JOURNAL OF FOREST SCIENCE, *59*, 2013 (11): 458–473

Application and limitations of growth models for silvicultural purposes in heterogeneously structured forest in Sweden

L. Drössler[1], **N. Fahlvik**[1,3], **B. Elfving**[2]

[1]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Alnarp, Sweden

[2]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences,, Umeå, Sweden

[3]Institute of Silviculture and Forest Protection, Technical University Dresden, Tharandt, Germany

ABSTRACT: The paper addresses the problem of estimating future stand development in heterogeneously structured forests in Sweden; specifically, multi-layered spruce stands and mature pine stands with advanced spruce undergrowth. We first introduce various supporting concepts and models with their empirical databases, model validation and constraints. Secondly, Swedish single-tree growth functions designed for more heterogeneously structured forest are tested using data from inventory plots, a thinning experiment in an uneven-aged forest stand, and yield plots in pristine forest. Future growth of a managed, multi-layered forest was simulated and is compared with other selected functions. Simulation results, expected errors and time constraints are discussed. For most models, projected stand basal area growth deviated 10–20% from the observed growth in individual stands. In single stands, the deviation ranged from 0 to 60%. Validation periods were often 5–15 years, sometimes even more than 30 years. For Swedish single-tree basal area growth functions, on average, a 5% overestimate was found for heterogeneously structured forest across Sweden. Observed growth in a boreal single-tree selection forest was underestimated by 12.5% fifteen years after thinning from above.

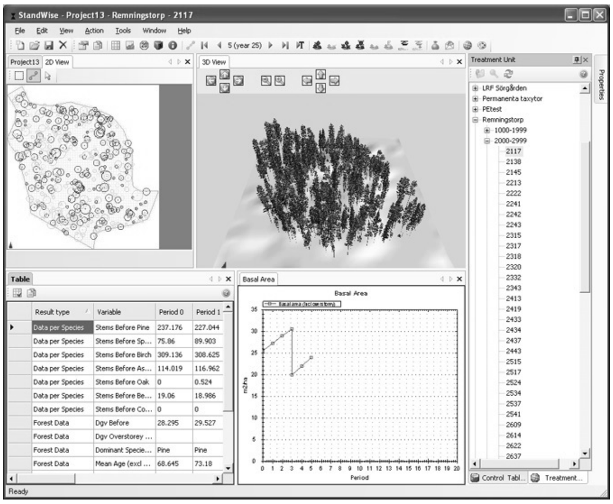
Keywords: continuous cover forestry; heterogeneous forest structure; forest growth; stand development; growth models; Heureka; Sweden

The Swedish University of Agricultural Sciences has developed free software for forest management planning and analysis, with particular focus on multi-purpose forestry (the Heureka system), including management of heterogeneously structured stands. The software package is divided into three main applications: an interactive stand simulator, an optimization tool for long-term forest planning at the landscape level, and a simulator for regional analyses. The system includes empirical models for growth projections and the simulation of treatments, and also procedures for estimating recreation values, carbon sequestration, and habitat suitability (Wikström et al. 2011). At the core of the system are single-tree growth functions developed for management purposes by Söderberg (1986) and Elfving (2004). At the stand level, the simulator StandWise can be used for projections of future forest stand development (Fig. 1).

The Heureka system is commonly used by forest planners, consultants, and researchers; mainly at scales above the single-tree level. However, with its single-tree growth functions, the system provides a tool to compare future stand development if alternative methods to clearfelling are applied, i.e. target diameter cutting. In Heureka StandWise, users can enter tree characteristics such as species, diameters and site variables when running stand simulations. They can even specify whether or not the stand is even-aged (Wikström 2007). If the stand is considered uneven-aged, functions for uneven-aged forest are used to estimate the growth

---

Supported by the Swedish research programs Future Forests and TC4F, and the Southern Swedish Forest Research Centre.



Result type	Variable	Period 0	Period 1
Data per Species	Stems Before Pine	237.176	227.044
Data per Species	Stems Before Sp...	75.86	89.903
Data per Species	Stems Before Birch	309.136	308.625
Data per Species	Stems Before As...	114.019	116.962
Data per Species	Stems Before Oak	0	0.524
Data per Species	Stems Before Be...	19.06	18.986
Data per Species	Stems Before Co...	0	0
Forest Data	Dgv Before	28.295	29.527
Forest Data	Dgv Overstorey ...		
Forest Data	Dominant Specie...	Pine	Pine
Forest Data	Mean Age (excl ...	68.645	73.18

Fig. 1. User interface of StandWise (example with stand map, 3D view, a table with selected stand characteristics, basal area development over time, and a list to select one stand or several sample plots to define the treatment unit)

of single trees. However, the simulation results are more difficult to interpret than for typical even-aged pine or spruce stands.

Generally, models are simplifications of the real world and simulations include uncertainty. In addition, when applying forest growth models with alternative management scenarios for decision support, extrapolation can occur. The extrapolation capability can be higher for general stand growth projections, while it can be more limited for single-tree dependent projections or other long-term sustainability assessments. The purpose of this paper is to explore stand and single-tree growth validations of selected models to assess the reliability of projections for heterogeneously structured stands over different time periods. Since both validation and documentation of growth in heterogeneously structured forests is very limited in Sweden, we also looked over models developed in surrounding countries. The goal of the study was to estimate the length of time over which stand growth models were applicable when simulating future stand growth, harvest or target diameters in multi-layered forest types. Therefore, we address the following questions in the first part of the paper:

– what is a typical validation period for forest models parameterized for Scots pine and Norway spruce stands regardless of the stand structure and mixture?
– what types of forest and data have been selected for parameterization and validation?
– how accurate are the projections in general?

We did not try to identify the best modelling approach, but strived to explore the range of possible errors when applying the Standwise simulator in heterogeneous forest. We then estimated the range of errors for particular forest types, based on the few existing observations and model comparisons. It was hypothesized that (*i*) the prediction of stand basal area growth over 50 years involves errors larger than 10% for single multi-layered stands. We also hypothesized that (*ii*) future tree removals based on target diameter cutting according to predicted diameters in 25 years involve errors of 10% (in terms of removed tree number). To demonstrate how simulation outcomes can be interpreted, the single-tree growth functions for uneven-aged forest were used to predict the future development of a multi-layered stand in southern Sweden.

One aim, here, is to share our experience of applying the Heureka system in forestry practice to assess target diameter cuttings. Future possible developments of the system or ways to complement it with alternative model approaches are also addressed. The tentative validation results were presented and discussed at the annual meeting of the Ertragskunde section of the DVFFA (German Union of Forest Research Organizations) 2013 in Rychnov nad Kněžnou, Czech Republic.

MATERIAL AND METHODS

Typical forest types with a multi-layered stand structure in Sweden

Most Swedish forests are located in the boreal vegetation zone, as part of a transition to the temperate forests in southernmost Sweden (Ahti et al. 1968; Bohn, Weber 2000). Planting after clearfelling and natural regeneration by seed-trees are the dominant regeneration methods on productive forest land (increment > 1 $m^3 \cdot ha^{-1}$). Only 10–20% of the productive forest in northern Sweden and 1–2% in southern Sweden has been classified as "forest with continuous tree cover", which has been described as forest with very rare stand-replacing disturbance regimes (Axelsson et al. 2007). Lundström (2008) identified 0.6 million ha of spruce-dominated forest on mesic and fertile sites with stand structures classified as "not even-aged" (according to the Swedish National Forest Inventory – NFI; Ranneby et al. 1987). Apart from various definitions used by previous authors, Table 1 explains the term "uneven-aged" a bit more as it is used in this paper. In southern Sweden, Drössler (2010) classified 0.9 of 5 million ha of forest as pine-spruce mixtures, half of them older than 80 years and presumably containing a considerable proportion of mature pine with younger, naturally regenerated spruce trees. Two-layered birch-spruce mixtures were not considered in the category of multi-layered stands because they are mostly even-aged and will develop a uniform stand layer (Mård 1996). The proportion of beech forest was too small to assess, both as pure stands and in mixtures (Drössler 2010). The proportion of oak in hemiboreal forest mixtures is higher than that of beech (Drössler et al. 2012a), but spruce is a successful competitor. Nevertheless, there is a certain potential for oak to grow under pine shelter, but only 0.4% of forests (equal to 20,000 ha) were estimated to be pine-oak mixtures in Götaland (Drössler 2010). Therefore, our main focus was on two forest types: pure, uneven-aged spruce stands and mature pine stands with advanced natural regeneration of spruce. Both forest types were considered by the authors to be suitable for continuous cover forestry, in line with ecological theory and experiences in forestry practice.

