewski et al., 2007), making use of time series that do not include the base age, and making models independent of the choice of base age. The algebraic difference approach was used earlier (Bailey and Clutter, 1974), but here only one parameter can be site-specific and such models produce height curves that are either anamorphic or have a single asymptote. The generalized algebraic difference approach (GADA) (Cieszewski and Bailey, 2000) allows more than one parameter to be site-specific, and models can therefore be polymorphic with multiple asymptotes (Cieszewski, 2001, 2002; Cieszewski et al., 2007). Short time series of dominant height with no common base age can also be used with this approach (e.g. García,

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2005; De los Santos-Posadas et al., 2006; Nord-Larsen, 2006a; Tiwari and Singh, 2009). GADA has become a standard for dominant height growth modelling (Diéguez-Aranda et al., 2006a; Nord-Larsen, 2006a; Cieszewski et al., 2007; Bravo-Oviedo et al., 2008; Martin-Benito et al., 2008).

Dominant height growth models can be developed from different data sources: stem analysis (Martin-Benito et al., 2008), repeated measurements on permanent sample plots established for experimental purposes or in the context of national forest inventories. Accuracy of the height growth data varies and is typically higher for stem analysis data than for permanent sample plots (García, 2005). A bias may occur with stem analysis data, however, if changes in tree dominance over time go undetected (Dahms, 1963; Zeide and Zakrzewski, 1993; Cherubini et al., 1998). Experimental plots tend to be established in well-managed stands on better sites while permanent sample plots of national forest inventories are usually representative for growth conditions for large areas.

Records from permanent sample plots of national forest inventories are increasingly used for growth modelling, such as basal area growth models (Monserud and Sterba, 1996; Sterba and Monserud, 1997; Andreassen and Tomter, 2003), diameter growth models (Bollandsås and Næsset, 2009), basal area and height growth models (Condés and Sterba, 2008), and height growth models (Hasenauer and Monserud, 1997). Huuskonen and Miina (2007) developed dominant height growth models from national forest inventory data for young and even-aged stands of Scots pine in Finland. Designed for another purpose, national forest inventory data might cause special problems for growth modelling (Seynave et al., 2005). Short time series and poor age records are among the most prominent problems. Short time series require special consideration in dominant height growth modelling and raise a general concern of how well the data represent average growing conditions with regard to climatic variation (Monserud and Sterba, 1996). Stand age of experimental plots can be recorded precisely, whereas stand age of permanent sample plots for national forest inventories are often recorded with much lower precision. Uneven-aged stands included in the sample cause special problems for age recording and dominant height growth modelling. Insufficient representation of the dominant trees due to the sampling approach for height measurements and the small plot sizes (García, 1998; Magnussen, 1999) might also question the use of such data for dominant height growth modelling.

The objective of our study was to develop dominant height growth models for Norway spruce and Scots pine in Norway. The models are intended to be used as to predict site index and potential height growth in individual tree based growth models. Data from the national forest inventory were available for this study, and we wanted to test the models against data from long-term experiments and stem analysis data specifically collected for this purpose. Given the lack of dominant height growth models developed from national forest inventory data, we wanted to test if it was possible to use this data despite the different purpose of the data collection. Short time series and poor age records are of special concern for our Norwegian data and will be addressed specifically.

2. Methods

2.1. Data

Following the objective of our study we initially used data from the Norwegian national forest inventory for model calibration and tested the models against two independent data sets, i.e. existing data from long-term experiments and stem analysis data specifically collected for our project. After the first tests of the model against data from the experiments we detected a bias for young stands due to missing data in that age range. We therefore decided to combine the two data sets for calibration of another set of models, leaving the stem analysis data as the only test data set for those combined data models.

2.1.1. National forest inventory data

The Norwegian national forest inventory (NFI) has established 10,500 permanent sample plots in productive forests systematically located in a 3 × 3 km grid across most of Norway except Finnmark county (Tomter, 2000). The size of the circular plots was 100 m^2 during the establishment phase (1986–1993) and was later increased to 250 m^2. Plots were remeasured every fifth year. We excluded plots that had a stand border within the plot, plots without age records, and plots with land use types other than forestry. We excluded plots if less than 70% of the standing volume was neither Scots pine nor Norway spruce. For all the trees above 5 cm in diameter at breast height (dbh) the coordinates and dbh are known. For our purpose we used data for the period 1986–2008, including up to three remeasurements of the height of the dominant trees.

Height was measured on a sample of trees at each remeasurement. The trees were selected based on a gauge angle factor of 6 $m^2\,ha^{-1}$, resulting in only one height sample tree per plot for about 30% of all plots, and between two and six height sample trees for the remaining plots. Due to the angle gauge sampling approach, dominant trees had a higher probability of being included in the height samples than smaller trees. Height of the sample trees was measured using hypsometers such as Suunto or Vertex and recorded to the nearest 0.1 m. Given the low precision of height measurements with those hand-held instruments relative to a 5 year height increment, large measurement errors can be expected. According to Norwegian traditions, tree height has been recorded as height difference between the tree top and an estimated stump height. We therefore converted to total tree height by adding 0.3 m to all recorded heights.

For a sample plot size of 250 m^2, the largest two to three trees by diameter can be expected to be among the 100 largest per ha and therefore fulfill the criteria for dominant trees. We identified those individual trees in our data using a combination of height and dbh ranking. This reflects a typical field procedure where both height and dbh are considered simultaneously to identify dominant trees. The selection algorithm resulted most often in one to two height sample trees per plot being selected as dominant trees.

We excluded plots with shelter trees to avoid suppressed height growth. Shelter trees were identified on the basis of dbh distributions for each plot and measurement occasion. Top breakage was identified in the field and those trees were removed from the data set. Still many dominant trees that were selected due to their large dbh had a low height relative to the dbh. A linear regression of height–dbh ratio over dbh for all height sample trees per species was used to identify such trees and exclude them.

Stand age for the NFI is defined as the basal area weighted mean breast height age. This means that in cases where the field crew considered the stand to be uneven-aged, the recorded stand age is lower than the age of the dominant trees. The recorded stand age is, in other words, a rough estimate of the age of the dominant trees, especially when considering the fact that large forest areas in Norway are uneven-aged. Recorded height and age did often not match with the recorded site index, indicating an age correction. We found such inconsistencies for 19% and 12% of the plots, for spruce and pine, respectively. We did not exclude these plots, because preliminary analysis indicated no significant bias of the models fitted to the entire data as compared to models fitted to data excluding such plots. Stand age was estimated from an increment core taken at breast height of one dominant tree outside the permanent sample plot during recordings in inventory periods 6 (1986–1993) and 7 (1994–1999). In inventory period 8 (2000–2004) stand age was known from previous inventories and therefore only sporadically controlled by counting age on increment cores. In period 9 (2005–2009) no ages were recorded. We therefore considered stand ages given for period 7 and 8 to be consistent and calculated a mean of the discounted ages for period 7 and 8. The average of stand age for period 6 and mean stand age for periods 7 and 8 was used as stand age for our analyses. We converted the recorded total age back to age at breast height by subtracting the time to reach breast height given in the field instructions for different site index classes (Skog og landskap, 2007).

Because tree height was measured during the growing season, the increment period was not always a full year. To calculate the number of increment periods for the given records, we assumed that height growth occurs within the first 60 days of the growing season for spruce (Kozlowski, 1962; Ekberg et al., 1994) and pine (Kozlowski, 1962; Zhang et al., 1997; Kilpelainen et al., 2006). The start of the growing season was estimated as the day when the degree day sum exceeded 10 °C (Salminen and Jalkanen, 2007), using a degree day sum of daily temperatures above 5 °C. The earliest start of height growth was set to April 19 and the latest to July 1. Mean monthly temperatures for all sample plots were obtained from a spatial interpolation of the records from 797 weather stations (Skaugen and Tveito, 2004; Solberg et al., 2004). For the 29% of all trees that were measured during the growing season we calculated the corrected proportion of time (number of days) within the height growth period (T_s) assuming a sigmoid height growth over time

$$T_s = \frac{1}{1 + \exp[10(0.5 - T)]}$$

where T is the time within the height growth period relative to the total length of the height growth period.

For Norway spruce, 1299 dominant trees on 859 plots were selected as dominant trees, representing 34% of all sample plots with height sample trees. For Scots pine, 1372 dominant trees on 913 plots were selected as dominant trees, representing 37% of all sample plots with height sample trees. Between one and four dominant trees were identified on the plots, with the majority of the plots represented by only one tree. The selected plots cover most of the range of the distribution for those two species in Norway.

2.1.2. Long-term experiment data

The Norwegian Forest and Landscape Institute has series of permanent sample plots located on several hundred sites across the country. The first plots were established in 1915 and the last measurements used here were done in 2006. The sample plots are part of long-term experiments (LTE) testing thinning methods and other treatments or they have been established to monitor growth for modelling purposes. The sample plots have been remeasured regularly, creating time series of dominant height data with a length of 10–80 years. Stand age varied between 0 and 180 years. The distribution of sample plots across ages and site indices can be seen in Fig. 2. After 1960 dominant height on those plots was estimated based on height measurements of all trees representing the 100 largest trees by diameter per ha. Before 1960 dominant height on some plots was estimated using height–diameter relationships estimated from a number of sample trees (18% of the dominant heights in the LTE data). For our analysis we used 1704 plots on 542 sites for Norway spruce, and 724 plots on 191 sites for Scots pine.

For conversion of total age to breast height age, an average time to breast height per site index was used (Skog og Landskap, 2007), ignoring indications for a slightly longer time to breast height in Western Norway (Øyen and Nes, 1997). For individual plots this average time can be different from the real time to reach breast height, causing height at breast height age zero to be different from 1.3 m. For time series on 47 plots in young stands (breast height age <10 years) with large errors, we corrected breast height age by estimating time to breast height based on a linear regression fitted to the first four observations of the time series. In cases where age of the LTE data was estimated from increment cores that showed signs of growth suppression in the youth, ages were corrected to ages of stands without growth suppression.

Dominant height series from LTE and NFI are different in nature. Time series from the LTE are generally much longer than those from the NFI data. While NFI data are representative of the growing conditions and stand ages in Norway, LTE data have a bias towards better sites and younger stands (Fig. 2). Data from younger stands are missing in the NFI data because individual tree height is only sampled for trees with dbh > 5 cm. The height series in the NFI data are based on individual trees whereas those from LTE are based on means of dominant trees. In both cases the sampling design is unbalanced, i.e. one to three trees per plot and two to four remeasurements per tree in the NFI data and 1–36 plots per site and 2–20 remeasurements per plot in the LTE data.

2.1.3. Stem analysis data

In order to test the dominant height growth models, we collected 89 dominant trees from both species for stem analysis (SA), allowing us to reconstruct their height growth. Sampling was restricted to south-eastern Norway (counties Telemark, Buskerud, Oppland, and Hedmark), a region containing most of the forest resources and supplying the majority of the annual cut. By using forest management plan data we identified stands with an age of around 100 years covering the existing site index range in the given region. In total we sampled 89 trees in 31 stands. In each stand we identified three dominant trees and sampled 20 stem disks at regular intervals along the stem, recording the height of the disks along the stem. The number of annual rings was counted on each stem disk in the lab to determine the age at which this height was reached, always assuming that the height was reached half way through the growth period (Newberry, 1991). By comparing the height series of the three trees per stand we could identify periods of suppression for individual trees (Martin-Benito et al., 2008) and excluded 16 trees and the later part of the time series from 11 trees due to signs of suppressed height growth.

When comparing dominant height growth model predictions with the SA height series, we found many trees that were growing slower in the youth than predicted by the model, especially for Norway spruce but also in a few cases for Scots pine. Suppressed height growth in the youth can be a consequence of natural regeneration under shelter, which is much more likely to be represented in our SA series due to their origin about 100 years ago as compared to the model calibration data. As a consequence of suppression in the youth, the age of those trees is not comparable with that of trees of the same height growing in even-aged stands after clearcutting. We corrected time series of suppressed trees if we found a deviation from model prediction of more than 2 m using model 1 fitted to the combined data set. Declining trends in the youth in the residual plots were used to identify periods of suppressed growth and those periods were removed from the time series of 22 spruce and 9 pine trees. In order to correct the age for the remaining part of those time series the dominant height growth model with fixed global parameters and variable site index and age correction term were fitted to the data. Most of the age corrections were about 50% of the length of the suppression period. Because this correction of the time series is depending on the dominant height growth model used for the correction, we applied age corrections using models 1, 2, 8, 12, 14 fitted to combined data and found differences in the age correction between models of 0 and 4 years, and 9 years for one tree (age corrections varied from 0 to 58 years with a mean of 15 years). This indicates that the correction using those models identifies periods of suppression as patterns inherent in the data almost independently of the individual model.

A total of 36 Norway spruce trees and 37 Scots pine trees were available for our tests. The distribution of SA data across ages and site indices can be seen in Fig. 2. Representing individual dominant trees the SA data are more similar to the NFI data than to the LTE data. Due to their long time series, which are in some cases exceeding the length of the LTE series, they are well suited for testing the dominant height growth model.

2.2. Models

Models of dominant height growth describe the development of height over age for a range of site qualities. As site index models they are used to assess productivity of forest sites (Skovsgaard and Vanclay, 2008). Time series of dominant height over age are non-linear and often sigmoid. Modelling the effect of site quality on asymptote and shape parameters of these models is a complex task, which is further complicated by the fact that the site quality of each individual time series is unknown. The latter is especially true for the short time series of the NFI data. We therefore applied the generalized algebraic difference approach (GADA) (Cieszewski and Bailey, 2000), which allowed us to use short time series and is able to fit polymorphic models with variable asymptotes. GADA has frequently been used to model growth of dominant height and other variables (Anta et al., 2006; Diéguez-Aranda et al., 2006b; Nord-Larsen, 2006a; Cieszewski et al., 2007; Bravo-Oviedo et al., 2008; Martin-Benito et al., 2008). GADA models have been developed for a range of different base functions of fractional form, e.g. Hossfeld, King-Prodan (Cieszewski et al., 2007) and exponential form, e.g. Chapman–Richards, Sloboda (Cieszewski and Strub, 2008). Dominant height growth for various species in Scandinavia has been modeled mainly based on the Chapman–Richards and Hossfeld functions (Hägglund, 1973, 1974; Johansson, 1996; Elfving and Kiviste, 1997; Karlsson, 2000). Current dominant height growth models for Norway spruce and Scots pine in Norway (Tveite, 1977) are based on a fractional function (Strand, 1964). Due to the short time series of our NFI data, we were not able to identify the most suitable base function for our material by fitting models to individual time series. We therefore tested GADA models that have previously been used and derived GADA formulations of previously used growth functions, i.e. a total of 15 models (Table 1). Any number of parameters in the base growth function can be made site-specific by using an unobservable theoretical site variable X. Solving the base equation for X with initial values and replacing parameters in the original equation, gives the GADA models of the form $h_1 = f(h_0, t_0, t_1, b)$ (h_0 and h_1 are heights (in m) at age t_0 and t_1 (in years), respectively, b is the parameter vector).

2.3. Analysis

2.3.1. Parameter estimation

The model parameters were estimated with non-linear least-square regression using PROC NLIN (SAS Institute Inc., 2008), applying Marquardt's method due to correlation among parameter estimates. We used nested regression (Cieszewski et al., 2000; Krumland and Eng, 2005) to simultaneously estimate global and site-specific parameters. The site-specific parameters describing the site index of individual plots are unknown, and depending on the global parameters, and therefore need to be estimated simultaneously. Parameters were simultaneously estimated with the following iterative procedure: (1) estimation of global parameters, (2) estimation of the site-specific parameter (site index) using the global parameter estimates in step 1, (3) estimation of global parameters using the site-specific parameter values obtained from step 2. Step 2 and 3 of this procedure were repeated until the sum of squared errors changed less than 10^{-8}.

To calibrate the GADA models, data were reorganized from time series of dominant height into height differences for each observation period, where h_0 is height at age t_0 and h_1 is height at age t_1. The h_0 and t_0 describe the site specific starting height and may for example for an index age describe the site index. Because the site index is unknown we used for the first step of the iterative procedure the mean height of all measurements per tree and plot, for NFI and LTE data respectively, as h_0 and the mean age as t_0. In subsequent iterations, h_0 was estimated as a local parameter. By estimating GADA models with this data structure, the models are base-age invariant (Cieszewski and Strub, 2007).

Both our calibration data sets have an unbalanced sampling design. For NFI plots, different numbers of dominant trees have been identified and time series of their height growth are of different length. To avoid bias in our models introduced by NFI plots or LTE sites with many observations, we weighted our observations in a way that the sum of weights for all growth periods per NFI plot or LTE site was equal to one. Both calibration data sets represent a sample of repeated measurements with unequal intervals, from a number of trees per plot for NFI data or from a number of plots per site for LTE data. Therefore, the observations are likely to be correlated with each other, thus model errors might not be independent. Mixed models including random effects would be the appropriate method for this data structure, but could not be applied due to limited number of replicates in the NFI data. Autocorrelation of the time series was accounted for by including a linear first order autoregressive error structure (Greene, 2003) into the models, where p_1 is the parameter related to the autoregression term.

All models presented describe dominant height growth above 1.3 m (breast height). We therefore subtracted 1.3 m from all height records, shifting the origin of all models to 1.3 m height at breast height age of zero. When applying the models to predict dominant height, 1.3 m has to be added to all predictions.

Measurement errors in independent variables are known to cause biased parameter estimates in regression models (Goelz and Burk, 1996; Kangas, 1998). This problem is most relevant for the age data of the NFI that have been measured with a low precision. We therefore applied the simulation extrapolation method (Kangas, 1998) to correct for the bias in parameter estimates from the original data. The error variance of the age estimates in our data is unknown, but we assumed that the error is normally distributed around the true age with a variance of 2 years. This variance results in maximum age errors of about ±6.5 years, which is a reasonable assumption for the structure of the NFI data and the corrections applied to the age estimates. In the simulation part we added a random age errors to the observed ages that were normally distributed with a variance of once or twice the assumed age error variance (2 years). Mean parameter estimates from 1000 replications per age error variance alternative were used together with the parameter estimates from the observed data to investigate the relationship between age error variance and parameter values. This relationship was strongly linear for all parameters in the final model and a linear regression was therefore used to extrapolate to parameter estimates for the case of no age error.

2.3.2. Model evaluation

The models were evaluated using numerical fit and prediction statistics, graphs of residuals and prediction errors, and evaluation of their biological realism (Goelz and Burk, 1992), e.g. sigmoidal

Table 1
Models fitted to dominant height time series.

Base model form	Site-specific parameters	Solution for theoretical variable X	GADA model form
Hossfeld: $h = \frac{a_1}{1+a_2 t^{-a_3}}$	$a_1 = b_1 + X$ $a_2 = b_2/X$	$X_0 = \frac{1}{2}\left[\psi + \sqrt{\psi^2 + 4b_2 h_0 t_0^{-b_3}}\right]$ with $\psi = h_0 - b_1$	Cieszewski (2002): $h_1 = \dfrac{b_1 + X_0}{1 + b_2/X_0 t_1^{-b_3}}$ (1)
	$a_1 = b_1 + X$ $a_2 = b_2 X$	$X_0 = \frac{h_0 - b_1}{1 - b_2 h_0 t_0^{-b_3}}$	Cieszewski (2002): $h_1 = \dfrac{b_1 + X_0}{1 + b_2 X_0 t_1^{-b_3}}$ (2)
	$a_2 = X$	$X_0 = t_0^{b_3}(b_1/h_0 - 1)$	McDill and Amateis (1992) in Anta et al. (2006): $h_1 = \dfrac{b_1}{\left[1 - (1 - b_1/h_0)(t_0/t_1)^{b_3}\right]}$ (3)
Hossfeld: $h = \frac{a_1 t^2}{(t+a_2)^2}$	$a_2 = X$	$X_0 = t_0\left(\sqrt{b_1/h_0} - 1\right)$	Cieszewski and Zasada (2002) in Cieszewski et al. (2007): $h_1 = \dfrac{b_1 t_1^2}{(t_1 + t_0(b_1/h_0 - 1))^2}$ (4)
	$a_1 = b_1 + b_2 X$ $a_2 = X$	$X_0 = -\frac{1}{2h_0}\left(\psi - \sqrt{\psi^2 - 4h_0 t_0^2(h_0 - b_1)}\right)$ with $\psi = t_0(2h_0 - b_2 t_0)$	$h_1 = \dfrac{t_1^2(b_1 + b_2 X_0)}{(t_1 + X_0)^2}$ (5)
Hossfeld: $h = \frac{t^2}{a_1 + a_2 t + a_3 t^2}$	$a_2 = X$	$X_0 = t_0/h_0 - b_1/a_0 - b_3 t_0$	$h_1 = \dfrac{t_1^2}{b_1 + X_0 t_1 + b_3 t_1^2}$ (6)
	$a_2 = X$ $a_3 = b_1 + b_2 X$	$X_0 = \frac{t_0^2(1 - b_1 h_0) - b_1 h_0}{h_0 t_0(1 + b_2 t_0)}$	$h_1 = \dfrac{t_1^2}{b_1(1 + t_1^2) + X_0 t_1(1 + b_2 t_1)}$ (7)
Korf: $h = a_1 \exp(-a_2 t^{-a_3})$	$a_1 = \exp(X)$ $a_2 = (b_1 + b_2)/X$	$X_0 = \frac{1}{2} t_0^{-b_3}\left[\psi + \sqrt{4b_2 t_0^{b_3} + (-\psi)^2}\right]$ with $\psi = b_1 + t_0^{b_3} Lnh_0$	Anta et al. (2006): $h_1 = \exp(X_0)\exp\left[-\left(\dfrac{b_1 + b_2}{X_0}\right)t_1^{-b_3}\right]$ (8)
	$a_2 = X$	$X_0 = -Ln(h_0/b_1)t_0^{b_3}$	$h_1 = b_1 \exp\left(Ln(h_0/b_1)(t_0/t_1)^{b_3}\right)$ (9)
King-Prodan: $h = \frac{t^{a_1}}{a_2 + a_3 t^{a_1}}$	$a_2 = b_2 + b_3 X$ $a_3 = X$	$X_0 = \frac{t_0^{b_1}/h_0 - b_2}{b_3 + t_0^{b_1}}$	Krumland and Eng (2005): $h_1 = \dfrac{t_1^{b_1}}{b_2 + b_3 X_0 + X_0 t_1^{b_1}}$ (10)
Chapman–Richards: $h = a_1[1 - \exp(-a_2 t)]^{a_3}$	$a_1 = X$	$X_0 = h_0/(1 - \exp(-b_1 t_0))^{b_2}$	Krumland and Eng (2005): $h_1 = h_0\left[\dfrac{1 - \exp(-b_1 t_1)}{1 - \exp(-b_1 t_0)}\right]^{b_2}$ (11)
	$a_1 = \exp(X)$ $a_3 = b_2 + \frac{b_3}{X}$	$X_0 = \frac{1}{2}\left[\psi + \sqrt{\psi^2 - 4b_3\phi}\right]$ with $\psi = Lnh_0 - b_2\phi$ and $\phi = Ln[1 - \exp(-b_1 t_0)]$	Krumland and Eng (2005): $h_1 = h_0\left[\dfrac{1 - \exp(-b_1 t_1)}{1 - \exp(-b_1 t_0)}\right]^{(b_2 + b_3/X_0)}$ (12)
	$a_2 = X$	$X_0 = -Ln\left[1 - (h_0/b_1)^{1/b_3}\right]/t_0$	$h_1 = b_1\left(1 - \exp\left(Ln\left[1 - (h_0/b_1)^{1/b_3}\right]t_1/t_0\right)\right)^{b_3}$ (13)

Table 1 (*continued*)

Base model form	Site-specific parameters	Solution for theoretical variable X	GADA model form
Sloboda: $h = a_1 \exp\left[-a_2 \exp\left(\frac{a_3}{(a_4-1)t^{(a_4-1)}}\right)\right]$	$a_2 = X$	$X_0 = -\frac{Ln(h_0/b_1)}{\exp\left(\frac{b_2}{(b_3-1)t_0^{(b_3-1)}}\right)}$	Anta and Dieguez-Aranda (2005): $h_1 = b_1(h_0/b_1)^{\exp\left(\frac{b_2}{(b_3-1)t_1^{(b_3-1)}} - \frac{b_2}{(b_3-1)t_0^{(b_3-1)}}\right)}$ (14)
Strand (1964): $h = \left(\frac{t}{a_1+a_2t}\right)^{a_3}$	$a_1 = X$ $a_2 = b_1 + b_2X$	$X_0 = t_0\left(h_0^{-1/b_3} - b_1\right)/1 + b_2t_0$	$h_1 = \left[\frac{t_1}{X_0 + t_1(b_1 + b_2X_0)}\right]^{b_3}$ (15)

$a_1, a_2, \ldots, a_n$ are parameters in base models; $b_1, b_2, \ldots, b_n$ are parameters in dynamic models; h_0 and h_1 are heights (in m) at age t_0 and t_1 (in years), respectively; X_0 is the solution of X for initial height and age.

shape or variable asymptotes. As fit statistics we used mean residuals (MR), adjusted coefficient of determination ($R^2_{\text{adj.}}$), root mean squared error (RMSE), and the Akaike information criterion (AIC) (Greene, 2003). For AIC, we used the least-square version (Burnham and Anderson, 2002). Fit statistics describe the residual variation of the observed data around the model. Similar statistics were used to describe the variation of independent data around model predictions, and called prediction statistics, e.g. mean residuals become mean prediction errors (MPE). Fit and prediction statistics have been calculated by including the same weights for each observation that have been used for model fitting. Graphical analysis of residuals was used to detect trends in the residuals as an indication of poor model fit. We evaluated residual graphs for individual age classes, site index classes, and geographical regions in order to assure that the models fitted well across the range of data. To facilitate the detection of trends in the residuals, we calculated mean residuals for age and site index classes.

To test how appropriate the short observation periods in the NFI data are for long-term averages, we evaluated the effect of weather on height growth for our data. Firstly, we compared weather data for a 15-year-period where NFI data had been collected (1986–2000) with 44-year averages (1957–2000). We used temperature and precipitation sums during the growing period for those comparisons. The start of the growing period has been defined as described above, the end of the season was set to the 1st and 10th of August for spruce and pine, respectively, based on observations for radial growth from Finland (Mäkinen et al., 2008; Henttonen et al., 2009). Second, we calculated relative height growth of individual trees as observed height growth relative to height growth predicted with model 1 fitted to the NFI data. The correlation between relative height growth and growing season mean temperature and precipitation sums for the same period between two height measurements was analyzed. Trends in the mean relative height growth for individual plots would indicate an effect of the

Table 2
Parameter estimates and fit statistics of models fitted to NFI data.

	Models	Parameter estimates				Fit statistics (NFI data)			Prediction statistics (LTE data)		
		b_1	b_2	b_3	p_1	MR (m)	RMSE (m)	$R^2_{\text{adj.}}$	AIC	MPE (m)	$R^2_{\text{adj.}}$
Norway spruce	1	10.5152	7507.7107	0.9751	−0.1949	0.0002	0.6066	0.9824	−860	−0.0292	0.9949
	2	112.9358	−2.9640	0.9831	−0.1952	0.0003	0.6065	0.9824	−860	−0.0282	0.9948
	3	75.2604	0.9535		−0.1931	0.0002	0.6096	0.9822	−852	−0.0376	0.9937
	4	43.1132			−0.1725	0.0058	0.6315	0.9809	−792	0.0349	0.9911
	5	53.1844	−0.3893		−0.1792	0.0054	0.6252	0.9813	−809	0.0340	0.9930
	6	0.5832		0.0156	−0.1923	0.0012	0.6097	0.9822	−852	−0.0272	0.9942
	7	0.0097	0.0028		−0.1951	0.0005	0.6061	0.9824	−862	−0.0257	0.9949
	8	0.0046	49.7100	0.2036	−0.1932	0.0002	0.6075	0.9823	−857	−0.0242	0.9948
	9	651.7645	0.2004		−0.1930	0.0002	0.6101	0.9822	−851	−0.0310	0.9936
	10	0.9831	−2.9640	334.7379	−0.1952	0.0003	0.6065	0.9824	−860	−0.0282	0.9948
	11	0.0059	0.8545		−0.1920	−0.0006	0.6077	0.9823	−858	−0.0343	0.9941
	12	0.0088	0.1693	2.9127	−0.1959	0.0000	0.6068	0.9824	−859	−0.0296	0.9944
	13	47.2074		0.9080	−0.1929	0.0001	0.6095	0.9822	−853	−0.0396	0.9937
	14	24370.6848	−0.1546	0.8858	−0.1936	0.0003	0.6076	0.9823	−857	−0.0228	0.9948
	15	0.0080	0.0027	0.9751	−0.1952	0.0030	0.6079	0.9823	−856	−0.0100	0.9951
Scots pine	1	16.5350	2800.7197	1.0423	−0.2478	0.0004	0.4839	0.9836	−1329	−0.0178	0.9927
	2	61.4465	−5.9731	1.0541	−0.2478	0.0004	0.4838	0.9836	−1329	−0.0141	0.9927
	3	50.3382	0.9395		−0.2481	0.0003	0.4884	0.9833	−1313	−0.0350	0.9904
	4	34.0159			−0.2303	0.0026	0.4982	0.9826	−1277	0.0429	0.9901
	5	47.1462	−0.4627		−0.2378	0.0018	0.4874	0.9833	−1316	0.0535	0.9913
	6	8.5040		0.0259	−0.2494	0.0007	0.4846	0.9835	−1327	0.0320	0.9926
	7	0.0140	0.0033		−0.2479	0.0002	0.4839	0.9836	−1330	−0.0231	0.9922
	8	0.0080	34.9688	0.3230	−0.2456	0.0005	0.4844	0.9836	−1327	0.0081	0.9926
	9	154.4984	0.2795		−0.2485	0.0006	0.4886	0.9833	−1312	−0.0123	0.9910
	10	1.0541	−5.9730	367.0199	−0.2478	0.0004	0.4838	0.9836	−1329	−0.0141	0.9927
	11	0.0064	0.8077		−0.2396	−0.0004	0.4868	0.9834	−1319	−0.0451	0.9897
	12	0.0100	−0.0663	3.4053	−0.2442	0.0000	0.4852	0.9835	−1324	−0.0295	0.9912
	13	34.1900		0.8516	−0.2478	0.0002	0.4884	0.9833	−1312	−0.0440	0.9900
	14	334.5074	−0.4507	0.8097	−0.2490	0.0008	0.4836	0.9836	−1330	0.0322	0.9923
	15	0.0141	0.0033	0.9994	−0.2480	0.0001	0.4840	0.9836	−1328	−0.0234	0.9922

weather variables on dominant height growth. We had to limit this analysis to about one third of the plots because weather data were only available up to 2000 and only longer time series could be used to detect trends in relative height growth for individual plots.

Dominant height growth models are often only valid for limited regions. We, therefore, tested how well our models represented dominant height growth in four regions defined as north (county Troms), middle (Sør-Trøndelag, Nord-Trøndelag, Nordland), south-east (Østfold, Akershus, Oslo, Hedmark, Oppland, Buskerud, Vestfold, Telemark, Aust-Agder, Vest-Agder) and southwest (Rogaland, Hordaland, Sogn og Fjordane, Møre og Romsdal).

3. Results

Following our original objective, we first fitted the 15 different models (Table 1) to the NFI data. Parameter estimates and fit

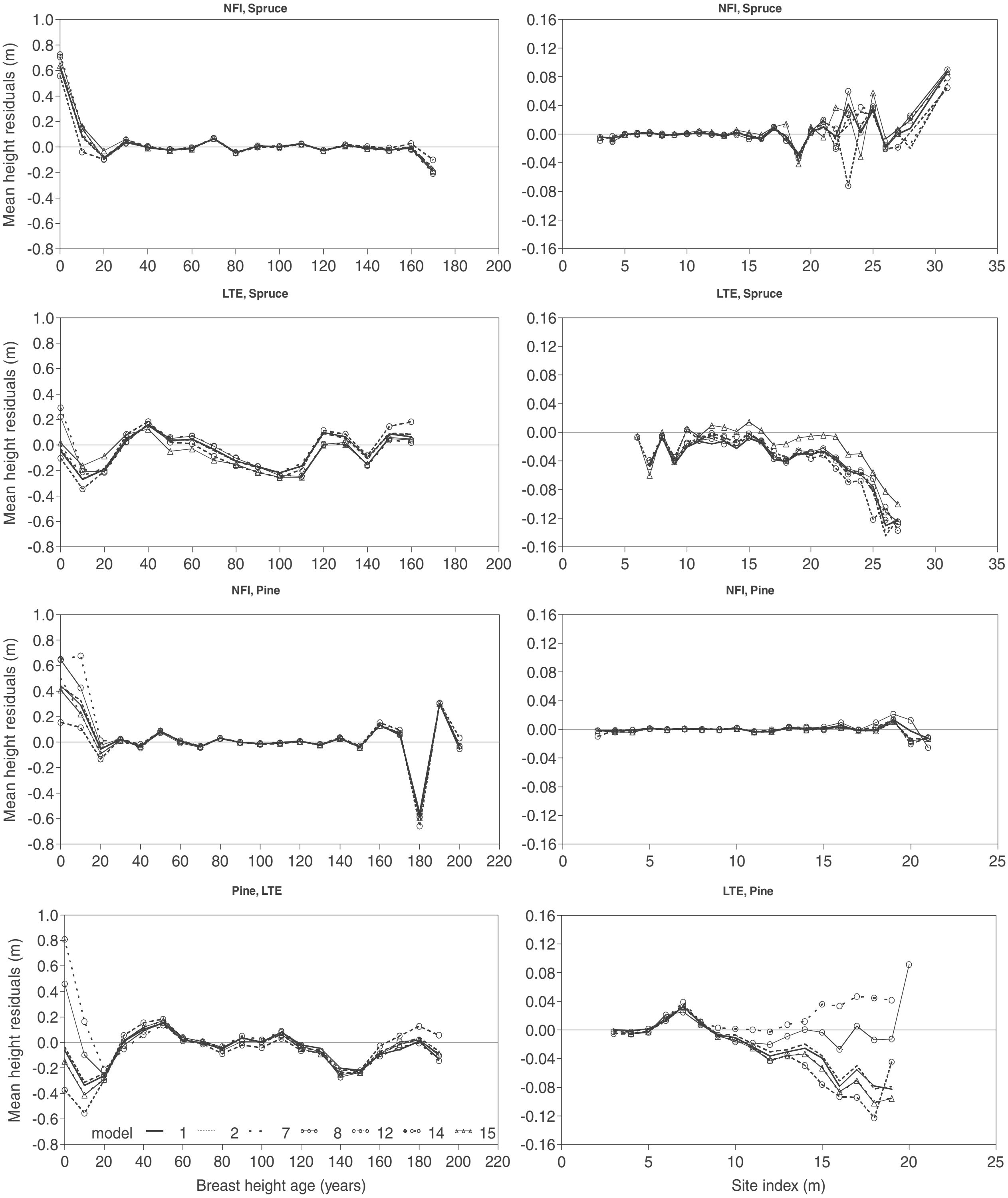

Fig. 1. Residuals of NFI and LTE data against models fitted to NFI data for Norway spruce (upper four panels) and Scots pine (lower four panels). The upper two panels per species are for NFI data and the lower two for LTE data. Legend for models: 1 = bold solid line; 2 = broken line; 7 = broken widely spaced line; 8 = solid line with circles; 12 = broken line with circles; 14 = broken widely spaced line with circles; 15 = solid line with triangles.

statistics of NFI data, and prediction statistics of LTE data are summarized in Table 2.

All 15 models showed good fit statistics with small differences between models. Models 1, 2, 7, 10, and 12 for spruce and models 1, 2, 7, 8 10, 14, and 15 for pine had the best fit statistics. Models 2 and 10 are different mathematical formulations of identical models as indicated by parameter estimates and fit statistics. We therefore only present graphical results for model 2 in the following. Prediction statistics of all models against LTE data (Table 2) are indicating a good representation for the complete LTE data set. For the NFI data the residual plots do not show any systematic bias, except for the youngest age class, which are only represented by very few data (Fig. 1). For the LTE data almost all models fitted to NFI data show significant bias for younger age classes (below 25 years) and for higher site indices. The poor fit of the models to younger age classes are caused by a few observations from very

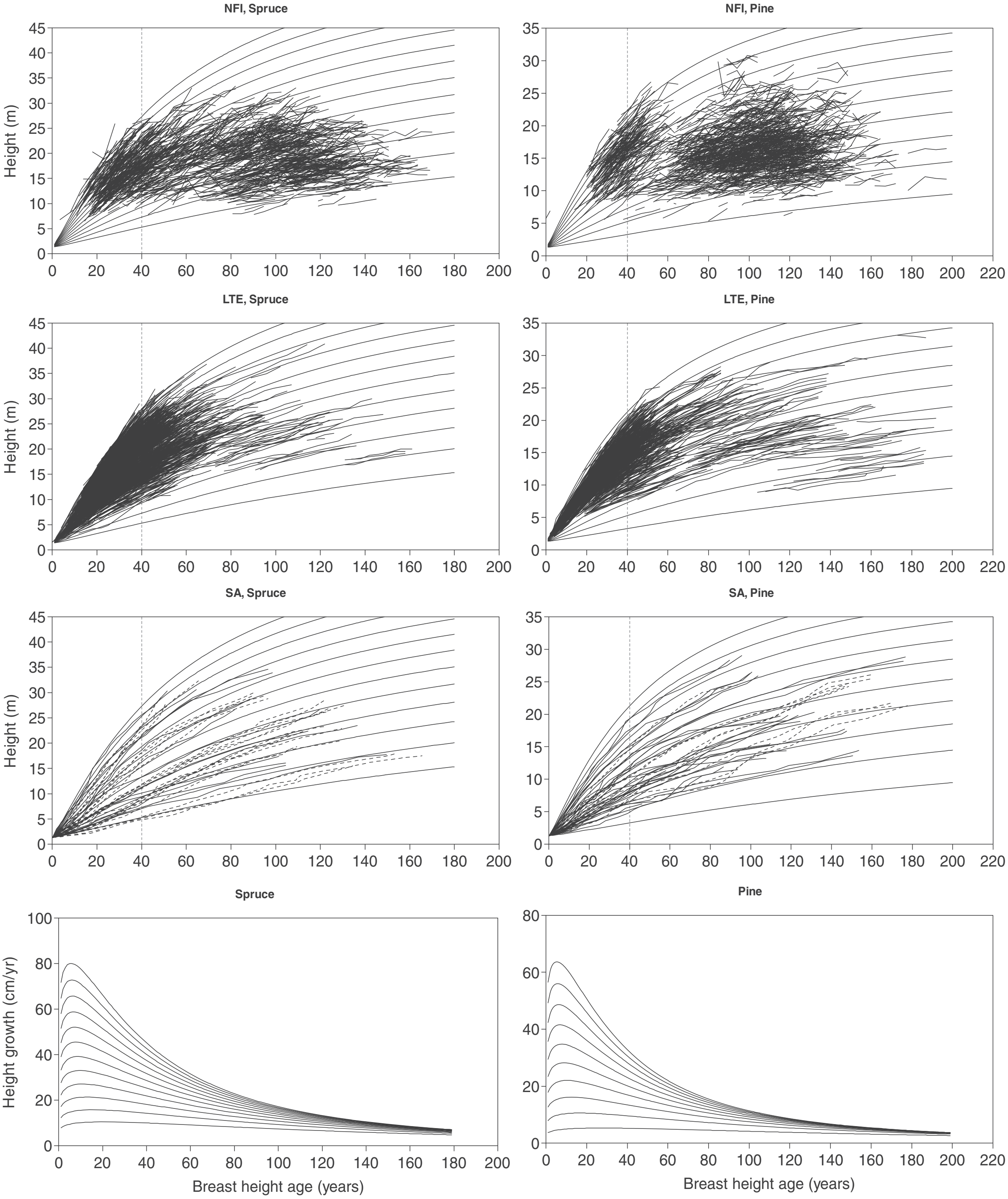

Fig. 2. Model 1 fitted to combined data vs. observed height series of all three data sets for Norway spruce (left panels) and Scots pine (right panels). Model predictions are for 2 m site index intervals (height at 40 years breast height age) for the range 4–26 m for spruce and 2–20 m for pine. For the SA data broken lines indicate trees where age has been corrected due to suppressed height growth in the youth.