Selection of concepts and models which might help to assess the future development of multi-layered spruce and pine-spruce forest in Sweden

The forest data used to parameterize and validate silvicultural and ecological models and concepts from Sweden and the neighbouring countries were assessed and summarized. In addition, Swedish growth models designed for even-aged stands were examined, because they provide valuable information under certain conditions (e.g. growth of old pine trees). Growth models from other countries for even-aged stands (i.e. Hynynen et al. 2002; Andreassen, Tomter 2003) were not considered, because Swedish models for even-aged stands were found to be reliable (Ekö 1985; Söderberg 1986; Fahlvik et al. 2013). One exception was the single-tree model of Nagel et al. (2006) from Germany, because it has been used to estimate and compare the future development of even-aged stands after target diameter cutting and under different silvicultural strategies (Duda 2006). During the literature search, the Austrian simulators MOSES and PROGNAUS, and a Belgian succession model (able to track different silvicultural pathways) also appeared to be relevant because they were parameterized and designed for heterogeneously structured forest containing the tree species we were interested in.

In addition, the ingrowth model by Wikberg (2004) that is currently in use was included, as well as the Finnish ingrowth model by Pukkala et al. (2009) for "uneven-sized" forest stands. Mortality models were not explored. The models by Ekö (1985) and Söderberg (1986) included mortality.

Model tests and evaluation

The two terms parameterization and validation were used according to definitions given by Kimmins et al. (2010). They are understood in terms of evaluating whether the output of a forest management model is useful for the intended objective. Validation tests whether the conclusions drawn on the basis of the model can be confirmed by independent data (Kimmins et al. 2010). In our study, validation was limited to independent observations in forest stands or forest inventory plots, while model components (i.e. growth response to temperature) were not considered.

Among the models parameterized under Swedish conditions, projections of single-tree growth functions for a multi-layered forest were compared with 15 years of observations in a managed and an unmanaged uneven-aged spruce forest. Later, the functions were also applied to simulate the development of a multi-layered pine-spruce forest. Based

Table 1. Clarification of the terminology used in this study.

Heterogeneously structured forest		Homogeneously structured forest
uneven-aged forest under quasi-equilibrium conditions	uneven-aged, **multi-layered** forest	Even-aged stands with a single stand height layer (i.e. Nilsson et al. 2010) and uniform shelterwoods (i.e. Holgén et al. 2003)
Single-tree selection forest (i.e. Lundqvist 1989) and pristine forest	i.e., stands managed by target diameter cutting (i.e. Drössler et al. 2012b), irregular shelterwoods and group selection	

we distinguish between uneven-aged stands under equilibrium conditions (= "uneven-aged") and other types of uneven-aged, multi-layered stands (= "multi-layered"). Both types of stands are included in the classification "heterogeneously structured" forest, which is distinct from even-aged stands with a single tree layer on a literature review and model assessments, reasonable time periods for simulating stand growth and structure were suggested. Possible and reasonable ranges of errors were considered. We used the validation criteria for models intended for predictive and decision-making processes according to Kimmins et al. (2010) to assess stand growth and single-tree growth predictions. Thus the following points were investigated or discussed: (1) the accuracy of predictions obtained from the model; (2) the quantitative correspondence between the behaviour of the model and the behaviour of the real forest; (3) the model usefulness; and (4) whether the accuracy of the model predictions is sufficient for the intended use.

RESULTS

Overview of concepts and models applicable to multi-layered coniferous forest types

Nineteen concepts and growth models were found to be relevant for estimating the future development of heterogeneously structured coniferous forests in Sweden (Fig. 2). Nine concepts and models were developed outside the country, of which five were designed for temperate regions. Five Swedish models and one German model were developed for even-aged stands. Fig. 2 gives an overview of the models, with the maximum time horizons applied in projections, and time periods used for parameterization and validation. The conceptual approaches consider fairly long time horizons, but are not parameterized by data. Instead, they are based on expertise (i.e. Engelmark, Hytteborn 1999; Larsen 2005). The longest model projections cover several centuries and estimate tree species composition or forest types (Fig. 2). Most ecological concepts, matrix and process-based models predicted an increase in spruce under continuous cover or close-to-nature forestry (Engelmark, Hytteborn 1999; Bollandsås 2007; Jönsson, Lagergren 2012). Two models predicted an increase in broadleaves: the first is a succession concept from Belgium; the second excluded, theoretically, any human influences in the future, and forecasted a replacement of spruce by beech, ash and oak in central south Sweden (Hickler et al. 2012). Components of this plant-physiological

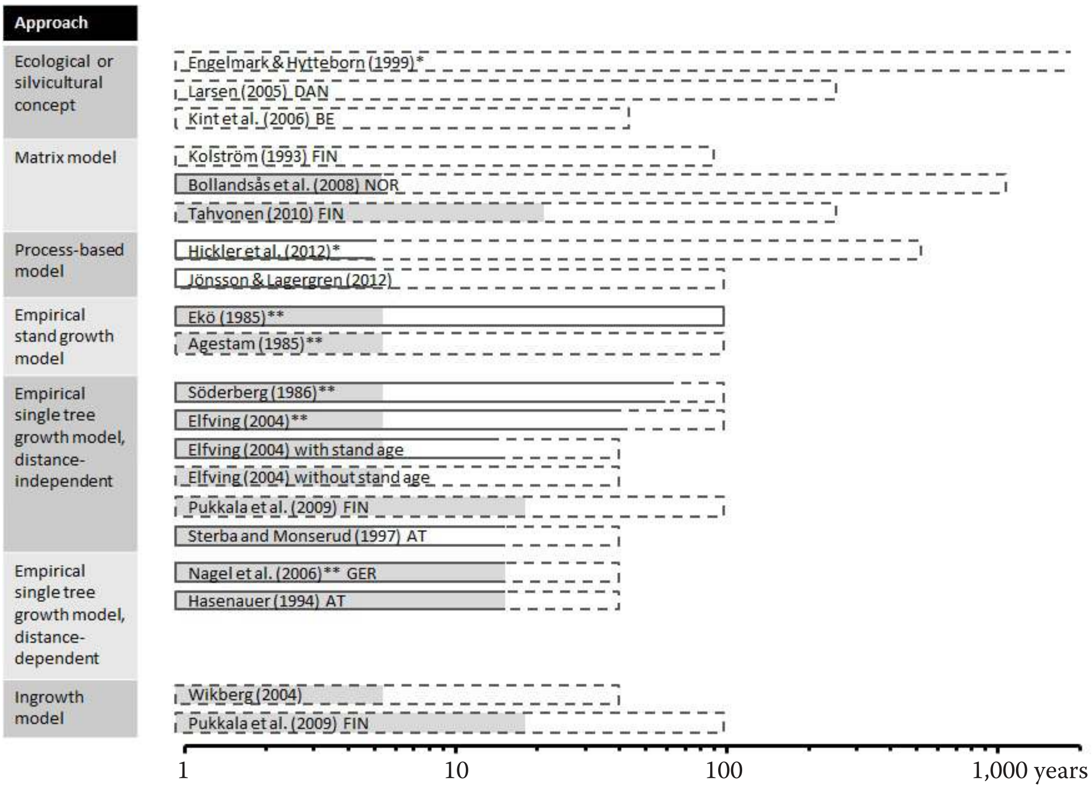


Fig. 2. Concepts, models used to assess the future forest development of more heterogeneously structured stands in Sweden

grey horizontal bars indicate time periods used for model parameterization, dotted lines show time periods applied in the associated literature or recommended by authors, continuous lines indicate time periods used for model validation by growth observation in forests (see the text), *assumed natural development without human influence, **for even-aged stands, DAN – Denmark, BE – Belgium, NOR – Norway, GER – Germany, FIN – Finland, AT – Austria model were validated on a monthly base, but biomass estimates were compared with data from the National Forest Inventory. When forest management was incorporated into the model, a strong increase in spruce under continuous cover forestry was predicted (Jönsson, Lagergren 2012). The matrix model from Norway for forecasting tree species gave similar predictions, but for longer time periods. Growth models applied in forest management usually project basal area (BA), tree numbers, or tree volume by species. For even-aged forests, they often cover one rotation cycle, but exclude the initial stages (the first 10–20 years). Two models for even-aged stands were validated using independent data from the first thinning to the end of the rotation (Ekö 1985; Söderberg 1986). The single-tree model for even-aged stands by Elfving (2004) was compared with 30 years of observations from long-term thinning experiments across Sweden (Nilsson et al. 2010; Fahlvik et al. 2013). Typical validation periods of single-tree growth models are 5–15 years (Sterba, Monserud 1997; Schmidt, Hansen 2007; Elfving 2009). Simulation periods longer than 30 or 40 years are not often recommended for individual tree models (Hasenauer, personal communication; Nagel et al. 2006). However, the Finnish model by Pukkala et al. (2009) was used for simulations over 100 years. The two Finnish matrix models for predicting the future stand structure in particular stands using transition probabilities between different tree size classes (Kolström 1993; Tahvonen et al. 2010) were also designed to cover the whole rotation period.

Description of parameterization and validation data

Information on the parameterization and validation data for the selected models is summarized in Table 2. Most of the validations of growth models showed that stand BA projections usually differ 10–20% from observations in particular stands. But conceptual design and data can vary considerably between models. All stand- and single-tree models from the Nordic countries in Table 2 were parameterized with data from National Forest Inventories (NFI) with systematic forest samples. According to Gadow (2005) such large-scale inventories cover a broader range of site conditions and stand structures than experimental plots. The German model BWinPro was parameterized with data from long-term experimental plots. The number of multi-layered forest stands is rather limited with respect to the data used for parameterization, both for the Nordic and the other models. One interesting exception is Pukkala (2009), who parameterized his model with data from experiments with "uneven-sized" trees and old NFI data originating from a time when multi-layered forest was more common. Hasenauer (1994) and Sterba and Monserud (1997) developed age-independent growth models suitable for mixed or uneven-aged stands in Austria. The latter model over- and underestimated BA growth in mixed pine-spruce stands by approximately 15% during three consecutive 5-year periods. The single-tree model by Hasenauer (1994) includes tree crown parameters and competition indices to reflect silvicultural interventions. It gives reasonable results for future stand BA (0–15% differences over 20 years in different forest districts covering several hundred hectares, as reported by Thurnher et al. 2011) and can estimate mean DBH and its standard deviation in uneven-aged forests (Hallenbarter et al. 2005). Even so, a particular old pure spruce stand 100 km outside the parameterized geographical range with a shifted observation period had 20% higher diameter growth in five years than expected (Hasenauer 1994). However, no general conclusions can be drawn from single observations. The Finnish stand simulator MOTTI (Hynynen et al. 2002) for even-aged stands overestimated growth in very old stands (Hynynen, personal communication). Meanwhile, the oldest thinning experiment in south Sweden (stand age 135 years) still has a current mean annual increment as estimated for the whole rotation period of 70 years (Ekö, personal communication). Such results highlight the difficulties in predicting growth in mature forests.

The data used for parameterization and calibration of the models for multi-layered forest do not allow us to distinguish between single-tree selection stands close to equilibrium conditions and heterogeneously structured stands originating from other types of selective cutting (e.g. shelterwood, target diameter cutting). In general, growth models designed for multi-layered stands are no less validated than models for even-aged stands, but different types of forest structure and species composition can easily outnumber the validated types of multi-layered forest.

Ingrowth

The ingrowth is the weakest component in many growth models designed for multi-layered stands (Hasenauer 2006; Pukkala 2009). Wikberg (2004) used information about new trees found on re-measured NFI plots, whilst Pukkala (2009) examined

Table 2. Concepts and models presented in Fig. 2 with projected features, description of parameterized and validated data, learning outcome and evaluation for the purpose of this study

Author	Projected feature	Parameterization		Validation			Insights	Evaluation
		data source	forest type	data source	forest type	period		
Engelmark and Hytteborn (1999)	Forest type	–		–			Development without management results in spruce-dominated coniferous forest, but with other tree species remaining.	In line with observations in nature reserves. Could be true in an unchanging environment.
Larsen (2005)	Forest type	–		–			Development under close-to-nature management resulting in beech-spruce, Douglas-fir-spruce-beech or pine-birch spruce stands is possible.	Long-term goal which can involve several stand generations. Reasonable for southern Sweden, but depends on silvicultural activity.
Kint et al. (2006)	Forest type	–		–			50% removal in more regularly distributed patterns would result in pine regeneration after 0–9 years in Belgium. Creating larger gaps with progressively increasing areas over 30 years from 15–90% would result in birch-oak regeneration after 0–30 years. Creating smaller gaps and longer shelter periods would result in beech-oak regeneration in 0–42 years.	Designed for Belgium. Longest time periods might be true for southern Sweden, especially when climate changes are taken into consideration. Heavy removals necessary to promote pine, otherwise competing tree species would take over.
Kolström (1993)	Diameter distribution and stand BA, plus regeneration and mortality	Cores from trees in temporary plots	Spruce, "uneven-sized", even-aged and uneven-aged	–			Sustainable harvest proportion for 5 years was 7–20% of BA, depending on initial BA. Extending the thinning interval from 5 to 10 years slightly reduced total removal during the 90-year simulation period.	Overestimated growth of small trees, underestimated growth of large trees. Might reflect stand growth of heterogeneously structured stands in eastern Finland, depending on regeneration.
Bollandsås et al. (2008)	Tree species composition and diameter distribution	Permanent NFI plots	General	Permanent NFI plots	Not specified	10 years	Development of mixed forest under continuous cover forestry results in massive spruce dominance with a small proportion of broadleaves in 400 years.	Spruce increase in line with observations in nature reserves, but the time line is questionable.
Tahvonen et al. (2010)	Diameter distribution and stand BA, plus regeneration, mortality and management costs	92 permanent plots	Spruce, uneven-sized	–			Highest growth occurred under even-aged management with artificial regeneration. Assuming future costs, prices and interest rates, uneven-aged management becomes superior, depending on initial stand state and conditions for natural regeneration.	Locally valid since modelling data comes from two experiments, located close to each other (Pukkala, von Gadow 2012).
Hickler et al. (2012)	Vegetation structure and composition	Climate and soil data, plant responses in different experiments	Species-specific	Sub-models validated			Development of current vegetation under future climate, but with no management, results in beech, ash and oak forest within the next 500 years, spruce would disappear in 300 years.	Indicates increasing beech and oak as a result of future climate change, but simulated proportions remain speculative due to browsing and recent ash die-back which was not incorporated into the model. The Time line questionable.