Table 3
Parameter estimates and fit statistics of models fitted to combined data.

	Models	Parameter estimates				Fit statistics							
						Combined data (NFI + LTE)				Separate data			
										NFI		LTE	
		b_1	b_2	b_3	p_1	MR(m)	RMSE(m)	$R^2_{adj.}$	AIC	MR(m)	$R^2_{adj.}$	MR(m)	$R^2_{adj.}$
Norway spruce	1	8.5507	6071.57	1.1160	−0.0517	0.0009	0.5492	0.9902	−1682	0.0028	0.9822	−0.0021	0.9957
	2	103.9762	−2.7885	1.1077	−0.0567	0.0006	0.5502	0.9902	−1677	0.0024	0.9822	−0.0024	0.9957
	3	64.2555	1.0636		−0.0047	0.0003	0.5655	0.9896	−1600	0.0045	0.9820	−0.0063	0.9948
	4	46.1701			0.0707	0.0213	0.6195	0.9875	−1344	0.0074	0.9807	0.0434	0.9920
	5	75.4352	−1.3279		−0.0021	0.0176	0.5892	0.9887	−1485	0.0050	0.9809	0.0379	0.9940
	6	3.6104		0.0162	−0.0387	0.0049	0.5558	0.9900	−1649	0.0051	0.9820	0.0046	0.9954
	7	0.0052	0.0048		−0.0273	−0.0056	0.5549	0.9900	−1654	0.0012	0.9824	−0.0163	0.9952
	8	0.0276	40.0930	0.3007	−0.0416	0.0024	0.5530	0.9901	−1662	0.0023	0.9822	0.0024	0.9955
	9	358.5910	0.2520		0.0048	0.0018	0.5688	0.9895	−1584	0.0040	0.9820	−0.0017	0.9946
	10	1.1076	−2.7671	288.81	−0.0487	0.0006	0.5502	0.9902	−1677	0.0024	0.9822	−0.0023	0.9957
	11	0.0118	0.9809		−0.0267	−0.0033	0.5591	0.9898	−1632	0.0007	0.9819	−0.0097	0.9953
	12	0.0137	0.2637	2.8764	−0.0367	−0.0007	0.5546	0.9900	−1654	0.0018	0.9821	−0.0048	0.9955
	13	44.5841		1.0155	−0.0052	−0.0004	0.5655	0.9896	−1600	0.0045	0.9820	−0.0081	0.9948
	14	122921.4490	−0.1798	0.7940	−0.0394	0.0022	0.5538	0.9900	−1658	0.0022	0.9822	0.0022	0.9954
	15	0.0052	0.0048	0.9982	−0.0273	−0.0056	0.5551	0.9900	−1651	0.0012	0.9823	−0.0164	0.9952
Scots pine	1	12.0763	3089.0547	1.1548	−0.1047	0.0005	0.4788	0.9871	−1629	0.0006	0.9835	−0.0002	0.9934
	2	55.5556	−6.9771	1.1557	−0.1037	0.0005	0.4790	0.9871	−1629	0.0004	0.9835	0.0009	0.9934
	3	38.6516	1.1033		−0.0757	−0.0002	0.4920	0.9863	−1570	0.0014	0.9832	−0.0081	0.9919
	4	33.8200			−0.0301	0.0094	0.5083	0.9854	−1499	0.0025	0.9826	0.1195	0.9758
	5	48.2447	−0.5785		−0.0630	0.0090	0.4911	0.9864	−1574	0.0011	0.9833	0.0470	0.9917
	6	6.6752		0.0254	−0.0941	0.0036	0.4830	0.9868	−1611	0.0005	0.9835	0.0187	0.9927
	7	0.0106	0.0050		−0.0867	−0.0044	0.4842	0.9868	−1606	−0.0002	0.9836	−0.0244	0.9924
	8	0.0229	33.6920	0.3671	−0.0960	0.0020	0.4818	0.9869	−1615	−0.0001	0.9835	0.0121	0.9929
	9	91.6744	0.3617		−0.0753	0.0017	0.4929	0.9863	−1566	0.0010	0.9832	0.0051	0.9916
	10	1.1557	−6.9771	387.6167	−0.1037	0.0005	0.4790	0.9871	−1629	0.0004	0.9835	0.0009	0.9934
	11	0.0120	0.9592		−0.0680	−0.0028	0.4897	0.9865	−1580	0.0001	0.9831	−0.0169	0.9924
	12	0.0147	−0.3495	4.7058	−0.0844	−0.0014	0.4849	0.9867	−1601	0.0003	0.9833	−0.0097	0.9927
	13	29.6082		1.0036	−0.0709	−0.0011	0.4934	0.9863	−1564	0.0018	0.9831	−0.0149	0.9917
	14	2401.1132	−0.3160	0.7704	−0.0947	0.0025	0.4825	0.9869	−1612	−0.0001	0.9836	0.0145	0.9927
	15	0.0106	0.0049	0.9989	−0.0866	−0.0045	0.4843	0.9868	−1604	−0.0003	0.9836	−0.0245	0.9924

young stands in the NFI data (Fig. 2). Only 16 and 3 plots younger than 15 years are present in the NFI data for spruce and pine, respectively. In Fig. 2 it can also be seen that LTE data, while adequately representing stands of all ages, are biased towards better site indices. This might explain the bias of NFI models on better sites that are only poorly represented in the data.

The two data sets complement each other to cover the whole range of age and site index classes. We therefore fitted models to the combined data in order to find models free of bias for individual age and site index classes. Model parameters and fit statistics for all 15 models are summarized in Table 3. All 15 models showed good fit statistics with small differences between models. For both species, models 1, 2, and 10 had better fit statistics than all other models. Also here, models 2 and 10 are different mathematical formulations of the same models as indicated by parameters and fit statistics. Model fit to individual age and site index classes can be seen from residual plots in Fig. 3. Compared to the model fitted to NFI data only (Fig. 1), less bias for younger age classes and better site indices of the LTE data indicates that the models based on the combined data set are better fitted to the total range of available data.

The advantage of the NFI data is that they are a representative sample of ages and site indices across the country, while LTE data are biased towards younger stands and better sites. By combining these data we wanted to avoid the biases of the model fitted to NFI data alone, without introducing a new bias caused by the LTE data. Residual plots for NFI data in Fig. 3 confirm that these models also fit unbiased to NFI data. In addition we calculated fit statistics of the models fitted to combined data separately for NFI and LTE data (Table 3). For NFI data the $R^2_{adj.}$ of the best models is only slightly lower for the combined data models than for the NFI data models (Table 2). For LTE data $R^2_{adj.}$ is clearly higher for models fitted to the combined data, compared to prediction statistics based on models fitted to NFI data alone, indicating that models fitted to combined data avoid the bias of models fitted to NFI data alone.

Models 1, 2, and 10 fitted to the combined data set are all similar in their fit statistics and do not show any systematic bias in the residual plots. Since model 1 has slightly better fit statistics for both species (RMSE) than model 2 and 10, this model is recommended for further use. Parameter estimates for this model have been corrected for bias caused by errors in the age variable and are presented in Table 4. The same model with biased parameter estimates (Table 3), predicts heights at age 100 that are 0.19 and 0.56 m lower for pine and spruce, respectively, for the site index with the largest bias. Model 1 for spruce and pine is presented in Fig. 2 in comparison with calibration data (NFI and LTE) and test data (SA).

When applying the model for predictions of dominant height growth, it should be noted that model predictions are only for heights above breast height and that 1.3 m has to be added in order to predict dominant height. When fitting the models to height series over breast height age rather than total age, we are accounting for slow initial height growth in uneven-aged stands that are frequent in our data and following Norwegian traditions (Tveite, 1977). As indicated in Fig. 2 we are also proposing to continue using a breast height age of 40 years to derive site indices from those models, but we would like to note that due to the base-age invariant methods used here, any other base age could be selected.

Dominant height growth models are often only valid for limited regions. Differences in dominant height growth of the same species between regions have been reported also for Norway. We therefore tested how well dominant height growth in four separate regions

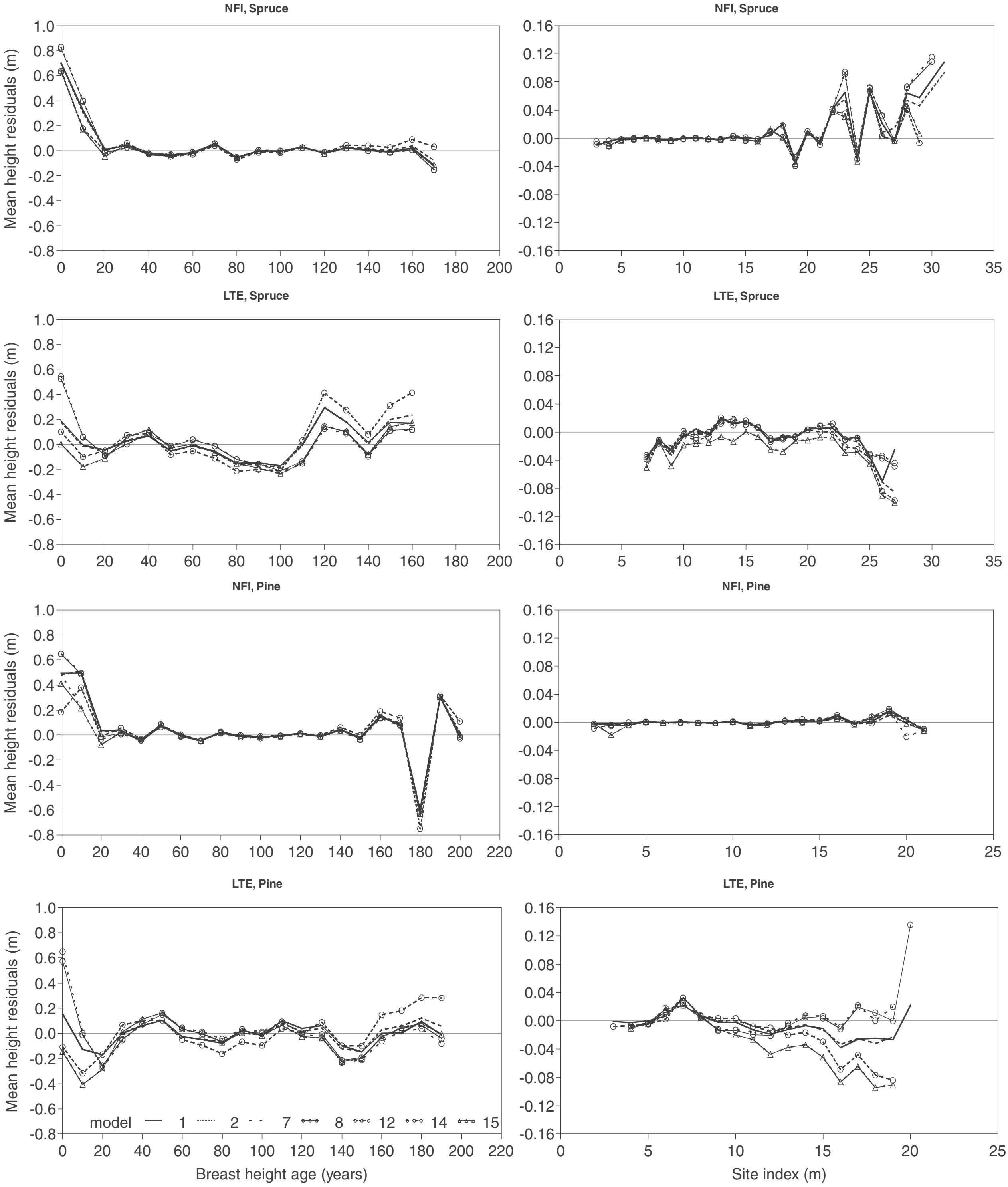

Fig. 3. Residuals of NFI and LTE data against models fitted to combined data for Norway spruce (upper four panels) and Scots pine (lower four panels). The upper two panels per species are for NFI data and the lower two for LTE data. Legend for models: 1 = bold solid line; 2 = broken line; 7 = broken widely spaced line; 8 = solid line with circles; 12 = broken line with circles; 14 = broken widely spaced line with circles; 15 = solid line with triangles.

was predicted by model 1 fitted to the combined data set (Table 5). Fit statistics in this table for individual regions are comparable with those for the entire data set. We did not find any systematic bias in residual plots for age and site index classes.

We tested model 1 fitted to the combined data against the independent data set derived from stem analysis of individual dominant trees (SA data). Prediction statistics for all trees (MPE = −0.0269 m, $R^2_{\mathrm{adj.}} = 0.9931$, $N = 36$ for spruce; MPE = 0.0007 m, $R^2_{\mathrm{adj.}} = 0.9909$, $N = 37$ for pine) and for trees without corrected ages due to suppression in the youth (MPE = −0.0561 m, $R^2_{\mathrm{adj.}} = 0.9987$, $N = 14$ for spruce; MPE = 0.0078 m, $R^2_{\mathrm{adj.}} = 0.9890$, $N = 28$ for pine) indicated a good fit of the model also to this data set. Prediction errors were for the major part of the time series of all 73 trees within ±1 m (Fig. 4).

Due to the sampling approach of the NFI, we were not able to use data representing exactly the 100 dominant trees per ha. For

Table 4
Parameter estimates for model 1 after correction of bias due to age measurement errors.

Species	b_1	b_2	b_3
Norway spruce	18.9206	5175.18	1.1576
Scots pine	12.8361	3263.99	1.1758

Table 5
Prediction statistics for regional data using model 1 fitted to combined data.

Species	Data source	Region	Number of plots	MPE (m)	$R^2_{\text{adj.}}$
Norway spruce	NFI	Southeast	592	0.0035	0.9829
		Southwest	33	−0.0260	0.9719
		Middle	234	0.0053	0.9772
	LTE	Southeast	910	0.0059	0.9957
		Southwest	319	−0.0245	0.9939
		Middle	443	0.0107	0.9967
		North	32	−0.0048	0.9892
Scots pine	NFI	Southeast	698	0.0003	0.9828
		Southwest	128	0.0014	0.9797
		Middle	82	0.0026	0.9731
		North	5	−0.0053	0.9607
	LTE	Southeast	544	−0.0150	0.9946
		Southwest	64	0.0206	0.9828
		Middle	30	0.0154	0.9864
		North	86	0.0125	0.9881

57% of the plots only one dominant tree per plot was identified and used. If this happens to be the largest tree on the plot, the height growth of these plots might be larger than for the mean height growth of the 100 dominant trees per ha, and models fitted to those data might have a positive bias. We therefore looked specifically at data from plots containing only one sample tree and their effect on the model. Single tree sample plots covered the same range of age and site index classes as the other plots (data not shown). For model 1 fitted to the NFI data only, we examined residual graphs for plots with different numbers of dominant height sample trees, but did not find any bias for the single tree plots relative to all other plots (data not shown). For plots containing more than one dominant height sample tree, we were able to rank trees according to their height, using only plots with complete time series for all trees, and calculating a mean rank for all remeasurements. We then compared residuals from the same model for the trees of different height ranks with residuals for trees from single tree plots, but did not find a significant bias for any of the height ranks (data not shown).

To test how representative the short observation periods in the NFI data are for long-term averages, we first compared weather data for a 15-year-period where NFI data had been collected (1986–2000) with 44-year averages (1957–2000). Growing season temperature sums for the NFI period were on average 2.6% (s.d. = 2.2) and 2.8% (s.d. = 2.0) higher than 44-year averages for spruce and pine, respectively. Growing season precipitation sums for the NFI period were on average 4.3% (s.d. = 5.7) and 3.5% (s.d. = 5.4) higher than 44-year-averages for spruce and pine, respectively. All differences were significantly different from zero (t-test, $p < 0.001$). This indicates that the weather during the period for which NFI data were available was on average only slightly warmer and moister than long-term averages. Relative height growth based on model 1 fitted to NFI data showed both increasing and decreasing trends per plot when plotted against mean temperature or precipitation sums for the growing period for spruce or pine. For about 60% of the plots a positive effect of both weather variables on relative height growth could be observed. On average relative height growth increased by about 20% as a consequence of the observed increase in temperature or precipitation between the two observation periods within the period 1986–2000 for spruce and pine. This result indicates that variation in temperature and precipitation between 5-year-periods might explain variation in dominant height growth. The observed variation of climate variables within the 15-year-period used for this analysis was about three times the difference between averages for this period and the 44-year average. The year 1997 is recorded as the warmest average growing season within the 44-year-period, the period 1995–2000 is recorded with above average precipitation sums for all years. Temperature and precipitation sums for the rest of the 15-year-period were not substantially different compared with the 44-year-period. By analyzing the correlation between weather data and height growth including the extreme years in the 1990s, we have been looking at weather variation that is clearly exceeding the long-term variation, and therefore likely having a larger than average influence on height growth.

4. Discussion

Fit statistics of the dominant height growth models developed from NFI data alone and tests against independent LTE data sets indicated that all models describe dominant height growth well within certain ranges of the NFI data, but had biased predictions for young stands and better sites that are insufficiently covered by NFI data. We, therefore, combined the data sets and recommend

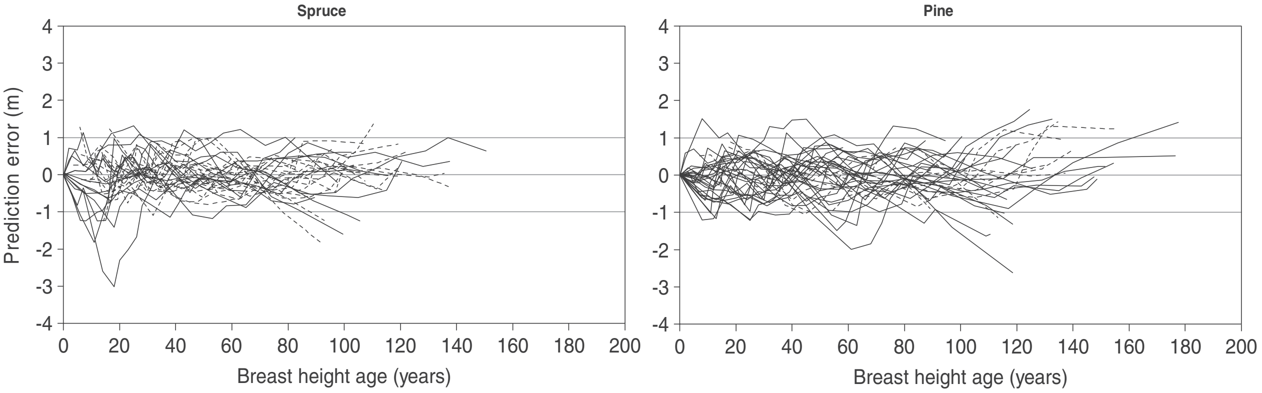

Fig. 4. Prediction errors of model 1 fitted to combined data against independent stem analysis data for Norway spruce (left) and Scots pine (right). Broken lines indicate trees where age has been corrected due to suppressed height growth in the youth.

the models fitted to these data for further use. They showed unbiased predictions with little residual variation for the independent SA data set. The 15 different functional forms fitted resulted in very similar models, but based on the fit statistics we recommended one of Hossfeld's models (model 1) (Cieszewski, 2002) for future use. The same functional form has also been used in other dominant height growth models (Diéguez-Aranda et al., 2006a,b). By using the GADA approach we could develop polymorphic models with multiple asymptotes from this base equation (Cieszewski et al., 2007).

The main advantage of the NFI data is that they are representative for most of the growing conditions and stand ages in the country, even though some ages and/or site index classes might be underrepresented as indicated by the biased predictions against LTE data. Still, NFI data cover a wider range of site indices and ages than LTE data (Fig. 2). A significant co-variation between age and site index is obvious in the NFI data (Fig. 2) and is caused by younger stands being established during the last 60 years when the clearfelling system was introduced and replaced uneven-aged stands, mostly on better sites. Based on our results when testing the models against independent data, we do not expect that this co-variation is leading to biased models.

In contrast to many other data sources for dominant height growth models, we used time series from individual trees on the NFI sample plots that were not specifically sampled to represent dominant height. The data recorded for all trees on the plot allowed us to identify dominant trees with measured heights, but for 57% of the plots only one tree could be used. We could demonstrate that the number of dominant trees selected or their height rank did not lead to biases in the models. This can be explained by the fact that variation in height growth of dominant trees is not affected by competition (Brunner and Nigh, 2000) for a large range of stand densities, as also indicated by the underlying assumption for using dominant height growth models as indicators of stand productivity (Skovsgaard and Vanclay, 2008). Effects of stand density on dominant height growth have been reported frequently (MacFarlane et al., 2000; Mäkinen and Isomäki, 2004; Nord-Larsen, 2006b; Nord-Larsen and Johannsen, 2007; Martin-Benito et al., 2008; Skovsgaard and Vanclay, 2008; Nilsson et al., 2010), most pronounced for light demanding pine species at extremely low or high density. We addressed that question during the development of an individual tree height growth model from the same data. We did not find any indication that the individual trees we selected as dominant here had less than maximum height growth due to intensive or missing competition. On a larger scale, site index estimates from smaller plots are biased relative to estimates from larger plots (García, 1998; Magnussen, 1999), which is amongst others caused by spatial variation of growing conditions within the one hectare which is defining dominant height. We were unable to address this question with our data, but our models will typically be applied for plot sizes similar to the ones in the data. The large spatial variation of growing conditions in Norway within any hectare of forest questions the area reference in the traditional definition of dominant height.

A limitation when using NFI data for growth modelling is the poor precision in registering stand age. A large part of the total forest area in Norway consists of uneven-aged stands as indicated by 37% of the productive forest area being classified as two- or multilayered (NIJOS, 2000). Even though dominant trees in those stands might have grown up without suppression and can therefore be used for dominant height growth modelling, the recorded stand ages reflect mean ages for those stands rather than the age of the dominant trees. Age records in the NFI data are therefore uncertain, and an unknown proportion of uneven-aged stands was included. We considered several indications in the data to identify stands with uncertain ages, but were unable to filter the data. For 15% of the plots inconsistent age and site index records indicated age corrections and thus uneven-aged stands, but we did not find any significant bias for those data compared to the rest in preliminary analyses. We interpret the successful test of the NFI data models with uncertain ages against LTE and SA data as a confirmation that the models are valid despite the large age errors involved. Age errors are likely random and not systematic, despite systematic reduction of stand age from dominant age for an unknown number of uneven-aged stands. Errors in predictor variables are known to cause biased parameter estimates (Goelz and Burk, 1996; Kangas, 1998). By using a simulation and extrapolation approach we were able to correct for this bias, but would like to note that the bias of the uncorrected parameter estimates was very small. We would also like to note that even though concepts of dominant height growth and site index are based on monospecific stands, part of our data are from mixed species stands, because we only excluded stands if less than 70% of the standing volume was neither pine nor spruce.

Another limitation of the NFI data is the short time series, i.e. only about 20 years. By applying the GADA approach we were able to use the time series despite a missing common base age for all time series. Another concern related to short time series is the insufficient representation of average growing conditions due to climatic variation (Monserud and Sterba, 1996). We found some indication that variation in climate between 5-year periods in our data might affect dominant height growth as also indicated in previous reports (Martin-Benito et al., 2008). However, we want to note that the climate in this period varied considerably and that smaller effects on height growth can be expected in periods with less variation in climate. We also showed that the period where NFI data were collected was slightly warmer and moister than the long-term averages. Due to global change it might be possible that the period 1986–2008 is more representative of future climate and growing conditions than long-term historical records. NFI height growth data might be a representative sample for height growth in the future, but due to the uncertainty about future climate we are unable to judge this. Models fitted to the combined data overcome this potential limitation of NFI data, because LTE data have been collected for the period 1915–2006 and are therefore less likely to be biased due to periods with more favorable growing conditions. We therefore conclude that our height growth models are likely unbiased with respect to effects of climate variation on height growth when applied for growth prediction into the future.

NFI data were not originally sampled for this purpose and therefore have many problems for height growth modelling. Despite this we were able to develop dominant height growth models based on those data, which again also fitted reasonably well to the independent data sets. We interpret this as a confirmation of our assumption that none of the problems discussed above is leading to biased models, and that, despite the rather large residual variation in the NFI data caused by various errors, the models reliably describe the height growth of dominant trees.

In order to reduce the bias of models fitted to NFI data alone, we combined NFI and LTE data to develop dominant height growth models. The two data sets supplement each other well to cover the range of site indices and ages. However, combining time series of the mean height of the 100 largest trees per ha (LTE) and time series of individual dominant tree heights (NFI) is an unconventional approach for dominant height growth modelling. We discussed earlier that dominant height growth is largely unaffected by competition and that individual trees, whose dominant status has been confirmed, therefore might be able to represent dominant height growth unbiased. The large variation of the NFI height data due to the sampling approach and other error sources did not allow us to test this assumption. But we see the unbiased predictions of the NFI models for LTE data for most of the data range sufficiently covered by the NFI data (Fig. 1) as a support for our assumption.

Models fitted to NFI data alone showed substantial bias for young stands (breast height age 5–25 years) in the LTE data set (Fig. 1) due to the lack of young stands in the NFI data. We were able to reduce this bias by fitting models to the combined data set (Fig. 3), but still some underprediction for these age classes in the LTE data is left for Scots pine. Even though the bias is minor, it might have large consequences if height growth of mixed young stands is simulated and pine looses in competition with spruce due to unrealistic dominant height growth models. No such bias was observed in the test against SA data (Fig. 4) and we therefore conclude that the observed minor bias describes a specialty of the LTE data set rather than a failure of the model.

The dominant height growth models presented (Fig. 2) show a very early culmination of height growth with little variation in the culmination age between site indices. For both species height growth culminates between breast height ages of 9 and 5 years for site indices 8 and 21 m respectively. This is also indicated by almost linear height time series in the LTE data for very young stands. It should be noted however, that these time series are not describing total height growth of individual trees, where we would expect a clearer sigmoidal form. Firstly, height growth is only described above 1.3 m, and secondly, mean dominant height rather than individual tree height is described. Given the problems of identifying dominant trees in very young and dense stands with frequently shifting dominance of individual trees, it is likely that in very young stands mean dominant height shows different growth patterns than individual tree height. Also for the individual trees in our SA data we found close to linear growth for the first years above breast height (Fig. 2). Nevertheless, the conversion from total age to breast height age is responsible for most of the loss of the exponential height growth in young stands. When comparing our models with dominant height growth models for Scots pine in Sweden and Norway (Hägglund, 1974; Tveite and Braastad, 1981; Elfving and Kiviste, 1997) we found similar ages for culmination of dominant height growth. Swedish dominant height growth models for Norway spruce (Hägglund, 1972, 1973) show maximum height growth at breast height.

Dominant height growth models are often only valid for limited regions. Norway is a large country with considerable differences in growing conditions. Regional deviations from the current Norwegian dominant height growth models (Tveite, 1977; Tveite and Braastad, 1981) have been reported, especially for western Norway (Blingsmo, 1985; Øyen and Nes, 1997; Orlund, 2001) but less so for northern Norway (Tveite, 1994). We did not find any bias of our models when applied to individual regions using the calibration data (Table 5). The independent SA data were only sampled in the southeastern part of the country and we were therefore unable to test our model against independent data from the rest of the country. Southeastern Norway contains most of the productive forests and contributes the majority of the annual harvest and is therefore the most important region for application of the model. From the regional distribution of the sample plots in Table 5 it can be seen that about 65% of all plots are within the southeastern region for our calibration data, indicating the distribution of the productive forest (NFI data) and the interest in forest management (LTE data). Because we did not find any indication for a bias of the models in the other regions, we recommend them for use in these regions as well, despite limited calibration data and a lack of independent test data.

Compared to existing Norwegian dominant height growth models for Norway spruce (Tveite, 1977) and Scots pine (Tveite and Braastad, 1981) our models predict similar dominant height growth for ages up to 60 years, but significant faster height growth for older stands, especially for better sites. Similarities between the old and new models are to be expected, because the data used to fit the old models have also been included in our data set (LTE data). Differences between the models are due to longer time series of the LTE data, combination with the NFI data, and model fitting procedures. The models that we fitted to the data can be used to predict site index as well as dominant height growth, which was not the case nor intended for the old dominant height growth models. Compared to Swedish dominant height growth models for Norway spruce (Hägglund, 1972, 1973) and Scots pine (Hägglund, 1974; Elfving and Kiviste, 1997) our models predict similar height growth for ages up to 60 years and increasing deviations with increasing age, as also observed in the comparison between old and new Norwegian models. Compared to the existing dominant height growth models for the same species in Norway and Sweden, our models predict a less asymptotic height growth for very old stands on good sites, a range of the model that is not covered by data and where the model will not be applied frequently.

Based on our results, we conclude that the Norwegian NFI data can be used to develop dominant height growth models, despite their short time series and large age errors. Biased predictions for young stands and good sites that were not appropriately covered by the NFI data made it necessary to include other data into the calibration of the models. We, therefore, recommend the models fitted to the combined data set for further use.

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References

Andreassen, K., Tomter, S.M., 2003. Basal area growth models for individual trees of Norway spruce, Scots pine, birch and other broadleaves in Norway. For. Ecol. Manag. 180, 11–24.

Anta, M.B., Dieguez-Aranda, U., 2005. Site quality of pedunculate oak (*Quercus robur* L.) stands in Galicia (northwest Spain). Eur. J. For. Res. 124, 19–28.

Anta, M.B., Dorado, F.C., Dieguez-Aranda, U., Gonzalez, J.G.A., Parresol, B.R., Soalleiro, R.R., 2006. Development of a basal area growth system for maritime pine in northwestern Spain using the generalized algebraic difference approach. Can. J. For. Res. 36, 1461–1474.

Bailey, R.L., Clutter, J.L., 1974. Base-age invariant polymorphic site curves. For. Sci. 20, 155–159.

Blingsmo, K.R., 1985. Overhøydeutviklingen i granbestand på Vestlandet (Top height development of Norway spruce in Western Norway). Norwegian Forest Research Institute. Research paper, 1/85: 1–8.

Bollandsås, O.M., Næsset, E., 2009. Weibull models for single-tree increment of Norway spruce, Scots pine, birch and other broadleaves in Norway. Scand. J. For. Res. 24, 54–66.

Bravo-Oviedo, A., Tomé, M., Bravo, F., Montero, G., del Rio, M., 2008. Dominant height growth equations including site attributes in the generalized algebraic difference approach. Can. J. For. Res. 38, 2348–2358.

Brunner, A., Nigh, G., 2000. Light absorption and bole volume growth of individual Douglas-fir trees. Tree Physiol. 20, 323–332.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Inference: A practical Information-Theoretic Approach. Springer-Verlag, New York.

Cherubini, P., Dobbertin, M., Innes, J.L., 1998. Potential sampling bias in long-term forest growth trends reconstructed from tree rings: a case study from the Italian Alps. For. Ecol. Manag. 109, 103–118.

Cieszewski, C.J., 2001. Three methods of deriving advanced dynamic site equations demonstrated on inland Douglas-fir site curves. Can. J. For. Res. 31, 165–173.

Cieszewski, C.J., 2002. Comparing fixed- and variable-base-age site equations having single versus multiple asymptotes. For. Sci. 48, 7–23.

Cieszewski, C., Bailey, R.L., 2000. Generalized algebraic difference approach: theory based derivation of dynamic site equations with polymorphism and variable asymptotes. For. Sci. 46, 116–126.

Cieszewski, C.J., Strub, M., 2007. Parameter estimation of base-age invariant site index models: which data structure to use? – A discussion. For. Sci. 53, 552–555.

Cieszewski, C.J., Strub, M., 2008. Generalized algebraic difference approach derivation of dynamic site equations with polymorphism and variable asymptotes from exponential and logarithmic functions. For. Sci. 54, 303–315.

Cieszewski, C.J., Harrison, M., Martin, S.W., 2000. Practical methods for estimating non-biased parameters in self-referencing growth and yield models. Daniel B. Warnell School of Forest Resources, University of Georgia Athens, Georgia. Plantation Management Research Cooperative (PMRC) Technical Report 2000–7.

Cieszewski, C.J., Strub, M., Zasada, M., 2007. New dynamic site equation that fits best the Schwappach data for Scots pine (*Pinus sylvestris* L.) in Central Europe. For. Ecol. Manag. 243, 83–93.

Condés, S., Sterba, H., 2008. Comparing an individual tree growth model for *Pinus halepensis* Mill. In the Spanish region of Murcia with yield tables gained from the same area. Eur. J. For. Res. 127, 253–261.

Dahms, W.G., 1963. Correction for possible bias in developing site index curves from sectioned tree data. J. For. 61, 25–27.

De los Santos-Posadas, H.M., Montero-Mata, M., Kanninen, M., 2006. Dynamic dominant height growth curves for *Terminalia amazonia* (Gmel.) Excell in Costa Rica. Agrociencia 40, 521–532.

Diéguez-Aranda, U., Burkhart, H.E., Amateis, R.L., 2006a. Dynamic site model for loblolly pine (*Pinus taeda* L.) plantations in the United States. For. Sci. 52, 262–272.

Diéguez-Aranda, U., Grandas-Arias, J.A., Alvarez-Gonzalez, J.G., von Gadow, K., 2006b. Site quality curves for birch stands in north-western Spain. Silva Fenn. 40, 631–644.

Ekberg, I., Eriksson, G., Namkoong, G., Nilsson, C., Norell, L., 1994. Genetic correlations for growth rhythm and growth capacity at ages 3–8 years in provenance hybrids of *Picea abies*. Scand. J. For. Res. 9, 25–33.

Elfving, B., Kiviste, A., 1997. Construction of site index equations for *Pinus sylvestris* L. using permanent plot data in Sweden. For. Ecol. Manag. 98, 125–134.

Eriksson, H., Johansson, U., Kiviste, A., 1997. A site-index model for pure and mixed stands of *Betula pendula* and *Betula pubescens* in Sweden. Scand. J. For. Res. 12, 149–156.

Fries, J., 1969. Boniteringskurvor för tall och gran (Site index curves for pine and spruce). Skogen 56, 1–20.

García, O., 1998. Estimating top height with variable plot sizes. Can. J. For. Res. 28, 1509–1517.

García, O., 2005. Comparing and combining stem analysis and permanent sample plot data in site index models. For. Sci. 51, 277–283.

Goelz, J.C.G., Burk, T.E., 1992. Development of a well-behaved site index equation-Jack pine in North central Ontario. Can. J. For. Res. 22, 776–784.

Goelz, J.C.G., Burk, T.E., 1996. Measurement error causes bias in site index equations. Can. J. For. Res. 26, 1585–1593.

Greene, W.H., 2003. Econometric Analysis, third ed. Pearson Education (pp. 1026).

Gustavsen, H., 1980. Talousmetsein kasvupaikkaluokittelu valtapituuden avulla (Site index curves for Finland). Folia For. 45, 1–31.

Hägglund, B., 1972. Om övre höjdens utveckling för gran i norra Sverige (Site index curves for Norway Spruce in northern Sweden). Royal College of Forestry, Department of Forest Yield Research. Report 21, pp. 298.

Hägglund, B., 1973. Om övre höjdens utvekling för gran i södra Sverige (Site index curves for Norway spruce in southern Sweden). Royal College of Forestry, Department of Forest Yield Research. Report 24, pp. 49.

Hägglund, B., 1974. Övre höjdens utveckling i tallbestånd (Site index curves for Scots pine in Sweden). Royal College of Forestry, Department of Forest Yield Research. Report 31, pp. 54.

Hasenauer, H., Monserud, R.A., 1997. Biased predictions for tree height increment models developed from smoothed ‘data’. Ecol. Model. 98, 13–22.

Hasenauer, H., Kindermann, G., Steinmetz, P., 2006. The tree growth model MOSES 3.0. In: Hasenauer, H. (Ed.), Sustaianble Forest Management, Growth Models for Europe. Springer-Verlag, Berlin, Heidelberg, p. 388.

Henttonen, H.M., Mäkinen, H., Nöjd, P., 2009. Seasonal dynamics of the radial increment of Scots pine and Norway spruce in the southern and middle boreal zones in Finland. Can. J. For. Res. 39, 606–618.

Huuskonen, S., Miina, J., 2007. Stand-level growth models for young Scots pine stands in Finland. For. Ecol. Manag. 241, 49–61.

Johansson, T., 1996. Site index curves for Norway spruce (*Picea abies* (L) Karst.) planted on abandoned farm land. New For. 11, 9–29.

Kangas, A., 1998. Effect of errors-in-variables on coefficients of a growth model and on prediction of growth. For. Ecol. Manag. 102, 203–212.

Karlsson, K., 2000. Height growth patterns of Scots pine and Norway spruce in the coastal areas of western Finland. For. Ecol. Manag. 135, 205–216.

Kilpelainen, A., Peltola, H., Rouvinen, I., Kellomaki, S., 2006. Dynamics of daily height growth in Scots pine trees at elevated temperature and CO2. Trees-Struct. Funct. 20, 16–27.

Kozlowski, T.T., 1962. Tree Growth. Ronald Press Company, New York.

Krumland, B., Eng, H., 2005. Site index systems for major young-growth forest and woodland species in northern California. California Department of Forest and Fire Protection, Sacramento, CA. Forestry report 4: 1–219.

MacFarlane, D., Green, J., Burkhart, H.E., 2000. Population density influences assessment and application of site index. Can. J. For. Res. 30, 1472–1475.

Magnussen, S., 1999. Effects of plot size on estimates of top height in Douglas-fir. West. J. Appl. For. 14, 17–27.

Mäkinen, H., Isomäki, A., 2004. Thinning intensity and growth of Scots pine stands in Finland. For. Ecol. Manag. 201, 311–325.

Mäkinen, H., Seo, J.W., Nöjd, P., Schmitt, U., Jalkanen, R., 2008. Seasonal dynamics of wood formation: a comparison between pinning, microcoring and dendrometer measurements. Eur. J. For. Res. 127, 235–245.

Martin-Benito, D., Gea-Izquierdo, G., del Rio, M., Canellas, I., 2008. Long-term trends in dominant-height growth of black pine using dynamic models. For. Ecol. Manag. 256, 1230–1238.

Monserud, R.A., 1984. Height growth and site index curves for inland Douglas-fir based on stem analysis data and forest habitat type. For. Sci. 30, 943–965.

Monserud, R.A., Sterba, H., 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. For. Ecol. Manag. 80, 57–80.

Newberry, J.D., 1991. A note on Carmean estimate of height from stem analysis data. For. Sci. 37, 368–369.

NIJOS, 2000. Skog 2000. Statistics of forest conditions and resources in Norway. Norwegian Institute of Land Inventory, Ås, Vol. 7.

Nilsson, U., Ekö, P.-M., Elfving, B., Fahlvik, N., Johansson, U., Karlsson, K., Lundmark, T., Wallentin, C., 2010. Thinning of Scots pine and Norway spruce monocultures in Sweden: effects of different thinning programmes on stand level gross- and net stem volume production. Studia Forestalia Suecica 219, 46.

Nord-Larsen, T., 2006a. Developing dynamic site index curves for European beech (*Fagus sylvatica* L.) in Denmark. For. Sci. 52, 173–181.

Nord-Larsen, T., 2006b. Modelling individual-tree growth from data with highly irregular measurement intervals. For. Sci. 52, 198–208.

Nord-Larsen, T., Johannsen, V.K., 2007. A state-space approach to stand growth modelling of European beech. Ann. For. Sci. 64, 365–374.

Orlund, A., 2001. Bonitering av plantet gran (*Picea abies* L. Karst) og sitkagran (*Picea sitchensis* Bong. Carr.) på vestlandet (Site quality classification of planted Norwray spruce and Sitka spruce in west coast of Norway). Skogforsk 2/01, 1–17.