Author	Projected feature	Parameterization		Validation			Insights	Evaluation
		data source	forest type	data source	forest type	period		
Jönsson and Lagergren (2012)	Vegetation structure and composition, and predisposition to storm damage	Climate and soil data, plant responses in different experiments	Species-specific	Sub-models validated			Continuous cover forestry implemented across the whole landscape would cause a higher predisposition to storm damage than traditional management. Strong increase in spruce within the next 100 years.	Points to the risk of storm damage and includes climate change. Very large difference in tree species composition compared to Hickler et al. (2012) without management. Time line questionable.
Ekö (1985)	BA of tree species	Temporary NFI plots	General	376 permanent plots	Pure spruce and pine, even-aged	40–100 years	Assuming an example similar to the multi-layered pine-spruce stand described in the last section of this paper (with 95-year-old pine and birch trees, and an average of 60 years for spruce and 50 years for oak and beech), CAI of 8–9 $m^3{\cdot}ha^{-1}$ was estimated before cutting. After cutting, 6–7 m^3ha^{-1} CAI was estimated.	Not validated for multi-layered stands, but data used for parameterization should contain a considerable number of more heterogeneous stands. Indicated about 20% (4–60%) differences between observed and projected total volume production per stand over 40 years and more.
Agestam (1985)	BA of tree species	Cores from trees in temporary plots	Mixed forest	61 permanent plots	Mixed forest	5–10-year intervals	No significant growth differences in even-aged, mature spruce-pine mixtures compared to average growth in pure stands.	Not validated, but supports the estimates from the model of Ekö (1985) in even-aged, mature spruce-pine forests.
Söderberg (1986)	Single-tree BA and volume	Temporary NFI plots	General	44 permanent plots	Pure spruce and pine, even-aged	19–63 years	Single-tree functions improved stand growth estimations.	Not validated for multi-layered stands, but data used for parameterization should contain a considerable number of more heterogeneous stands. Reliable BA projection over several decades in even-aged stands, confirming Ekö (1985) with more precise projections.
Elfving (2004) for even-aged stands	Single-tree BA	Permanent NFI plots	Min. 80% volume in one layer	277 permanent plots and 1711 NFI plots	Pure spruce and pine, even-aged, plus other forest types	5–41 years	In general, 5% overestimation (not at the plot level). Small trees were associated with greater overestimates than large trees (in general by 0.6 and 0.3 mm per year). Future tree size variation underestimated.	Not designed for multi-layered stands. More specific than previous Swedish models because more independent variables were used.
Pukkala et al. (2009)	Single tree diameter	Experiments and old NFI (1951–1953)	Uneven-sized	–			Parameterized under Finnish conditions, a simulation on a very fertile *Oxalis-Myrtillus* site (pine H_{100} = 30 m) for 100 years indicated growth similar to estimates by Elfving (2004). Post-thinning basal area above 24 $m^2{\cdot}ha^{-1}$ not recommended. The authors conclude that thinning large trees more heavily than small ones would increase ingrowth. Infrequent heavy thinning may be better for ingrowth than frequent light thinning.	Not validated. Tree clustering and stand history not considered. Data cover different developmental stages of heterogeneously structured stands but not the whole rotation cycle.

Table 2 to be continued

Author	Projected feature	Parameterization		Validation			Insights	Evaluation
		data source	forest type	data source	forest type	period		
Elfving (2004) for multi-layered stands with stand age	Single-tree BA	Permanent NFI plots	Max. 80% volume in one layer	2 permanent plots and 462 NFI plots	Multi-layered, both managed and unmanaged	5–15 years	5% overestimation compared to NFI data. 12.5% underestimation compared to observations in a single-tree selection stand, 5% underestimation in a pristine forest. 2/3 of variation included in the model, but 50–200% deviation from single tree sizes. Assuming a stand age of 60 or 80 instead of 70 years changed total growth projections by 2.5 and 0.8% over 50 years in the simulation example.	Partly validated. Presumably representative of the multi-layered forest types in the data set. Does not reflect silvicultural release of single trees. Most advanced tool for estimates under Swedish conditions.
Elfving (2004) for multi-layered stands without stand age	Single-tree BA	Permanent NFI plots	Max. 80% volume in one layer	–			Estimated CAI before cutting 7 $m^3 \cdot ha^{-1}$, and after cutting 5–6 $m^3 \cdot ha^{-1}$ with a strong thinning effect (5.2 $m^3 \cdot ha^{-1}$ during the first 5 years and 5.8 during the first 10 years). Similar average rates were projected for 50 years. Unexpectedly low increment for a site where 10 $m^3 \cdot ha^{-1}$ MAI for planted spruce was expected.	Not validated. Presumably representative of the multi-layered forest types in the data set. Supported by estimates derived using the model with stand age, but the same model structure and data.
Nagel et al. (2006)	Single-tree volume	Experiments	General	Permanent NFI plots	Pure beech and spruce, even-aged	15 years	A mixed stand with 50–year-old pine and 30–year-old spruce on glacially formed soils produced 13 $m^3 \cdot ha^{-1}$ MAI during a 40-year simulation period with thinning. The authors recommended simulation periods of 30–40 years, not longer.	Parameterized by single-tree observations in long-term measurement plots in Germany. Distance-dependent. Not validated for uneven-aged stands. Compared to Sweden, very high increment on sites where H_{100} = 28 m for pine and 31 m for spruce.
Hasenauer (1994)	Single-tree volume	36 permanent plots	Uneven-aged pine-spruce and beech-spruce	Permanent NFI plots	Not specified	5 years	For a single stand 100 km away from the region used for parameterization, single-tree diameter projections can differ 20% on average. Tree height projections differed by as much as 50% from the growth observed for 5 years.	The distance- and age-dependent model is supposed to reflect silvicultural interventions. Parameterized for a region in Austria originally, the model was recently parameterized for heterogeneous forests in Switzerland and Scotland.
Sterba and Monserud (1997)	Single-tree BA	Permanent NFI plots	General	22 permanent plots	Uneven-aged pine-spruce mixtures	15 years in three 5-year periods	15% over- and underestimated stand BA growth possible within five-year validation intervals.	Distance-independent and based on NFI data from Austria. Similar growth variation between 5-year periods as found by examining cores from trees on NFI plots in Sweden (Elfving 2004).
Wikberg (2004)	Ingrowth (trees with DBH > 4 cm), proportion of saplings	Permanent NFI plots	General	–			Estimated a general 11% probability of ingrowth across all Swedish forest types, decreasing with stand density and age, but increasing with site index.	Data do not refer to silvicultural measures to promote ingrowth. On the contrary, harvest activity reduces ingrowth probability. Field experiments demonstrate larger natural variation.
Pukkala et al. (2009)	Ingrowth, number of new trees (DBH > 5 cm)	Experiments	Uneven-sized	–			Projected 2–7 new trees/ha per year in heterogeneously structured forests with 20–35 $m^2 \cdot ha^{-1}$ BA in Finland.	Data do not refer to silvicultural measures to promote ingrowth. Natural variation can be higher in particular stands than reflected by the model, parameterized for Finnish conditions.

262 experimental plots in Finland. The two models reflect general trends in the occurrence of small trees during the first decades of growth. However, management should not rely on ingrowth predicted after several decades. Simulated ingrowth should be interpreted as representing an overall average for a certain forest type and managers should rely on the assessment of regeneration conditions in the field rather than on the predicted number of new trees. A limited number of experimental plots can show, for instance, that the large variation in tree numbers in particular stands of spruce under single-tree selection can be close to zero or twice as much as expected (Lundqvist 1989; Lähde et al. 2002). Preliminary models to explain the large variation of small trees were developed by Eerikäinen et al. (2007) in Finland using mixed-effects models with components for spatial measures. Even specific process-based models might help to characterize variation better in the future.

Growth models parameterized under Swedish conditions

Conventional Swedish growth functions. Two of the most widely applied and validated growth models in Sweden were developed by Ekö (1985) and Söderberg (1986). The first represents stand growth in 14,000 temporary NFI plots across all typical Swedish forest types measured between 1973 and 1977. Initial state and growth were reconstructed using increment cores from sample trees. To project future stand BA, the model requires species-specific initial stand BA, stem number and age at breast height, in combination with latitude, altitude, climate zone, site index, field vegetation type and soil moisture class as site variables (Ekö 1985). The model was designed to provide estimates of stand BA and volume in an even-aged, pure and mixed forest under different thinning regimes (0–40% removals, thinning from above and below). The validation using 363 permanent experimental plots of pure pine and spruce stands with different thinnings revealed 13% overestimation of BA growth for pine (especially in old stands) and 3% underestimation for spruce. The measurement period was, on average, 50 years and no systematic trend over time was observed. The model was validated with well managed research plots and differences of 7 to 33% in total growth after 40–70 years were found (Ekö 1985). In addition, the extensive data set demonstrated up to 50% deviation from projected growth for single plots (plots with old and mixed forest; Ekö 1985).

At the same time, a stand growth model for mixed forest stands (Agestam 1985) was developed which was parameterized on the basis of tree cores from temporary plots and validated with data from permanent plots. Agestam (1985) reported only small differences from the average yield of pure pine and spruce stands and confirmed projections made by Ekö (1985). Söderberg (1986), for his single-tree model, used the same data set as Ekö (1985) but included single-tree information. He selected a smaller number of plots for validation, but was, therefore, able to predict stand BA growth more precisely: the annual BA growth projections deviated by +11 to –26% for 44 years of observations in 18 permanent plots, residuals (obs/est) were –4.2 ± 11.8 %. The parameterization data used by Ekö (1985) and Söderberg (1986) also contained a considerable proportion of stands managed by selective fellings, the traditional harvesting method before clearfelling became dominant in the 1950s (see Pukkala 2009, who used Finnish NFI data from 1951–1955 to parameterize his model for an uneven-sized forest; see also Elfving, Tegnhammar 1996).

Two decades later, new single-tree and stand growth functions were developed by Elfving (2004) on the basis of ca. 18,500 permanent NFI plots laid out in the period 1983–1987 and re-measured in 1988–1992. Like Ekö (1985) and Söderberg (1986), the NFI data represented both even-aged and more heterogeneously structured forest. Since 1983, plots have been classified as even-aged and uneven-aged (where the latter was defined by > 20% of volume not allocated to the dominant age class; class width 20 years; 27% of plots were classified as uneven-aged according to the definition used in the inventory). However, plots of both classes were used together to parameterize a single function per species to estimate single-tree BA growth (Table 3). In Heureka, the single-tree growth function is controlled by a stand-wise BA growth function which was derived from the same data set (Elfving 2005). Since forest growth was higher than usual during the observation period, the measured increment was corrected specifically to tree species and to regional year ring indices based on tree core samples from the NFI plots (Elfving 2004). Important variables used in these single-tree BA growth functions were tree diameter and tree age, especially for spruce, pine and birch. For pine and spruce, the site index and temperature sum were also important (Elfving 2004). Site index was calculated based on site factors (Hägglund, Lundmark 1977).

Both the new and Söderberg's (1986) functions were implemented in the Heureka package and can be selected separately for simulations. Recently, these functions have been validated with data from 1711 permanent NFI plots covering 5-year periods during the interval 1999–2007 and with 277 permanent plots in a thinning experiment followed for an average of 30 years (Fahlvik et al. 2013) and compared with functions by Ekö (1985). For the NFI data, BA increment could be projected satisfactorily by all models (except the general underestimation at very high BA levels). Single-tree projections had a tendency towards overestimation, especially for unthinned stands. In general, basal area growth was 5% overestimated for the test data set; the residual variation had a magnitude of 0.22 for even-aged and 0.23 for multi-layered plots. The growth of small trees was overestimated more than the growth of large trees. Within the thinning from above treatment, the smallest spruce trees grew ca. 0.6 mm less per year than estimated. Large spruce tree growth was overestimated by ca 0.3 mm per year on average (Fig. 3). The large variation seen in Fig. 3 at the end of the observation period was caused by a lower tree number. Projections for pine were more accurate, overestimating diameter growth of the largest trees by less than 0.1 mm per year.

Swedish growth functions designed specifically for uneven-aged stands. Tree age was an important independent variable in the growth functions of Elfving (2004) described above. Additional functions have been developed to estimate the age at breast height for single trees, separately for even- and uneven-aged forests (Elfving 2003). The functions were based on sampled cores from trees in NFI plots. For multi-layered forest, 9,262 trees were used to derive two single-tree age functions ($R^2 = 0.66$): One function used the basal area weighted mean age as an independent variable, the other one did not use this parameter.

Therefore, two different types of growth functions for multi-layered forests exist. While the first function is the same as that used for even-aged stands (but uses a different age function parameterized by tree cores from uneven-aged forests), the second growth function is stand age-independent and designed for uneven-aged forests only.

Table 3. Number of trees used for the parameterization of single-tree growth functions by Elfving (2004)

Tree species	In even-aged plots	In uneven-aged plots
Pine	64,929	14,870
Spruce	80 060	24,650
Birch	19,568	9,451
Beech	1,157	332
Oak	1,436	686

The basal area growth functions were parameterized with ca 50,000 trees in multi-layered NFI plots (Table 3). While the functions predict mean BA growth very well (error of predicted basal area = 1 cm^2, which is much less than 1 mm of diameter in five years), the variation in tree growth is not fully reflected (i.e. spruce, 26 cm^2 standard deviation of predicted basal area increment compared to an observed value of 42 cm^2, Table 4). Both natural variation and measurement errors can be assumed to cause the large variation.

Tests on data from long-term yield plots indicated that the growth functions did not work well over time when used without stand age as a variable. For this data, for instance, it was necessary to include mean stand age. A residual analysis indicated that the mean age should be reduced by 10% in multi-layered stands to predict growth. In this case, no systematic deviation was found between plots classified as even-aged and "uneven-aged".