Øyen, B.H., Nes, K., 1997. Growth patterns of Scots pine (*Pinus sylvestris* L.) in western Norway. Meddelelser fra Skogforsk 47.18, 24.

Pretzsch, H., Biber, P., Dursky, J., 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. For. Ecol. Manag. 162, 3–21.

Reed, D.D., Jones, E.A., Tome, M., Araujo, M.C., 2003. Models of potential height and diameter for *Eucalyptus globulus* in Portugal. For. Ecol. Manag. 172, 191–198.

Salminen, H., Jalkanen, R., 2007. Intra-annual height increment of *Pinus sylvestris* at high latitudes in Finland. Tree Physiol. 27, 1347–1353.

SAS Institute Inc., 2008. SAS/ETS1 9.1 User’s Guide. SAS Institute Inc., Cary, NC.

Seynave, I., Gegout, J.C., Herve, J.C., Dhote, J.F., Drapier, J., Bruno, E., Dume, G., 2005. Picea abies site index prediction by environmental factors and understorey vegetation: a two-scale approach based on survey databases. Can. J. For. Res. 35, 1669–1678.

Skaugen, T.E., Tveito, O.E., 2004. Growing-season and degree-day scenario in Norway for 2021–2050. Climate Res. 26, 221–232.

Skog og Landskap, 2007. Landsskogtakseringens Feltinstruks 2007 (National Forest Inventory Field Instructions 2007). Norwegian Forest and Landscape Institute, Ås.

Skovsgaard, J.P., Vanclay, J.K., 2008. Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. Forestry 81, 12–31.

Solberg, S., Andreassen, K., Clarke, N., Torseth, K., Tveito, O.E., Strand, G.H., Tomter, S., 2004. The possible influence of nitrogen and acid deposition on forest growth in Norway. For. Ecol. Manag. 192, 241–249.

Spurr, S.H., 1952. Forest Inventory. Ronald press, New York.

Sterba, H., Monserud, R.A., 1997. Applicability of the forest stand growth simulator PROGNAUS for the Austrian part of the Bohemian Massif. Ecol. Model. 98, 23–34.

Strand, L., 1964. Numerical construction of site curves. For. Sci. 10, 410–414.

Tiwari, V.P., Singh, B., 2009. Site index model for Tecomella undulata (Sm.) Seem. (Bignoniaceae) plantations in a hot arid region of India. J. Arid Environ. 43, 490–493.

Tomter, S.M., 2000. Skog 2000. Statistikk over skogforhold og -ressurser i Norge (Statistics of forest conditions and resources in Norway). Norwegian Forest and Landscape Institute, Ås, 84.

Tveite, B., 1977. Bonitetskurver for gran (Site index curves for Norway spruce (*Picea abies* (L.) Karst.)). Report of Norwegian Forest Research Institute 33, 1–84.

Tveite, B., 1994. Høgdeutvikling og volumproduksjon i gran- og furuskog nord for Saltfjellet (Height development and volume production in spruce and pine forests north for Saltfjellet). In: Bergan, J. (Ed.), Faglige emner innen primærproduksjonen i skogbruket i Nord-Norge. Norwegian Forest Research Institute, Ås, pp. 92–99 (**in Norwegian**).

Tveite, B., Braastad, H., 1981. Bonitering for gran, furu og bjørk (Site index for Norway spruce, Scots pine and birch). Norsk Skogbruk 27, 17–22.

Vuokila, Y., Väliaho, H., 1980. Growth and yield models for conifer cultures in Finland. Commun. Inst. For. Fenn. 99, 1–271.

Zeide, B., Zakrzewski, W.T., 1993. Selection of site trees- the combined method and its application. Can. J. For. Res. 23, 1019–1025.

Zhang, S.S., Allen, H.L., Dougherty, P.M., 1997. Shoot and foliage growth phenology of loblolly pine trees as affected by nitrogen fertilization. Can. J. For. Res. 27, 1420–1426.

PAPER II

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ORIGINAL ARTICLE

Site index prediction from site and climate variables for Norway spruce and Scots pine in Norway

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Abstract

Site index prediction models for Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) were developed using Norwegian National Forest Inventory data. A number of multiple linear regression models with different combinations of site and climate variables were developed in order to facilitate their application to a range of situations where the accessibility of various explanatory data differs. The best models used year of stand origin, temperature sum, vegetation type groups, soil depth, aspect, slope and latitude to predict site index. These models explained a large part of the total variation ($R^2_{adj.} = 0.86$ and 0.72 for spruce and pine, respectively) and had little residual variation (RMSE = 2.04 and 1.95 m for spruce and pine, respectively). Alternative models using only year of stand origin, temperature sum and vegetation type groups, or soil depth in addition, had slightly lower but still useful predictive power. All the developed models exhibited a strong non-linear effect of the year of stand origin on site indices, which varied when temperature sum was included. The increase in site indices along with increasing year of stand origin was significantly faster after about 1940 for both species. Similar time trends were observed for mean temperature and precipitation sums for the periods of stand growth, but only exhibited a faster increase after about 1960. Even though increased temperature and precipitation after 1990 seem to contribute to increased site indices, increased nitrogen availability and atmospheric CO_2 levels may also be important factors.

Keywords: Picea abies, Pinus sylvestris, *site index prediction model, site index trends.*

1. Introduction

Forest site productivity may be defined as the potential of a site to produce timber or forest biomass (Skovsgaard & Vanclay, 2008). Information on site productivity is an important prerequisite for forest management planning. Different approaches can be used to assess site productivity (e.g. Carmean, 1975; Pokharel & Dech, 2011; Skovsgaard & Vanclay, 2008; Vanclay, 1994). A frequently applied approach is based on the strong correlation between volume and height growth. Consequently, dominant height for the given tree species at a specified reference age (site index) serves as a proxy for site productivity. However, this approach is restricted to fully stocked, monospecific, even-aged stands (e.g. Vanclay, 1994). The site index approach fails if dominant trees are not present, if stands are mixed species or uneven-aged, if the area is unstocked, stocked with a different species than the one that should be predicted, or stocked with young stands where small errors in age or dominant height cause large errors in site index predictions. An alternative way to estimate site index is to predict it from site variables describing location, topography, soil, understory vegetation or climate (Carmean, 1975; Hägglund, 1981; Pokharel & Dech, 2011). We use the term "site index prediction models" for this frequently applied approach (e.g. Farrelly et al., 2011; Hägglund & Lundmark, 1977; Klinka & Carter, 1990; Nilsen & Larsson, 1992; Schadauer, 1999; Seynave et al., 2005). Most of the site variables used in these types of models can be easily measured in the field or extracted from existing maps or databases.

Most previously developed site index prediction models were calibrated based on limited data sets. Only a few studies have used extensive data from national forest inventories or other sources (Beaulieu et al., 2011; Chen et al., 2002; Elfving, 1994;

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Hägglund & Lundmark, 1977; Schadauer, 1999; Seynave et al., 2005; Tegnhammar, 1992). In Norway, the national forest inventory (NFI) has been recording tree and stand variables as well as site variables related to location, topography, soil and understory vegetation on permanent sample plots systematically located across the country for the last 25 years. Temperature and precipitation records from a network of weather stations managed by the Norwegian Meteorological Institute have been geographically interpolated to estimate climate variables for the NFI sample plots (Skaugen & Tveito, 2004; Solberg et al., 2004). These data can be used for site index prediction models and have the advantage of being a representative sample for the total forest area. Site index models for Norway spruce and Scots pine in Norway have been developed using the same data (Sharma et al., 2011).

Site indices for Norway spruce and Scots pine have been reported to vary with year of stand origin in Norway (Bøhler & Øyen, 2011; Nilsen & Larsson, 1992), Sweden (Elfving, 1994; Elfving & Nyström, 1996a; Elfving & Tegnhammar, 1996; Elfving et al., 1996; Hägglund & Lundmark, 1977), Finland (Mielikäinen & Timonen, 1996; Tamminen, 1993), and other regions in Europe (Hassall et al., 1994; Schadauer, 1999; Socha, 2008; Spiecker et al., 1996). Under the same site conditions, site indices for stands established later tend to be higher than for stands established earlier. We use the term "site index trend" for these trends in dominant height growth. Trends in site indices can be caused by changes in growing conditions or management practice over time. The role of individual factors contributing to the complex causes of site index trends has only rarely been quantified (Tegnhammar, 1992). However, even without site index trends site indices in inventory data are often correlated with stand age, which is caused by shorter rotation periods for stands on better sites as compared to poorer sites (Tegnhammar, 1992). Site index prediction models have frequently included age as a variable in order to correct for the site index trend. Tegnhammar (1992) found trends in site indices for Sweden based on NFI data and proposed a correction function for site index that is age dependent and varies with latitude. Elfving and Nyström (1996b) applied this correction function on independent data and found similar trends in site indices. Elfving (1994) introduced age as a variable into Swedish site index prediction models (Hägglund & Lundmark, 1977). Schadauer (1999) included age into site index prediction models for Norway spruce in Austria after he identified significant site index trends in the NFI data. A significant interaction of the site index trend with temperature sum in these models indicated regional variation in site index trends. By applying different site index models, Schadauer (1999) could also demonstrate that the observed site index trends are more likely caused by a real shift in growing conditions over time than by inappropriate time trends implicit in the site index models. Applying a site index concept that is different from the traditional ones applied in all other studies, Albert and Schmidt (2010) described strong trends in site indices after 1970.

For Norway, Nilsen and Larsson (1992) developed site index prediction models for Norway spruce and Scots pine based on temporary sample plots and NFI data from southeastern Norway using previous site index models (Tveite, 1977). Significant age trends in the residuals of the site index prediction models were observed, but age was only included into preliminary models for Norway spruce, leaving the final models with a significant age bias. Bøhler and Øyen (2011) tested these models for samples of Norway spruce and found a large bias, most likely due to a lack of site index trends in these models.

The aim of our study was to develop site index prediction models based on site and climate variables for the most important tree species in Norway, Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). Using NFI data for these models will make it possible to apply them across Norway. We also tested for the existence of trends in site indices recorded for NFI plots. Site index prediction models that include site index trends will allow for better predictions of future growth. Trends in site indices derived from site index prediction models might also be used to correct site indices that are predicted from observed age and dominant height.

2. Materials and methods

2.1. Data

The NFI database comprises information from approximately 10,500 sample plots established from 1986 and onwards in productive forests (Tomter, 2000). The 250 m^2 plots are systematically distributed over the entire country (except in Finnmark county where the plots were established later) in a 3×3 km grid and are remeasured every fifth year (Landsskogtakseringen, 2007). Data up to 2008 were used in our study. We only used plots where heights for dominant Norway spruce or Scots pine trees were recorded inside the 250 m^2 plot, applying the criteria described in Sharma et al. (2011). These selection criteria significantly reduced the number of plots, but based our analyses on more precise registrations of dominant height and therefore site index as opposed to height measured on individual site index trees recorded outside the 250 m^2 plot for all plots. A total of 1711 NFI plots (832 spruce dominated and 879 pine dominated) were selected based on the following additional criteria: forestry land use; no interception by roads, water bodies or agricultural land; more than 70% of the total standing volume is comprised of spruce or pine; site and climate variables available; one of the eight most frequent vegetation types. Frequency distributions of site index, age, dominant height and altitude for the sample plots used here are presented in Figure 1. Frequency distributions for all NFI sample plots in productive forests were very similar, but some deviations indicate a slight bias in our data selection. For stands on the lowest site indices (< 14 m for spruce, < 11 m for pine) the data used here has significantly lower proportions of stands below 100 years and higher proportions of stands above 100 years as compared to the total NFI data-set. The sampled data also have a small over-representation of stands from higher elevations (above 350 m) for spruce and lower elevations (below 400 m) for pine.

The site index, to be used as the dependent variable, was calculated for each plot using the following dominant height growth model (Sharma et al., 2011):

$$h - 1.3 = \frac{b_1 + X_0}{1 + b_2/X_0 \cdot t^{-b_3}} \tag{1}$$

$$\text{with } X_0 = 0.5 \cdot \left(\psi + \sqrt{\psi^2 + 4 \cdot b_2 \cdot (h_{40} - 1.3) \cdot 40^{-b_3}}\right)$$

$$\text{and } \psi = (h_{40} - 1.3) - b_1$$

where h is dominant height (m), t is breast height age (years) and h_{40} is site index (m) at the reference age of 40 years. The parameter estimates for spruce are: $b_1 = 18.9206$, $b_2 = 5175.18$, $b_3 = 1.1576$, and for pine: $b_1 = 12.8361$, $b_2 = 3263.99$, $b_3 = 1.1758$. The dominant height at the last observation was used to calculate site index for each plot. The observed site index varied from 5 to 30 m for spruce, and from 3 to 23 m for pine (Table III).

A large number of variables describing the site are available for the NFI sample plots. In order to develop simple and easily applicable models, only variables that could be measured in the field or recorded relatively easily from other sources at low costs were chosen. The latest registration of site variables was used here, assuming constant values for the same plot and that errors from previous measurements have been corrected. Vegetation types

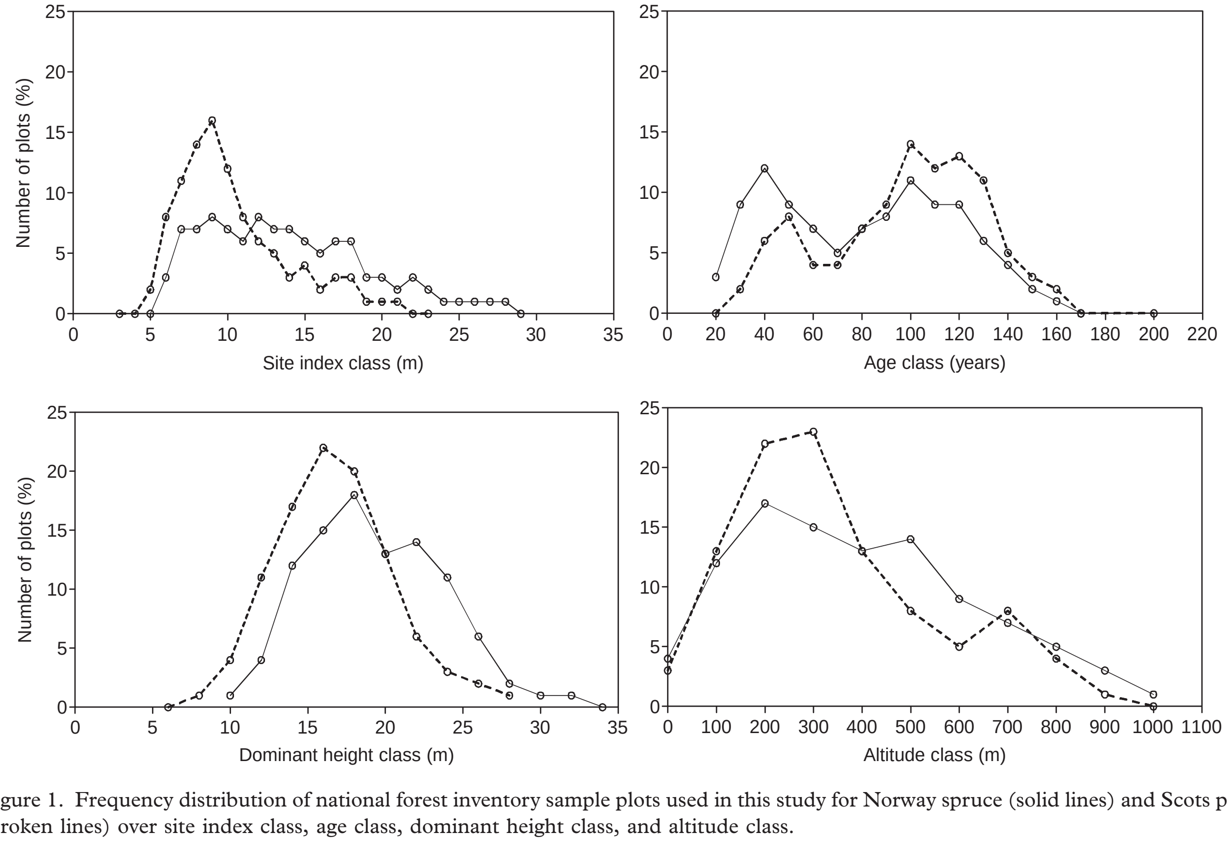


Figure 1. Frequency distribution of national forest inventory sample plots used in this study for Norway spruce (solid lines) and Scots pine (broken lines) over site index class, age class, dominant height class, and altitude class.

Table I. Continuous site and climate variables.

Site variable	Abbreviation, unit	Description
Altitude	*ALT*, m	Elevation above mean sea level
Latitude	*LAT*, ^{0}N	Latitude of the plot centre
Aspect	*ASP*, radian	Orientation of slope, measured in clockwise direction from magnetic North
Slope	*SLP*, %	Rise in altitude with respect to horizontal distance
Temperature sum	*TSUM*, degree days (d.d.)	Mean growing season temperature sum for period 1957–2000
Precipitation sum	*PSUM*, mm	Mean growing season precipitation sum for period 1957–2000

were classified according to Larsson (2000), who also ranks vegetation types according to availability of water and nutrients, or productivity. We used only plots with the eight most frequent vegetation types that represent 95% of the conifer forest area in Norway (Tomter, 2000). The final selection of site variables were therefore continuous ones such as altitude, latitude, aspect and slope (Table I), and discrete ones such as soil depth and understory vegetation type (Table II).

Mean monthly temperature and precipitation recorded by the Norwegian Meteorological Institute at 797 weather stations from 1957 to 2000 were used to estimate those variables for each NFI plot through spatial interpolation from the nearest weather stations (Skaugen & Tveito, 2004; Solberg et al., 2004). Temperature sum (*TSUM*, degree days above 5°C) and precipitation sum (*PSUM*, mm) were calculated for the growing season as a mean of the 44-year period (Figure 2, Table I). The start of the growing season was defined as the day when the degree day sum (sum of temperatures above 5°C) exceeded 10°C, using observed intraannual height growth as a criterion (Salminen & Jalkanen, 2007). The earliest start of the growing season was limited to April 19 and the latest to July 1. Since only mean monthly temperature data were available, the growing season length was estimated on the basis of daily mean temperatures interpolated from mean monthly temperatures. The end of the growing season was defined based on observations on intraannual diameter growth from Finland (Henttonen et al., 2009; Mäkinen et al., 2003; Schmitt et al., 2004). Diameter growth terminated in August in these studies, when mean daily temperatures were around 15°C, but there was no indication that the termination of diameter

Table II. Discrete site variables, their statistics, grouping, and dummy variable coding.

		Number of observations		Variable level group		Dummy variable					
						Spruce			Pine		
Site variable	Type	Spruce	Pine	Spruce	Pine	*SD1*	*SD2*	*SD3*	*SD1*	*SD2*	*SD3*
Soil depth	1 = depth < 25cm	36	226			0	0	0	0	0	0
	2 = depth 25–50cm	173	232			1	0	0	1	0	0
	3 = depth 51–100cm	215	116			0	1	0	0	1	0
	4 = depth >100cm	408	305			0	0	1	0	0	1
						VT1	*VT2*		*VT1*	*VT2*	*VT3*
Vegetation type (order according to increasing productivity)	1 = Lavskog (*Cladonio-Pinetum boreale*)	1	102	Type 1,2,3	Type 1	0	0		0	0	0
	2 = Blokkebærskog (*Barbilophozio-Pinetum*)	4	178	Type 4	Type 2	1	0		1	0	0
	3 = Bærlyngskog (*Vaccinio- Pinetum*)	107	411	Type 5,6,7,8	Type 3	0	1		0	1	0
	4 = Blåbærskog (*Eu-Pceetum myrtillitosum*)	369	160		Type 4,5,6,7,8				0	0	1
	5 = Småbregneskog (*Eu-Pceetum dryopteridestosum*)	219	11								
	6 = Storbregneskog (*Eu-Pceetum arthyrietosum*)	17	1								
	7 = Lågurtskog (*Melico-Piceetum typicum*)	71	12								
	8 = Høgstaudeskog (*Melico-Piceetum aconitetosum*)	44	4								

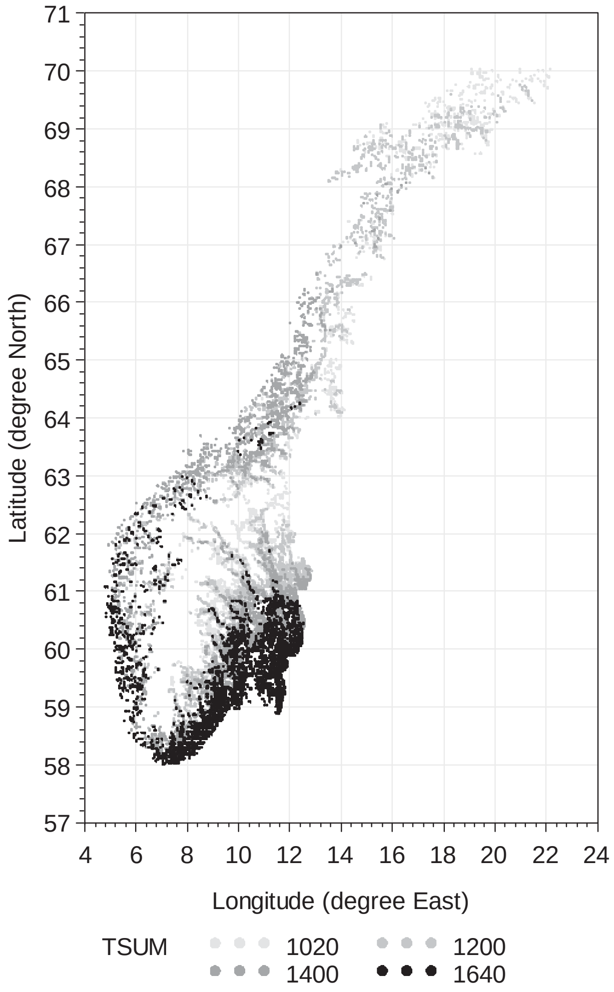


Figure 2. Growing season temperature sum (*TSUM*, d.d.) for all national forest inventory plots in productive forests (*TSUM* classes are ≤1100, 1100 – 1300, 1300 – 1500, >1500; TSUM in the legend are observed means of those classes).

growth was triggered by temperature signals. In order to describe the large regional variation in termination of tree growth across Norway, we used the day when the daily mean temperature dropped below 15°C as a criterion for the end of the growing season. Statistics of all continuous site and climate variables are presented in Table III.

2.2. Analyses

A significant trend of site indices over year of stand origin was observed for spruce and pine (Figure 3). We used year of stand origin rather than age for this analysis, because in contrast to previous studies, our data were collected over a 23-year period and therefore stands with the same age at the recording might have different years of stand origin, not allowing us to use stand age as a proxy for stand origin year. Preliminary site index prediction models without stand origin year as a variable could not remove this trend in the residuals with any combination of site and climate variables. Stand origin year was therefore included as a variable into all models. The observed site index trend (Figure 3) was not linear, but the increase in site indices with increasing stand origin year was faster for the last 60 years. The site index prediction models will be applied mostly in the extrapolation range, for stands established after 1990. Because the change in the site index trend is only estimated based on few observations from the stands established recently, we avoided the use of non-linear models that might in the extrapolation range predict further changes in the trend for which no indication is given in the data. A segmented linear model has the advantage of linear extrapolation and was therefore applied to describe the site index trend. Residual plots of the segmented linear models did not indicate additional non-linearity, which would have implied the use of non-linear models. The breakpoint of the segmented linear model, that is, the year when the site index trend changes, was estimated from the data. The segmented linear model is defined as

$$\mathrm{SI} = \mathrm{c}_0 + \mathrm{c}_1\mathrm{STORG} + \mathrm{c}_2\mathrm{STORG2} + \varepsilon \qquad (2)$$

where SI is site index; c_0, c_1, c_2 are parameters to be estimated, and ε is the residual error. STORG is the calendar year of stand origin, STORG2 is an additional time variable for the second segment and calculated as the difference between STORG and the breakpoint year for stands originated after

Table III. Statistics for continuous variables (832 Norway spruce sample plots; 879 Scots pine sample plots).

Species	Statistic	*SI* (m)	ALT (m)	*LAT* (°N)	*ASP* (radian)	*SLP* (%)	*TSUM* (d.d.)	*PSUM* (mm)
Norway spruce	Minimum	4.8	5.0	58.1	0.0	0.0	845.3	135.9
	Maximum	29.8	1005.0	68.7	6.3	99.0	1877.0	926.7
	Mean	13.7	389.4	61.4	3.0	22.8	1360.1	341.9
	Standard deviation	5.4	234.6	2.0	1.8	16.6	227.2	88.4
Scots Pine	Minimum	3.2	10.0	58.0	0.0	1.0	941.9	119.4
	Maximum	23.2	950.0	69.4	6.3	105.0	1879.3	878.8
	Mean	10.3	341.1	60.7	3.1	20.3	1436.7	368.5
	Standard deviation	3.7	207.9	1.9	1.7	16.5	210.7	131.0

SI, dominant height at breast height age 40; Other abbreviations as in Table I.

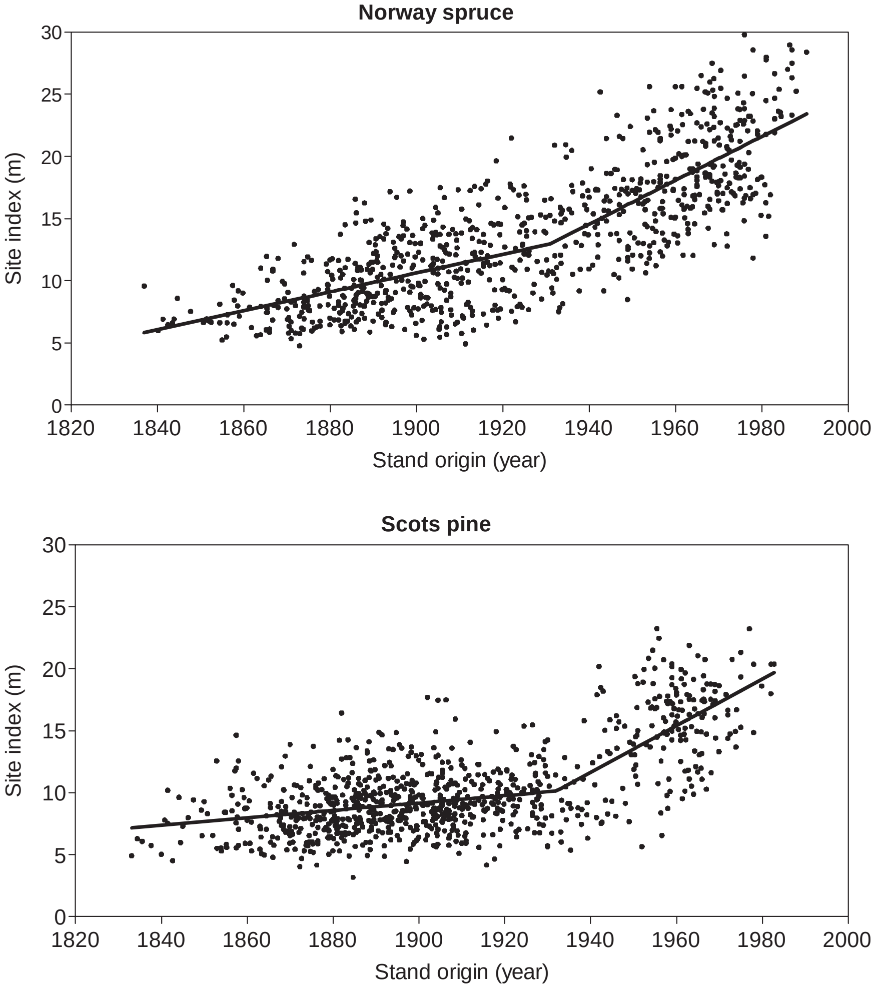


Figure 3. Observed site index over stand origin year for Norway spruce and Scots pine. Parameters of regression models are given in Tables V and VI (model 1).

the breakpoint year and set to zero for all other stands. In order to estimate the breakpoint year from the data, models were estimated with all possible breakpoint years between 1920 and 1960, and the model with the lowest root mean squared error was selected. Preliminary analyses also showed significant interaction between site index trend variables and *TSUM*, *LAT* or *ALT*, indicating a regional variation of site index trends. These interaction terms were therefore included into the initial set of variables before variable selection for individual models.

Scatter plots of site index against all potential independent variables, and scatter plots of the independent variables among themselves did not show significant non-linear relationships. Multiple linear models were therefore used to estimate site index from site and climate variables. For the discrete variables, dummy variables were used in the models (Table II). Discrete variable levels having similar characteristics and few observations were grouped into a single level to avoid over-parameterisation. Significant interactions of two site variables were only found in a few cases. The interaction of slope (*SLP*) and aspect (*ASP*) is one example. This interaction has previously been quantified with trigonometric expressions (Stage, 1976; Wykoff, 1990). The interaction term $SLP \times sin(ASP)$ describes that stands on east facing slopes are growing better than on west facing slopes, and that this effect increases with increasing slope. The interaction term $SLP \times cos(ASP)$ describes a similar pattern, favouring north facing slopes versus south facing slopes.

Site and climate variables can be grouped into categories describing location (altitude, latitude), topography (aspect, slope), soil properties (soil depth), understory vegetation (vegetation type) and climate (temperature sum, precipitation sum). These variables can be obtained either directly through field measurements or indirectly from digital maps, for example, location, topography and climate. Even though digital maps will be increasingly available in the future, most of the variables will still have to be estimated in the field and site index estimation models purely based on field data will still be needed. For similar reasons models with fewer variables are more easily applied. Based on these considerations we prepared for a number of different site index prediction models containing different combinations of site and climate variables. The site index trend and its regional variation were included in all models, but also as separate models. Alternative models were prepared using different site and climate variables to explain the regional variation in site index trends. The complete list of models aimed at was therefore:

1) Uniform site index trend only, no site and climate variables.
2) Region specific site index trend only, no additional site and climate variables.
3) Understory vegetation.
4) Understory vegetation and soil.
5) Climate.
6) Climate and understory vegetation.
7) Climate, understory vegetation and soil.
8) Location, topography and climate.
9) All site and climate variables (location, topography, soil, understory vegetation and climate).
10) All site variables, no climate variables (location, topography, soil and understory vegetation; regional variation of site index trend described without climate variables).

The parameters of the models were estimated with PROC REG (SAS Institute Inc., 2008) by applying backward elimination to select the significant variables ($\alpha = 0.05$). Some independent variables included may be significantly correlated with each other, and therefore the estimated parameters will be biased (Montgomery et al., 2001). The variance inflation factor (VIF) was therefore applied, and a VIF value of less than 10 was used as a threshold to avoid multicolinearity among independent variables (Montgomery et al., 2001; O'Brien, 2007). Partial R^2 was used to remove the correlated variables that explained least variation of the dependent variable when VIF was above the threshold. Residuals were examined graphically in relation to all available variables.

To explore possible causes for trends in site indices (Figure 3), we analyzed time trends in climate data. Long-term series of mean monthly temperature and monthly precipitation sums were used to describe the climate during the entire period when stands developed. This set of long-term climate data from meteorological stations is different from the data described earlier where climate data were interpolated for all NFI plots for the period 1957–2000 only. Series for the years 1900–2009 were available from four stations for temperature and 55 stations for precipitation (eklima.met.no, downloaded 9 September 2011). In order to confirm that time trends in temperature observed by these four stations reflect a general time trend, data from another 10 stations covering the period 1930–2009 were compared. Stations used for all analyses cover southern Norway, where most of the productive forest is located. Annual mean temperature and precipitation sum were calculated for each station and year and normalised using the mean of the entire 110-year series per station. Whole year data rather than growing season data were used, because they implicitly include effects of growing season length and soil water availability. Normalised trends were tested for similarity between stations graphically before a mean trend for all stations was calculated. From these mean trends that are reflecting the variation in temperature and precipitation across the region, mean relative temperature and precipitation were calculated for periods ranging from 2009 back to stand origin years between 1900 and 1989. Segmented linear regressions were fitted to these time series using the same methods as described above for site index data.

3. Results

All continuous site and climate variables were significantly correlated with site index (Table IV) except for aspect where a linear relationship was not expected. For spruce and pine, the strongest correlations were found for the year of stand origin and temperature sum. Spruce site index was negatively correlated with altitude and latitude and positively correlated with year of stand origin, temperature and precipitation sum. Pine site index was also negatively correlated with altitude and latitude and positively correlated with year of stand origin and temperature sum, but, as opposed to spruce, negatively correlated with precipitation sum. When considering correlations between different variables, temperature sum showed strong negative correlations with altitude and latitude for both species. The correlation between these variables is also visible in Figure 2 where temperature sums are higher in the south and at lower altitudes.

Model 1, describing the uniform site index trend (Figure 3, Tables V and VI), explained 66% and 53% of the site index variation for spruce and pine, respectively. Site index increased more with increasing stand origin year in the second period of stand origin, after the breakpoint in the segmented linear regression, than in the first (Figure 3). For model 2,

Table IV. Pearson's correlation coefficients between continuous variables and observed site index.

Species	Variable	*SI*	*ALT*	*LAT*	*ASP*	*SLP*	*TSUM*	*PSUM*
Norway spruce	*ALT*	−0.49						
	LAT	−0.30	−0.20					
	ASP	−	+	+				
	SLP	−0.08	−	0.14	−0.06			
	TSUM	0.64	−0.76	−0.45	−	−0.16		
	PSUM	0.20	−0.38	0.09	+	0.19	0.19	
	STORG	0.80	−0.39	−0.10	+	−0.15	0.42	0.18
Scots pine	*ALT*	−0.21						
	LAT	−0.17	0.10					
	ASP	−	−	0.10				
	SLP	−0.15	−0.07	−	−			
	TSUM	0.34	−0.81	−0.57	−	−		
	PSUM	−0.13	−0.43	−0.25	−	0.28	0.28	
	STORG	0.66	−0.16	0.07	+	−0.13	0.11	−

Non-significant correlation ($p > 0.05$) is symbolised with + or −, depending on the sign of the correlation.
All abbreviations as in Table I.

describing region specific site index trends by using temperature sums, $R^2_{adj.}$ was even higher. An interaction of stand origin year and temperature sum was significant for both periods of stand origin. The parameter estimate for *STORG* × *TSUM* is very small, indicating that the site index trend is only changing very little with increasing temperature sum for the first period of stand origin (Figure 4). The

Table V. Parameter estimates and fit statistics for Norway spruce.

	Model						
Variable	1	2	3	4	8	9	10
Intercept	−133.65240	−96.57398	−77.87344	−76.29319	−83.97164	−59.94881	−80.34282
Location							
LAT					−0.24019	−0.35694	
Topography							
SLP					0.02429	0.03245	0.02022
ASP						−0.00236	
SLP × *sin (ASP)*						−0.01162	
SLP × *cos (ASP)*						−0.00805	
Soil							
SD1				0.85849		1.06598	1.02772
SD2				1.68124		1.95140	1.78465
SD3				2.14027		2.63731	2.58080
Understory vegetation							
VT1			1.76652	1.57874		1.56397	1.57260
VT2			3.70176	3.39037		3.47510	3.53569
Trend							
STORG	0.07593	0.05091	0.04021	0.03841	0.05237	0.04185	0.07599
STORG2	0.10015						0.11236
STORG × *TSUM*		0.00000426	0.00000405	0.00000424	0.00000377	0.00000361	
STORG2 × *TSUM*		0.00007779	0.00007198	0.00007880	0.00007185	0.00007770	
STORG × *ALT*							−0.00000338
STORG × *LAT*							−0.00046852
Breakpoint year	1931	1937	1933	1937	1933	1937	1937
Fit statistic							
$R^2_{adj.}$	0.6580	0.7743	0.8263	0.8373	0.7845	0.8576	0.8539
RMSE	3.16	2.57	2.25	2.18	2.51	2.04	2.06

$R^2_{adj.}$, adjusted coefficient of determination; RMSE, root mean squared error (m); other abbreviations are the same as in Tables I and II. Dummy variable levels are defined in Table II. Models 5, 6 and 7 are not presented here, because they are similar to models 2, 3 and 4, respectively.

Table VI. Parameter estimates and fit statistics for Scots pine.

	Model						
Variable	1	2	3	4	8	9	10
Intercept	−47.590	−40.10336	−32.01432	−32.68569	−28.73058	−15.52333	4.02461*
Location							
ALT							−0.00296
LAT					−0.18005	−0.26061	−0.57751
Topography							
SLP						0.01262	
SLP × sin (ASP)					0.00768		
SLP × cos (ASP)					−0.02090	−0.01663	−0.01691
Soil							
SD1				0.70537		0.87601	0.81941
SD2				1.72277		1.91351	1.75905
SD3				2.56274		2.88112	2.68337
Understory vegetation							
VT1			−1.21844	−0.65945		−0.50898	−0.64305
VT2			0.46793	0.69075		0.65361	0.67191
VT3			1.08818	1.24962		1.33244	1.32105
Trend							
STORG	0.02988	0.02284	0.01850	0.01666	0.02320	0.01646	0.02074
STORG2	0.15848						0.16048
STORG × TSUM		0.00000215	0.0000022	0.0000032	0.00000171	0.00000260	
STORG2 × TSUM		0.00009460	0.0000907	0.0000925	0.00008921	0.00008397	
STORG2 × ALT × LAT							−0.00000155
Breakpoint year	1932	1928	1927	1932	1925	1927	1928
Fit statistic							
$R^2_{adj.}$	0.5281	0.6030	0.6445	0.7061	0.6168	0.7240	0.6961
RMSE	2.56	2.34	2.22	2.02	2.30256	1.95	2.05

*Not significantly different from zero.

$R^2_{adj.}$, adjusted coefficient of determination; RMSE, root mean squared error (m); other abbreviations are the same as in Tables I and II. Dummy variable levels are defined in Table II. Models 5, 6 and 7 are not presented here, because they are similar to models 2, 3 and 4, respectively.

parameter estimate for *STORG2 × TSUM* is significantly larger, indicating that the site index trend is substantially larger in warmer than in colder regions in the second period of stand origin. The breakpoint years between the two different periods of stand origin differed between models, but within a limited range. The estimated breakpoint years were in most cases a few years earlier for pine than for spruce.

In model 3 only vegetation types were used in addition to site index trends to predict site index. The $R^2_{adj.}$ and RMSE of those models (Tables V and VI) indicate that these few variables explain a large part of the variation in site indices. However, the inclusion of temperature sum in the site index trend interactions does also explain regional variation in site indices. The parameter estimates confirm the ranking of vegetation types according to increasing productivity for spruce (Table II). For pine, vegetation type 2 (Blokkebærskog) has a lower site index than vegetation type 1 (Lavskog). Parameter estimates for vegetation type groups are indicating large differences in sites indices among them for both species.

Model 4 uses soil depth in addition to variables in model 3 to predict site index. The improvement in $R^2_{adj.}$ and RMSE is larger for pine than for spruce (Tables V and VI). Parameter estimates for soil depth are similar for both species and indicate significantly higher site indices for stands on deeper soils. Site index predictions from this model are given in Figure 4, showing the effects of varying a few important independent variables. In this figure it should be noted that the interaction terms between site index trends and *TSUM* are not only causing varying trends of site index for different values of *TSUM*, but *TSUM* is a major variable in predicting the general level of site indices. Even though *TSUM* is not represented as an individual variable in the models, it explains a large part of the variation in site indices.

Models 5, 6 and 7 are similar to models 2, 3 and 4, respectively, with the addition of climate variables. Only for pine, an additional climate variable, *PSUM*,

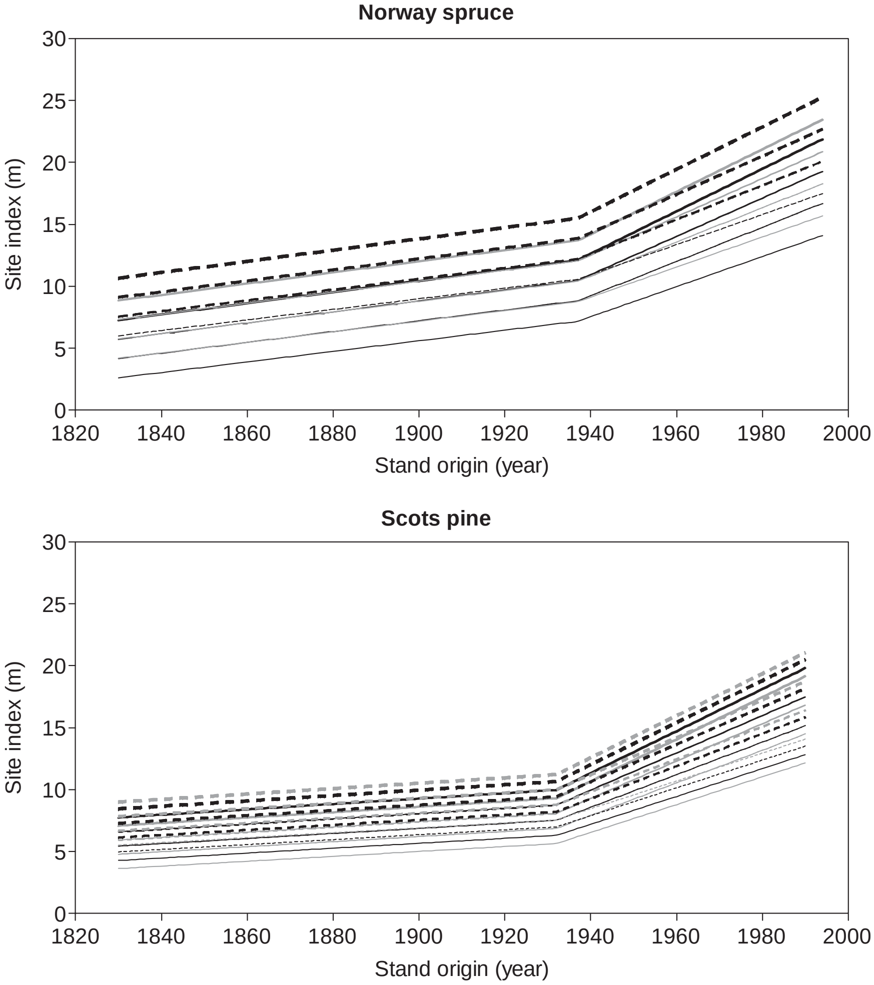


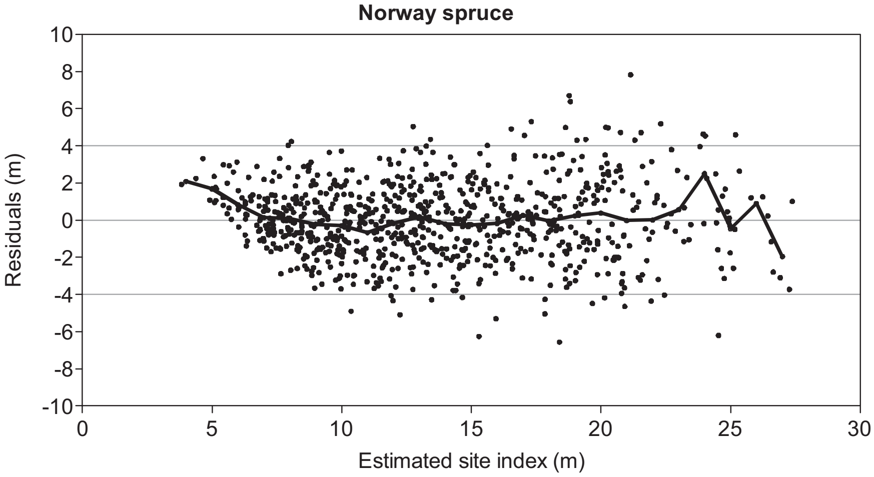
Figure 4. Site index for Norway spruce and Scots pine predicted with model 4 for soil depth type 2, vegetation types (type 1: black solid, type 2: grey solid, type 3: black broken, type 4: grey broken), and four temperature sums (1000, 1200, 1400 and 1600 d.d., displayed with increasing line thickness).

entered the models, but with a negative parameter estimate for this variable in all three models. A negative correlation between *PSUM* and site index was also found for this species (Table IV). However, older stands are overrepresented in regions with high *PSUM* in the data. Site index trends rather than negative effects of increasing precipitation on growth are therefore responsible for the observed correlation. Models 5, 6 and 7 are therefore not presented here for pine and *PSUM* was excluded in models 8 and 9 for this species as well.

In model 8, location and topography are used to predict site index instead of vegetation type and soil variables. For both species, the improvement in $R^2_{adj.}$ and RMSE compared to model 2 was much smaller than for model 3 (Tables V and VI). With increasing latitude site index decreases for both species. This effect of latitude was significant in addition to the effect of *TSUM* that shows a strong latitudinal gradient (Figure 2, Table IV). With increasing slope site index of spruce increased (Table V), reaching about one meter difference in site index between slopes of 0 and 41%. In contrast to this relationship, slope was negatively correlated with site index for both species (Table IV), because stands on steeper hillsides were on average older than other stands. Due to the trend in site indices, stands on steeper hillsides therefore had on average lower site indices. For Scots pine, effects of slope were described by the interaction variables between aspect and slope. The interaction $SLP \times sin(ASP)$, describing better site index on east facing slopes, got a positive parameter estimate. The interaction $SLP \times cos(ASP)$, describing better site index on north facing slopes, got a larger but negative parameter estimate in model 8. In combination, these two variables and their parameters predict that Scots pine site index is higher on south facing slopes slightly oriented towards east (160 degrees) than on slopes facing the opposite direction, and this effect increases with increasing slope (reaching about one meter difference in site index between slopes of 0 and 24%).

For model 9, all available site and climate variables could be chosen. The variables selected describing location, soil, vegetation and site index trend were identical in these models with those in models 2, 3, 4 and 8 for both species and parameter estimates were similar. The combination of variables describing topography was different in model 9 than in model 8 for both species. For pine, the model predicts higher site index on south facing slopes, which increase with increasing slope (reaching about one meter difference in site index between slopes of 0 and 30%). For spruce, site index is highest for slopes oriented towards southwest (235 degrees) and this effect increases with increasing slope (reaching about one meter difference in site index between slopes of 0 and 27%). The $R^2_{adj.}$ and RMSE of model 9 indicate for both species that a large part of the variation in site indices can be explained with the given combinations of site and climate variables. However, the improvement is only minor as compared to model 4.

Residuals for model 9 are shown in Figure 5 to illustrate the residual variation of the observed site indices. Even though the residuals of model 9 for all observations do only show small trends for the lowest site indices, larger trends and bias have been observed when observations from different regions were analysed separately. For spruce, models 3, 4 and 9 underestimated the average site index in Western Norway (from Rogaland to Møre og Romsdal) by 2.5, 2.7 and 2.0 m, respectively (all significantly different from 0 at $p < 0.05$, *t*-test). Model 9, which includes slope as a variable, shows a smaller bias for this region, which is characterised by steep hillsides. For Mid-Norway (from Sør-Trøndelag to Nordland), average site index was overestimated by about 1.1 m for spruce using models 3 and 4, and for pine by 1.3 and 0.9 m using models 3 and 4, respectively (all significantly different from 0 at $p < 0.05$, *t*-test). For the same



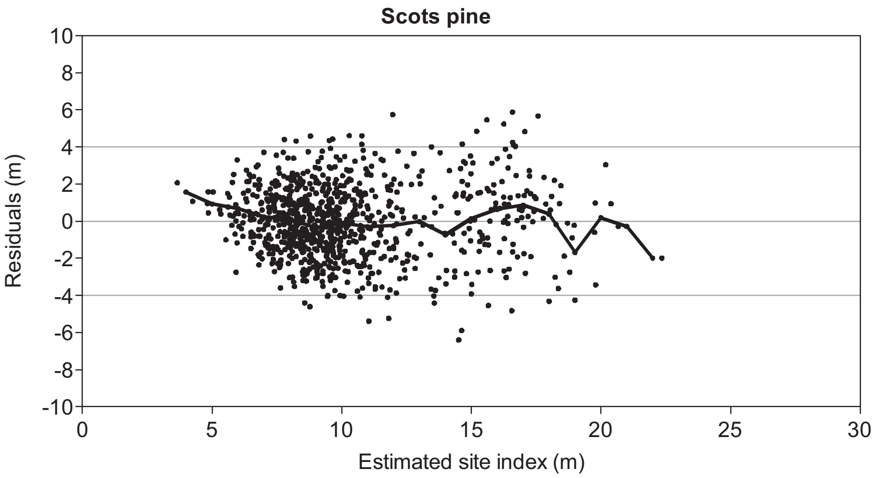


Figure 5. Residuals for model 9 over estimated site index for Norway spruce and Scots pine. Mean residuals (solid line) were calculated for one meter site index classes.

region, model 9 was free of bias for both species. In model 9, a strong effect of latitude is included, which reduces site index when moving from 60 to 64 degrees north by the same order of magnitude as in the observed bias for Mid-Norway. For pine stands and old spruce stands (established before the breakpoint year) in Mid-Norway, models 3, 4 and 9 underpredicted lower site indices and overpredicted higher site indices, with a maximum bias of less than 1 m (significantly different from 0 at $p < 0.05$, *t*-test, for models 3 and 4 only). This might indicate that the variable mostly responsible for the differentiation of site index, temperature sum, has different effects in Mid-Norway than in other regions. Most observations are from Southeastern Norway, where temperature sum varies greatly (Figure 2) and describes steep elevational gradients. The range of temperature sums and the elevational gradient are much smaller in Mid-Norway.

In model 10, the regional variation in site index trends should be explained without using climate variables. Altitude, latitude and their interaction with site index trend variables were used to explain the regional variation in site index and trends for both species. For spruce, model 10 had almost the same fit statistics as model 9 (Table V). For pine, fit statistics of model 10 indicated only a slightly larger residual variation (Table VI). Different combinations of the variables altitude, latitude and their interactions with site index trend variables were selected in model 10 for spruce than for pine. For both species, these variable combinations describe that site index decreases with increasing altitude and latitude. For pine, a faster increasing site index trend for stands established after the breakpoint year on sites at lower altitudes (interaction $STORG2 \times ALT \times LAT$) is predicted with model 10. This interaction is similar to the interaction described in other models by the temperature sum variable (Figure 4). For spruce, altitude and latitude could not describe the regional variation in site index trends for stands established after the breakpoint year. This interaction could be described in model 9 using temperature sums, but interaction variables using altitude or latitude were only significant with higher probabilities of error ($\alpha = 0.05$–0.10) in preliminary alternatives to models 2 and 10. Spruce stands established after the breakpoint year were mostly from lower altitudes and latitudes. However, in combination there were still enough stands established after the breakpoint year on sites with lower temperature sums to explain the interaction with a single variable, temperature sum. But using two variables, altitude and latitude, too few observations remained to model this interaction. For pine, the stands established after the breakpoint year had a distribution across altitudes and latitudes that was more similar to the ones established before the breakpoint year.

To explore possible causes for trends in site indices (Figures 3 and 4), time trends in a second set of long-term climate data for selected weather stations were analyzed. A similar time trend was observed for all weather stations across southern Norway for the period 1900 to 2009, both for mean annual temperatures and precipitation sums. From this common trend, mean temperatures and precipitation sums for the periods of stand development ranging back from 2009 to stand origin years between 1900 and 1989 were calculated (Figure 6). The trend in these climate variables could be described with a segmented linear regression that is similar to trends in site indices (Figure 3). However, the breakpoint

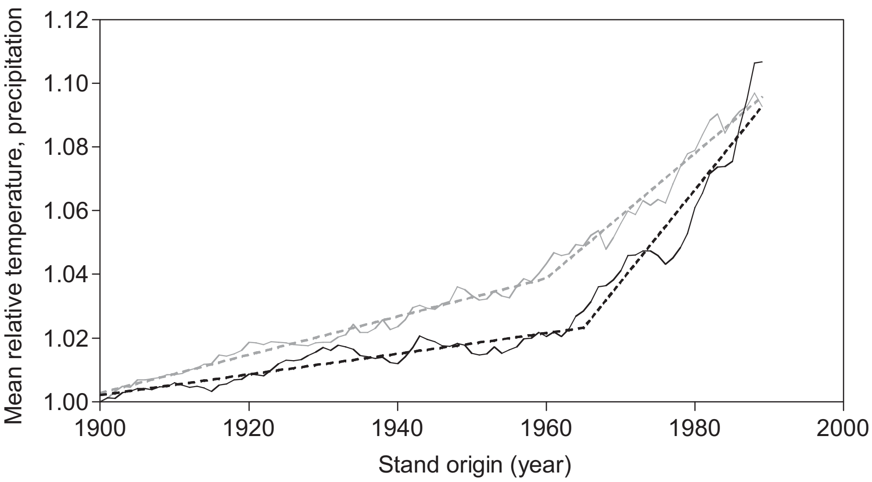


Figure 6. Mean relative temperature (black solid lines) and precipitation (grey solid lines) for periods ranging from 2009 back to stand origin years between 1900 and 1989. The segmented linear regressions (broken lines) have breakpoints at year 1965 for temperature and 1960 for precipitation.

for the trends in climate variables is about 30 years later than the breakpoint for site indices.

4. Discussion

A strong trend of site indices was observed in our data (Figures 3 and 4) and was therefore included in the site index prediction models (Tables V and VI). Trends in site indices have been reported frequently (e.g. Elfving et al., 1996; Nilsen & Larsson, 1992; Schadauer, 1999). In a Europe wide study, Kahle et al. (2008b) demonstrated increased height growth of young Norway spruce and Scots pine stands between 1960 and 2000. This study compared stands of the same age but different year of germination and is therefore independent of site index models. Site index prediction models have therefore frequently included age as a variable in order to correct for the trend (Elfving, 1994; Elfving & Nyström, 1996a; Nilsen & Larsson, 1992; Schadauer, 1999; Tegnhammar, 1992). Unlike most others, we observed an abrupt change in the relationship between site index and stand establishment year around 1930, which we modelled using a segmented linear model. For forest stands established after the 1930s the increase in site index was stronger than for stands established before. Covering about 50 years for stands established between 1940 and 1990, our data might have enabled us to detect a change in the site index trend that was not detected in earlier reports from Fennoscandia due to shorter time series. The data selected for this study include fewer stands on the lowest site indices (<14 m for spruce, <11 m for pine) below an age of 100 years as compared to the total NFI data set. Model predictions for this range of ages and site indices are therefore more uncertain than for all other situations. Nevertheless, due to the variation of site index trends with temperature sum in all models, an uncertain site index trend for stands on poorer sites may not bias trends for stands on better sites.

For spruce, site index for stands established after 1983 tends to be underpredicted by the site index trend model (Figure 3). Similar patterns were seen in the residuals for model 9. These young stands grew up during the 20-year period with much higher than average temperatures (Figure 6). The linear site index trend applied to the stands established after the breakpoint does therefore only poorly predict the trend for these stands. For pine, no stands established after 1983 were in the data. Due to the limited amount of data indicating non-linear trends, we did not apply other trend models. However, site index trends should be updated as soon as more data are available that describe current growth conditions.

In our data, trends of site indices differed between regions and temperature sum could be used to describe the regional variation. But only after the 1930s was the regional variation in site index trends large enough to indicate significantly larger trends in warmer regions than in colder regions (Figure 4). A significant interaction of the site index trend with temperature sum was also found in site index prediction models for spruce in Austria (Schadauer, 1999).

Following Tegnhammar (1992), site indices in inventory data can be positively correlated with stand age or year of stand origin, if rotation periods are shorter for stands on better sites. The relationship in Figure 3 can partly be caused by stands on better sites being harvested at lower ages than stands on poorer sites. However, if a correlation between site index and harvest age was the only factor responsible for the observed relationship, no trend should be observed below the minimum final harvest ages (applied on the best sites) under the assumption that final harvest has not been favouring stands of certain site indices within this range of ages. The last assumption is unlikely to be fulfilled in our Norwegian data. Introduction of the clearfelling system after 1950 might have favoured harvesting of better sites in the beginning, gradually moving to lower quality sites later in this 50-year period. In the very beginning of this era, predominantly low density stands on poorer sites were clearfelled based on concepts to increase stocking, but this only happened on small areas for a limited period. Given this history of harvesting, one would expect to see a declining trend of site indices. On the contrary, we observe a sharply increasing trend in site indices within the last 50 years (Figure 3). This might be a clear indication that changes in growing conditions and management practices rather than differences in harvesting practices are responsible for the observed trends in site indices in this period. To a larger degree, trends in site indices before the breakpoint years might be explained by different rotation times for stands of different site quality.

Similar trends in site indices (Figures 3 and 4) and climate variables (Figure 6) indicate that the warmer and moister climate during the last 20 years may have contributed to the trends in site indices. However, the different breakpoint years between the time trends also indicate that climate variables alone might not explain the observed trends in site indices. Climate data interpolated to the location of the sample plots were not available for the entire growth period of the stands and it was therefore only possible to use a mean time trend in temperature and precipitation for southern Norway to evaluate the contribution of climate trends to the site index trends. Previously published trends in site indices in Fennoscandia (e.g. Elfving, 1994; Nilsen & Larsson 1992) did not include the last 20 years with an exceptionally warm and moist climate, which might explain the contrast between the non-linear trends observed in this study and the linear trends in previous reports.

A number of changes in growing conditions and management practices during the last century have been discussed as causes for observed trends in site indices (Elfving & Tegnhammar, 1996; Kahle et al., 2008a; Solberg et al., 2009; Spiecker et al., 1996; Spiecker, 1999; Tegnhammar, 1992). Our results do not allow identifying individual causes for the observed site index trends, but some causes are more likely than others based on the magnitude of the changes that have been observed in Norway. Nitrogen input has been identified as a main factor behind observed growth trends (Kahle et al., 2008a) and is very likely to affect forest productivity in the nitrogen limited boreal forest ecosystems in Norway (Solberg et al., 2004, 2009). Nitrogen deposition in Norway is characterised by a steep spatial gradient with considerable input along the southern coast and very little input further north (Solberg et al., 2004). Even though the nitrogen deposition in Norway has been rather constant for the last 30 years, nitrogen accumulates in forest ecosystems leading to increasing effects on growth over time. Climate change has been documented to increase forest productivity as a consequence of increased temperatures and precipitation, longer growth periods and increased atmospheric CO_2 levels (Andreassen et al., 2006; Bergh et al., 2003; Cannell, 1999; Zheng et al., 2002a, 2002b). The observed similarity of time trends for site indices and climate variables in our data make it likely that increased temperature and precipitation during the last two decades have caused increased site indices. Recovery from previous exploitation can lead to increased forest productivity. Even though forests in Norway had been exploited heavily until the beginning of the twentieth century (Fritzbøger & Søndergaard, 1995; Tveite, 1964), the low population density might indicate that depletion of nutrient pools due to litter raking and husbandry was limited to a few locations.

The breakpoints in observed trends of site indices coincide with the introduction of the clearfelling system in Norway after 1945 (Vennesland et al., 2006). The clearfelling system leads to a number of differences in stand treatment as opposed to the previously practised selective cutting. Some of those treatments might improve forest productivity and result in higher site indices. Stands established on clearcuts are typically denser and grow faster while young. Site preparation is often combined with clearfelling in boreal forests but very little used in Norway, where it is mostly used for natural regeneration of pine. Clearcutting has led to a significant increase in planted spruce stands (Rognstad & Steinset, 2008), while pine is predominantly regenerated naturally using the seed tree method. A selection of suitable microsites for planted seedling might also lead to increased growth because forests in Norway are characterised by large variation on this scale. For Scots pine in Sweden, Elfving and Nyström (1996a) observed higher site indices for stands planted after 1940, most likely caused by differences in stand establishment and early thinning. Planting of pine has never been a common practice in Norway. Genetic improvement might have contributed to increased growth of spruce after the introduction of Central European provenances in Norway in the 1950s and 1960s. Spruce seedlings from first generation seed orchards have only been used in Norway during the last few years. Previously seeds have been collected from selected plus trees in forest stands, leading to a limited but unknown effect on stand growth. Ditching was used mainly in the 1950s and 1960s at a rate of about 10,000 ha per year (Rognstad & Steinset, 2008) and has improved forest productivity of these stands. Only about 4000 ha per year have been fertilised between 1960 and 1990 in Norway (Rognstad & Steinset, 2008) and this treatment is therefore unlikely to be a major cause of the observed site index trends. Afforestation of spruce during the 1960s and 1970s along the west coast, where spruce was not present before and where site indices for spruce are often higher than in the rest of the Norway, has little effect on observed site index trends, because only a few observations from this region are included. Sites of intermediate productivity, where spruce and pine coexist in mixed stands, have frequently been regenerated with pine. Even though this species conversion can cause increasing trends in site indices for both species, it has not been applied systematically enough to explain the observed trends. The moose population has increased significantly after 1970 and as a consequence has delayed height growth of young pine stands possibly causing decreasing trends of site indices.

The changes in management practices observed in Norway during the last century are more likely to affect the growth of Norway spruce than that of Scots pine. The fact that we observed similar trends in site indices for both species might indicate that they, to a larger extent, are caused by changes in growing conditions, for example, nitrogen input, increased temperature and precipitation. The faster site index trends in regions with higher temperature sums might have been caused by larger nitrogen deposition rather than by effects of increased temperature, because temperature sum and nitrogen deposition are highly correlated across Norway.

The site and climate variables that were best able to predict site index, that is, temperature sum, altitude, latitude, vegetation type or soil depth (Tables II–IV), often vary greatly across the country and describe regional differences rather than differences in growing conditions at local scales. Other variables with much less variation or coarse classifications, were only selected occasionally (aspect, slope). Temperature sum was the only climate variable included in the site index prediction models. Even though temperature sum was represented as an interaction term with year of stand origin in the models, it explained significant parts of the variation in site indices (Figure 4) and was the individual variable that explained most of the variation (Table IV). In model 8, latitude enters the model in addition to temperature sum, that also has a strong latitudinal gradient, because temperature sum also has a strong altitudinal gradient (Table II) and therefore not only describes the effect of latitude. This is also indicated by similar fit statistics for models 9 and 10 (Tables V and VI), where temperature sum is replaced by latitude and altitude to describe the regional variation in site indices and site index trends.

Along with temperature sum, vegetation type improved the predictive power of the site index prediction models significantly (model 3 in Tables V and VI). Vegetation type also explained much of the variation in earlier site index prediction models from Fennoscandia (Hägglund & Lundmark, 1977; Nilsen & Larsson, 1992; Tamminen, 1993) and the common use of vegetation types for site classification in the boreal forests of this region indicates the importance of this variable. Nevertheless, vegetation type cannot be used to predict site index in a number of situations, for example, in dense stands, after clearcuts, or after forest fires. In the site index prediction models, significant effects were only found for a small number of groups of vegetation types. This facilitates the use of this variable, but also indicates that vegetation type alone is a rather poor predictor of site index.

Including soil depth into site index prediction models in addition to temperature sum and vegetation type improved their predictions significantly (model 4 in Tables V and VI). Soil depth improved the models for pine more than those for spruce. Pine forests grow on average on shallower soils than spruce forests (Table II) and therefore differences in soil depth might describe the observed restrictions to growth, whereas additional soil depth above a certain minimum soil depth might not be as strongly correlated to height growth. Soil depth, even though conceptually easy to record, is expensive to sample due to the manual labour involved and the large spatial variation within stands in Norway. If soil depth therefore is estimated rather than measured, site index estimates might not become more precise than without soil depth information.

We found significantly higher site indices on steeper slopes. For site indices estimated from dominant height, differences in competition between individual trees depending on the slope might explain increased height growth on steeper slopes (Bachmann, 1997), but this does not necessarily indicate increased productivity. The effect of slope on site index was small in our models and in the same order of magnitude than for previous site index prediction models (Nilsen & Larsson, 1992). Aspect has affected site index in our data, but only on steeper slopes as indicated by the significant interactions between aspect and slope. On steeper slopes, site indices were higher on south-facing slopes than on north-facing slopes, indicating effects of increased temperature and growth period length. Aspect can also affect site index in cases where sheltering from strong winds can increase growth (Farrelly et al., 2011), but the differences of site index by aspect observed in our data do not indicate such an effect.

Site index prediction models are difficult to compare with previously published models because different site and climate variables were used, the total variation of site indices varies, the variation of site and climate variables in the study area varies, different species react differently to site variables, the size of the sample varies, and different factors act in different regions. However, some site and climate variables are frequently selected for those models, indicating that they are able to predict site indices. Focussing on site index models for conifers in Europe, we found that the most important variables in our models were also selected in other models. Climate variables (Albert & Schmidt, 2010; Ercanli et al., 2008; Farrelly et al., 2011; Fontes et al., 2003; Romanya & Vallejo, 2004; Schadauer, 1999; Seynave et al., 2005; Tamminen, 1993), vegetation type (Hägglund & Lundmark, 1977; Farrelly et al., 2011; Nilsen & Larsson, 1992; Schadauer, 1999; Seynave et al., 2005; Tamminen, 1993), soil depth (Ercanli et al., 2008; Farrelly et al., 2011; Fontes et al., 2003; Hägglund & Lundmark, 1977; Nilsen & Larsson, 1992; Romanya & Vallejo, 2004; Seynave et al., 2005; Tamminen, 1993) and aspect and slope (Ercanli et al., 2008; Farrelly et al., 2011; Fontes et al., 2003; Nilsen & Larsson, 1992; Schadauer, 1999; Socha, 2008; Tamminen, 1993) have frequently been included in site index prediction models.

The size of the region for site index prediction models can have consequences for the site and climate variables that are selected in these models. Factors that are only acting in subregions might not explain the variation of site indices across the entire region, making it necessary to introduce submodels for the subregions (e.g. Chen et al., 2002; Farrelly et al., 2011; Romanya & Vallejo, 2004). We found some indications for the need for subregional models in our data, but were unable to fit separate models due to the limited data from those regions. For spruce in western Norway, models 3, 4 and 9 have biased site index predictions and should therefore not be applied in this region. For Mid-Norway, predictions of model 3 and 4 were biased for both species. Model 9, which is using latitude in addition to temperature sum to describe regional variation of site indices, did not show this bias and we therefore recommend using model 9 for Mid-Norway rather than models 3 and 4. Different effects of temperature sum have been observed in Mid-Norway than for other regions. For spruce, the observed bias in Mid-Norway does not restrict model application, because site indices are only predicted for younger or not yet established stands. For pine, a small bias was also observed for younger stands, with some uncertainty due to very few observations. Applying the models for pine in Mid-Norway will therefore not result in significantly biased predictions.

For practical use in forest management planning, we are recommending models 3, 4 and 9 for both species. These three models have similar fit statistics and the choice of model will depend on the accessible site and climate variables. Model 9 clearly has the best predictive performance, because it includes all available site and climate variables. Model 4 has only slightly poorer fit statistics but needs fewer and more easily accessible site and climate variables. Model 3 will be the best choice where soil depth data are too expensive to collect. When applying the models it is important to use temperature sums for the same period that have been used to calibrate the models provided in Figure 2 or in more detail upon request from the authors. Temperature sums used here are 44-year averages and describe the regional variation in climate rather than dynamical changes in climate. The models will mostly be used to predict site index of young or not yet established stands. Therefore only the models after the breakpoint year or their extrapolation will be used. The higher correlation coefficients (Table IV) and $R^2_{adj.}$ (Tables V and VI) for spruce than for pine are caused by a larger variation in site indices for spruce than for pine (Figure 3), but both species have similar RMSEs, indicating that the models predict site index for both species with a similar precision.

The observed trends in our site index prediction models can also be used to correct site index for old stands observed from dominant height and age to site index for younger or future stands. For this correction we recommend to use the parameters related to the year of stand origin in model 9, *STORG*, *STORG* × *TSUM*, *STORG2* × *TSUM* and breakpoint year. Bøhler and Øyen (2011) supplied similar site index correction functions for a subregion in Norway based on a limited data-set. Elfving (1994) supplied models that can be used to correct site index of spruce and pine in Sweden and found site index trends of a similar order of magnitude as observed in our data.

In conclusion, we would like to emphasise that the non-linear trend in site indices of Norway spruce and Scots pine in Norway is most likely caused by dynamic changes in growing conditions, and that increased temperature, precipitation, nitrogen availability and atmospheric CO_2 level are major contributions to the improved growing conditions. The site index prediction models presented here are able to predict site index with a few easily accessible site and climate variables. Temperature sum, vegetation type groups and soil depth explained most of the variation in site indices, when used in combination with regionalised site index trend models.

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References

Albert, M. & Schmidt, M. (2010). Climate-sensitive modelling of site-productivity relationships for Norway spruce (*Picea abies* (L.) Karst.) and common beech (*Fagus sylvatica* L.). *Forest Ecology and Management*, *259(4)*, 739–749.

Andreassen, K., Solberg, S., Tveito, O. E. & Lystad, S. L. (2006). Regional differences in climatic responses of Norway spruce (*Picea abies* L. Karst) growth in Norway. *Forest Ecology and Management*, *222(1–3)*, 211–221.

Bachmann, M. (1997). About the effects of competition on individual tree growth in mountain forests. *Allgemeine Forst und Jagdzeitung*, *168(6–7)*, 127–130.

Beaulieu, J., Raulier, F., Prégent, G. & Bousquet, J. (2011). Predicting site index from climatic, edaphic, and stand structural properties for seven plantation-grown conifer species in Quebec. *Canadian Journal of Forest Research*, *41(4)*, 682–693.

Bergh, J., Freeman, M., Sigurdsson, B., Kellomäki, S., Laitinen, K., Niinistö, S. et al. (2003). Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. *Forest Ecology and Management*, *183(1–3)*, 327–340.

Bøhler, F. & Øyen, B.-H. (2011). Estimation of site index in old, semi-natural stands of Norway spruce at high altitude. *Forskning fra Skog og Landskap 1(11)*, 17. (In Norwegian with English summary)

Cannell, M. G. R. (1999). Relative importance of increasing atmospheric CO2, N deposition and temperature in promoting European forest growth. In T. Karjalainen, H. Spiecker & O. Laroussinie (Eds.), *Causes and consequences of accelerating tree growth in Europe. European Forest Institute proceedings*, *27*, 25–41.

Carmean, W. H. (1975). Forest site quality evaluation in the United States. *Advanced Agronomy*, *27*, 209–269.

Chen, H. Y. H., Krestov, P. V. & Klinka, K. (2002). Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. *Canadian Journal of Forest Research*, *32(1)*, 112–119.

Elfving, B. (1994). Analser av bonitering med ståndortsfaktorer, grundade på rikstax-data från 1983–1986 [Analysis of site classification from site variables based on national forest inventory data from 1983–1986]. *Institutionen för skogsskötsel, Arbetsrapporter Nr 75*. (in Swedish)

Elfving, B. & Nyström, K. (1996a). Stability of site index in Scots pine (*Pinus sylvestris*, L.) plantations over year of planting in the period 1900–1977 in Sweden. In: H. Spiecker, K. Mielikäinen, M. köhl, & J. P. Skovsgaard (Eds.), *Growth trends in European forests. European forest research report 5*, pp. 71–77. Leiden, Boston: European Forest Institute.

Elfving, B. & Nyström, K. (1996b). Yield capacity of planted *Picea abies* in Northern Sweden. *Scandinavian Journal of Forest Research*, *11*, 38–49.

Elfving, B. & Tegnhammar, L. (1996). Trends of tree growth in Swedish forests 1953–1952: An analysis based on sample trees from the national forest inventory. *Scandinavian Journal of Forest Research*, *11*, 26–37.

Elfving, B., Tegnhammar, L. & Tveite, B. (1996). Studies on growth trends of forests in Sweden and Norway. In: H. Spiecker, K. Mielikäinen, M. Köhl, & J. P. Skovsgaard (Eds.), *Growth trends in European forests. European Forest Research Report 5*, pp. 61–70. Leiden, Boston: European Forest Institute.

Ercanli, I., Gunlu, A., Altun, L. & Baskent, E.Z. (2008). Relationship between site index of oriental spruce [*Picea orientalis* (L.) Link] and ecological variables in Macka, Turkey. *Scandinavian Journal of Forest Research*, *23(4)*, 319–329.

Farrelly, N., Dhubháin, Á. N. & Nieuwenhuis, M. (2011). Site index of Sitka spruce (*Picea sitchensis*) in relation to different measures of site quality in Ireland. *Canadian Journal of Forest Research*, *41(2)*, 265–278.

Fontes, L., Tomé, M., Thompson, F., Yeomans, A., Luis, J. S. & Savill, P. (2003). Modelling the Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) site index from site factors in Portugal. *Forestry*, *76(5)*, 491–507.

Fritzbøger, B. & Søndergaard, P. (1995). A short history of forest uses. In: M. Hytönen (Ed.), *Multiple-use forestry in the Nordic countries*, pp. 11–41. Vantaa: The Finnish Forest Research Institute.

Hägglund, B. (1981). Evaluation of forest site productivity. *Forestry Abstract*, *42*, 515–527.

Hägglund, B. & Lundmark, J. E. (1977). Site estimation by means of site properties: Scots pine and Norway spruce in Sweden. *Studia Forestalia Suecica*, *138*, 1–38.

Hassall, R. B., Macmillan, D. C. & Miller, H. G. (1994). Predicting Sitka spruce yields in the Buchan area of north-east Scotland. *Forestry*, *67(3)*, 219–235.

Henttonen, H. M., Mäkinen, H. & Nöjd, P. (2009). Seasonal dynamics of the radial increment of Scots pine and Norway spruce in the southern and middle boreal zones in Finland. *Canadian Journal of Forest Research*, *39(3)*, 606–618.

Kahle, H.-P., Karjalainen, T., Schuck, A., Ågren, G. I., Kellomäki, S., Mellert, K., et al. (Eds.). (2008a). *Causes and consequences of forest growth trends in Europe. European Forest Research Report 21*, p. 261. Leiden, Boston: European Forest Institute.

Kahle, H.-P., Spiecker, H., Unseld, R., Pérez-Martínez, P.-J., Prietzel, J., Mellert, K.-H. et al. (2008b). Temporal trends and spatial patterns of height growth in relation to changes in air temperature and precipitation, and in relation to levels of foliar nitrogen and nitrogen deposition. In: H.-P. Kahle, T. Karjalainen, A. Schuck, G. I. Ågren, S. Kellomäki, K. Mellert, J. Prietzel, K.-E. Rehfuess, & H. Spiecker (Eds.), *Causes and consequences of forest growth trends in Europe. European Forest Research Report 21*, pp. 127–168. Leiden, Boston: European Forest Institute.

Klinka, K. & Carter, R. E. (1990). Relationship between site index and synoptic environmental variables in immature coastal Douglas-Fir stands. *Forest Science*, *36*, 815–830.

Landsskogtakseringen. (2007). Landsskogtakseringens feltinstruks 2007 [Field manual of the national forest inventory 2007]. *Håndbok fra Skog og Landskap, 06/2007*, 116 + appendix. (In Norwegian)

Larsson, J. Y. (2000). Veiledning i bestemmelse av vegetasjonstyper i skog [Guideline for identification of vegetation types in forests]. *NIJOS rapport, 11/2000*, 30. (In Norwegian)

Mäkinen, H., Nöjd, P. & Saranpää, P. (2003). Seasonal changes in stem radius and production of new tracheids in Norway spruce. *Tree Physiology*, *23*, 959–968.

Mielikäinen, K. & Timonen, M. (1996). Growth trends of Scots pine (*Pinus sylvestris*, L.) in unmanaged and regularly managed stands in southern and central Finland. In: H. Spiecker, K. Mielikäinen, M. Köhl & J. P. Skovsgaard (Eds.), *Growth trends in European forests. European Forest Research Report 5*, pp. 41–59. Berlin: Springer-Verlag.

Montgomery, D. C., Peck, E. A. & Vining, G. G. (2001). *Introduction to linear regression analysis*, 3rd ed, p. 641. New York: Wiley.

Nilsen, P. & Larsson, J. (1992). Site index estimation from vegetation type and site properties. *Rapport fra Skogforsk*, *22/92*, 1–43. (In Norwegian with English summary)

O'Brien, R. M. (2007). A caution regarding rules of thumb for variance inflation factors. *Quality and Quantity*, *41(5)*, 673–690.

Pokharel, B. & Dech, J. P. (2011). An ecological land classification approach to modeling the production of forest biomass. *Forestry Chronicle*, *87(1)*, 23–32.

Rognstad, O. & Steinset, T. A. (2008). Landbruket i Norge 2007 [Agriculture in Norway 2007]. *Statistical Analyses, Statistics Norway*, 182. Oslo-Kongsvinger. (In Norwegian)

Romanya, J. & Vallejo, V. R. (2004). Productivity of *Pinus radiata* plantations in Spain in response to climate and soil. *Forest Ecology and Management*, *195*, 177–189.

Salminen, H. & Jalkanen, R. (2007). Intra-annual height increment of Pinus sylvestris at high latitudes in Finland. *Tree Physiology*, *27(9)*, 1347–1353.

SAS Institute Inc. (2008). *SAS/ETS1 9.1 User's Guide*. SAS Institute Inc., Cary, NC.

Schadauer, K. (1999). Site index and site characteristics of Norway spruce according to data of the Austrian Forest Inventory. *Mitteilungen der Forstlichen Bundesversuchsantalt Wien. Report 171*, 138. (In German with English summary)

Schmitt, U., Jalkanen, R. & Eckstein, D. (2004). Cambium dynamics of Pinus sylvestris and Betula spp. in the northern boreal forest in Finland. *Silva Fennica*, *38(2)*, 167–178.

Seynave, I., Gegout, J. C., Herve, J. C., Dhote, J. F., Drapier, J., Bruno, E. et al. (2005). *Picea abies* site index prediction by environmental factors and understorey vegetation: A two-scale approach based on survey databases. *Canadian Journal of Forest Research*, *35(7)*, 1669–1678.

Sharma, R. P., Brunner, A., Eid, T. & Øyen, B.-H. (2011). Modelling dominant height growth from national forest inventory individual tree data with short time series and large age errors. *Forest Ecology and Management*, *262(12)*, 2162–2175.

Skaugen, T. E. & Tveito, O. E. (2004). Growing-season and degree-day scenario in Norway for 2021–2050. *Climate Research*, *26(3)*, 221–232.

Skovsgaard, J. P. & Vanclay, J. K. (2008). Forest site productivity: A review of the evolution of dendrometric concepts for even-aged stands. *Forestry*, *81(1)*, 12–31.

Socha, J. (2008). Effect of topography and geology on the site index of *Picea abies* in the west Capthian, Poland. *Scandinavian Journal of Forest Research*, *23(3)*, 203–213.

Solberg, S., Andreassen, K., Clarke, N., Torseth, K., Tveito, O. E., Strand, G. H. et al. (2004). The possible influence of nitrogen and acid deposition on forest growth in Norway. *Forest Ecology and Management*, *192(2–3)*, 241–249.

Solberg, S., Dobbertin, M., Reinds, G. J., Lange, H., Andreassen, K., Fernandez, P. G. et al. (2009). Analyses of the impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: A stand growth approach. *Forest Ecology and Management*, *258(8)*, 1735–1750.

Spiecker, H. (1999). Overview of recent growth trends in European forests. *Water, Air, and Soil Pollution*, *116*, 33–46.

Spiecker, H., Mielikäinen, K., Köhl, M. & Skovsgaard, J. P. (Eds.). (1996). *Growth trends in European forests. European Forest Research Report 5*: European Forest Institute. Berlin: Springer-Verlag, 372.

Stage, A. R. (1976). An expression of the effect of aspect, slope and habitat type on tree growth. *Forest Science*, *22(4)*, 457–460.