Estimated and observed increment in uneven-aged stands. The growth functions for multi-layered forest using mean stand age were tested with 15 years of observations from an uneven-aged spruce stand in Central Sweden (Elfving 2009) managed by single-tree selection (Lundqvist et al. 2007). The initial diameter distribution was characterized by a large number of small trees (on average 500 trees·ha^{-1}

Table 4. Mean, standard deviation and extreme values of observed 5-year basal area increment (cm^2) of trees in multi-layered plots, and the increment predicted using an estimated mean stand age (Elfving 2004)

Tree species	BA increment	*N*	Mean	SD	Min	Max
	observed	14,870	44.1	43.1	–133.4	460.5
Pine	predicted	14,870	43.5	26.9	1.5	301.8
	residuals	14,870	0.6	33.6	–270.3	280.0
	observed	24,650	37.9	42.4	–249.4	836.3
Spruce	predicted	24,650	36.9	25.8	1.1	266.3
	residuals	24,650	1.0	32.1	–330.6	734.6

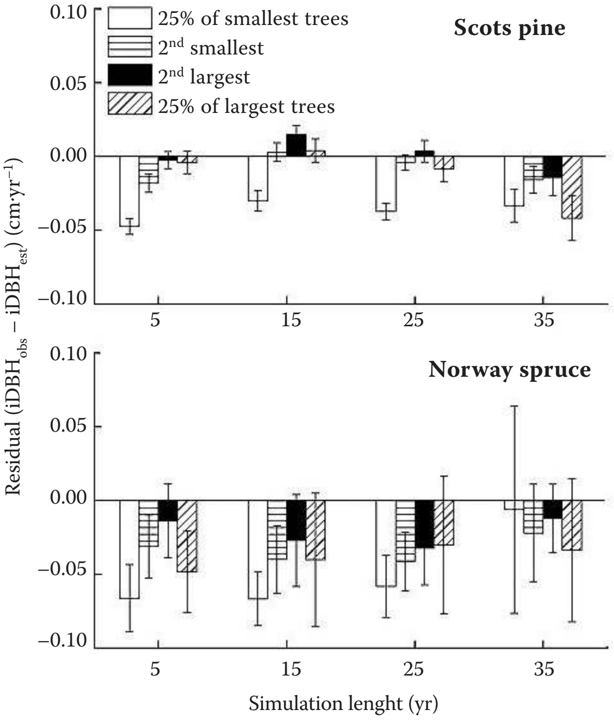


Fig. 3. Residuals between the observed and estimated diameter growth of single spruce and pine trees treated by thinning from above in long-term experiments across Sweden (residuals were analysed in four relative tree size classes with 25% of trees in each class, referring to the diameter at the start of the simulation)

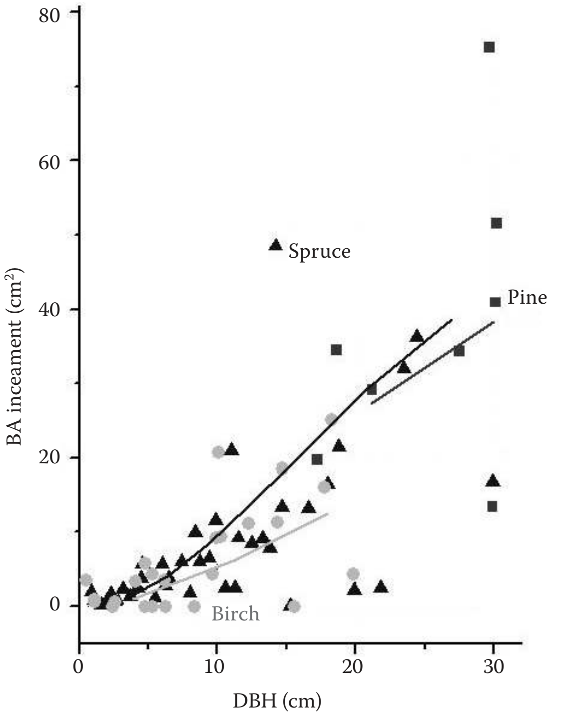


Fig. 4. Single-tree basal area increment in one plot of the pristine forest after 15 years [triangle – spruce, square – pine, circle – birch, lines indicate the relationship between diameter and increment calculated using the tree species-dependent growth function with basal area weighted mean stand age as an additional parameter, which was calculated from single-tree ages estimated by age functions from uneven-aged forests (Elfving 2006)]

with 5–10 cm DBH), a pronounced exponential decrease in tree numbers, and about 50 cm DBH maximum. The model underestimated basal area growth by 12.5% after harvest of the largest trees (Elfving 2009). In the control treatment with no thinning, growth was underestimated by 4%. For small trees with 5–10 cm DBH, the observed values were 20–50% higher than expected (Elfving 2009). Another test was undertaken involving 14 yield plots in pristine forest reserves followed over 16 years. The reserves were described by Linder (1998). The test showed that increment was underestimated by 5% on average, while 2/3 of the variation in single-tree growth could be explained by the model (Elfving 2006). However, these two tests in uneven-aged forest do not allow us to draw a final conclusion. For instance, a preliminary comparison with the most recent 20-year observation period indicated greater underestimates in the selection forest stand (Elfving, personal communication).

More unreliable than stand growth projection was the estimation of future tree diameters. Observations were much more variable than projected by the model, ranging from 50 to 200% of the projected single-tree diameters after 15 years (Fig. 4). In addition, underestimation can occur, as mentioned earlier (Fig. 3).

A third test was carried out to compare estimates of Swedish growth functions with each other in a multi-layered forest in southwest Sweden managed by target diameter cutting. The stand was located on a mesic site, with ground vegetation dominated by *Vaccinium myrtillus* and a podzolic soil developed over sandy moraine. Tree diameters were measured before cutting in systematically distributed plots covering 1.5 ha. No tree coordinates were recorded. The stand was characterized by a 95-year-old Scots pine overstorey and naturally regenerated Norway spruce trees in all height classes (Figs 5 and 6). In addition to spruce, a considerable number of Sessile oaks were present in the lower stand layers. Drössler et al. (2012b) provided a detailed description of the stand, harvest method and simulation approach.

In the first step, stand BA growth without management was projected using different functions. Using a mean stand age of 70 years (based on the recorded age of pine trees and estimates from counting spruce whorls) as an additional independent variable gave similar results to those achieved using the function without stand age. Using stand ages of 60 and 80 years resulted in a range of BA values from 52.5 to

Fig. 5. Part of the example stand

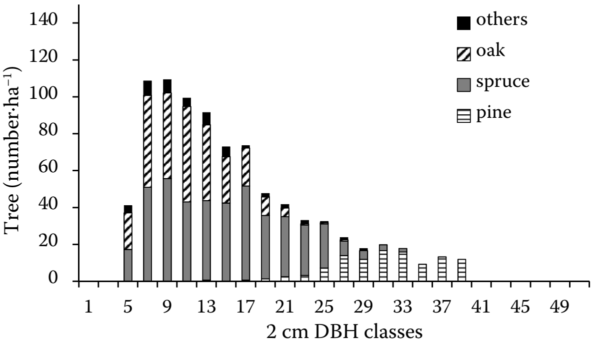


Fig. 6. Diameter distribution and tree species distribution of the example stand after the initial target diameter cutting (target diameter of pine: 40 cm, spruce: 36 cm in the highest quality class, otherwise 26 cm)

54.4 $m^2 \cdot ha^{-1}$ (Fig. 7). The difference is equal to 10% of the projected growth.

In the second step, the single-tree growth functions by Elfving (2004) were applied, both with and without mean stand age, to estimate future BA and diameter distributions. The simulation indicated BA levels between 20 and 35 $m^2 \cdot ha^{-1}$ for managed forest (Fig. 8). Expecting 10% BA growth deviation, an error of 1 $m^2 \cdot ha^{-1}$ within the next 15 years is possible. Assuming 20% growth deviation, an error of 2.5 $m^2 \cdot ha^{-1}$ would occur. In 25 years, at the time of the next cutting, BA could deviate even more since uncertainty increases with every simulation step. At the time of the third cutting, BA growth may differ by 3–8 $m^2 \cdot ha^{-1}$, which would be equal to 9–25% of BA before harvest.

The projected diameter distribution in 25 years (Fig. 9) had fewer trees than today in many DBH classes. The relative proportion of pine trees will decrease and oak trees can be expected to grow more slowly than spruce trees. Fig. 3 indicates that the growth of large trees can be overestimated. Assuming an annual overestimate of 0.3 mm diameter growth for the largest trees, the trees would be 0.75 cm thinner than expected after 25 years. This would result in 5-10 trees·ha^{-1} fewer than the predicted harvest of 120 trees·ha^{-1} in the simulation example (Fig. 9). In addition, projected diameter distributions cannot be expected to reflect the large natural variation in actual single-tree growth (as demonstrated by the two documented examples in this section) and ingrowth. This larger variation in single-tree growth than predicted causes errors which are very difficult to assess. If a similar variation in single-tree growth occurred in the simulation example as that observed in the pristine forest, a tree with 20 cm DBH could grow to any DBH between 25 and 40 cm, compared to 30 cm as projected. In the best case, the error would lead to an underestimate of harvestable trees which could counterbalance their overestimated number caused by diameter growth overestimation. On the other hand, fairly large errors are possible when one or two target diameter harvests are simulated.

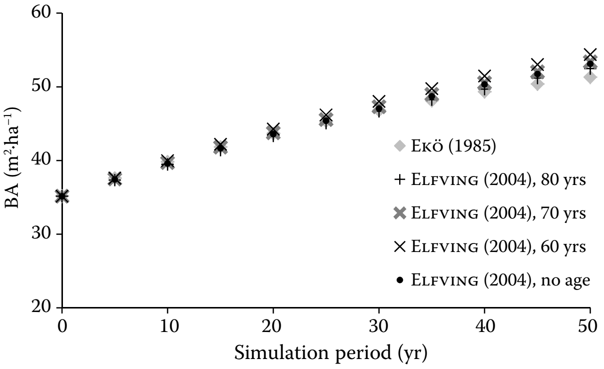


Fig. 7. Comparison of the basal area projections of different growth models for the multi-layered pine-spruce-oak stand without management as described by Drössler et al. (2012b)

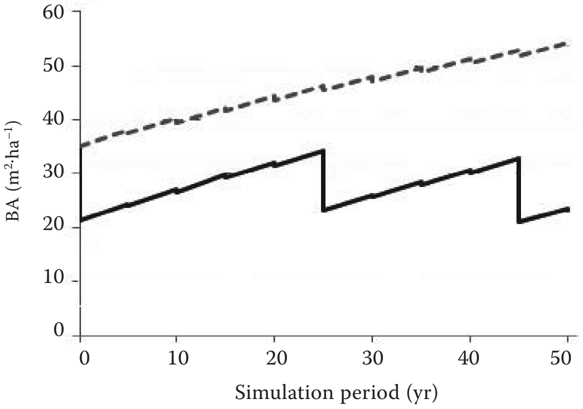


Fig. 8. Projected basal area development without management (dashed line) and after target diameter cutting (straight line) according to the model by Elfving (2004) for a multilayered forest without stand age incorporated as a variable

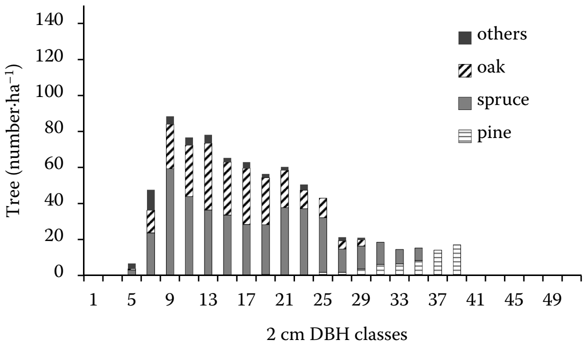


Fig. 9. Projected diameter distribution after the second cutting in 25 years according to the model by Elfving (2004) for a multi-layered forest without stand age incorporated as a variable

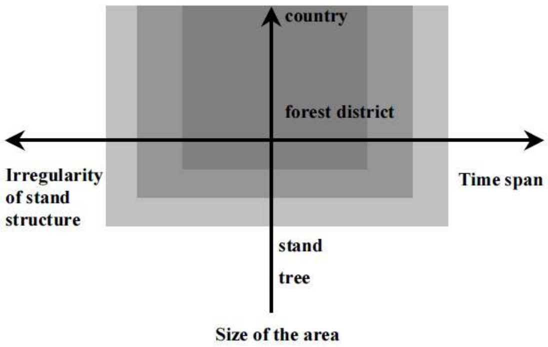


Fig. 10. Schematic representation of the applicability of models used in forest management planning according to Hynynen et al. (2002): the darker the background, the more reliable the model behaviour

DISCUSSION

Conclusions from the very few tests carried out in this study can be only tentative. Over all the models, the validation for multi-layered stands was limited (also due to the variety of possible forest types). At the stand level, 10–20% growth deviation from predicted values was not unusual. In single study plots, the observed deviation could be close to 0 or even amount to 50% of estimated growth. While whole stand models are more robust (Vanclay 1994), simple growth estimates for a single tree are hampered by the large natural variation in individual tree growth. Therefore, growth estimates for a particular tree size class may involve large errors. On the other hand, single-tree models have a better ability to represent complex forest structures and selective cuttings in the long run (Weiskittel et al. 2011).

In general, if simulation periods are longer than validation periods, the reliability is expected to decrease due to inherited errors from previous simulation steps and uncertainties associated with extrapolation. Larger errors can occur with an increasing heterogeneity of forest structure in the long run. Fig. 10 demonstrates how Hynynen et al. (2002) interpreted their growth model at different spatial scales along the time line and a gradient of different forest structures.

Originally, we hypothesized that (*i*) the prediction of stand basal area growth in multi-layered stands over a period of 50 years involves errors larger than 10% for single stands. This hypothesis was not disproven by our tentative results. Using Elfving's (2004) single-tree model, we found a 12.5% underestimate of growth for a single stand just after 15 years. Validations of other models suggested similar deviations, around 10–20%. This finding is not directly comparable to the tested model, but was a pattern repeatedly found in the forest models assessed. More validation of the tested model is required here.

We also hypothesized that (*ii*) future tree removals based on target diameter cutting according to predicted diameters in 25 years involve errors of 10%. This hypothesis could not be tested satisfactorily using the few comparisons available from multi-layered forest. It seems unlikely that the slight overestimation of the average growth of large trees can be the main reason for imprecise projections. In our preliminary conclusion, the large variation in single-tree growth is the greatest uncertainty associated with predicting future tree harvest. Testing the model with even-aged stands suggested similar problems (Fig. 3). When predicting the future stand structure, part of the unknown variation in single-tree growth can be hidden by using wider diameter classes (i.e. only four classes in total; see also Lundqvist et al. 2009). To overcome the modelling problem with increasing differences between observed and estimated diameter distribution ranges, a successive, small adjustment in the diameter class width in proportion to the unexplained growth variation might help. However, more comparisons with single-tree observations in multi-layered forests are necessary to assess the deviation better (see Albrecht et al. 2009, 2012 i.e.). Additional sources of error can occur in association with the mortality and the ingrowth model used in Heureka (Fridman and Ståhl 2001; Wikberg 2004). Ingrowth does not substantially affect total growth during the first two decades in a simulation, but it is crucial when assessing the sustainable yield in the long run.

If mentioned at all, maximum simulation periods of 30–40 years were recommended for different single-tree simulators. Two studies suggested a possibility that quality forecast can be improved when stand- and single-tree-models are combined (Yue et al. 2008; Elfving 2010). The single-tree model by Elfving (2004) provided reasonable results for the 50-year simulation period considered. However, growth after the release of suppressed trees is inadequately reflected by the model. Eventually, particular trees could continue to grow as before cutting or respond according to their biological age. Eventually, the local experiences of the manager might provide a better picture of the development of those trees so far. If sustainability analyses of different silvicultural systems over time horizons longer than 50 years using the Heureka system are required, errors larger than 20% have to be considered. In that case, conceptual models might have a similar precision. Nevertheless, Heureka is used to forecast wood production, to plan forest operations, and to simulate silvicultural management alternatives. The use of such software is required for many reasons and seems to be inevitable (Wikström et al. 2011). Therefore, expected errors and the range of possible errors for single stands should be highlighted when running the simulations.