Tamminen, P. (1993). Estimation of site index for Scots pine and Norway spruce stands in South Finland using site properties. *Folia Forestalia*, 819, 1–26. (In Finish with English summary)

Tegnhammar, L. (1992). On the estimation of site index for Norway spruce. *Department of Forest Survey, Swedish University of Agricultural Sciences. Report 53*, 259. (In Swedish with English summary)

Tomter, S. M. (2000). Skog 2000. Statistikk over skogforhold og -ressurser i Norge [Statistics of forest conditions and resources in Norway]. *Norwegian Forest and Landscape Institute, Ås*, 84. (In Norwegian)

Tveite, B. (1977). Site index curves for Norway spruce (*Picea abies* (L.) Karst.). *Report of Norwegian Forest Research Institute*, *33*(*1*), 1–84. (In Norwegian with English summary)

Tveite, S. (1964). Skogbrukshistorie [Forest history]. In: H. K. Seip (Ed.), *Skogbruksboka*, Vol. 3, pp. 17–75. Skogforlaget, Oslo. (In Norwegian)

Vanclay, J. K. (1994). *Modelling forest growth and yield*. Oxon: Applications to mixed tropical forests: CAB International, 312.

Vennesland, B., Hobbelstad, K., Bolkesjø, T., Baardsen, S., Lileng, J. K. & Rolstad, J. (2006) Skogresursene i Norge 2006. Muligheter og aktuelle strategier for økt avvirkning [Forest resources in Norway 2006. Options and strategies for increased harvest]. *Viten fra Skog og Landskap, 03/2006*, 94. (In Norwegian)

Wykoff, W. R. (1990). A basal area increment model for individual conifers in the Northern Rocky Mountain. *Forest Science*, *36(4)*, 1077–1104.

Zheng, D., Freeman, M., Bergh, J., Røsberg, I. & Nilsen, P. (2002a). Production of *Picea abies* in south-east Norway in response to climate change: A case study using process-based model simulation with field validation. *Scandinavian Journal of Forest Research*, *17(1)*, 35–46.

Zheng, D., Nilsen, P. & Øyen, B.-H. (2002b). Kortsiktige effekter av klimaendringer på skogproduksjonen i furuskog på Sørlandet – en prosessbasert modellsimulering [Short-term effects of climate change on forest production in pine forests in Southern Norway – a process-based model simulation]. *Aktuelt fra skogforskningen, 6/02*, 5–6. (In Norwegian)

PAPER III

Modelling individual tree height growth of Norway spruce and Scots pine from national forest inventory data in Norway

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Abstract

We developed individual tree height growth models for Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) in Norway based on national forest inventory data. Potential height growth is based on existing dominant height growth models and reduced due to competition by functions developed in this study. Three spatially explicit and two spatially non-explicit competition indices were tested. Distance effects and diameter ratio effects were estimated from the data simultaneously with parameters of the potential modifier functions. Large height measurement errors in the national forest inventory data caused large residual variation of the models. However, the effects of competition on height growth were significant and plausible. The potential modifier functions show that height growth of dominant trees is largely unaffected by competition. Only at higher levels of competition, height growth is reduced as a consequence of competition. However, Scots pine also reduced height growth at very low levels of competition. Distance effects in the spatially explicit competition indices indicated that the closest neighbours are most important for height growth. However, for Scots pine also competitors at larger distance affected height growth. The five competition indices tested in this study explained similar proportions of the variation in relative height growth. The small plot size of the national forest inventory in Norway (250 m^2) introduces large edge effects into spatially explicit indices and limits the spatially non-explicit indices to the nearest neighbours, making both types of indices more similar than in theory. Given that unbiased predictions can only be expected for the same plot size, we recommend a spatially explicit index, which describes the distance function with a negative exponential, for use in growth simulators.

Keywords: Individual tree height growth model; national forest inventory data; Norway spruce; Scots pine; Norway

1. Introduction

Individual tree-based forest growth models are frequently used to simulate structurally complex and mixed species stands (e.g., Pretzsch 2009; Vanclay 1994). They can also be used to extrapolate to a certain degree from empirical to novel stand treatments. In contrast to stand level growth models, they supply additional information about individual tree dimensions. In these models, competition indices are used to modify potential growth of individual trees. Spatially explicit competition indices (also called distance-dependent) use information about the position of competitors relative to the subject tree (also called target tree or focal tree). Spatially non-explicit competition indices (also called distance-independent) do not use information about the spatial arrangement of trees and therefore only use some metric about the rank of the subject tree within the list of trees on the plot to estimate competition. The large within-stand variation in stand density in many of the managed boreal forest stands in Fennoscandia makes it necessary to include a rather detailed description of stand structure into growth models (Pukkala 1990). Spatially explicit individual-based growth models are therefore a preferred choice. For Norway, individual-based models have been supplied for diameter growth (Bollandsås and Næsset 2009) and mortality (Eid and Tuhus 2001), and a first version of a simulator is available (Gobakken et al. 2008). All models are based on data from the national forest inventory. However, individual-based height growth models are still lacking.

Individual tree diameter or basal area increment models are often the starting point for individual-based growth models. Individual tree height increment data are much rarer, explaining the comparatively low number of such models (Huang and Titus 1999; Uzoh and Oliver 2006; Pretzsch et al. 2002; Mitchell 1975; Vaughn et al. 2010; Courbaud et al. 1993; Hasenauer and Monserud 1997; Biging and Dobbertin 1995, 1992; Hann and Ritchie 1988; Ritchie and Hann 1986; Nord-Larsen 2006). National forest inventory data can supply a representative sample of individual tree height growth data. However, only few models (e.g., Hasenauer and Monserud 1997) are based on national forest inventory data, which are often characterised by large measurement errors of periodical height growth measured from the ground. Stem analysis data avoid the problems of measurement errors, but suffer from missing descriptions of the competitive situation at the time of height growth and the missing representation for larger forest regions. Height growth of individual trees has an asymptotic response to competition. Height growth of dominant trees is often not affected by competition. Only above a certain amount of competition height growth is reduced as competition increases (Brunner and Nigh 2000). Diameter or basal area growth is much more affected by competition, resulting in responses that are much more linear than for height growth. Potential growth of individual trees is often estimated simultaneously with a modifier for competition (e.g., Uzoh and Oliver 2006; Vaughn et al. 2010; Huang and Titus 1999; Courbaud et al. 1993; Hasenauer and Monserud 1997) rather than estimated separately (e.g., Pretzsch et al. 2002).

Competition indices in forest growth models have become more flexible during the last decades. Whereas early competition indices assumed certain effects of distance (e.g., Pukkala 1989) and size ratios (e.g., Hegyi 1974), more recent growth models included more parameters into the competition index and estimate these effects from the data (Miina and Pukkala 2002; Pommerening et al. 2011; Sabatia and Burkhart 2012; Boyden et al. 2008; Miina and Pukkala 2000; Richards et al. 2008; Bøhler et al. 2008; Canham et al. 2004; Peltoniemi and Makipaa 2011). Ledermann and Stage (2001) described the distance effect of individual competitors for a number of different spatially explicit competition indices, which were all based on assumptions by the modeller. Comparing distance effects that have been estimated from the data (e.g., Pommerening et al. 2011; Sabatia and Burkhart 2012; Boyden et al. 2008) will allow us to analyze how they vary by species, age, site type and other growing conditions.

Competition between trees in a forest varies depending on a range of factors (Nord-Larsen et al. 2006; Pretzsch and Biber 2010). However, it is uncertain whether competition indices represent all of this variation. Species-specific effects of competitors and responses of subject trees are often built into growth models. Competition increases as stand density increases (Nord-Larsen et al. 2006). Competition often decreases as stands develop, trees get older or increase in size. Stand structure, especially as a consequence of thinning types, can change structural variability and thereby affect competition (Nord-Larsen et al. 2006). With increasing site quality, the relationship between above-ground and below-ground competition changes, giving much more weight to above-ground competition on good sites (Pretzsch and Biber 2010). Weather can also affect the relationship between competition for above-ground and below-ground resources and thereby change competition (Wichmann 2001). Variation in initial tree sizes, caused by genetic variation or microsite differences, causes differences in stand structure and thereby affects competition (Boyden et al. 2008; Sabatia and Burkhart 2012). Microsite conditions and genes vary at the individual tree level. Competition indices assume uniformity in both, resulting in either lack of explanatory power, or covariation with these factors, making competition indices vulnerable when applied to other populations and sites.

National forest inventory data are increasingly used for growth modelling purposes (e.g., Sharma et al. 2012; Sharma et al. 2011; Monserud and Sterba 1996; Condes and Sterba 2008; Seynave et al. 2005). The sampling of these data is designed to represent the forest of the region. However, data collection is often not designed primarily for growth modelling. Large measurement errors and other sampling details therefore often cause substantial trouble to growth modellers (e.g., Sharma et al. 2011).

The objective of this study was to develop individual tree height growth models for Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) in Norway based on national forest inventory data. Norway spruce and Sots pine are the two commercially most interesting species in Norway. Spatially explicit and spatially non-explicit competition indices where tested in potential modifier functions. Distance and diameter ratio effects of the competition indices where estimated from the data rather than assumed in the choice or construction of competition indices. We wanted to test if it is possible to extract the complex competitive interactions from data that are characterized by large measurement errors.

2. Materials and methods

2.1. Data

The Norwegian national forest inventory

The Norwegian national forest inventory collects information on approximately 10,500 sample plots established from 1986 and onwards in productive forests (Tomter 2000). The circular 250 m^2-plots are systematically distributed over the entire country (except in Finnmark county where the plots were established later) in a 3 x 3 km grid and were remeasured every fifth year after 1993. Data up to 2008 were used in our study. Sample plots were only selected if they were registered as forestry land use and without stand border within the plot. Position and diameter at breast height (dbh) were registered for all trees with a dbh > 5 cm. Height was measured on a sample of trees at each remeasurement. The trees were selected based on a gauge angle factor of 6 m^2 ha^{-1}. On average 2 - 3 trees per plot were sampled for height (Table 1). Due to the angle gauge sampling approach, larger trees had a higher probability of being included in the samples than smaller trees. Height of the sample trees was measured using hypsometers such as Suunto or Vertex and recorded to the nearest 0.1 m. Given the low precision of height measurements with these hand-held instruments relative to a five-year height growth, large measurement errors can be expected. Tree height was recorded according to a Norwegian definition as height above stump and, therefore, 0.3 m were added to the recorded heights to convert to total tree height.

Height growth

Height increments were calculated as differences in measured individual tree heights between successive inventories and divided by the length of the growth period. Because tree height was measured during the growing season, the increment period was not always a full year. To calculate the number of increment periods for the given records, we used the methods described in Sharma et al. (2011), which is based on weather records for individual years. Missing weather data were supplemented using methods described in Gizachew and Brunner (2011). For some plots, individual remeasurements were taken at periods much shorter than five years. Given the low precision of the height measurements, uncertainties in the estimation of the increment period length, and the weather effects on height growth of individual years, periodical height increment for shorter periods varies much more than for longer periods. Therefore only height increment periods of at least 3 years were used.

For trees with registered broken tops, only height increments up to this event were used.

Tree diameter and position

All competition indices in this study use dbh to describe the competition from neighbouring trees. Tree height and crown data were only available for a small sample of trees in each plot. All living trees registered at the beginning of the increment period were considered as competitors. Spatially explicit competition indices use tree positions in addition to dbh. Therefore, only records where positions were registered for all trees on the plots were used. The latest recorded position per tree was used, assuming that errors in earlier recordings were corrected during remeasurements. Tree positions were used to calculate the distance between subject trees and their competitors. If a competitor was registered at the same position as the subject tree, the distance was set to 0.001 m. Between 1986 and 1993, position and dbh for all trees with a dbh > 5 cm was only recorded on the central 100 m^2-plot and for all trees with dbh > 20 cm on the 250 m^2-plot. In order to use height increment data from the first period, it was therefore necessary to estimate the dbh at the beginning of the increment period based on the dbh recorded at the end of the increment period for trees with dbh between 5 and 20 cm located on the 150 m^2-annulus of the plot. An individual tree based dbh growth model that was calibrated using the same national forest inventory data (Bollandsås and Næsset 2009) was used for this purpose. Only trees with an estimated dbh > 5 cm were included as competitors in accordance with the registration method. Dbh was estimated with the same method in a few cases where trees significantly larger than the 5-cm dbh registration threshold were registered at the end of an increment period, but not registered at the beginning of the increment period.

Site index

Site index models (Sharma et al. 2011) are used to define the potential height growth. Site indices recorded in the data were for earlier site index models and could therefore not be used. Identification of dominant trees among the height sample trees (Sharma et al. 2011) for estimation of site index would have restricted the data unduly, excluding height growth data from a large number of suppressed trees. Therefore, the dominant height estimated by inventory field crews (based on height sample trees inside the 250 m^2-plot and additional dominant heights measured on a 1000 m^2-plot surrounding the 250 m^2-plot) were used together with recorded stand ages to estimate site index. However, we observed that the crew-recorded dominant tree height was systematically deviating from that of height sample trees identified on the 250 m^2-plot in an earlier study (Sharma et al. 2011). On better sites, crew-recorded dominant stand height was lower and on poorer sites higher than heights of dominant trees inside the 250 m^2-plot with a consistent trend over site index. We therefore used dominant heights from the 250 m^2-plot for the plots used in Sharma et al. (2011) for site index estimation. For the remaining plots (56%), the crew-recorded dominant tree height was used for site index estimation. Site index estimates for the latter plots were corrected for systematic differences between site index estimates using linear regressions between the two site indices calibrated from plots where both site index estimates were available.

Stand ages were recorded with large errors (Sharma et al. 2011), which affects the precision of all site index estimates. The use of recorded stand ages followed the procedures described in (Sharma et al. 2011). In order to prepare site indices for both spruce and pine on each plot, recorded site indices for spruce, pine, and birch had to be converted to site indices of another species. Site index conversion functions only exist for earlier site index models in Norway (Braastad 1983). We applied these conversion functions, but used the mean of the two given regressions in order to correct for errors-in-variables (Goelz and Burk 1996; Nigh 1995). The site indices (Tveite 1977, 1981) for species conversion were estimated using dominant height estimated by inventory field crews or dominant height estimated from the site index models (Sharma et al. 2011) for the given age for plots where dominant trees were identified inside the plot. After site index for missing species had been estimated with the conversion function, site index was transformed to the new model (Sharma et al. 2011) using dominant heights predicted by the old model (Tveite 1977, 1981) for the observed ages. Height data from birch trees were only used in a few cases where no data for spruce and pine were available.

Data selection

The height growth data used in this study were measured with large errors (Figure 1). Based on the time series of height development for individual trees it would be possible to eliminate the most extreme registration errors. We initially chose not to correct height records or exclude height growth data in order to avoid bias in the models. Nevertheless, height growth of two trees was excluded because height differences were larger than 10 m for a 5-year growth period. In preliminary analyses, interactions between competition indices and site index or competition index and tree height explained the variation in relative height growth. However, this interaction was caused by covariation of measurement errors with height and site index. Measurement errors are larger for trees with slow growth, i.e. trees with larger heights on lower site indices. Many large negative height increments are responsible for the fact that mean relative height increments are much lower in certain groups of height and site index even though the competitive status is on average not different in these groups compared to the rest of the data. In order to avoid biased models we therefore excluded data from height and site index ranges that had large measurement errors. Data were grouped in 5-m height classes within 3-m site index classes and mean relative height growth calculated for each group. Data from groups with mean relative height growth of less than 0.6 for both spruce and pine, and larger than 1.4 for pine were excluded (191 height increments for spruce trees with heights above 20 m in site index class 8 m or heights above 25 m in site index class 11 m; 256 height increments for pine trees with heights above 17.5 m for site index class 5 m, heights above 20 m for site index class 8 m, or heights above 25 m in site index classes 14 to 20 m). The effects of excluding data above certain heights for given site index classes can be seen in Figure 1.

2.2. Model

The height growth model follows the potential modifier concept. Potential height growth is derived from dominant height development models and modified using competition indices for each individual tree. Site index models that describe the development of dominant height for Norway spruce and Scots pine (Sharma et al. 2011) are used to define potential height growth of individual trees:

$$h - 1.3 = \frac{b_1 + X_0}{1 + b_2 / X_0 \cdot t^{-b_3}} \qquad [1]$$

with $X_0 = 0.5 \cdot \left(\psi + \sqrt{\psi^2 + 4 \cdot b_2 \cdot (h_{40} - 1.3) \cdot 40^{-b_3}}\right)$

and $\psi = (h_{40} - 1.3) - b_1$

where h is dominant height (m) at breast height age t (years) and h_{40} is site index (m) at breast height age of 40 years. The parameter estimates for spruce are: $b_1 = 18.9206$, $b_2 = 5175.18$, $b_3 = 1.1576$, and for pine: $b_1 = 12.8361$, $b_2 = 3263.99$, $b_3 = 1.1758$. The dominant height development model needs to be applied independently of age to derive potential height increment. Therefore, for any given tree height, the increment in dominant height for the following period is derived by adding the period length to the age corresponding to the dominant height that is equal to the observed tree height. For the model calibration data, the period length for the estimation of potential height growth was equal to the period length of observed height increment. Relative height growth (ih_{rel}) is the dependent variable in the height growth models, and defined as the ratio of observed height growth and potential height growth. The potential modifier function describes ih_{rel} as a function of a competition index (*CI*). We selected the following model, because it is flexible enough to describe the reduction of relative height growth for trees growing under strong competition as well as for trees growing under extremely low competition, e.g., Scots pine seed trees:

$$ih_{rel} = a \cdot \exp\left[b \cdot (1 - CI)^c\right] \cdot (1 - CI)^c + \varepsilon \qquad [2]$$

where *a*, *b*, and *c* are parameters and ε is the residual error.

Competition indices

To calculate a competition index, the contribution of individual competitors is described for selected competitors and summed per subject tree. In the case of spatially explicit competition indices a correction for edge effects is needed. For further use in growth models, competition indices have to be scaled. We tested three spatially explicit competition indices and two spatially non-explicit competition indices in the potential modifier functions (Table 2). All five competition indices use dbh as the only variable to describe the competitors and subject trees. Tree height and crown dimension might better describe competition between trees, but were not available in our data and will not be available in most model applications. Distance between competitors and subject trees are used in spatially explicit indices as the only additional variable.

The three spatially explicit competition indices describe how the competitive effect of each competitor decreases with decreasing dbh and increasing distance. *CI*1 is a modified version of the view angle based competition indices (Pukkala 1989; Lin 1974; Pukkala and Kolström 1987). By adding one parameter to the distance term, the shape of the decline in competitive effect with increasing distance will be estimated from the data rather than assumed. By adding one parameter to the dbh of the competitor, the competitive effect of trees of different sizes is not assumed to be linearly correlated with dbh, but differences between trees of different dbh in their competitive effect are estimated from the data. *CI*2 is based on the competition index by (Hegyi 1974) which has been frequently used in forest growth models.

*CI*3 is based on competition indices that use the negative exponential to describe the distance function (Martin and Ek 1984; Pommerening et al. 2011). Similarly to *CI*1, parameters were introduced for *CI*2 and *CI*3 to estimate the distance function and the dbh effect from the data. The same formulation of *CI*2 was applied by Sabatia and Burkhart (2012) who also addressed the problems of correlations between competition index parameters and other parameters in the growth model.

The spatially non-explicit competition index *CI*4 is the basal area sum of larger trees (Wykoff et al. 1982) without any modification. *CI*5 is the ratio between the subject tree’s dbh and the quadratic mean diameter (Bollandsås and Næsset 2009; Huang and Titus 1999) without any modification.

For the identification of competing trees to be included in the spatially explicit competition indices, we used the maximum distance of recorded competitors, i.e., 17.84 m which is two times the plot radius. The small plot size and the fact that distance effects were estimated from the data did not allow applying flexible search radii.

For the spatially explicit competition indices, competitors located outside the plot boundary are of concern. The number of registered competitors is systematically lower for trees closer to plot boundaries than for trees in the plot centre, leading to biased estimates of competition. To correct for the plot edge bias, the linear expansion method (Martin et al. 1977; Pretzsch 2009; Haefner et al. 1991) is often applied. For the circular plots, we calculated the linear expansion factor for each competitor *c* relative to a given subject tree *s*, if the distance of the subject tree from the plot center ($dist_s$, m) plus the distance between subject tree and competitor ($dist_{sc}$, m) exceeded the plot radius (r = 8.92 m), as

$$\gamma_{sc} = \frac{360}{2 \cdot ar\cos\left(\frac{dist_s^{\,2} + dist_{sc}^{\,2} - r^2}{2 \cdot dist_s \cdot dist_{sc}}\right)} \qquad [3]$$

This expansion factor is using $dist_{sc}$ as the radius of a circle around the subject tree and calculates the portion of the perimeter inside the sample plot, which is equivalent to the probability of a competitor with the given distance to be inside the plot. The factor needed to expand this perimeter portion to a full circle is given as γ_{sc} and was applied to each competitor's contribution to the competition index (Table 2). For potential competitors with a distance larger than $dist_{sc} + r$, but still at distances assumed to influence the subject tree (here defined with a maximum distance of $2 \cdot r$), no competitors inside the plot are available to apply the linear expansion method. We therefore followed the proposal of Martin et al. (1977) and simulated competitors to correct for edge effects from unobserved areas. All trees on the plot were sorted into ten 5-cm dbh classes. The mean dbh for each dbh-class was used to simulate competitors in 1-m concentric zones at a distance equal to the midpoint of the zone. The sum of the frequency- and area-weighted simulated competition index contributions (δ_s) was added to the unscaled competition index (Table 2).

With increasing distance of subject trees from the plot centre, information about the competitors becomes increasingly less accurate because an increasing portion of the competitors is located outside the plot. This effect also applies to the spatially non-explicit competition indices that use all trees on the plot and are therefore more accurate descriptions of the neighbourhood for subject trees in the centre of the plot than for subject trees at the edge. Consequently, the error of the estimated competition indices increases with increasing distance from the plot centre. This covariation is of special concern for the data used here due to the sampling approach. The angle gauge method results in the minimum dbh of height sample trees to increase from 5 cm up to 1.02 m distance from the plot centre to 43.7 cm at the plot edge. As a consequence of these two covariations with distance, the error of the competition index estimates increases with increasing dbh.

The unscaled values of all five competition indices were transformed to the range 0 to 1 using the transformation function introduced by Pommerening et al. (2011) with specific modifications for each competition index (Table 2). This transformation results in a common scale for all competition indices and introduces variation in competitive effects with subject tree dbh for $CI1$, $CI3$, and $CI4$. For $CI2$, this effect is already included in the unscaled competition index. Competition indices are transformed by relating them to the competitive effect of a competitor with the same size of the subject tree in $CI1$ and $CI3$. For $CI2$, $CI4$ and $CI5$, the competitive effect of the subject tree cannot be described with the same formulation and therefore alternative formulations were introduced. For $CI5$, the transformation equation was further modified to reflect the variation of the effect of competition with tree size. Introducing QMD as a variable into the transformation equation causes varying effects of $CI5$ depending on the mean tree size in the stand. Parameters p and q, which describe this effect, were estimated from the data, in the same way as for the other four competition indices. The minimum value of all scaled competition indices was set to 0.001 to avoid invalid mathematical operations when using a competition index of 0 in the potential modifier function. Statistics for all five competition indices are compiled in Table 3.

Due to the small size of the sampling plots, even spatially non-explicit competition indices describe the closest competitors. The small plot size is also responsible for the fact that spatially explicit competition indices are only precise for trees close to the plot centre, but estimated with random errors due to edge bias corrections.

2.3. Parameter estimation

The model parameters were estimated with non-linear least-squares regression using the NLIN procedure in SAS, applying Marquardt's method due to correlation among parameter estimates. All model parameters were estimated simultaneously, i.e., three parameters of the potential modifier function (Eq. 2) and up to two parameters of the competition index (Table 2). Due to trees sampled on the same plot and repeated height measurements on the same trees, model errors are not be independent. Mixed models including random effects on the plot and tree level would be the appropriate method for this data structure. However, random effects could not be estimated due to the small number of height sample trees per plot (Table 1), which was below the number of parameters in the models for about 90% of the plots. Autocorrelated errors in the height growth time series were accounted for by including a linear first order autoregressive error structure with an autocorrelation parameter φ into the potential modifier function (Eq. 2) (cf. Wang et al. 2011). Models were evaluated using fit statistics (root mean squared error, *RMSE*, and adjusted coefficient of determination, $R^2_{adj.}$) and graphical analysis of trends in residuals when plotted against tree height, site index, *CI*, and subject tree dbh. A significance level of $p = 0.05$ was used unless otherwise stated.

3. Results

Potential modifier functions for height growth of Norway spruce and Scots pine were fitted to the data using five different competition indices (Table 3, Figure 2). The models explained only about 4 and 7% of the total variation, for spruce and pine respectively, irrespective of the competition index used in the models. RMSE exceeded the theoretical range of the response variable (0 to 1) for spruce (RMSE = 1.04) and pine (RMSE = 1.62) for all models. However, the observed relative height growth had a much larger variation than the theoretical range (Figure 1, Table 1). Large measurement errors of periodical height growth measured with hand-held instruments from the ground might be responsible for the large residual variation as indicated by the large amount of negative height increments (Figure 1). Larger variation of relative height increment for pine as compared to spruce (Figure 1, Table 3) might be caused by lower absolute height growth of pine (Table 1), but measurement errors of the same order of magnitude. Also the lack of response of height growth to competition across a wide range of competitive situations (Figure 2) might explain the large residual variation.

Despite the large residual variation, the models describe effects of competition on height growth in the data. For Norway spruce, height growth is mostly unaffected by competition at low levels of competition (Figure 2). Only for trees growing under very strong competition height growth is reduced to a larger degree. For Scots pine, also trees growing under no or very little competition reduced their height growth compared to trees growing under moderate levels of competition. For Scots pine, trees with little competition can be dominating trees in open stands or seed trees. However, no seed trees were included in our data. *CI4* for the largest tree on the plot differs from the other *CIs* and therefore the model for *CI4* differs from the other models for pine. While *CI4* = 0 for the largest tree on a plot, irrespective if smaller competitors are present, all other *CIs* assign 0 only to trees that are the only tree on the plot and *CI* > 0 for the largest tree on the plot that has smaller competitors. Consequently, the reduction in height growth at *CI4* = 0 is less than for other *CIs* because all the largest trees are given that value for *CI4* whereas the largest trees are more evenly distributed over larger values for the other *CIs*.

All five competition indices explained a similar proportion of the variation in relative height growth, as indicated by similar fit statistics (Table 3). Ranking of the five models according to fit statistics differs between species, but differences between models are often too small to allow firm conclusions. Spatially explicit competition indices (*CI1 – CI3*) performed on average slightly better than spatially non-explicit competition indices (*CI4* and *CI5*), but also this difference in fit statistics is small. The small plot size makes *CI1 – CI3* less spatially explicit by estimating considerable portions of the competition for edge trees using edge expansion. At the same time the small plot size is responsible for making *CI4* and *CI5* more spatially explicit by only using neighbors close to the subject tree. In total, the small plot size might explain the small difference in fit statistics between spatially explicit and spatially non-explicit competition indices.

Scaling of the competition indices (Table 2) resulted in similar means and ranges for all competition indices (Table 3). For *CI4* and *CI5,* scaling functions were designed to result in distributions of the scaled competition index similar to *CI1 – CI3*. Earlier versions of the scaling equations for *CI4* and *CI5* resulted in models with significantly higher residual variation (not shown). The poorer fit statistics of *CI2* for Norway spruce as compared to *CI1* and *CI3* (Table 3) might be caused by a scaling, leading to differences in the range of competition indices (Figure 2, Table 3).

The functions describing the decrease of competition with increasing distance from the competitor were estimated from the data in this study. Figure 3 shows examples of the distance functions for a range of competitor sizes for all three spatially explicit competition indices. For spruce, competition from trees of the same size or smaller decreases rapidly with distance and approaches zero at about 3 m distance. Only for competitors significantly larger than the subject tree, competition also from trees at larger distances contributes to the total competition. It is also interesting to note how little competition is contributed from trees growing further away than one sample plot radius (8.92 m). For pine, the effect of individual competitors declines much less than for spruce, especially for competitors which are of the same size or larger. This indicates a competitive effect that reaches further, but also a stronger effect of the competitor’s size on the competition as compared to the effects observed for spruce. The distance functions (Figure 3) are similar for all three spatially explicit competition indices, both regarding the decline over distance, but also regarding the effect of competitor tree size. However, using *CI2* a slightly different distance effect was found. The distance effect can only be fully evaluated if it is combined with the potential modifier function. Figure 5 shows the effect of one competitor at different distances from the subject tree for the models using *CI3*. In the combined model, the reduction in height growth is stronger for spruce than for pine. However, the model also indicates a larger reduction in height growth due to competitors at larger distances in pine as compared to spruce, as also indicated in Figure 3.

For *CI1 – CI3* and *CI5*, the effect of a given competitor varies, depending on the size of the subject trees (Table 2, Figures 3 and 4). These effects have been estimated from the data and show in all models larger competitive effects on smaller trees than on larger trees. However, due to different mathematical formulation and parameterization of the models, the effects differ between models. Effects of dbh-ratios between subject tree and competitors are described by the same formulations and parameters as the distance function for *CI1 – CI3* (Table 2). For spruce, *CI2* predicts a larger competitive effect on smaller subject trees than *CI1* and *CI3* (Figure 3). For *CI4*, the competitive effect does not vary by subject tree size. This might partly explain why the models for *CI4* have lower fit statistics than other models (Table 3).

A significant negative first-order autocorrelation was included in all models (Table 3). This negative correlation between residuals of successive observations in a time series of periodic height increment indicates oscillation around the height development predicted by site index models, which might be caused by weather conditions or measurement errors. Higher negative autocorrelation for pine than for spruce might be caused by larger relative measurement errors, i.e., same absolute height measurement error, but larger error relative to smaller heights in pine than in spruce.

4. Discussion

The individual tree height growth models for Norway spruce and Scots pine presented here have a large residual variation. The main factor contributing to the large residual variation are the measurement errors in the data. Tree heights have been measured on the national forest inventory plots with hand-held instruments from the ground at intervals of five years. The error of this measurement procedure is large relative to the height increment during that period, resulting in a large number of unreasonable height increments in the data (Table 1, Figure 1). Despite these large measurement errors in the response variable, it was possible to detect significant effects of competition on individual tree height growth in the data. We therefore conclude that the national forest inventory data, which were not originally designed for height growth modeling, can also be used for this purpose. All other sources of the residual variation, e.g., periodic variation in height increment, random variation between plots and trees, site index estimation errors, or errors of the dominant height growth model, are producing residual variation that are at least one order of magnitude smaller than the errors caused by the measurement procedure. Hasenauer and Monserud (1997) reported measurement errors in height increment data from national forest inventory data causing residual variation in a height growth model in the same order of magnitude as in our models. However, their model estimated height increment directly using tree size, site descriptions and competition indices, and therefore the model still explained larger parts of the total variation than the potential modifier functions presented here (cf. Nord-Larsen 2006). Large measurement errors can result in biased models if the measurement errors are correlated to independent variables in the model. We found some indication for this kind of correlation in our data due to slower height growth of trees with larger heights on poorer sites and therefore excluded groups of data where large measurement errors biased the response of height growth to competition. However, we did not find any further indication for correlations between measurement errors and independent variables, based on the analyses of residuals vs. independent variables (not shown). Zobel (2011) evaluated the effect of data selection, fitting methods, autocorrelation, and hierarchical model structure on models fitted to regional inventory data and found negligible effects, as long as simple and robust models were used. Their basal area yield models for aspen forest types were most problematic in the extrapolation range, or at the edges that were not covered by many data.

As a consequence of the angle gauge approach used to sample height increment data, smaller trees have a higher probability to be selected close to the plot center. Due to the small plot size, both spatially explicit and non-explicit competition indices are more precise for subject trees located in the plot center than for trees closer to the plot edge. The description of the competition is therefore more accurate for smaller trees than for larger trees. Larger trees are also sampled at larger distances from the plot center and therefore edge expansion contributes a larger proportion of the competition index for some of the larger trees. Trees of small diameter might grow in young stands or as suppressed trees in older stands. In both cases they likely experience high competition and therefore a more precise description of the competition for smaller than for larger trees is desirable. However, we were unable to evaluate the effect of this sampling approach on the models, because no data for larger plots were available, which are necessary to analyze the errors induced by the small plot size.

The shape of the potential modifier functions agrees with previous reports that describe height growth as being less affected by low levels of competition and only significantly reduced at higher levels of competition (Brunner and Nigh 2000; Mitchell 1975; Huang and Titus 1999; Vaughn et al. 2010; Courbaud et al. 1993; Nord-Larsen 2006). In contrast to height growth, diameter growth is more affected by competition also for dominating trees, and therefore the response of diameter growth to competition is more linear than the asymptotic response of height growth (Brunner and Nigh 2000; Pretzsch et al. 2002; Nord-Larsen 2006).

However, Scots pine also reduced height growth at very low levels of competition in the data presented here. Dominant height growth of Scots pine and other shade-intolerant species has been reported to be reduced in very dense or very open stands (e.g., Mäkinen and Isomäki 2004; MacFarlane et al. 2000; Nilsson et al. 2010; Martin-Benito et al. 2008; Anton-Fernandez et al. 2011). Reduced height growth of Scots pine at low competition must therefore be considered when dominant height growth models are used to estimate site index. Models for pine have better fit statistics than models for spruce (Table 3), indicating a larger sensitivity of this shade-intolerant species to competition than for shade-tolerant spruce. Based on the difference in shade tolerance between the two species, one would expect reduction in height growth at lower levels of competition in pine than in spruce. This difference between the species cannot be seen by comparing the modifier functions (Figure 2). The different species-specific parameters of the competition indices (Table 3) do not allow such a direct comparison. However, the comparison of the distance functions (Figure 3) clearly indicates that the level of competition from each competitor is much higher for pine trees of the same size and at the same distance as compared to spruce trees. As a consequence, *CI*1 to *CI*3 get higher values for pine trees than for spruce trees (Table 3) and consequently the reduction of height growth due to competition occurs at higher *CI*s for pine (0.9 – 1.0) than for spruce (0.2 – 1.0) (Figure 2). The reduction in height growth is therefore similar for both species at comparable levels of competition in the models presented here. However, when evaluating the combined effect of distance function and potential modifier function (Figure 5) spruce appears to reduce height growth more, whereas pine is more sensitive to competition from trees at larger distances. The models do not account for the species of the competitor. However, most of the data are from pure stands (Table 1) and therefore the same *CI* for a spruce tree might indicate heavier competition from the neighboring spruce trees as compared to competition from neighboring pine trees for a pine subject tree. One other individual tree height growth model for Norway spruce and Scots pine also indicates similar reductions in height growth due to competition for both species (Pretzsch et al. 2002). However, also in this model species-specific effects built into the competition indices prevent a full evaluation of differences between species in potential modifier functions.

In our model approach the height growth potential is set by the dominant height growth model (Sharma et al. 2011). An alternative approach is to estimate the potential height growth simultaneously with competition effects. However, the potential height growth in our model was estimated using the same data source. Due to the insensitivity of height growth of dominating trees to competition, the assumption is valid that the dominant trees selected for the potential height growth model in Sharma et al. (2011) are showing potential height growth.

The three spatially explicit competition indices used in this study explained similar proportions of the variation in relative height growth than the two spatially non-explicit competition indices (Table 3). The plot size in this study is small (250 m^2) compared to plot sizes often used for research plots in forests (≥ 1000 m^2). The plot radius of 8.92 m is well below the tree height of most of the competitors in the data, and therefore some competition from large trees outside the plot is likely, also for a tree located close to the centre of the plot. For spatially explicit and spatially non-explicit competition indices, the small plot size causes less accurate estimates of competition for most trees due to large edge effects compared to larger plots. However, for spatially non-explicit competition indices, the small plot size results in a more accurate description of competition for most trees in the plot center compared to larger plots. Therefore the small plot size might explain the small differences in fit statistics between both types of competition indices in this study. Stage and Ledermann (2008) introduced the term “semi-distance-dependent” for competition indices that are not considering tree positions but have a large degree of spatially explicit representation of competition due to the small plot size they are applied to or due to the sampling design (cf. Ledermann 2010). Similar predictive properties of spatially explicit vs. spatially non-explicit competition indices might be restricted to the small plot sizes or the homogeneous stand structures used in these studies (Contreras et al. 2011; Filipescu and Comeau 2007; Mailly et al. 2003; Rivas et al. 2005; Biging and Dobbertin 1995, 1992). For larger plots, heterogeneous stand structures, or mixed species stands, spatially explicit competition indices offer a more precise description of the neighborhood for each subject tree and are therefore more likely to outperform non-explicit competition indices.

Our results also emphasize the effect of plot size on estimates of competition. Application of growth models to data from plot sizes significantly different than those of the calibration data will give biased predictions (Stage and Ledermann 2008; Stage and Wykoff 1998; Lappi 2005; Ledermann and Eckmüllner 2004; Hynynen and Ojansuu 2003; Pukkala et al. 2011). The spatially non-explicit competition indices in our models can therefore not be applied to plot sizes larger than 250 m^2. The initial advantage of spatially non-explicit indices, not to rely on expensive registrations of tree positions, might therefore be lost if the sample plot size is too small.

All five competition indices tested in this study resulted in similar fit statistics for the potential modifier function of the two species (Table 3). This might indicate that all models can be used in growth simulators. Spatially explicit competition indices performed slightly better than spatially non-explicit, but in the absence of tree positions also the latter might be useful, if the plot size is comparable to the plot size of the calibration data. *CI3* had the best fit statistics for spruce and the second best for pine. We therefore recommend *CI3* for use in individual-based forest growth simulators in Norway. This spatially explicit competition index will allow simulating heterogeneous structures and mixed species stands better than the spatially non-explicit indices. Tree positions required to initiate model simulations might in the future also be available from airborne laser scanning (Hyyppä et al. 2012) or generated based on empirical spatial distribution patterns (Pretzsch 1997).

Following the example of previous studies (e.g., Pommerening et al. 2011; Sabatia and Burkhart 2012; Canham et al. 2004; Richards et al. 2008) we estimated the effects of distance and diameter ratios from the data simultaneously with other model parameters. Parameters *p* and *q* for *CI1* to *CI3* were significantly different from 1 in all cases (Table 3), indicating the need for a more flexible description of these effects compared to their original versions. No search radius for competitors was applied in this study, because the distance effect was estimated from the data and because of the small plot size. Sabatia and Burkhart (2012) discuss the correlation between parameters describing the distance effect and parameters defining the search radius. Estimating both parameters simultaneously is therefore a complex task and earlier studies (Miina and Pukkala 2000; Canham et al. 2004; Richards et al. 2008) did not address this correlation problem. All three studies used different methods for the numerical optimization of both groups of parameters and it is therefore hard to judge, how the correlation between parameters affected their results. Sabatia and Burkhart (2012) got inconclusive results based on simultaneous estimation of both types of parameters and therefore only optimized the search radius, but not the distance function parameters. We chose the other option and only estimated distance function parameters without search radius, following the example of Pommerening et al. (2011). Only the maximum search radius (17.84 m) is given by the plot size.

The interpretation of the distance effects in our models (Figure 3 and 5) has to consider the small plot size. Up to one plot radius (8.92 m) most data are from real competitors, with a decreasing proportion as subject trees are located closer to the plot edge, due to edge expansion. Between one and two plot radii, most data are from simulated competitors, and beyond two plot radii no data on competitors were available. The short range of severe competition might therefore be a consequence of the small plot size. However, Pommerening et al. (2011) estimated distance functions, which are almost identical to the functions in this study, for Norway spruce and a competition index equivalent to *CI3* using data from a larger plot in Austria. Also for other species a short range of competitive effects was estimated with flexible competition indices (Boyden et al. 2008; Miina and Pukkala 2000; Pukkala and Kolström 1987; Miina and Pukkala 2002; Richards et al. 2008; Canham et al. 2004; Sabatia and Burkhart 2012). Even though all previous attempts to quantify distance effects from the data were for diameter increment models, it is unlikely that height increment responds significantly different. The short range of the competitive effects indicates that the closest neighbors are the most serious competitors and therefore have the largest effect on the growth of the subject trees. The construction of many competition indices assumes a short range of competitive effects (Ledermann and Stage 2001; Stage and Ledermann 2008), often justified by the competition being mostly for above-ground resources. Comparing distance functions between studies will ultimately lead to more knowledge about how they vary with species, age, site, and growing conditions.

Distance functions for pine indicate a substantially larger range of competitive effects for subject trees of this species (Figure 3 and 5). This might be caused by a lower shade tolerance of Scots pine as compared to Norway spruce. Pine stands are also on average more open (Table 1) resulting in a larger distance to the nearest neighbors. Miina and Pukkala (2000) report much smaller differences in distance functions between Norway spruce and Scots pine for their *CI3*, which is comparable to our *CI2*. However, their diameter increment model explicitly considers the species of the competitor and therefore the combined distance effect on growth cannot be compared with our models.

The competitive effect varies with the diameter ratio between subject tree and competitor in four of the five competition indices in this study (Figure 3 and 4). Lower fit statistics for *CI4* (Table 3), which did not consider the variation of competition with subject tree size, might indicate the need to consider diameter ratio effects in competition indices. Diameter ratio effects estimated from the data in this study are similar to the effects reported earlier for diameter growth models (Pommerening et al. 2011; Richards et al. 2008; Miina and Pukkala 2000). However, the mathematical formulations used to describe diameter ratio effects in our models tightly link the diameter ratio effect to the distance effect. We were therefore unable to optimize one effect independently of the other effect, a task left for future research. Diameter ratio effects introduce more focus on above-ground competitors compared to competition indices that are considering above- and below-ground competition by counting all competitors irrespective of their size.

Competition has been shown to vary with stand density, tree size, site quality, climate, and stand structure. Pretzsch and Biber (2010) reported significant variation of potential modifier functions for diameter increment models by site index and interpreted these results as decreasing importance of competition for light on less productive sites due to increasing competition for below-ground resources. In our study, we did not observe bias for any site index class, when residuals of the models were plotted over competition indices (results not shown). Different response of growth to competition for diameter growth vs. height growth might explain the difference between the two studies. However, also the construction of the competition indices varied between the studies. Whereas Pretzsch and Biber (2010) selected only competitors that reduced light availability of the crown by using inverted cones, all our *CI*s except for *CI4* quantified the contribution from all competitors and thereby also described competition for below-ground resources. *CI4* (*BAL*) only describes competition from trees larger than the subject tree. In order to also include competition for below-ground resources, *BAL* is frequently combined with total stand basal area in growth models (e.g., Nord-Larsen 2006). We did not follow this approach, which might be another reason for the poor predictive power of *CI4* compared to the other *CI*s which included competition from competing trees of all sizes.

The effect on the subject tree varies by tree species of the competitor (e.g., Pretzsch et al. 2002; Canham et al. 2004; Richards et al. 2008; Miina and Pukkala 2000; Liu and Burkhart 1994; von Oheimb et al. 2011; Zhao et al. 2006). We did not test this with our data, because the large residual variation in our data due to measurement errors made it difficult to include additional variables. We also expect this species effect to be stronger for diameter growth than for height growth.

Competition changes over time due to growth of competitors, but also due to mortality or removal of competitors. The sudden change in competition induced by tree removals in connection with delayed growth responses to the improved growing conditions calls to treat this effect separately from other changes in the competition index. Growth models therefore frequently include the change in competition index (e.g., Pretzsch et al. 2002) or crown length (e.g., Ledermann 2010; Mailly et al. 2003) as additional variables. Diameter increment data from the Norwegian national forest inventory (Gizachew and Brunner 2011) indicated that delayed responses to thinning are blurred due to the length of the growth period (5 years) being similar to the typical response time and due the unknown time of the thinnings within the 5-year period. Based on this source of noise in our data and an assumption that height growth is generally less affected by competition than diameter growth and therefore also less affected by sudden changes in competition, we chose not to include a variable describing a lagged height growth response to thinning into our models.

Competition can be modified by the slope of the stand (Bachmann 1998). A substantial part of the forest area in Norway is located on slopes of varying steepness. Preliminary versions of our models (not shown) had negligible effects of slope corrections and we therefore excluded this variable in the final model. We did not consider directional effects of competitors either, in order to keep the competition indices in our models as simple as possible. However, such effects have been documented for the species that we analyzed and included in other competition indices (Miina and Pukkala 2002; Pretzsch et al. 2002; Pukkala 1989). Future work should also test if the additive effect of competitors should be replaced by multiplicative effects (Miina and Pukkala 2002).

The competition indices used as independent variables in the potential modifier models are estimated with errors and a basic assumption of regression analysis is therefore violated, which might cause biased parameter estimates. A number of methods have been proposed to correct for errors in variables (e.g., Kangas 1998). However, the magnitude of the errors in our competition indices are mostly caused by edge expansions and therefore unknown. In addition, the errors in the competition indices might be correlated to the distance from the plot centre and due to the sampling approach also correlated to the size of the subject tree. We were therefore unable to apply previously applied correction methods (Kangas 1998; Sharma et al. 2011).

The models presented in this study describe the relationship between periodical height growth and competition indices. The competition index only describes the situation at the start of the growth period. However, for the five-year periods that most of the data represent, the competition index might only change slightly due to diameter growth of subject tree and competitors. For longer increment periods, the non-linearity of the height growth and the changes in competition indices during this period can lead to biased models (Cao 2000; Nord-Larsen 2006). However, less than 12% of the data have increment periods longer than 7 years (Table 1). The linear interpolation within this short period will only cause small bias during growth predictions. Even though our data cover a period of 22 years, periodical height growth might be affected by variation and trends in weather conditions. The warm climate during this period might not represent long-term historic climates. However, it might be representative of future climate to which model predictions are applied.

5. Conclusions

Even though the national forest inventory data in Norway are sampled for a different purpose and contain rather larger height measurement errors, it was possible to develop height increment models for individual trees in our study using this data source. Simultaneous estimation of parameters of the competition indices together with parameters of the potential modifier function allowed us to estimate effects of competitor's distance from the subject tree and diameter ratios between competitor and subject tree on height growth from the data. These flexible competition indices are more likely to describe the competition realistically by avoiding the assumption that earlier versions of the same competition indices have built into growth models. In this study the three spatially explicit competition indices performed only slightly better than the spatially non-explicit versions. The small plot size used for data collection made spatially explicit competition indices less accurate and spatially non-explicit competition indices much more spatially explicit than for the larger plot sizes typically in use for growth modeling. The models describe a substantial reduction in height growth only at high levels of competition for Norway spruce and Scots pine. For Scots pine, height growth was also reduced at low levels of competition, a process also observed for other shade-intolerant species.

Acknowledgements

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References

Anton-Fernandez C, Burkhart HE, Strub M, Amateis RL (2011) Effects of initial spacing on height development of Loblolly pine. Forest Science 57 (3):201-211

Bachmann M (1998) Indizes zur Erfassung der Konkurrenz von Einzelbäumen. Methodische Untersuchungen in Bergmischwäldern. Forstliche Forschungsberichte München vol 171.

Biging GS, Dobbertin M (1992) A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. Forest Science 38 (3):695-720

Biging GS, Dobbertin M (1995) Evaluation of competition indexes in individual tree growth models. Forest Science 41 (2):360-377

Bollandsås OM, Næsset E (2009) Weibull models for single-tree increment of Norway spruce, Scots pine, birch and other broadleaves in Norway. Scandinavian Journal of Forest Research 24 (1):54-66. doi:10.1080/02827580802477875

Boyden S, Binkley D, Stape JL (2008) Competition among Eucalyptus trees depends on genetic variation and resource supply. Ecology 89 (10):2850-2859. doi:10.1890/07-1733.1

Brunner A, Nigh G (2000) Light absorption and bole volume growth of individual Douglas-fir trees. Tree Physiology 20 (5-6):323-332

Braastad H (1983) Forholdet mellom høydebonitet og produksjonsevne for gran, furu og bjørk på samme voksested. Aktuelt fra Statens Fagtjeneste for Landbruket (3/83):50-59

Bøhler F, Brunner A, Øyen B-H (2008) Toppkapping i ungskogpleie av gran: Vekstreaksjoner på toppkappede trær. Forskning fra Skog og landskap, vol 4/08. Skog og Landskap, Ås

Canham CD, LePage PT, Coates KD (2004) A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Canadian Journal of Forest Research 34 (4):778-787

Cao QV (2000) Prediction of annual diameter growth and survival for individual trees from periodic measurements. Forest Science 46 (1):127-131

Condes S, Sterba H (2008) Comparing an individual tree growth model for Pinus halepensis Mill. in the Spanish region of Murcia with yield tables gained from the same area. European Journal of Forest Research 127 (3):253-261. doi:10.1007/s10342-007-0201-7

Contreras MA, Affleck D, Chung W (2011) Evaluating tree competition indices as predictors of basal area increment in western Montana forests. Forest Ecology and Management 262 (11):1939-1949. doi:10.1016/j.foreco.2011.08.031

Courbaud B, Houllier F, Rupe C (1993) Un model de croissance en hauteur des arbres en pessiere pure irreguliere de montagne. Annals of Forest Science 50(4):337-351

Eid T, Tuhus E (2001) Models for individual tree mortality in Norway. Forest Ecology and Management 154 (1-2):69-84

Filipescu CN, Comeau PG (2007) Aspen competition affects light and white spruce growth across several boreal sites in western Canada. Canadian Journal of Forest Research 37 (9):1701-1713. doi:10.1139/x07-011

Gizachew B, Brunner A (2011) Density-growth relationships in thinned and unthinned Norway spruce and Scots pine stands in Norway. Scandinavian Journal of Forest Research 26 (6):543-554. doi:10.1080/02827581.2011.611477

Gobakken T, Lexerod NL, Eid T (2008) T: A forest simulator for bioeconomic analyses based on models for individual trees. Scandinavian Journal of Forest Research 23 (3):250-265. doi:10.1080/02827580802050722

Goelz JCG, Burk TE (1996) Measurement error causes bias in site index equations. Canadian Journal of Forest Research 26 (9):1585-1593. doi:10.1139/x26-178

Haefner JW, Poole GC, Dunn PV, Decker RT (1991) Edge effects in computer models of spatial competition. Ecological Modelling 56 (1-4):221-244. doi:10.1016/0304-3800(91)90201-b

Hann DW, Ritchie MW (1988) Height growth rate of Douglas-fir: a comparison of model forms. Forest Science 34 (1):165-175

Hasenauer H, Monserud RA (1997) Biased predictions for tree height increment models developed from smoothed 'data'. Ecological Modelling 98 (1):13-22

Hegyi F A simulation model for managing jack-pine stands. In: Fries J (Ed.) Growth models for tree and stand simulation, 1974. Royal College of Forestry, Stockholm, pp 74-90

Huang SM, Titus SJ (1999) An individual tree height increment model for mixed white spruce-aspen stands in Alberta, Canada. Forest Ecology and Management 123 (1):41-53. doi:10.1016/s0378-1127(99)00015-8

Hynynen J, Ojansuu R (2003) Impact of plot size on individual-tree competition measures for growth and yield simulators. Canadian Journal of Forest Research 33 (3):455-465. doi:10.1139/x02-173

Hyyppä J, Holopainen M, Olsson H (2012) Laser scanning in forests. Remote Sensing 4 (10):2919-2922. doi:10.3390/rs4102919

Kangas AS (1998) Effect of errors-in-variables on coefficients of a growth model and on prediction of growth. Forest Ecology and Management 102:203-212

Lappi J (2005) Plot size related measurement error bias in tree growth models. Canadian Journal of Forest Research 35:1031-1040

Ledermann T (2010) Evaluating the performance of semi-distance-independent competition indices in predicting the basal area growth of individual trees. Canadian Journal of Forest Research 40 (4):796-805. doi:10.1139/x10-026

Ledermann T, Eckmüllner O (2004) A method to attain uniform resolution of the competition variable Basal-Area-in-Larger trees (BAL) during forest growth projections of small plots. Ecological Modelling 171 (1-2):195-206

Ledermann T, Stage AR (2001) Effects of competitor spacing in individual-tree indices of competition. Canadian Journal of Forest Research 31 (12):2143-2150

Lin JY Stand growth simulation models for Douglas-fir and western hemlock in the northwestern United States. In: Fries J (Ed.) Growth models for tree and stand simulation, 1974. Royal College of Froestry, Stockholm, pp 102-118

Liu JP, Burkhart HE (1994) Modeling inter-specific and intra-specific competition in Loblolly pine (*Pinus taeda* L) plantations on cutover, site-prepared lands. Annals of Botany 73 (4):429-435. doi:10.1006/anbo.1994.1053

MacFarlane D, Green J, Burkhart HE (2000) Population density influences assessment and application of site index. Can J For Res 30:1472-1475

Mailly D, Turbis S, Pothier D (2003) Predicting basal area increment in a spatially explicit, individual tree model: a test of competition measures with black spruce. Canadian Journal of Forest Research 33 (3):435-443

Martin-Benito D, Gea-Izquierdo G, del Rio M, Canellas I (2008) Long-term trends in dominant-height growth of black pine using dynamic models. Forest Ecology and Management 256 (5):1230-1238. doi:10.1016/j.foreco.2008.06.024

Martin GL, Ek AR (1984) A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. Forest Science 30 (3):731-743

Martin GL, Ek AR, Monserud RA (1977) Control of plot edge bias in forest stand growth simulation models. Canadian Journal of Forest Research 7:100-105

Miina J, Pukkala T (2000) Using numerical optimization for specifying individual-tree competition models. Forest Science 46 (2):277-283

Miina J, Pukkala T (2002) Application of ecological field theory in distance-dependent growth modelling. Forest Ecology and Management 161 (1-3):101-107

Mitchell KJ (1975) Dynamics and simulated yield of Douglas-fir. Forest Science Monograph 17:1-39

Monserud RA, Sterba H (1996) A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Autria. Forest Ecology and Management 80:57-80

Mäkinen H, Isomäki A (2004) Thinning intensity and growth of Scots pine stands in Finland. Forest Ecology and Management 201 (2-3):311-325

Nigh GD (1995) The geometric mean regression line - A method for developing site index conversion equations for species in mixed stands. Forest Science 41 (1):84-98

Nilsson U, Ekö P-M, Elfving B, Fahlvik N, Johansson U, Karlsson K, Lundmark T, Wallentin C (2010) Thinning of Scots pine and Norway spruce monocultures in Sweden: effects of different thinning programmes on stand level gross- and net stem volume production. Studia Forestalia Suecica 219:46

Nord-Larsen T (2006) Modeling individual-tree growth from data with highly irregular measurement intervals. Forest Science 52 (2):198-208

Nord-Larsen T, Damgaard C, Weiner J (2006) Quantifying size-asymmetric growth among individual beech trees. Canadian Journal of Forest Research 36 (2):418-425

Peltoniemi M, Makipaa R (2011) Quantifying distance-independent tree competition for predicting Norway spruce mortality in unmanaged forests. Forest Ecology and Management 261 (1):30-42. doi:10.1016/j.foreco.2010.09.019

Pommerening A, Lemay V, Stoyan D (2011) Model-based analysis of the influence of ecological processes on forest point pattern formation-A case study. Ecological Modelling 222 (3):666-678. doi:10.1016/j.ecolmodel.2010.10.019

Pretzsch H (1997) Analysis and modeling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in Lower Saxony. Forest Ecology and Management 97 (3):237-253. doi:10.1016/s0378-1127(97)00069-8

Pretzsch H (2009) Forest dynamics, growth and yield. Springer-Verlag, Berlin, Heidelberg

Pretzsch H, Biber P (2010) Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. Canadian Journal of Forest Research 40 (2):370-384. doi:10.1139/x09-195

Pretzsch H, Biber P, Dursky J (2002) The single tree-based stand simulator SILVA: construction, application and evaluation. Forest Ecology and Management 162 (1):3-21

Pukkala T (1989) Methods to describe the competition process in a tree stand. Scandinavian Journal of Forest Research 4:187-202

Pukkala T (1990) A method for incorporating the within-stand variation into forest management planning. Scandinavian Journal of Forest Research 5 (1-4):263-275. doi:10.1080/02827589009382611

Pukkala T, Kolström T (1987) Competition indices and the prediction of radial growth in Scots pine. Silva Fennica 21 (1):55-67

Pukkala T, Lähde E, Laiho O (2011) Using optimization for fitting individual-tree growth models for uneven-aged stands. European Journal of Forest Research 130 (5):829-839. doi:10.1007/s10342-010-0475-z

Richards M, McDonald AJS, Aitkenhead MJ (2008) Optimisation of competition indices using simulated annealing and artificial neural networks. Ecological Modelling 214 (2-4):375-384. doi:10.1016/j.ecolmodel.2008.03.008

Ritchie MW, Hann DW (1986) Development of a tree height growth model for Douglas-fir. Forest Ecology and Management 15 (2):135-145. doi:10.1016/0378-1127(86)90142-8

Rivas JJC, Gonzalez JGA, Aguirre O, Hernandez F (2005) The effect of competition on individual tree basal area growth in mature stands of *Pinus cooperi* Blanco in Durango (Mexico). European Journal of Forest Research 124 (2):133-142. doi:10.1007/s10342-005-0061-y

Sabatia CO, Burkhart HE (2012) Competition among loblolly pine trees: Does genetic variability of the trees in a stand matter? Forest Ecology and Management 263:122-130. doi:10.1016/j.foreco.2011.09.009

Seynave I, Gégout J-C, Hervé J-C, Dhôte J-F, Drapier J, Bruno É, Dumé G (2005) Picea abies site index prediction by environmental factors and understorey vegetation: a two-scale approach based on survey databases. Canadian Journal of Forest Research 35:1669-1678

Sharma R, Brunner A, Eid T (2012) Site index prediction from site and climate variables for Norway spruce and Scots pine in Norway. Scandinavian Journal of Forest Research online 18-04-2012

Sharma RP, Brunner A, Eid T, Øyen BH (2011) Modelling dominant height growth from national forest inventory individual tree data with short time series and large age errors. Forest Ecology and Management 262 (12):2162-2175. doi:10.1016/j.foreco.2011.07.037

Stage AR, Ledermann T (2008) Effects of competitor spacing in a new class of individual-tree indices of competition: semi-distance-independent indices computed for Bitterlich versus fixed-area plots. Canadian Journal of Forest Research 38 (4):890-898. doi:10.1139/x07-192

Stage AR, Wykoff WR (1998) Adapting distance-independent forest growth models to represent spatial variability: Effects of sampling design on model coefficients. Forest Science 44 (2):224-238

Tomter SM (2000) Skog 2000. Statistikk over skogforhold og -ressurser i Norge. [Statistics of forest conditions and resources in Norway.]. Norsk Institutt for jord- og skogkartlegging, Ås

Tveite B (1977) Bonitetskurver for gran [Site-index curves for Norway spruce (Picea abies (L.) Karst)]. Meddelelser fra Norsk Institutt for Skogforskning 33.1:84

Tveite B (1981) Bonitering for gran, furu og bjørk. Norsk Skogbruk 27 (4):17-22

Uzoh FCC, Oliver WW (2006) Individual tree height increment model for managed even-aged stands of ponderosa pine throughout the western United States using linear mixed effects models. Forest Ecology and Management 221 (1-3):147-154. doi:10.1016/j.foreco.2005.09.012

Vanclay JK (1994) Modelling forest growth and yield. Applications to mixed tropical forests. CAB International, Oxon, UK, 321pp

Vaughn NR, Turnblom EC, Ritchie MW (2010) Bootstrap evaluation of a young Douglas-fir height growth model for the Pacific Northwest. Forest Science 56 (6):592-602

von Oheimb G, Lang AC, Bruelheide H, Forrester DI, Wasche I, Yu MJ, Hardtle W (2011) Individual-tree radial growth in a subtropical broad-leaved forest: The role of local neighbourhood competition. Forest Ecology and Management 261 (3):499-507. doi:10.1016/j.foreco.2010.10.035

Wang ML, Bhatti J, Wang YH, Varem-Sanders T (2011) Examining the gain in model prediction accuracy using serial autocorrelation for dominant height prediction. Forest Science 57 (3):241-251

Wichmann L (2001) Annual variations in competition symmetry in even-aged sitka spruce. Annals of Botany 88 (1):145-151. doi:10.1006/anbo.2001.1445

Wykoff WR, Crookston NL, Stage AR (1982) User's guide to the stand prognosis model. Gen. Tech. Rep. INT-133. USDA Forest Service, Intermountain Forest and Range Experiment Station,

Zhao D, Borders B, Wilson M, Rathbun SL (2006) Modeling neighborhood effects on the growth and survival of individual trees in a natural temperate species-rich forest. Ecological Modelling 196 (1-2):90

Zobel JM, Ek AR, Burk TE (2011) Comparison of Forest Inventory and Analysis surveys, basal area models, and fitting methods for the aspen forest type in Minnesota. Forest Ecology and Management 262 (2):188-194. doi:10.1016/j.foreco.2011.03.022

Table 1. Tree and stand characteristics for the national forest inventory sample plot data used in this study.

Variables	Norway spruce	Scots pine
	Mean ± std. (range)	Mean ± std. (range)
Number of sample plots	2385 (pure 1807, mixed 578)	2151 (pure 1573, mixed 578)
Number of height sample trees	6697	5360
Number of height sample trees per plot and period	2.7 ± 1.9 (1 - 17)	2.2 ± 1.5 (1 - 11)
Site index (m)	14.1 ± 5.4 (3.8 - 36.2)	10.8 ± 3.9 (2.1 - 25.4)
Stand age (yrs)	74 ± 36 (9 - 191)	85 ± 32 (8 - 192)
Number of stems ha^{-1}	1388 ± 705 (80 - 5000)	966 ± 576 (80 - 4400)
Basal area (m^2 ha^{-1})	27.9 ± 12.3 (0.7 - 87.3)	22.2 ± 9.9 (0.9 - 60.9)
QMD (cm)	16.8 ± 4.6 (6 - 41.7)	18.2 ± 4.9 (6.4 - 49.1)
Sample tree height (m)	15.6 ± 5.1 (2.9 - 34.2)	14.6 ± 3.9 (3.5 - 26.5)
Height growth (m yr^{-1})	0.21 ± 0.22 (-1.54 - 1.83)	0.13 ± 0.17 (-1.35 - 1.44)
Relative height growth	0.9 ± 1.1 (-18.2 - 16.4)	0.90 ± 1.7 (-28.2 - 24.1)
Height growth period (yrs)	5.5 ± 1.5 (3 - 18.8)	5.5 ± 1.4 (3 - 19.6)
BAL (m^2 ha^{-1})	12.5 ± 10.8 (0 - 76.6)	8.4 ± 8.1 (0 - 55.5)
dq	1.34 ± 0.47 (0.22 - 4.24)	1.44 ± 0.52 (0.26 - 4.86)

Table 2. Competition indices

Competition from individual competitor	Unscaled competition index	Scaled competition index
$CI1_c = 2 \cdot \arctan\left(\frac{\left(\frac{0.5 \cdot d_c}{100}\right)^p}{dist_{sc}^{\,q} + 1}\right)$	$CI1u = \sum_{c=1}^{n} (\gamma_{sc} \cdot CI1_c) + \delta_s$	$CI1 = \frac{CI1u}{CI1u + CI1_s}$, $dist_{sc} = 0$ for $CI1_s$
$CI2_c = \left(\frac{d_c}{d_s}\right)^p \cdot \frac{1}{dist_{sc}^{\,q}}$	$CI2u = \sum_{c=1}^{n} (\gamma_{sc} \cdot CI2_c) + \delta_s$	$CI2 = \frac{CI2u}{CI2u + \frac{d_s}{QMD}}$
$CI3_c = d_c^{\,p} \cdot \exp(q \cdot dist_{sc})$	$CI3u = \sum_{c=1}^{n} (\gamma_{sc} \cdot CI3_c) + \delta_s$	$CI3 = \frac{CI3u}{CI3u + CI3_s}$, $dist_{sc} = 0$ for $CI3_s$
	$BAL = \sum_{c=1}^{n} (ba_c \mid ba_c > ba_s)$	$CI4 = \frac{BAL}{BAL + \kappa \cdot ba_s}$, $\kappa = 500$ for spruce, $\kappa = 100$ for pine
	$dq = \frac{d_s}{QMD}$	$CI5 = 1 - \frac{dq^3}{\kappa + dq^3} \cdot \left[1 + \frac{1}{dq} \cdot p \cdot (QMD - q)\right]$, $\kappa = 2$ for spruce, $\kappa = 4$ for pine

Note: d is diameter at breast height (cm), ba is basal area of individual trees (m^2), QMD is the quadratic mean diameter (cm), $dist_{sc}$ is the distance between subject tree and competitor (m), n is the number of competitors per plot, c is an index for competitors, s is an index for the subject tree, γ_{sc} is the edge expansion factor for a given competitor and subject tree, p and q are parameters.

Table 3. Parameter estimates and fit statistics of the potential modifier functions. Standard errors of parameter estimates are given in parentheses below the parameter estimates.

Species	Competition index	Parameter estimates						Fit statistics		*CI* statistics
		a	*b*	*c*	*p*	*q*	φ	*RMSE*	$R^2_{adj.}$	Mean ± std. (range)
Norway spruce	*CI1*	2.55	-0.910	0.745	2.02	2.53	-0.187	1.0425	0.0403	0.408 ± 0.226 (0.0024 - 0.979)
		(0.363)	(0.156)	(0.0998)	(0.251)	(0.189)	(0.00498)			
	CI2	2.97	-1.077	0.428	1.66	1.59	-0.185	1.0434	0.0386	0.660 ± 0.219 (0.018 - 1.000)
		(0.410)	(0.161)	(0.0531)	(0.351)	(0.122)	(0.00497)			
	CI3	2.44	-0.868	0.745	2.07	-0.829	-0.187	1.0423	0.0406	0.383 ± 0.233 (0.001 - 0.983)
		(0.375)	(0.165)	(0.110)	(0.255)	(0.101)	(0.00497)			
	CI4	3.14	-1.16	-0.354			-0.184	1.0448	0.0361	0.399 ± 0.285 (0.001 - 0.980)
		(0.433)	(0.129)	(0.0526)			(0.00498)			
	CI5	2.05	-0.683	0.335	0.0380	21.8	-0.180	1.0470	0.0321	0.571 ± 0.215 (0.010 - 0.996)
		(0.515)	(0.282)	(0.166)	(0.0146)	(10.9)	(0.00500)			
Scots pine	*CI1*	8.23	-2.96	0.505	2.92	0.755	-0.336	1.6223	0.0676	0.789 ± 0.167 (0.043 - 0.999)
		(0.699)	(0.251)	(0.113)	(0.466)	(0.324)	(0.00558)			
	CI2	8.52	-3.05	0.460	2.25	0.590	-0.336	1.6214	0.0686	0.819 ± 0.164 (0.055 - 0.999)
		(0.703)	(0.251)	(0.0905)	(0.462)	(0.273)	(0.00555)			
	CI3	7.99	-2.87	0.517	2.88	-0.203	-0.336	1.6220	0.0679	0.767 ± 0.182 (0.021 - 0.999)
		(0.628)	(0.217)	(0.0839)	(0.409)	(0.0471)	(0.00561)			
	CI4	5.29	-1.90	0.525			-0.333	1.6245	0.0650	0.490 ± 0.333 (0.001 - 0.994)
		(0.292)	(0.0737)	(0.0482)			(0.00551)			
	CI5	6.71	-2.35	0.874	0.0579	9.42*	-0.336	1.6222	0.0677	0.449 ± 0.226 (0.001 - 0.985)
		(0.713)	(0.242)	(0.114)	(0.0120)	(6.04)	(0.00557)			

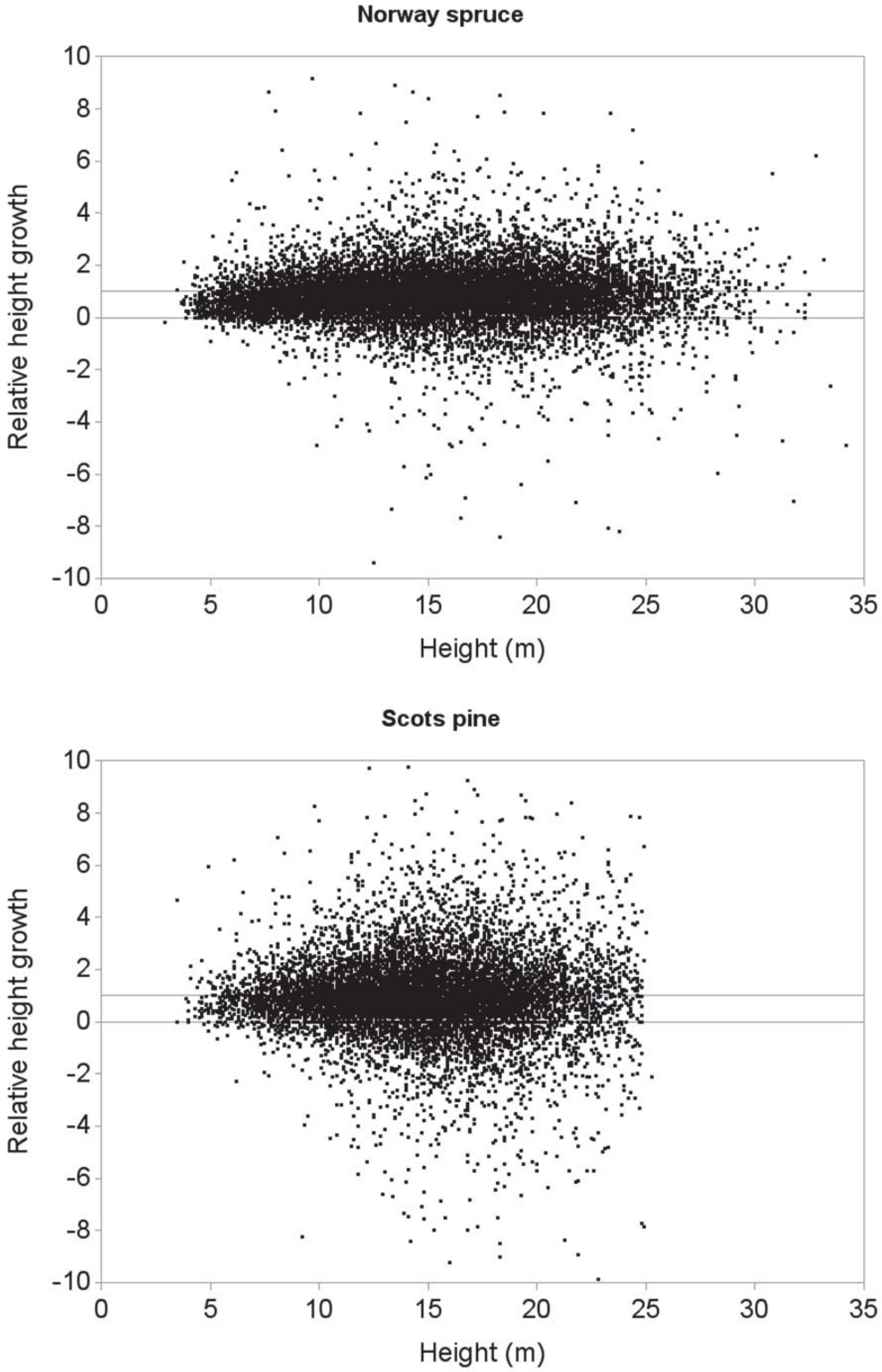


Figure 1. Height growth relative to potential height growth over height for Norway spruce and Sots pine.

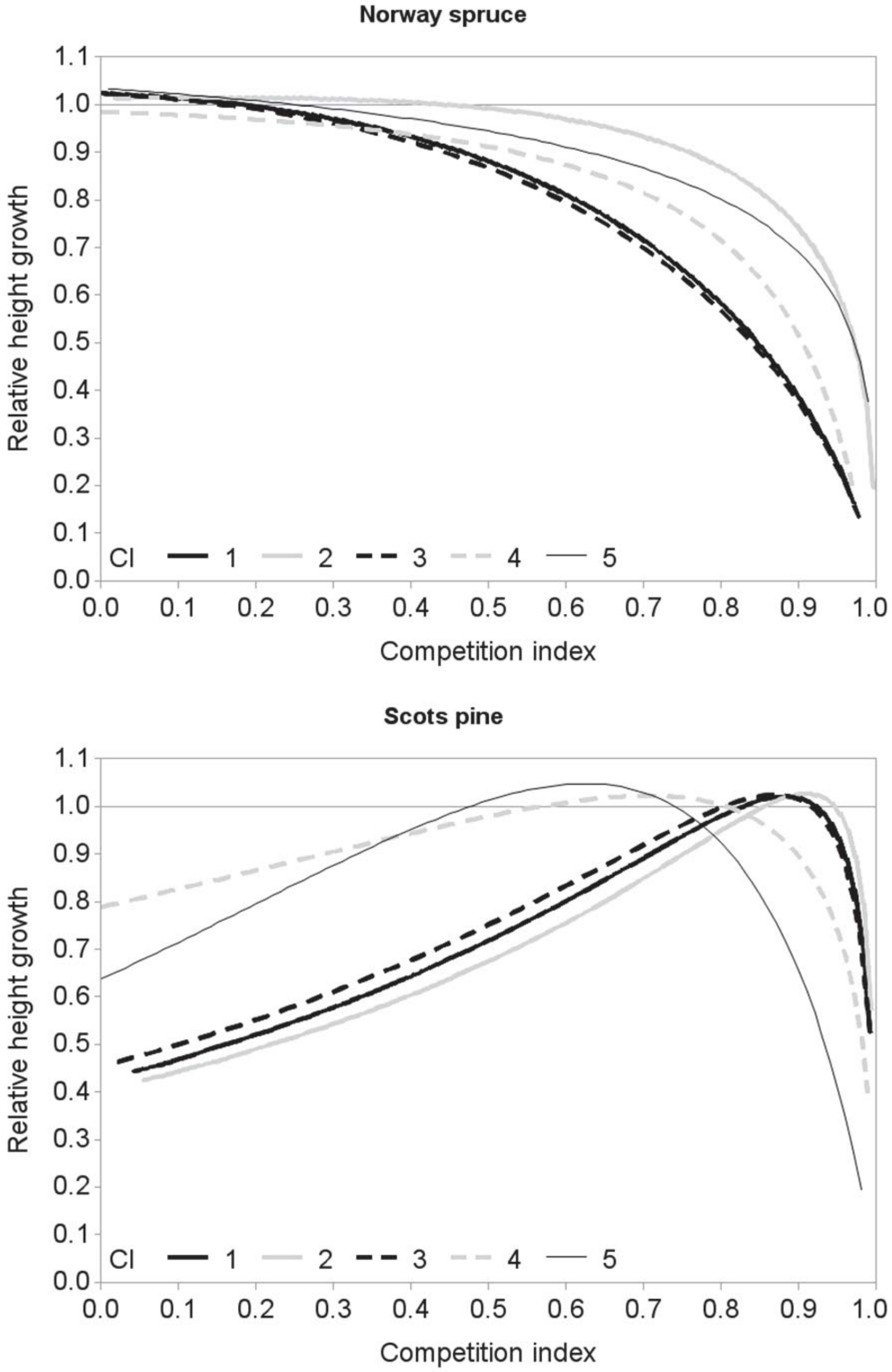


Figure 2. Potential modifier functions for individual tree height growth of Norway spruce and Scots pine for five different competition indices (Table 2).

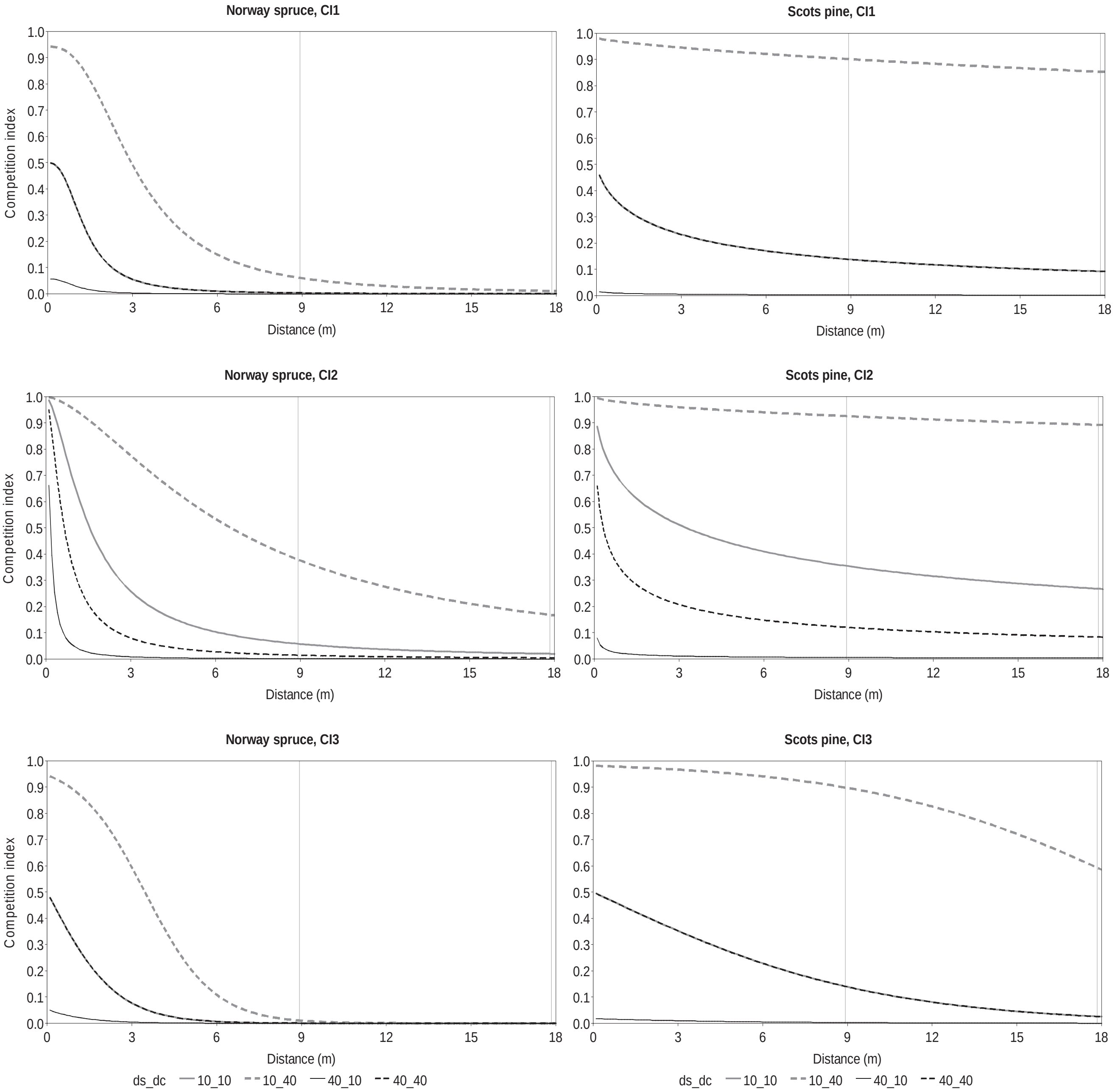
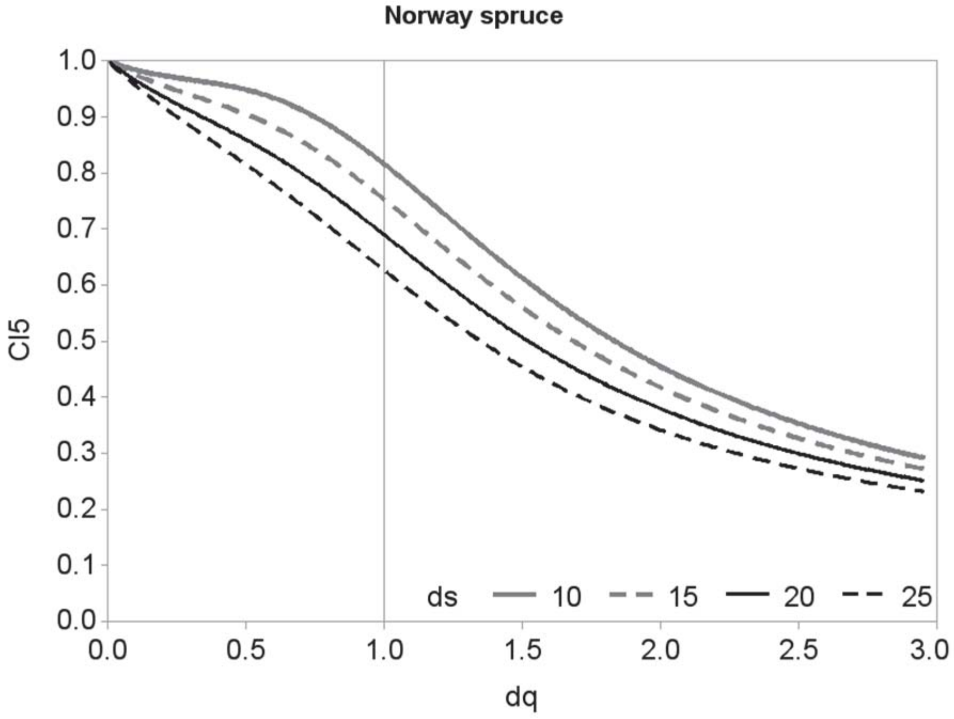


Figure 3. Effect of the distance of individual competitors on their contribution to the spatially explicit competition indices CI_1, CI_2, and CI_3, (Table 2 and 3). Each line is for a given diameter ratio between subject tree and competitor, ds = dbh of subject tree in cm, dc = dbh of competitor in cm.



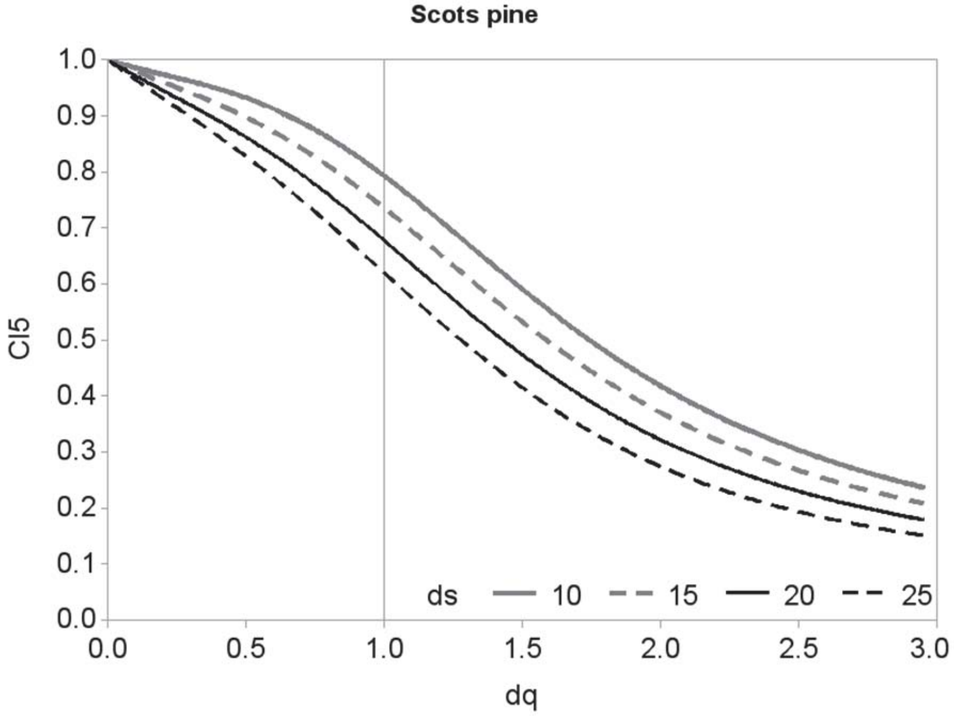
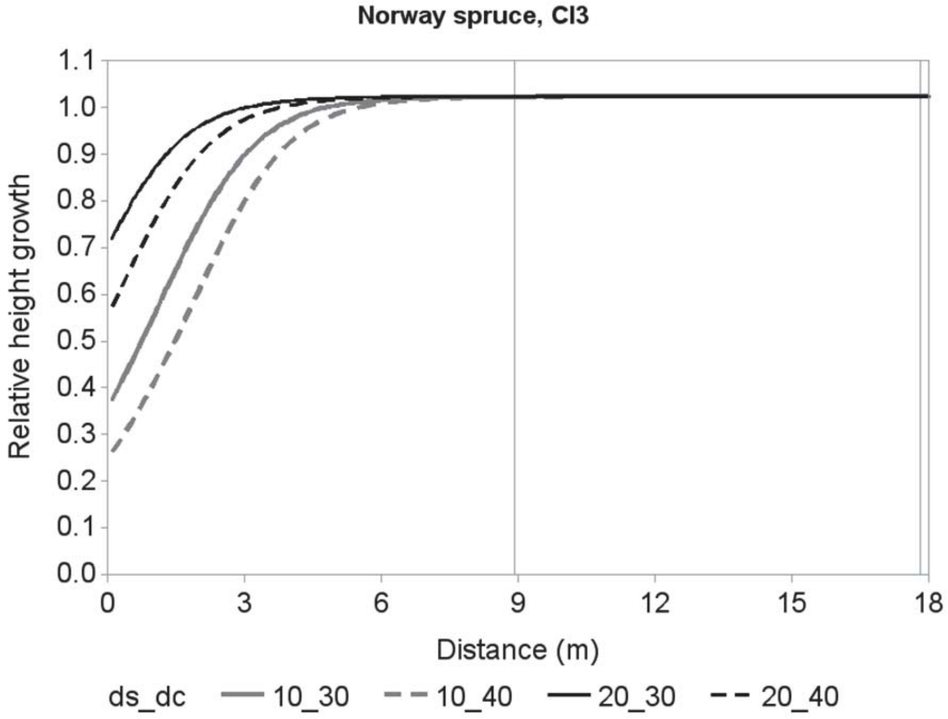


Figure 4. Effect of the diameter of subject tree (d_s = dbh of subject tree in cm) relative to quadratic mean dbh of all trees ($d_q = d_s / QMD$) on the competition index CI_5. For both species the effect is given for four different d_s.



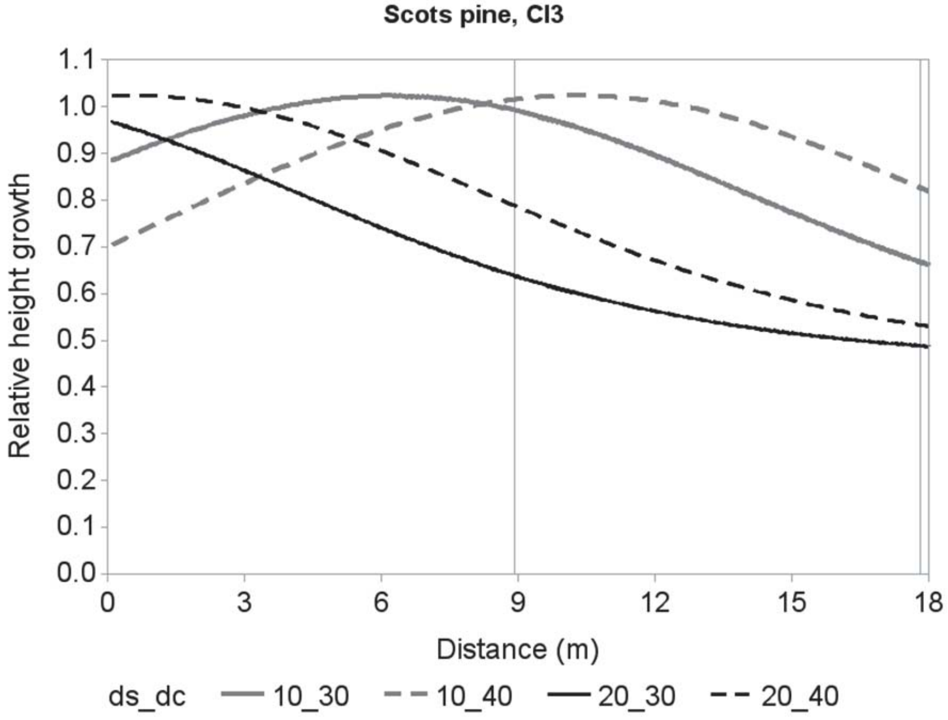


Figure 5. Effect of the distance of one competitor on the relative height growth in the models using CI_3. Each line is for a given diameter ratio between subject tree and competitor, ds = dbh of subject tree in cm, dc = dbh of competitor in cm.

PAPER IV

Modelling height-diameter relationships for Norway spruce, Scots pine, and downy birch using Norwegian national forest inventory data

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Abstract

We developed nonlinear mixed effects height-diameter models for three major tree species: Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), and downy birch (*Betula pubescens (*Ehrh.)) in Norway. We used data from four Norwegian National Forest Inventory (NFI) cycles (7th - 10th NFI cycle) as model fitting data and data from the 6th NFI cycle as validation data. Among several bi-parametric functions tested as base functions in a preliminary analysis, the Näslund function showed the smallest residual variations, and therefore it was generalized by incorporating stand variables as covariates that act as modifiers of the original parameters of the Näslund function. Sample plot-level random effects were also included in order to account for inter-plot variations within the populations. Unlike a basic mixed effects model, a generalized mixed model described larger parts of variations in the height-diameter relationships and predicted heights without significant bias for validation data from the sample plots, where all measured heights of the focused species (species used for species-specific model) were used to predict random effects. For all species, when measured heights of other than focused species were used to predict random effects, a significant height prediction bias occurred. This bias could be reduced for certain diameter ranges by applying generalized ordinary least square model. We thus recommend using generalized mixed effects models to estimate the missing heights on NFI sample plots and other sample plots, where measured tree heights of the focused species are available for prediction of random effects. When measured heights are not available, generalized ordinary least square model can be used.

Key words: Height-diameter models; nonlinear mixed effects model; Näslund function prediction error; EBLUP

1. Introduction

Tree diameters and heights are fundamental measurements in forest inventories and are used as input parameters of models or decision support systems in forest management planning. Diameter and height measurements are used to estimate tree volume, site index, growth and yield, succession and carbon budget models. Diameter is easily measured for all standing trees, but measuring height may be difficult, time consuming and hence expensive. Therefore, height-diameter models are commonly used to estimate the heights of trees for which only diameters are measured.

The height-diameter relationship differs from one stand to another due to differences in site quality, stand age and silvicultural treatments, and even within the same stand due to differing competitive situation among the trees (e.g. Vanclay, 1994; Calama & Montero, 2004; Sharma & Parton, 2007; Trincado et al., 2007; Schmidt et al., 2011). The height-diameter relationship is thus highly site- and stands density-specific and varies over time even within the same stand (Curtis, 1967; Zeide & Curtis, 2002; Pretzsch, 2009). Errors of height predictions can be significantly reduced by incorporating stand and site variables into height-diameter models (e.g. Sharma & Zhang, 2004; Temesgen and Gadow, 2004; Castedo-Dorado et al., 2006; Lei et al., 2009) which enables the establishment of stand- or time-specific height-diameter relationships. Furthermore, inclusion of both stand variables as covariates and possible sources of subject-specific variation (e.g. plot-level variation) as random effects into the model better describes the variation in the height-diameter relationship on stand level than a model with no random effects included (Mehtatalo, 2004, 2005; Adame et al., 2008; Meng et al., 2008; Crecente-Campo et al., 2010; Schmidt et al., 2011).

In recent years, national forest inventory (NFI) data are becoming useful for forest modellers to develop various models as decision support tools in forest management planning. The height and diameter data from NFI cover a wide range of tree sizes and ages, site conditions, and silvicultural treatments. Even though NFI data is primarily acquired for other objectives, they have been frequently used for modelling individual tree growth such as basal area growth (e.g. Monserud & Sterba, 1996; Sterba & Monserud, 1997), height growth (Condés & Sterba, 2008; Hasenauer & Monserud, 1997; Huuskonen & Miina, 2007), and height-diameter relationships (Mehtatalo, 2004, 2005; Nanos et al., 2004; Adame et al., 2008; Crecente-Campo et al., 2010). Also in Norway, various individual tree based forest models have been developed, such as basal area growth models (Andreassen & Tomter, 2003), diameter growth models (Bollandsås & Næsset, 2009), height growth models (Sharma et al., 2011; Sharma & Brunner (in review)), mortality models (Eid & Tahus, 2001; Bollandsås, 2007) and height-diameter models (Bollandsås, 2007).

Existing height-diameter models for Norway (Øyen & Andreassen, 2002; Bollandsås, 2007) did not take sample plot-level random effects into account when they were developed. The models presented by Bollandsås (2007) lack dominant trees height as covariate that represents stand development stage over time. In stead, these models used basal area as covariate which is not independent of thinning. In the Norwegian NFI, a tariff method is used, where mean height-diameter curves (Fitje and Vestjordet, 1977; Vestjordet, 1968) are adjusted to individual sample plots using measured heights. Height prediction errors of this method are unknown and changes in the number of sampled heights between inventories can affect predictions. A main concern is also that this method is not flexible enough to modify the shape of the mean height-diameter curves for individual sample plots.

This study aims at developing species-specific height-diameter models for three major tree species using longitudinal data from the Norwegian NFI. These species are Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), and downy birch (*Betula pubescens (*Ehrh.)). Different stand variables and sample-plot level random effects have been integrated in the models in order to improve height prediction accuracy. The proposed models are primarily meant for predicting heights of trees with a measured diameter at breast height (*DBH*) on the Norwegian NFI sample plots. However, they may also be used to predict tree height from *DBH* measurements for other sample plots in Norway. The models are expected to overcome the disadvantages of the existing tariff method and provide more accuracy than other existing alternatives (Øyen & Andreassen, 2002; Bollandsås, 2007).

2. Materials and methods

2.1. The Norwegian National Forest Inventory

The Norwegian National Forest Inventory is a permanent and rotating sample plot inventory. The sample plots are located at the intersections of a 3 × 3 km grid in areas below the coniferous forest border. Circular plots with an area of 100 m^2 were established between 1986 and 1993. The sample plot size was increased to 250 m^2 in the second period (1994 - 1998) and plots were re-measured every five year. The NFI data contain approximately 10,500 sample plots in the productive forest (minimum production of 1 m^3 ha^{-1} yr^{-1}) (Tomter, 2000). Since 2005, also mountain forests and the northern part of the country are sampled with a lower intensity (sample plots on a 3 × 9 and 9 × 9 km grid, respectively). While *DBH* and tree species are recorded for all trees with a *DBH* >5 cm, tree height is only measured for a subsample selected using a relascope sampling approach based on angle gauge factor of 6 m^2 ha^{-1}. The numbers of height sample trees per plot in earlier inventories (1986 - 2003) were smaller than that in later inventories (2004 - 2011). Details of NFI design and methods of data acquisition are found in inventory handbooks (e.g. Landsskogtakseringen, 2007).

2.2. Height-diameter data

Single-tree height measurements of up to 25 years (1986 - 2011) were used in the study. Only data from undivided sample plots (one forest type, not intercepted by road, water body, agriculture field and so on) were used. The height of the sample trees in the NFI is measured using hypsometers such as Suunto or Vertex and recorded to the nearest 0.1 m. According to NFI field instruction, tree height is defined from the stump height to top. All living trees as defined in Landsskogtakseringen (2007) with measured pairs of height and *DBH* were used. For trees with broken tops, only height and *DBH* measurements up to this event were used. Due to the relascope sampling approach, larger trees had a higher probability of being included in the sample than smaller ones. More than one height tree was not available for a large number of sample plots in earlier NFI cycles (i.e., about 30% plots in1986 - 2004). Since 2004, the number of height sample trees was increased to at least 10 per plot in order to improve the estimation of volume increments from the inventories. During the 6th NFI cycle (1986 - 1993) all trees with *DBH* > 5 cm were measured within an inner circle of 100 m^2 but only trees with *DBH* > 20 cm were measured outside this circle, but within a concentric circle of 250 m^2. Most of the measured heights were thus from 100 m^2 and only a few were measured for height outside the inner circle. We used data from this NFI cycle to validate the height-diameter models developed with data from 7th - 10th NFI cycles (1994 - 2011). Sample plots with at least four height sample trees that were measured during at least two consecutive measurement occasions were used for model fitting. The height-diameter data used for model fitting and validation are shown in Figure 1. Since the main objective of this study was to develop height-diameter models that will be used for estimating missing heights on NFI sample plots, data from the 6th NFI cycle allow evaluating model precision for the intended use. The validation data covers most of ranges of height and *DBH* of the model fitting data. In both data sets, there are few observations available for above 35 cm *DBH* of downy birch and above 50 cm *DBH* of both Norway spruce and Scots pine.

2.3. Stand variables

Various stand variables that were available in the NFI data were tested as covariates in our height-diameter models. Dominant tree height defined as the average height of the 100 thickest trees per hectare is not available for most of the sample plots and measurement occasions in the Norwegian NFI data (Sharma et al., 2011). Therefore, we used the measured height of the tallest tree per plot and measurement occasion as a proxy of dominant height (*hdom)* and its *DBH* (*ddom*) were used as covariates. Dominant height and dominant diameter have often been used as covariates in height-diameter models (e.g. Crecente-Campo et al., 2010; Castedo-Dorado et al., 2005; 2006; Lei et al., 2009), but only a few studies (e.g. Sharma and Parton, 2007) have used a proxy for dominant height. In addition, we also calculated basal area (*BA*), number of stems (*N*) and quadratic mean diameter (*qmd*) using all living trees regardless of tree species at each measurement. These stand variables also describe the competitive situation of all trees in the stand, and have therefore frequently been used in height-diameter models (e.g. Calama & Montero, 2004; Sharma & Zhang, 2004; Newton & Amponsah, 2007; Adame et al., 2008; Schmidt et al., 2011). Additionally, we calculated the difference in *DBH* (*dbhrange*) between the thickest and the thinnest tree using all living trees regardless of tree species at each measurement occasion on each sample plot. Similarly, the difference between the tallest and the shortest tree heights (*htrange*) was calculated using all living trees regardless of tree species at each measurement occasion on each sample plot. Summary statistics of modelling data are presented in Table I.

Both pure and mixed species sample plots are properly represented in both model fitting data and validation data. If at least one tree of another species was present on the plot, sample plots were defined as mixed species plots. Mixed species sample plots may consist of various species, but mostly from three species: Norway spruce, Scots pine, and downy birch. Other species are Sitka spruce, Silver fir, contorta pine, larch, yew, silver birch, and some other broad-leaved species. Sample plots were assigned to a dominating species >70% standing volume is from the mixed species plots. In the model fitting data of Norway spruce, 780 plots were dominated by Norway spruce, 79 plots by Scots pine, and 46 plots by downy birch. Of the mixed species sample plot in the model fitting data of Scots pine, 523 plots were dominated by Scots pine, 32 plots by Norway spruce, and 10 plots by downy birch. Of the mixed species sample plot in the model fitting data of downy birch, 379 plots were dominated by downy birch, 112 plots by Norway spruce, and 118 plots by Scots pine. These statistics show that most of the model fitting data that came from mixed species stands are still dominated by focused species. However, for the model validation data, larger numbers of the mixed species plots were dominated by other than the focused species. Of the mixed species sample plot in the model validation data of Norway spruce, 469 plots were dominated by Norway spruce, 336 plots by Scots pine, and 158 plots by downy birch. Of the mixed species sample plot in the model validation data of Scots pine, 464 plots were dominated by Scots pine, 224 plots by Norway spruce, and 106 plots by downy birch. Of the mixed species sample plot in the model validation data of downy birch, 132 plots were dominated by downy birch, 406 plots by Norway spruce, and 269 plots by Scots pine.

2.4. Selection of the base model

The height-diameter curve increases faster for small *DBH* than for larger *DBH* (Lappi, 1997; Pretzsch, 2009; Schmidt et al., 2011). We considered this shape while selecting mathematical functions to model height-diameter relationships. For a preliminary investigation, we used a number of bi-parametric functions to fit to our height-diameter data and evaluated on the basis of fit statistics and residual variations. Only bi-parametric functions were tested to fit height-diameter data separately for each sample plot and measurement occasion in order to get parameter estimates for all cases. Among all models tested in our preliminary analyses, Näslund’s function (Näslund, 1936) with one parameter fixed (i.e., $b_3 = 3$) was selected for further analyses. This function was also used in many earlier studies (e.g. Kangas & Maltamo, 2002; Nord-Larsen, 2006; Schmidt et al., 2011) to describe height-diameter data. This function is flexible enough to describe the height-diameter relationships. The base function in is given by

$$h_{jkt} = 1.3 + \left(\frac{DBH_{jkt}}{b_1 + b_2 DBH_{jkt}} \right)^3 + \varepsilon_{jkt} \qquad (1)$$

where h_{jkt} and DBH_{jkt} are height and diameter measured in measurement occasion t $(t = 1,\ldots,n_k)$ on the tree k $(k = 1,\ldots, m_j)$ for sample plot j $(j = 1,\ldots, m)$, respectively, b_1 and b_2 are parameters, and ε_{jkt} is a residual. A value of 1.3 was added to avoid the prediction of zero height when *DBH* approaches zero.

2.5. Selection of stand variables

Species-specific data were used for fitting models. Since the base model (Eq. 1) only described a small part of variation in the height-diameter relationships for each species, we included stand variables as covariates in the model to describe larger parts of the variation. For this, first, the base model (Eq. 1) was fitted to the species-specific data for each sample plot and measurement occasion individually using the ordinary least square method. The parameter estimates of b_1 and b_2 were then plotted against each stand variable. Secondly, stand variables were selected on the basis of their relationships with parameters b_1 and b_2 (Mehtatalo, 2004, 2005; Adame et al., 2008). Different combinations of stand variables and their transformations (square, logarithm, root, inverse) and interaction terms were also tested to improve the model fits. We identified those stand variables, which had significant relationships to parameters b_1 or b_2 of the base model (Eq. 1). We then generalized the base model redefining its parameters as a function of stand variables. Only five stand variables (*hdom*, *ddom, N, qmd*, and *dbhrange)* were significantly correlated to the parameters of the base model. We also tested a complex model that included all five variables as covariates, but our preliminary results did not show higher prediction accuracy than that of the model including only *hdom* and *ddom*. These two variables are more likely to be independent of thinning or any other cuttings than other stand variables, and have therefore frequently been used to model height-diameter relationships (e.g. Castedo-Dorado et al., 2005, 2006; Crecente-Campo et al., 2010).

2.6. Mixed-effect models

Our data have a hierarchical structure (measurement occasions within sample plot). The assumption of independent residuals does not hold and estimated parameters may be marginally biased or standard errors get inflated (Pinheiro & Bates, 2000; Fang & Bailey, 2001; Fox et al., 2001). We therefore, applied a mixed effects modelling approach to incorporate plot-level variations into the regression model. We also tried estimating models including both plot-level and measurement occasion-level random effects, but later random effects could not be estimated from our data. A single-level nonlinear mixed effects model in matrix form (Pinheiro and Bates, 2000, p. 307) is given by

$$y_j = f(\theta_j, x_j) + \varepsilon_j \text{, } \varepsilon_j \sim N(0, R_j) \tag{2}$$

with $\theta_j = A_j b + B_j u_j \text{, } u_j \sim N(0, D)$

where $\boldsymbol{y}_j$ is a response for repeated height measurements on plot j, $\boldsymbol{x}_j$ is a predictor for repeated *DBH* measurements on plot j, $\boldsymbol{b}$ is a ($p \times 1$) vector of fixed parameters with design matrix $\boldsymbol{A}_j$ (where p is number of fixed parameters), $\boldsymbol{u}_j$ is a ($q \times 1$) vector of the plot-level random parameters (u_{j1} and u_{j2}) and is assumed to have multivariate normal distribution with zero means and a variance-covariance matrix $\boldsymbol{D}$ (where q is number of mixed effects parameters). A vector $\boldsymbol{u}_j$, *is* assumed to be independent of residual vector $\boldsymbol{\varepsilon}_j$, and $\boldsymbol{B}_j$ is random effect design matrix for plot j. The vector of residuals ε_{jkt} is defined by $\boldsymbol{\varepsilon}_j \sim N(0,\boldsymbol{R}_j)$, where $\boldsymbol{R}_j$ is a within-plot variance-covariance matrix of dimension $n_j \times n_j$, that is given by

$$R_j = \sigma^2 G_j^{1/2} \Gamma_j G_j^{1/2} \tag{3}$$

where σ^2 is a residual variance common to all sample plots, diagonal matrix $\boldsymbol{G}_j$ of dimension $n_j \times n_j$ whose elements describe residual variance heterogeneity, and matrix $\boldsymbol{\Gamma}_j$ of dimension $n_j \times n_j$ was reduced to the identity matrix, because there was no autocorrelations among the observations on sample plot j.

Within-plot residual heteroskedasticity was taken into account by modelling variance as a function of the predicted height [i.e. $\mathrm{var}(\varepsilon_j) = \sigma^2 \hat{h}_{jkt}^{0.9}$]. Thus, $\boldsymbol{G}_j$ in Eq. 3 is a diagonal matrix of $n_j \times n_j$ dimension, which contains $\sigma^2 \hat{h}_{jkt}^{0.9}$ as diagonal elements (where h_{jkt} is height of tree k on sample plot j measured in time t). We constructed the mixed effects models incorporating plot-level random effects as below.

$$h_{jkt} = 1.3 + \left(\frac{DBH_{jkt}}{b_1 + u_{j1} + (b_2 + u_{j2}) DBH_{jkt}} \right)^3 + \varepsilon_{jkt} \text{; } \varepsilon_j \sim N(0, R_j) \text{; } u_j \sim N(0, D) \tag{4}$$

$$h_{jkt} = 1.3 + \left(\frac{DBH_{jkt}}{b_1 + u_{j1} + (b_2^* + u_{j2}) DBH_{jkt}} \right)^3 + \varepsilon_{jkt};\ \varepsilon_j \sim N(0, R_j);\ u_j \sim N(0, D) \tag{5}$$

with $b_2^* = a_1 \left(\sqrt{hdom}_{jt} \right)^{\alpha_2} + a_3 \sqrt{ddom}_{jt}$

Hereafter, a mixed effects model with *DBH* only (Eq. 4) will be termed as basic mixed effects model and a model with *DBH* and other covariates (Eq. 5) termed as a generalized mixed effects model. If a random parameter vector $\boldsymbol{u_j}$ is assumed zero in Eq. 4 - 5, models become the population average models. These models result in a larger prediction bias than ordinary least square (OLS) model (e.g. De-Miguel et al., 2012; Meng et al., 2009) as random parts or estimated variance-covariance components of mixed effects models are disregarded while predicting tree heights. Realizing this, we also fitted OLS models and presented in the paper.

2.7. *Parameter estimation and model evaluation*

The mixed effects models were estimated with maximum likelihood in SAS macro NLINMIX (SAS Institute Inc., 2008) using expansion- around-zero method (Littell et al., 2006). Other model versions were estimated using PROC MODEL (SAS Institute Inc., 2008) with the ordinary least square method. The Akaike's information criterion (*AIC*) (Akaike, 1972) and Schwarz's Bayesian information criterion (*BIC*) were used to compare the models. The estimated models were also evaluated for their residual variations using root mean squared error (*RMSE*) and adjusted coefficient of determination (R^2_{adj}). Residuals graphs for the estimated models were thoroughly examined. Since our main interest of using the mixed effects modelling approach was for sample plot-level predictions, we evaluated height predications for the validation data using the following statistical measures (Huang et al., 2009) *k* on sample plot *j*-level:

$$\bar{e}_j = \sum_{k=1}^{n_j} \left(h_{jk} - \hat{h}_{jk} \right) \Big/ n_j \tag{6}$$

$$bias(\%) = \frac{\bar{e}_j}{\bar{h}_j} \times 100 \tag{7}$$

where h_{jk} and $\hat{h}_{jk}$ are the observed and predicted heights for tree *k* on sample plot *j*, n_j is number of observations for sample plot *j*, $\bar{e}_j$ is a mean prediction error for sample plot *j*, and

$\bar{h}_j$ is the observed mean height for sample plot *j*. Prediction errors of the models and simulated height curves overlaid on the observed data for each sample plot were also examined.

2.8. Prediction of random effects

For application of the mixed effects model, prior information of the response variable (i.e., tree height) in Eq. 4 - 5 is needed. Measured heights of one or more trees per plot can be used to predict random effects parameters for plot *j* and adjust the population average model to the plot-specific conditions. The random effects parameters are predicted using the empirical best linear unbiased prediction (EBLUP) method (Vonesh & Chinchilli, 1997; Pinheiro & Bates, 2000). A vector of random effects parameters in Eq.8 was predicted using PROC IML in SAS (SAS Institute Inc., 2008).

$$u = DZ_j^T \left(Z_j D Z_j^T + R_j\right)^{-1} \varepsilon_j \qquad (8)$$

where ***u*** is a vector of random effects parameters, containing plot-level random parameters for plot *j* and within plot variance-covariance matrix $D = \begin{bmatrix} \sigma_{uj_1}^2 & \sigma_{uj_1uj_2} \\ \sigma_{uj_1uj_2} & \sigma_{uj_2}^2 \end{bmatrix}$ where σ_{uj}^2 and $\sigma_{uj_1uj_2}$ are plot-level variance and covariance components of random effects (u_{j1} and u_{j2}). The elements of $\boldsymbol{Z}_j$ matrix are the partial derivatives of the nonlinear function (Eq. 4 - 5) with respect to its fixed parameters (e.g. Pinheiro & Bates, 2000, p. 311; Calama & Montero, 2004), and it is defined by $z_{jkt} = \frac{\partial f\left(DBH_{jkt}, b, u_j\right)}{\partial b}$, where ***b*** is a fixed parameter vector, and $\boldsymbol{u}_j$ is random parameter vector. In our case, z_{jkt} was defined for tree *k* at measurement time *t* on the *j*th plot as

$$z_{jkt}(b_1) = -3DBH_{jkt}^3 \Big/ \left(b_1 + b_2 DBH_{jkt}\right)^4 \qquad (9)$$

$$z_{jkt}(b_2) = -3\left(\frac{DBH_{jkt}}{b_1 + b_2 DBH_{jkt}}\right)^4 \qquad (10)$$

The matrix $\boldsymbol{Z_j}$ has the dimension $\sum_{k=1}^{m_j} n_j \times q$ (i.e., number of its columns equal to the number of rows of the matrix $\boldsymbol{D}$), where m_j is number of trees for a plot j. The matrix $\boldsymbol{R}_j$ is a variance-covariance matrix obtained from Eq. 3. The error vector $\boldsymbol{\varepsilon}_j$ was obtained using the fixed part of the mixed effects models (Eq. 4 - 5).

We evaluated prediction errors of the mixed effects models only for the validation data using height measurement from differing numbers of trees that were selected either systematically or randomly to predict random effects by applying the EBLUP method (Eq. 8). The alternative methods to select height trees evaluated in our analyses were: randomly selected one to five height trees (alternative 1 to 5); one median height tree (alternative 6); one median height tree from each of two height classes (one class below the mean height and another above the mean height) (alternative 7); and all height trees (alternative 8). These all evaluations were made using data from only pure species sample plots. The best alternative identified was then subsequently used for further evaluations. We also tested whether measured heights of other than the focused species (species used for species-specific model) could be used to localize the models of the focused species. For this, we applied the Norway spruce model for prediction of random effects with measured heights of Scots pine (492 plots), downy birch (462 plots), or other species (184 plots) and heights of Norway spruce were predicted. We also applied the Scots pine model for prediction of random effects with measured heights of Norway spruce (394 plots), downy birch (224 plots), or other species (95 plots) and heights of Scots pine were predicted. Similarly, we applied the downy birch model for prediction of random effects with measured heights of Norway spruce (412 plots), Scots pine (269 plots), or other species (121 plots) and heights of downy birch was predicted.

3. Results

The parameter estimates and fit statistics of basic mixed effects model (Eq. 4) and generalized mixed effects model (Eq. 5) are presented in Table II and III, respectively. Fit statistics of their OLS versions are also listed there. All estimates of the fixed effects parameters and variance-covariance components of mixed effects models are significant ($p < 0.0001$). For all three species, both mixed effects models and their OLS versions described height-diameter relationships well. However, both basic mixed effects model and its OLS version showed poorer fit statistics than a generalized mixed effects model and its OLS version. The *hdom* showed the biggest reduction of AIC for all three species as it was strongly correlated to parameter b_2. Also *ddom* significantly contributed to the model improvements for all species. Inclusion of residual heteroskedasticity reduced AIC by 1% - 3% (Table II - III). This reduction varied with models and tree species. Also, values of the fixed parameters of each model changed significantly through integration of random effects in into the models. Through mixed modelling, reduction of unexplained variances (i.e. mean square residual or σ^2) relative to OLS models varied with tree species and models, ranging from 44% to 85% (i.e. largest reduction with a basic mixed effects model for Scots pine and smallest reduction with a generalized mixed effects model for Scots pine). This indicated that mixed effects models were able to describe much larger part of variations in height-diameter relationships than their OLS versions. For each species, variances of u_{j1} of the basic mixed effects model and generalized mixed effects model are closely comparable. However, variance of u_{j2} of the basic mixed effects model is about three times larger than that for a generalized mixed effects model. This indicated that covariates used in the generalized mixed effects model significantly reduced the effects of sample plot variations.

For all species, generalized mixed effects model showed smaller residual variations than basic mixed effects model (Table II - III). Using the validation data, we evaluated height prediction errors of generalized mixed effects models with various alternatives of tree selection methods for prediction of random effects (Figure 2). For all species, height prediction accuracy of the models increased with increasing number of height trees used to predict random effects. Height prediction accuracy of alternative 8 was higher as compared to all other alternatives. Hereafter, alternative 8 was chosen for evaluations of models. For all species, height prediction bias of a generalized mixed effects model occurred within ± 5% range for > 95% sample plots (out of 1588 spruce plots or 1709 pine plots or 924 birch plots). However, a basic mixed effects model showed significantly larger bias in the predicted heights for a number of sample plots (Figure 3). As compared to the generalized mixed effects model, the basic mixed effects models also have a tendency to larger over-prediction.

For the validation data, a generalized mixed effects model did not show substantial bias for pure stands, where all measured heights of the focused species were used to predict random effects (Figure 4, left panels). In general, this model with random effects predicted from the focused species did not show substantial biases for mixed species stands also (Figure 4, right panels). However, for small *DBH* ranges (< 15 cm) of Norway spruce and Scots pine and across all *DBH* ranges of downy birch, there is very small bias. For mixed stands, height prediction bias of a generalized mixed effects model occurred within ± 5% range for Norway spruce on 94% sample plots (out of 990 plots), for Scots pine on 96% sample plots (out of 794 plots) and for downy birch on 85% sample plots (out of 807 plots). For both pure and mixed stands, as indicated by height of the boxes of the prediction errors in both panels of this figure, most of the prediction errors of the focused species are falling within a range of ± 2 m. However, larger errors occurred for some samples plots, where two or more layers of height sample trees exist, and where their height ranges were large. When measured heights of other than focused species were used to predict random effects, height predictions for focused species were substantially biased for most of *DBH* ranges (Figure 5). As compared to generalized mixed effects model, its OLS version only showed a little improvement in height prediction accuracy (Figure 6) for the same sample plots as used in Figure 5. As expected, for both pure and mixed stands, where measured height of the focused species was used for prediction of random effects, a generalized mixed effects model showed significantly higher prediction accuracy than its OLS version (data not shown).

The height-diameter relationship varies with *hdom* and *ddom*, and this variation is also affected by sample plot-level effects even for the same *hdom* and *ddom*. To illustrate this, we selected few sample plots in the validation data, where similar *hdom* and *ddom* existed, and used all measured heights of Norway spruce to predict random effects. We then generated height curves using the generalized mixed effects model (Figure 7) for the observed data range on the plot. Variation of height-diameter relationships with random effects for observed *hdom* and *ddom* shows the generalized mixed effects model’s flexibility.

4. Discussion

The height-diameter data used in this study have large variation (Figure 1, Table 1), and cover most of the growth conditions and silvicultural treatments across Norway. Even though Näslund’s function has been reported to work well for even-aged and single-layered stands (cited in Pretzsch, 2009, p. 187), it has also been shown to work adequately for multi-layered forests after the base function (Eq. 1) was generalized through inclusion of stand variables and random effects (e.g. Kangas & Maltamo, 2002; Schmidt et al., 2011). A large value of estimated variance of random parameter u_{j1} (Table II - III) indicates that the parameter b_1 of mixed models (Eq. 4 - 5) highly varies across the sample plots. This justifies the use of plot-level mixed effects models.

Mixed effects height-diameter models can best predict the missing heights on the sample plots (Robinson & Wykoff, 2004), but large errors still remain to be accounted for. The main cause of large prediction errors is due to outlier observations. The prediction accuracy of the mixed effects model for each individual tree depends highly on the vertical heterogeneity of stands and numbers of height trees to be selected for prediction of random effects. Measured heights of any number of trees can be used to predict random effects by EBLUP method. But height prediction accuracy of the model largely depends on the representativeness of the chosen trees. The higher the number of trees used to predict random effect parameters, the higher is the height prediction accuracy. In our data, only one measured height is available for about one-third of the total sample plots inventoried in first three NFI cycles. If the vertical structure of the stand is homogenous, one measured height tree may work well (e.g. Trincado et al., 2007), otherwise height predictions may be biased. Except for Norway spruce, one or two median-sized trees (alternative 6 or 7) can also work well (Figure 2). For smallest height prediction bias, alternative 8 is obviously the best choice. Median-sized height trees are also reported to have significantly reduced the prediction bias in other studies as well (e.g. Crecente-Campo et al., 2010).

For mixed stands, where measured heights of the focused species are not available, either generalized OLS model or generalized mixed effects model with random effects predicted from the measured heights of other than the focused species need to be used. However, none of the models would be precise for all species (Figure 5 - 6). In general, a generalized OLS model outperforms its mixed effects version for all three stand conditions assumed. Using generalized OLS model is more logical than generalized mixed effects model for the stands, where measured height of the focused species is not available for prediction of random effects. The prediction errors for a different species than modelled one may be large, and therefore causes biased estimation of random effects in EBLUP (Eq. 8). Large height prediction bias for mixed species sample plots is due to layering among the tree species. Also, OLS models for both pure and mixed stands did not account for sample plot-level effects that are large in the data (Figure 7). Not only for pure stands, but also for mixed species stands, where measured height of the focused species is available for prediction of random effects, a generalized mixed effects model can be more accurate than generalized OLS model for height prediction. Therefore, wherever possible, only the focused species should be used to localize height-diameter models. For the conditions, when model users are not able to predict random effects or measured heights are not available for random effects prediction, application of the OLS model is more appropriate than population average model or only fixed parts of the mixed effects model (e.g. De-Miguel et al., 2012; Meng et al., 2009). However, access to computational facilities will make the application of mixed effetcs model much easier. For other species (except Norway spruce, Scots pine and downy birch) no test was perfomed for whether models were adeqaute for their height predcitons.

The height-diameter relationship varies with development stages over time in a stand. This is due to stand density effects (Curtis, 1967; Zeide & Curtis, 2002). To reduce height prediction errors, one or more stand variables (e.g. *N*, *BA*, *qmd*, *hdom*, and *ddom)* need be used to generalize the height-diameter models (Sharma & Zhang, 2004; Temesgen & Gadow, 2004; Castedo-Dorado et al., 2006; Lei et al., 2009). However, some stand variables are affected by thinning. Since thinning in Norway is mostly from below, using *hdom* and *ddom* as covariates is much more appropriate than other stand variables. Generally, height of dominant trees represents stand development stage, and has therefore frequently been used as covariate in height-diameter models (e.g. Calama & Montero, 2004; Castedo-Dorado et al., 2006; Sharma & Parton, 2007; Adame et al., 2008; Crecente-Campo et al., 2010; Paulo et al., 2011).

To conclude, a generalized mixed effects model predicted heights without substantial bias for all three species (Norway spruce, Scots pine and downy birch) not only for pure stands, but also for mixed stands, where measured heights of focused species are available for prediction of random effects. This model can be applied to estimate missing heights for NFI sample plots or other sample plots, where measured heights are available. Even though bias for certain *DBH* ranges is substantial, a generalized OLS model may be applicable for mixed stands, where measured heights of the focused species are not available for the application of mixed effects model.

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References

Adame, P., del Río, M., & Cañellas, I. (2008). A mixed nonlinear height-diameter model for pyrenean oak (*Quercus pyrenaica* Willd.). *Forest Ecology and Management, 256*(1-2), 88-98.

Akaike, H. (1972). A new look at statistical model identification. *IEEE Trans Automatic Control*, AC19(6), 716-723.

Andreassen, K. & Tomter, S.M. (2003). Basal area growth models for individual trees of Norway spruce, Scots pine, birch and other broadleaves in Norway. *Forest Ecology and Management*, 180(1-3): 11-24.

Bollandsås, O.M. (2007). *Uneven-age forestry in Norway: inventory and management models.* PhD thesis. Norwegian University of Life Sciences, Ås, Norway.

Bollandsås, O.M. & Næsset, E. (2009). Weibull models for single-tree increment of Norway spruce, Scots pine, birch and other broadleaves in Norway. *Scandinavian Journal of Forest Research*, 24(1), 54 - 66.

Calama, R. & Montero, G. (2004). Interregional nonlinear height-diameter model with random coefficients for stone pine in Spain. *Canadian Journal of Forest Research*, 34(1), 150-163.

Castedo-Dorado, F., Anta, M.B., Parresol, B.R. & Gonzalez, J.G.A. (2005). A stochastic height-diameter model for maritime pine ecoregions in Galicia (northwestern Spain). *Annals of Forest Science*, 62(5), 455-465.

Castedo-Dorado, F., Diéguez-Aranda, U., Anta, M.B., Rodriguez, M.S. & von Gadow, K. (2006). A generalized height-diameter model including random components for radiata pine plantations in northwestern Spain. *Forest Ecology and Management*, 229(1-3), 202-213.

Condés, S. & Sterba, H. (2008). Comparing an individual tree growth model for *Pinus halepensis* Mill. in the Spanish region of Murcia with yield tables gained from the same area. *European Journal of Forest Research*, 127(3), 253-261.

Crecente-Campo, F., Tomé, M., Soares, P. & Diéguez-Aranda, U. (2010). A generalized nonlinear mixed-effects height-diameter model for *Eucalyptus globulus* L. in northwestern Spain. *Forest Ecology and Management*, 259(5), 943-952.

Curtis, R.O. (1967). Height-diameter and height-diameter-age equations for second growth Douglas fir. *Forest Science*, 13, 365-375.

De-Miguel, S., Mehtatalo, L., Shater, Z., Kraid, B. & Pukkala, T. (2012). Evaluating marginal and conditional predictions of taper models in the absence of calibration data. *Canadian Journal of Forest Research*, 42(7), 1383-1394.

Eid, T. & Tuhus, E. (2001). Models for individual tree mortality in Norway. *Forest Ecology and Management*, 154(1-2), 69-84.

Fang, Z.X. & Bailey, R.L.(2001). Nonlinear mixed effects modeling for slash pine dominant height growth following intensive silvicultural treatments. *Forest Science*, 47(3), 287-300.

Fitje, A. & Vestjordet, E. (1977). Bestandshøydekurver og nye høydeklasser for gran. *Meddelelser fra Norsk institutt for skogforskning*, 34(2), 23-68.

Fox, J.C., Ades, P.K. & Bi, H. (2001). Stochastic structure and individual-tree growth models. *Forest Ecology and Management*, 154(1-2), 261-276.

Hasenauer, H. & Monserud, R.A. (1997). Biased predictions for tree height increment models developed from smoothed 'data'. *Ecological Modelling*, 98(1), 13-22.

Huang, S., Meng, S.X. & Yang, Y. (2009). Using nonlinear mixed model technique to determine the optimal tree height prediction model for black spruce. *Modern Applied Science*, 3(4), 3-18.

Huuskonen, S. & Miina, J. (2007). Stand-level growth models for young Scots pine stands in Finland. *Forest Ecology and Management*, 241(1-3): 49-61.

Kangas, A. & Maltamo, M. (2002). Anticipating the variance of predicted stand volume and timber assortments with respect to stand characteristics and field measurements. *Silva Fennica*, 36(4), 799-811.

Landsskogtakseringen (2007). Landsskogtakseringens feltinstruks 2007 [Field manual of the national forest inventory 2007], *Håndbok fra Skog og landskap*, 06/2007, 116 p.+ appendix (in Norwegian).

Lappi, J. (1997). A longitudinal analysis of height/diameter curves. *Forest Science*, 43(4), 555-570.

Lei, X.D., Peng, C.H., Wang, H.Y. & Zhou, X.L. (2009). Individual height-diameter models for young black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) plantations in New Brunswick, Canada. *Forestry Chronicle*, 85(1), 43-56.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D. & Schabenberger, O. (2006). *SAS for mixed models,* 2nd Ed. SAS Institute, Cary, NC. 814 p.

Mehtatalo, L. (2004). A longitudinal height-diameter model for Norway spruce in Finland. *Canadian Journal of Forest Research*, 34(1), 131-140.

Mehtatalo, L. (2005). Height-diameter models for Scots pine and birch in Finland. *Silva Fennica*, 39(1), 55-66.

Meng, S.X., Huang, S.M., Lieffers, V.J., Nunifu, T. & Yang, Y.Q. (2008). Wind speed and crown class influence the height-diameter relationship of lodgepole pine: Nonlinear mixed effects modeling. *Forest Ecology and Management,* 256(4), 570-577.

Meng, S.X., Huang, S.M., Yang, Y.Q., Trincado, G. & VanderSchaaf, C.L. (2009). Evaluation of population-averaged and subject-specific approaches for modeling the dominant or codominant height of lodgepole pine trees. *Canadian Journal of Forest Research*, 39(6), 1148-1158.

Monserud, R.A. & Sterba, H. (1996). A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. *Forest Ecology and Management*, 80(1-3): 57-80.

Nanos, N., Calama, R., Montero, G. & Gil, L. (2004). Geostatistical prediction of height/diameter models. *Forest Ecology and Management*, 195(1-2): 221-235.

Näslund, M. (1936). Skogsforsö ksastaltens gallringsforsök i tallskog [Thinning experiments in pine forest conducted by the forest experiment station]. *Meddelanden fran Statens Skogsforsöksanstalt,* 29,1-169 (In Swedish).

Newton, R.F. & Amponsah, I.G. (2007). Comparative evaluation of five height-diameter models developed for black spruce and jack pine stand-types in terms of goodness-of-fit, lack-of-fit and predictive ability. *Forest Ecology and Management*, 247(1-3), 149-166.

Nord-Larsen, T. (2006). Developing dynamic site index curves for European beech (*Fagus sylvatica* L.) in Denmark. *Forest Science*, 52(2), 173-181.

Paulo, J.A., Tomé, J. & Tomé, M. (2011). Nonlinear fixed and random generalized height-diameter models for Portuguese cork oak stands. *Annals of Forest Science*, 68(2), 295-309.

Pinheiro, J.C. & Bates, D.M. (2000). *Mixed-effects models in S and S-PLUS*. New York: Springer, 528 p.

Pretzsch, H. (2009). *Forest dynamics, growth and yield: from measurement to model*. Springer Verlag, Berlin, Germany, 664 pp.

Robinson, A.P. & Wykoff, W.R. (2004). Imputing missing height measures using a mixed-effects modeling strategy. *Canadian Journal of Forest Research*, 34(12), 2492-2500.

SAS Institute Inc. (2008). SAS/ETS1 9.1 *User's Guide*. SAS Institute Inc., Cary, NC

Schmidt, M., Kiviste, A. & von Gadow, K. (2011). A spatially explicit height-diameter model for Scots pine in Estonia. *European Journal of Forest Research*, 130(2), 303-315.

Sharma, M. & Zhang, S.Y. (2004). Height-diameter models using stand characteristics for Pinus banksiana and Picea mariana. *Scandinavian Journal of Forest Research*, 19(5), 442-451.

Sharma, M. and Parton, J. (2007). Height-diameter equations for boreal tree species in Ontario using a mixed-effects modeling approach. *Forest Ecology and Management*, 249(3), 187-198.

Sharma, R.P., Brunner, A., Eid, T. & Øyen, B.-H. (2011). Modelling dominant height growth from national forest inventory individual tree data with short time series and large age errors. Forest Ecology and Management, 262(12), 2162-2175.

Sharma, R.P. & Brunner, A. Modelling individual tree height growth of Norway spruce and Scots pine using national forest inventory data in Norway (in revision).

Sterba, H. & Monserud, R.A. (1997). Applicability of the forest stand growth simulator PROGNAUS for the Austrian part of the Bohemian Massif. *Ecological Modelling*, 98(1), 23-34.

Temesgen, H. & Gadow, K.V. (2004). Generalized height-diameter models: an application for major tree species in complex stands of interior British Columbia. *European Journal of Forest Research*, 123, 45-51.

Tomter, S.M. (2000). Skog 2000. Statistikk over skogforhold og -ressurser i Norge [Statistics of forest conditions and resources in Norway]. *Norwegian Forest and Landscape Institute, Ås*, 84 p. (in Norwegian).

Trincado, G., VanderSchaaf, C.L. & Burkhart, H.E. (2007). Regional mixed-effects height-diameter models for loblolly pine (*Pinus taeda* L.) plantations. *European Journal of Forest Research*, 126(2), 253-262.

Vanclay, J.K. (1994). *Modelling forest growth and yield. Applications to mixed tropical forests*. CAB International, Oxon, U.K., 312 p.

Vestjordet, E. (1968). Volum av nyttbart virke hos gran og furu basert på relativ høyde og diameter i brysthøyde eller ved 2,5 m fra stubbeavskjær. *Meddelelser fra Det Norske Skogforsøksvesen* 25, 411-459.

Vonesh, E.F. & Chinchilli, V.M. (1997). *Linear and nonlinear models for the analysis of repeated measurements*. Marcel Dekker, New York, 560 p.

Zeide, B. & Curtis, V. (2002). The effect of density on the height-diameter relationship. In: *Gen. Tech. Rep. SRS-48 (*pp. 463-466). Asheville, NC: USDA, Forest Service, Southern Research Station,.

Øyen, B.-H. & Andreassen, K. (2002). Modeller for å estimere trehøyde ved hjelp av diameter og bestandsdata. Norwegian Forest Research Institute. *Aktuelt* 6, 13-14 [in Norwegian].

Table I. Summary statistics of modelling data

Variables*	Model fitting data [Mean ± std. (range)]			Validation data [Mean ± std. (range)]		
	Norway spruce	Scots pine	Downy birch	Norway spruce	Scots pine	Downy birch
Number of sample plots (pure + mixed)	1583 (678 + 905)	1218 (653 + 565)	1061 (452 + 609)	2578 (1588 + 990)	2503 (1709 + 794)	1731 (924 + 807)
Number of height sample trees	10088	7670	6598	6903	5266	3017
Number of height sample trees per plot	6.4±2(4-19)	6.3±2(4-12)	6.2±2(4-13)	2.7±1.8(1-15)	2.1±1.4(1-10)	1.7±1(1-9)
Number of stems (*N* ha^{-1})	1312±688 (160-5288)	868 ±542(160-4440)	1167±760(160-5280)	1692±838(100-6300)	1204±704(100-5300)	1528±827(100-5300)
BA (m^{2} ha^{-1})	28±15(0.8-92)	20.8±12 (0.5-64)	12±8(0.4-51)	47±26(0.8-154)	38±23(0.8-132)	24±17(0.3-119)
qmd (cm)	16.7±5(5.9-42.6)	17.9±5.3(6-50.1)	11.6±3.6(5.5-35.3)	19.1±5.8(6- 40.9)	20.5±6.2(6 -50.6)	14.3±5.3(5.3-49.7)
hdom (m)	18.5±5.2(5-35.2)	27.5±4.8(3.5-31)	19.9±3.8(3.6-27.5)	27.8±5.3(3.4-34)	27.8±4.6(3-30)	20.3±4.5(3-31)
ddom (cm)	28.8±9.5(5.5-72.3)	27.5±8.2(6.5-0.9)	19.9±9.7(5-73.9)	27.8±10(5.1-74.3)	27.8±9.1(5-72.5)	20.3±10.1(5-58.2)
dbhrange (cm)	25.9±9.4(1.6-72.8)	24.6±8.5(2.4-61)	17.3±9.6(0.4-75.6)	24.5±8.6(0-68.8)	22.5±9.4(0-66.8)	18.2±9.6(0-74.5)
htrange (m)	8.9±4.3(0.7-26.4)	6.8±3.5(0.3-26.4)	5.7±3.2(0.3-22.6)	6.5±4.6(0-25.8)	4.1±3.7(0-21.7)	3.8±3.7(0-25.8)
Sample tree height (m)	14.6±5.7(1.6-35.2)	12.0±5.2(2.1-31)	8.83±3.2(2.2-24.5)	15±5.4(3-33.9)	13.5±4.5(2.9-30)	9.3±3.6(3-27.2)
DBH (cm)	20.7±9.3(5-72.3)	21.9±9.3(5-66)	12.5±5.7(5-68)	22±9.6(5-74.3)	25.2±9.7(5-72.5)	14.4±7.2(5-56.7)

*abbreviations are defined in the text.

Table II. Parameter estimates, variance and covariance components, and fit statistics of a basic mixed effects model and its OLS version (Eq. 4).

Components	Parameter estimates and fit statistics					
	Norway spruce		Scots pine		Downy birch	
	OLS model	Mixed model	OLS model	Mixed model	OLS model	Mixed model
Fixed						
b_1	2.2131	1.877	2.2845	1.5007	1.649	1.1962
b_2	0.3046	0.3276	0.3318	0.3747	0.373	0.4171
Variance & covariance						
σ^2_{uj1}		0.286		0.4334		0.2481
σ_{uj1uj2}		-0.00858		-0.00729		-0.01575
σ^2_{uj2}		0.000942		0.001891		0.002974
σ^2	0.7245	0.1905	1.2293	0.1784	0.6242	0.1568
Fit statistics						
RMSE	3.1155	1.4197	3.7536	2.2286	2.2575	1.556
R2adj	0.7023	0.9382	0.4704	0.8133	0.5131	0.7686
AIC	118472.5	93414.8	95221.1	67273	59705.4	45283.7
BIC	118496.8	93447	95244.5	67303.6	59728.1	45313.5
Reduction of *AIC* due to inclusion of heteroskedasticity (%)	2	1.5	1.5	1.2	1.6	1.6

OLS = ordinary least square, other abbreviations are defined in the text.

Table III. Parameter estimates, variance and covariance components, and fit statistics of a generalized mixed effects model (Eq. 5) and its OLS version

Components	Parameter estimates and fit statistics					
	Norway spruce		Scots pine		Downy birch	
	OLS model	Mixed model	OLS model	Mixed model	OLS model	Mixed model
Fixed						
b_1	1.6351	1.6974	1.3239	1.3872	1.1684	1.1444
a_1	1.0347	0.8523	1.2882	1.0265	1.0556	0.8154
a_2	-0.9592	-0.7339	-1.0580	-0.794	-0.9761	-0.6248
a_3	0.0148	0.007824	0.01442	0.005987	0.02121	0.00928
Variance & covariance						
σ^2_{uj1}		0.2858		0.4169		0.2129
σ_{uj1uj2}		-0.00849		-0.01249		-0.01169
σ^2_{uj2}		0.000317		0.000471		0.00107
σ^2	0.2924	0.1518	0.2919	0.1624	0.2976	0.1481
Fit statistics						
RMSE	1.8348	1.1799	1.76066	1.1505	1.5529	0.9533
R2adj	0.8967	0.9573	0.8835	0.9502	0.7695	0.9132
AIC	96185.9	85751.8	68755	62268.9	49125.3	42948.8
BIC	96226.4	85794.8	68794	62309.8	49163.1	42988.5
Reduction of *AIC* due to inclusion of heteroskedasticity (%)	0.9	2	1.5	2.3	3	3

OLS = ordinary least square, other abbreviations are defined in the text.

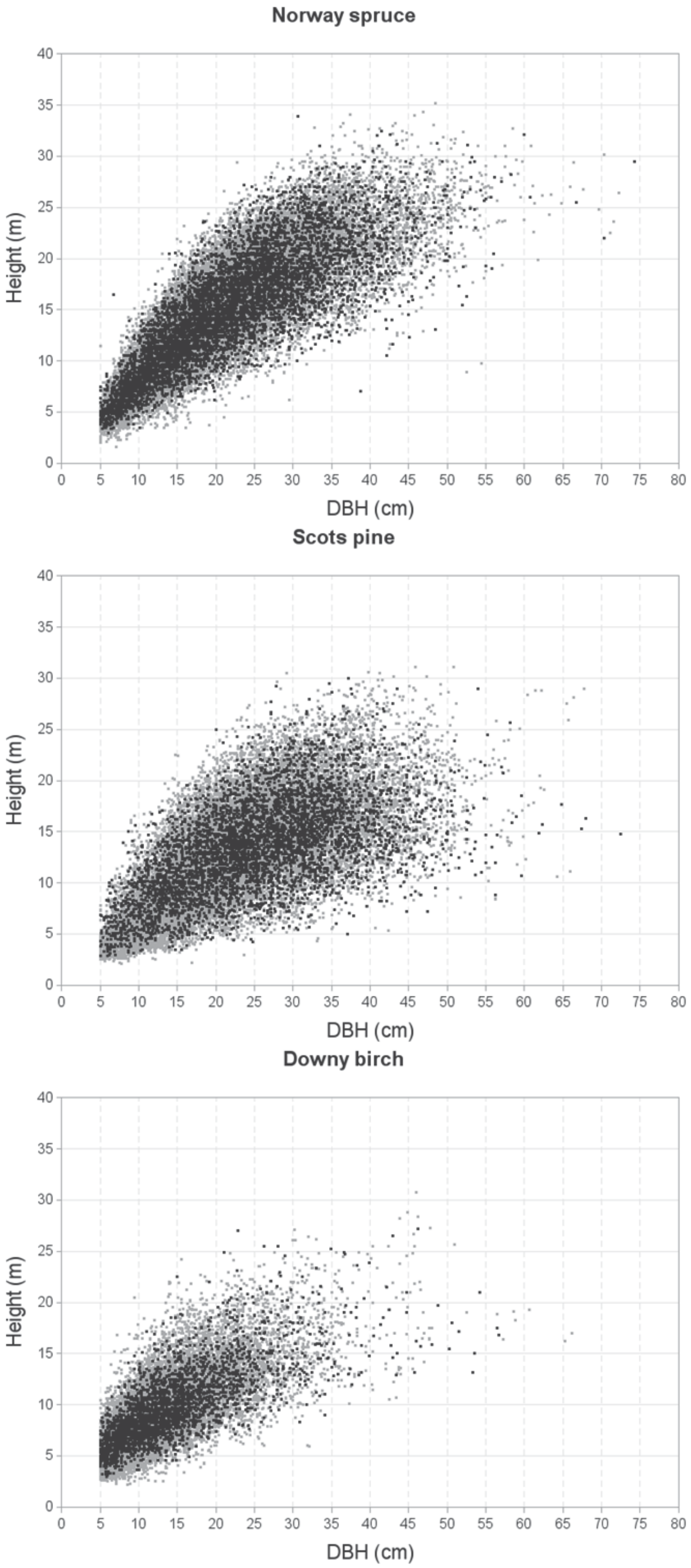

Figure 1. Height-diameter data: model fitting data (grey dots) and validation data (black dots).

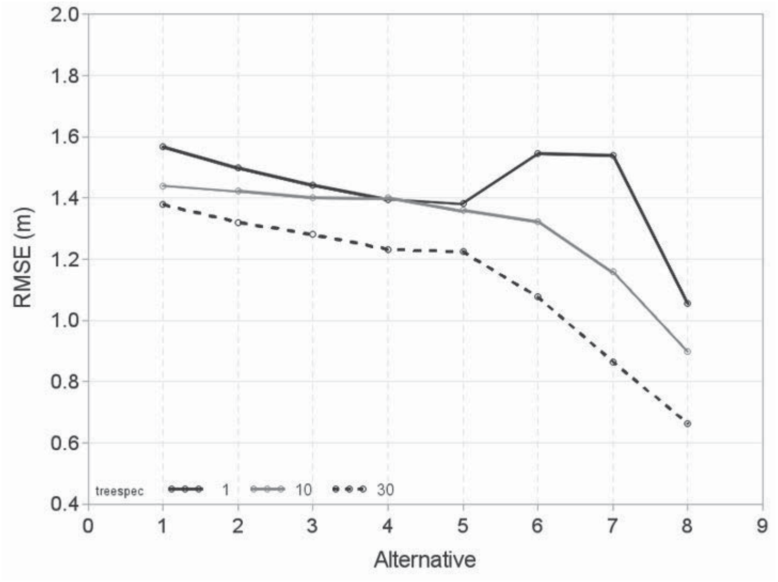

Figure 2. Prediction statistics of a generalized mixed effects model (Eq. 5) for various methods to select sample trees when predicting random effects using validation data (treespec =1: Norway spruce, 10: Scots pine, 30: downy birch).

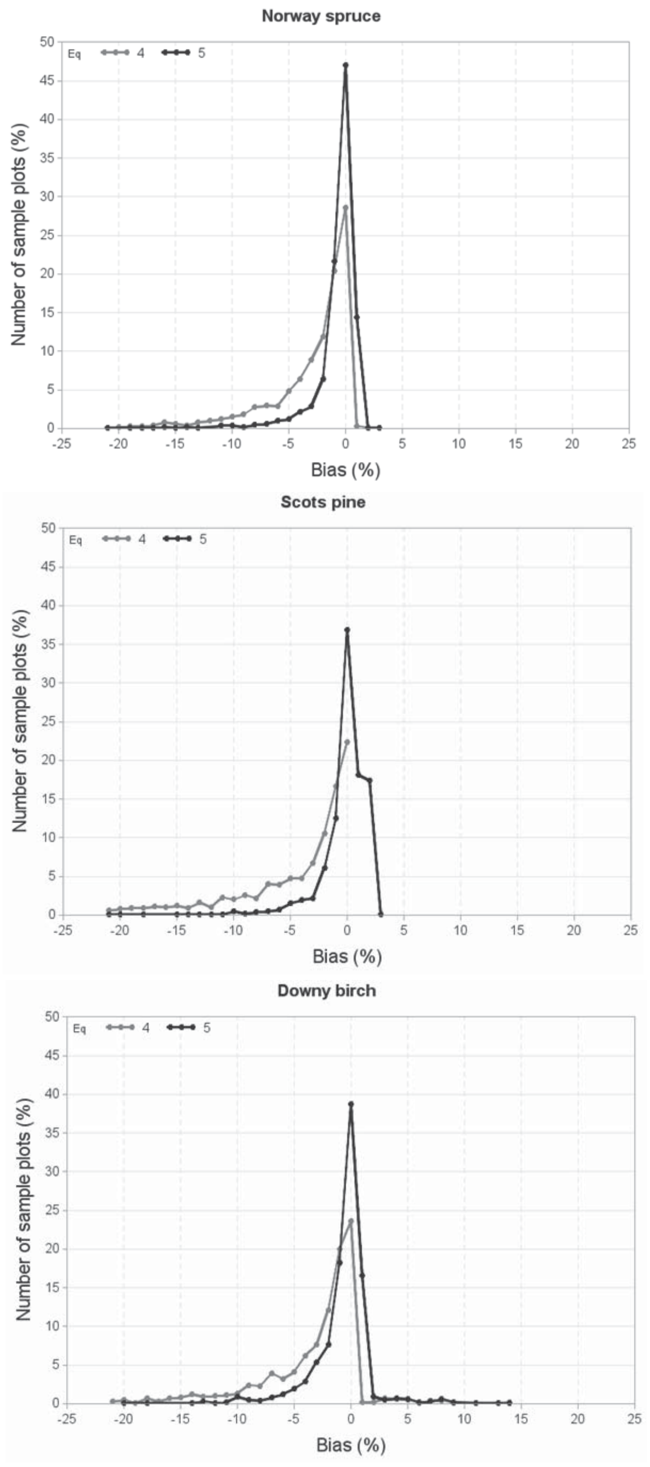

Figure 3. Bias of a basic mixed effetcs model (Eq. 4) and generalized mixed effetcs model (Eq. 5) for validation data, where random effetcs were estimated using all measured heights of the focused species on pure species sample plots in the validation data.

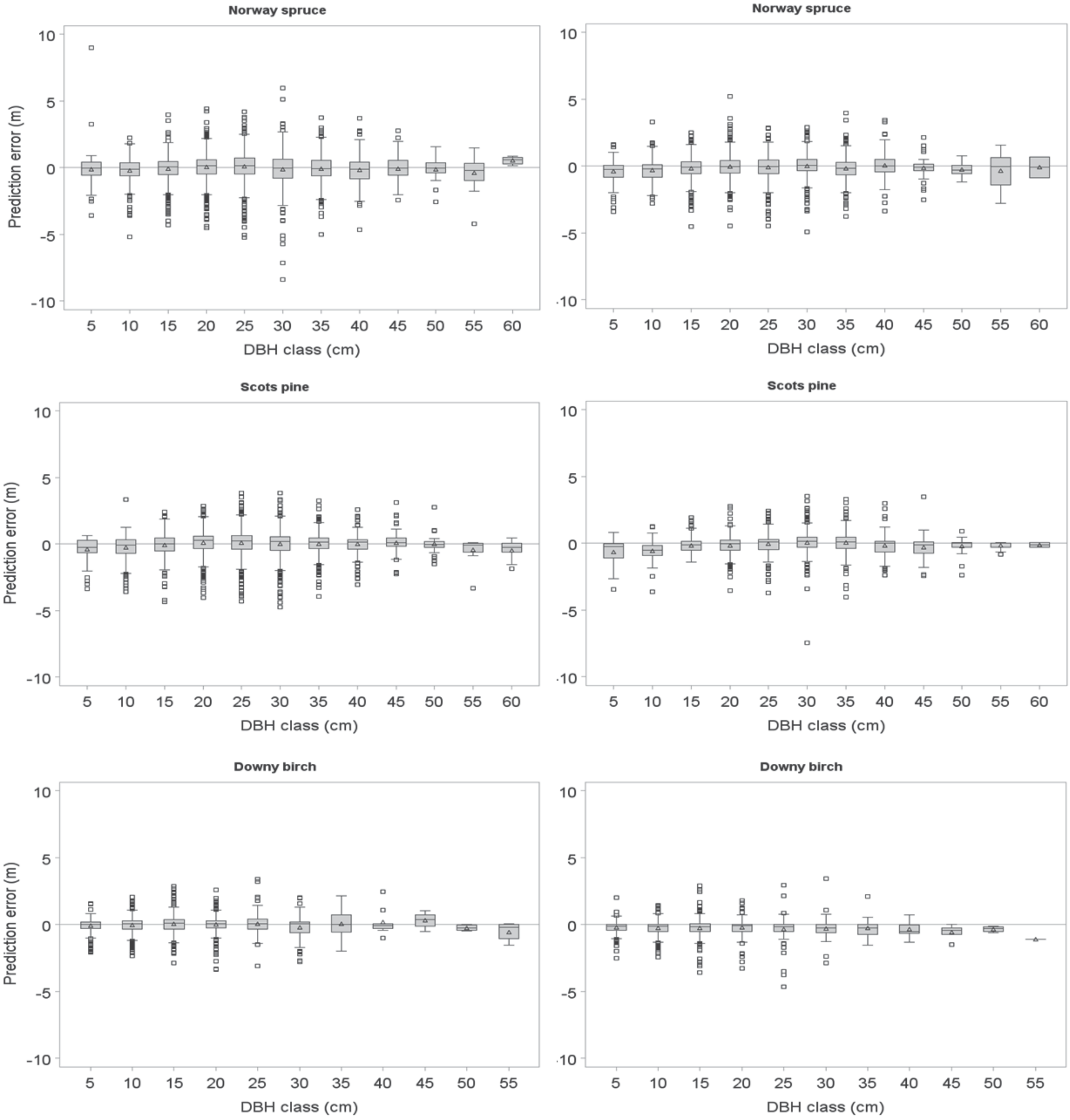

Figure 4. Height prediction errors of a generalized mixed effects model (Eq. 5) for pure stands (left panels) and mixed stands (right panels) in the validation data. All measured heights of the focused species were used for prediction of random effects. The number of sample plots used here is given in Table 1. The length of the box represents the interquartile range (IQR), length of the whisker represents class minimum and maximum values in IQR, and small boxes represent observations lying beyond 1.5 times IQR.

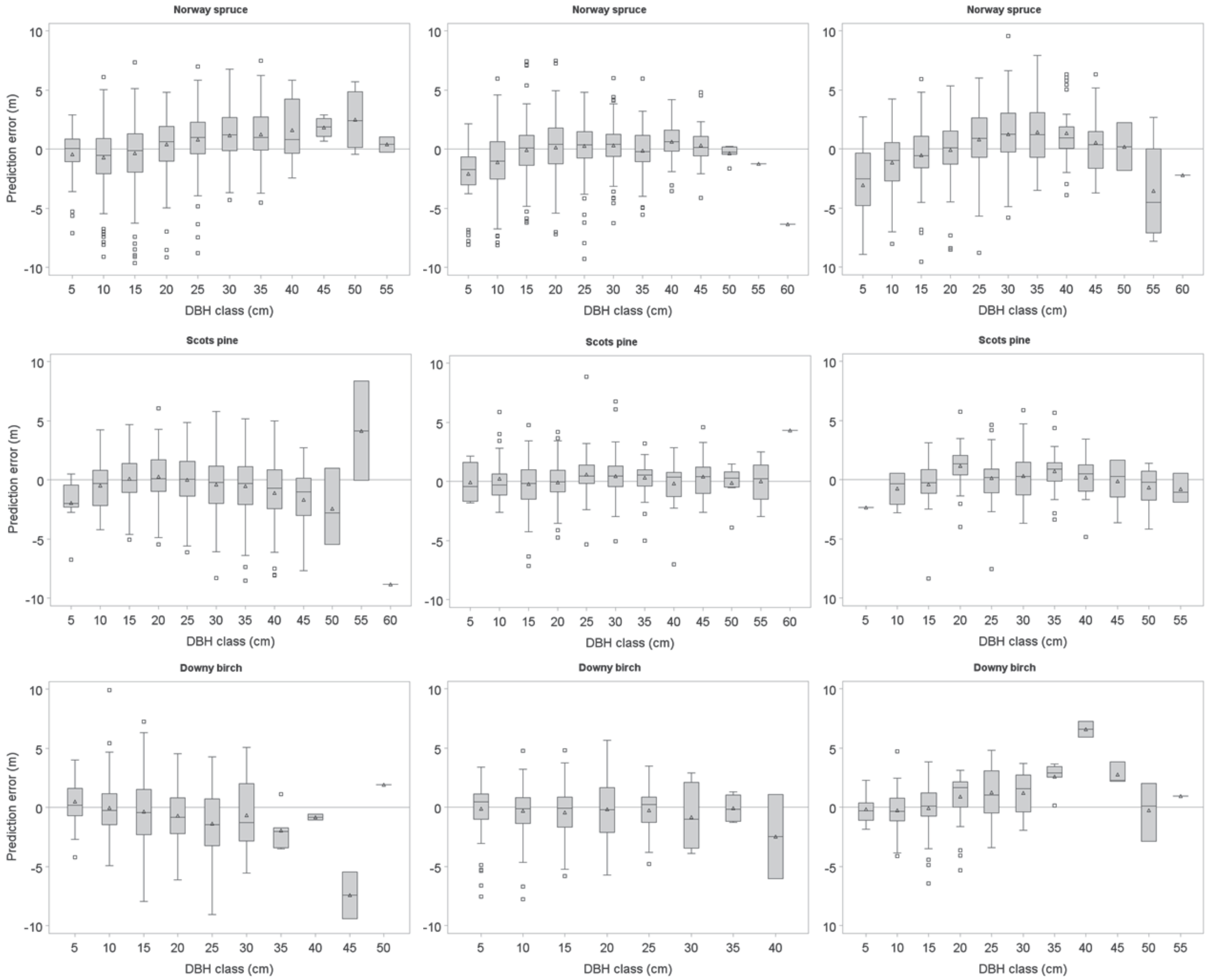

Figure 5. Height prediction errors of a generalized mixed effects model (Eq. 5) for mixed stands of the validation data, where other than the focused species were used for prediction of random effects. Height prediction errors of Norway spruce with random effects estimated from Scots pine, downy birch and other species, respectively (first row). Height prediction errors of Scots pine with random effects estimated from Norway spruce, downy birch and other species, respectively (second row). Height prediction errors of downy birch with random effects estimated from Norway spruce, Scots pine and other species, respectively (third row). Definitions of box-plots and whiskers are the same as in Figure 4.

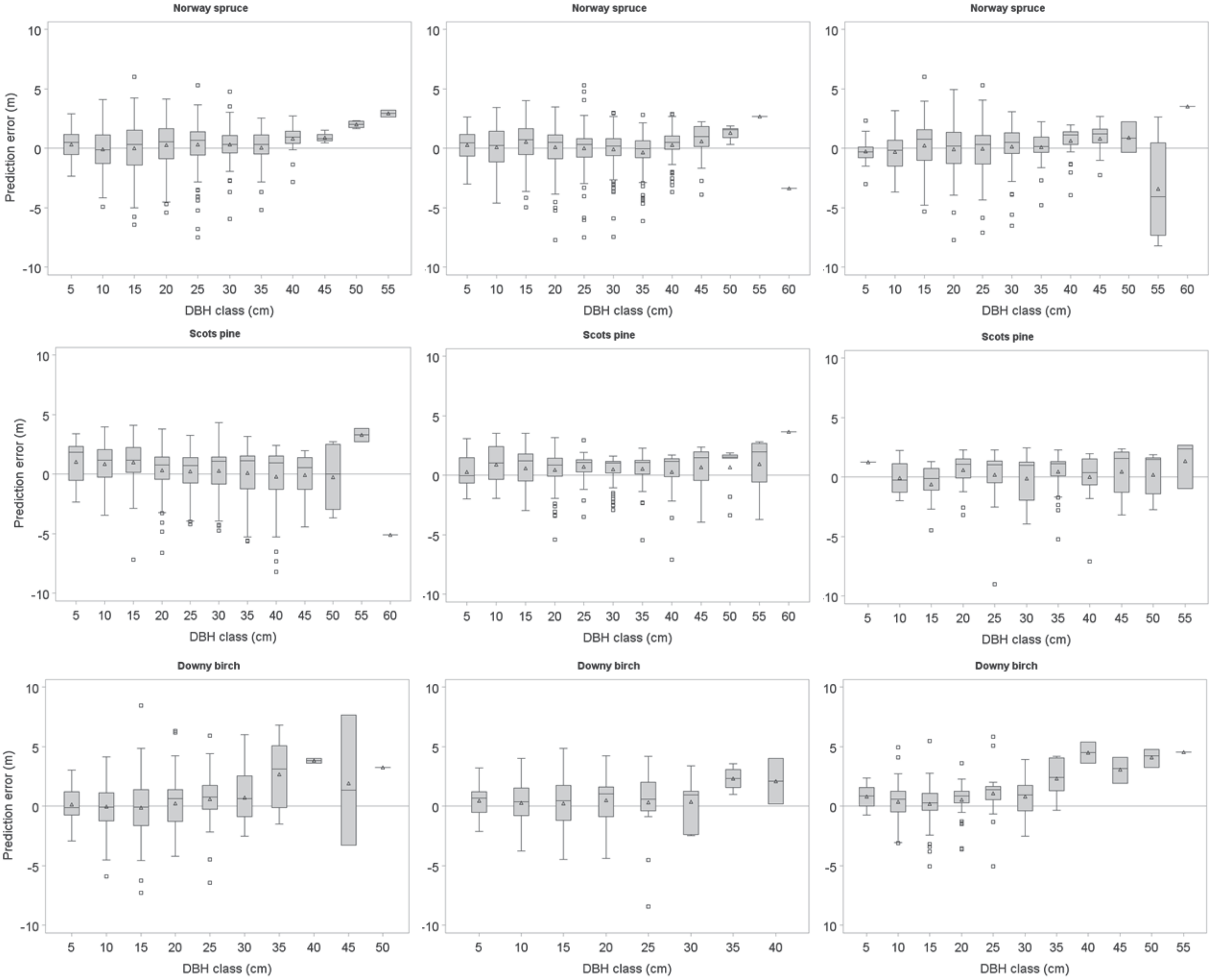

Figure 6. Height prediction errors of a generalized OLS model for mixed species plots of the validation data, where focused species are not available and various species composition exist [Norway spruce - Scots pine, Norway spruce - downy birch, and Norway spruce - other species, respectively (first row); Scots pine - Norway spruce, Scots pine - downy birch, and Scots pine -other species, respectively (second row), downy birch -Norway spruce, downy birch- Scots pine, and downy birch - other species, respectively (third row)]. The sample plots used in each case are the same as in Figure 5. Definitions of box-plots and whiskers are the same as in Figure 4.

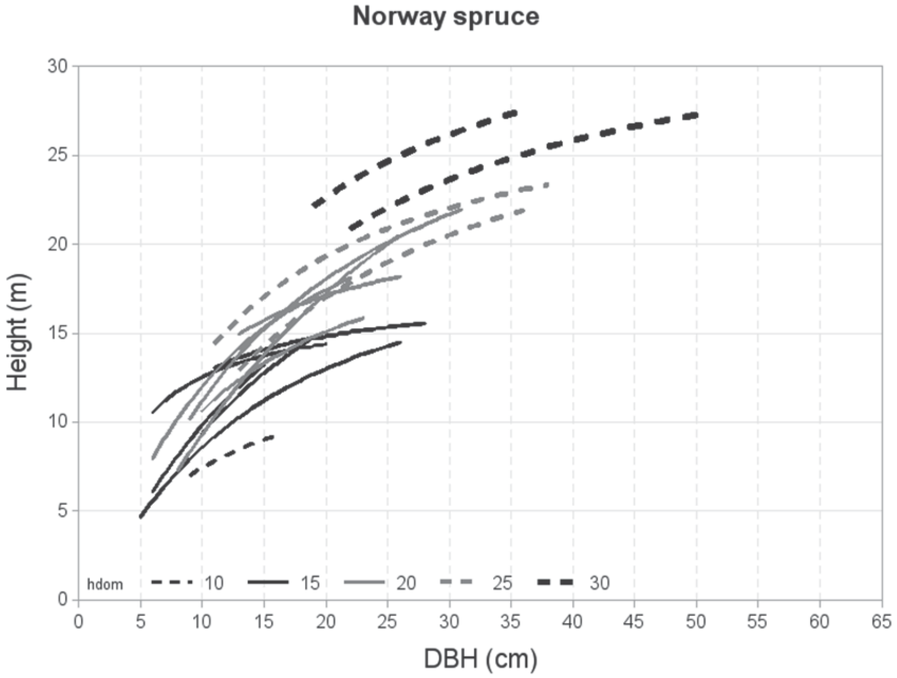

Figure 7. Predicted height-diameter curves of a generalized mixed effects model (Eq. 5) for Norway spruce for the sample plots, where similar *hdom* and *ddom* existed, and observed *hdom* and *ddom* and predicted random effects for such plots were used to generate the curves (*hdom* classes represent *hdom* < 12.5, 12.5 - 17.5, 17.5 - 22.5, 22.5 - 27.5, and > 27.7, respectively)

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