Outlook. To improve predictions of future stand development, both databases and models should be improved. First, the existing data from observations of experimental plots should be used for wider validation. Results from spruce single-tree selection stands over several decades in central and northern Sweden (Lundqvist 1989) are particularly valuable. Other data collected over 1–2 decades are available for shelterwood experiments across Sweden (e.g. Holgen et al. 2003) and the "NaturKultur" trial with intensive removal of mature trees (Hagner 2004). Secondly, cross-validations with other models could be used to evaluate and improve predictions. In particular, combinations of different modelling approaches seem to be beneficial in the long run (see for example Matala et al. 2003; Pretzsch et al. 2008; Yue et al. 2008). In the Heureka system, stand growth and single-tree growth models are already combined, with the stand growth function controlling total growth of single trees. To reflect the growth of small or large trees better, spatial tree distribution or competition indices for single trees could be incorporated. The trees in uneven-aged stands released after thinning from above responded more slowly than trees in even-aged stands, but seem to reach a higher permanent growth level. They continued to grow like younger trees and this rejuvenation effect should also be included in the model. The Heureka system would even allow the implementation of such additional sub-models.

In general, growth projections for multi-layered stands should be independent of stand age to ensure that simulated growth rates are not forced to slow down over time. One problem with stand age is that it seldom increases by 5 years in a 5-year period. Old trees die and young trees grow into the tree layer. From that point, age is not an ideal variable for growth predictions. On the other hand, validation tests of the Swedish growth functions for multi-layered forests indicated that mean age should be included in order to stabilize the function (Elfving 2010). At present, the age shift in uneven-aged stands is modelled in Heureka, but the models could certainly be improved. Considering the validation paucity, both types of growth model should be tested further in single-tree selection stands.

Management planning in Swedish forestry has a tradition of using stand- and single-tree models as applied in Heureka. While the development of Heureka strives for generalized models that can capture all forest types, every single model mentioned here has particular strengths, drawbacks, time horizons and resolution. To ensure application in forest practice and to avoid severe bias, a model needs to be tested against observed growth in forests on a representative base.

References

Agestam E. (1985): A Growth Simulator for Mixed Stands of Pine, Spruce and Birch in Sweden. Garpenberg, Swedish University of Agricultural Sciences: 150.

Ahti T., Hämet-Ahti L., Jalas J. (1968): Vegetation zones and their sections in northwestern. Annales Botanica Fennica, ***5***: 169–211.

Albrecht A., Hein S., Kohnle U., Biber P. (2009): Evaluierung des Waldwachstumssimulators Silva 2.2 anhand langfristiger ertragskundlicher Versuchsflächen in Baden-Württemberg. Allgemeine Forst- und Jagdzeitung, ***180***: 55–64.

Albrecht A., Kohnle U., Nagel J. (2012): Parametrisierung und Evaluierung von BWinPro für Baden-Württemberg anhand waldwachstumskundlicher Versuchsflächendaten. Freiburg, Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg: 40.

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***: 11–24.

Axelsson R., Angelstam P., Svensson J. (2007): Natural forest and cultural woodland with continuous tree cover in Sweden: How much remains and how is it managed? Scandinavian Journal of Forest Research, ***22***: 545–558.

Bohn U., Weber H. (2000): Map of Natural Vegetation of Europe. Bonn, Bundesamt für Naturschutz.

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

Drössler L. (2010): Tree species mixtures – a common feature of southern Swedish forests. Forestry, ***83***: 433–441.

Drössler L., Attocchi G., Jensen A.M. (2012a): Occurrence and management of oak in southern Swedish forests. Forstarchiv, ***83***: 163–169.

Drössler L., Fahlvik N., Ekö P.M. (2012b): Stand Structure and Future Development of a Managed Multi-Layered forest in Southern Sweden: Erikskö p – A Sase Study. Alnarp, Southern Swedish Forest Research Centre: 75.

Duda H.A.A. (2006): Vergleich forstlicher Managementstrategien. Umsetzung verschiedener Waldbaukonzepte in einem Waldwachstumssimulator. Available at http://resolver.sub.uni-goettingen.de/purl/?webdoc-1300 (accessed 12.6.2013).

Eerikäinen K., Miina J., Valkonen S. (2007): Models for the regeneration establishment and the development of established seedlings in uneven-aged, Norway spruce dominated forest stands of southern Finland. Forest Ecology and Management, ***242***: 444–461.

Ekö P.M. (1985): A Growth Simulator for Swedish Forests, Based on Data from the National Forest Survey. Umeå, Swedish University of Agricultural Sciences: 86.

Elfving B. (2003). Individual-Tree Basal Area Growth Functions for Forest Growth Predictions. Umeå, Swedish University of Agricultural Sciences: 44. (in Swedish with English summary)

Elfving B. (2004): Basal area growth functions for single trees, based on data of the Swedish national forest inventory. Unpublished manuscript. (in Swedish)

Elfving B. (2005): One basal area growth function for all tree species in Sweden. Unpublished manuscript. (in Swedish)

Elfving B. (2006): Pristine forest dynamics. Unpublished manuscript. (in Swedish)

Elfving B. (2009): Analysis of stand development on single-tree selection plot 2280 Fagerland/Hammerdal. (unpublished manuscript)

Elfving B. (2010): Growth modelling in the Heureka system. Unpublished manuscript. Available at http://heurekaslu.org/wiki/Heureka_prognossystem_(Elfving_rapportutkast).pdf (accessed June12, 2013).

Elfving B., Tegnhammar L. (1996): Trends of tree growth in Swedish forests 1953–1992: An analysis based on sample trees from the national forest inventory. Scandinavian Journal of Forest Research, ***11***: 26–37.

Engelmark O., Hytteborn H. (1999): Coniferous forests. Acta Phytogeographica Suecica, ***84***: 55–74.

Fahlvik N., Elfving B., Wikström P. (2013): Evaluation of growth functions used in the Heureka forest planning system. (submitted)

Fridman J., Ståhl G. (2001): A three-step approach for modelling tree mortality in Swedish forests. Scandinavian Journal of Forest Research, ***16***: 455–466.

Hägglund B., Lundmark J.E. (1977): Site index estimation by means of site properties. Studia Forestalia Suecica, ***138***: 38.

Hagner M. (2004): Naturkultur. Ekonomiskt skogsbruk kännetecknat av befriande gallring och berikande Plantering. [Naturkultur - Forest Management with Single Tree Release and Enrichment Planting.] Umeå, Mats Hagners bokförlag: 203.

Hallenbarter D., Hasenauer H., Zingg A. (2005): Validierung des Waldwachstumsmodells MOSES für Schweizer Wälder. Schweizerische Zeitschrift für Forstwesen, ***156***: 149–156.

Hasenauer H. (1994): Ein Einzelbaumwachstumssimulator für ungleichaltrige Fichten-, Kiefern- und Buchen-Fichtenmischbestände. Wien, Forstliche Schriftenreihe Universität für Bodenkultur: 152.

Hasenauer H. (2006): Sustainable Forest Management. Growth models for Europe. Berlin, Heidelberg, Springer: 398.

Hickler T., Vohland K., Feehan J., Miller P.A., Smith B., Costa L., Giesecke T., Fronzek S., Carter T.R., Cramer W., Kühn I., Sykes M.T. (2012): Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species based dynamic vegetation model. Global Ecology and Biogeography, ***21***: 50–63.

Holgén P., Söderberg U., Hånell B. (2003): Diameter increment in *Picea abies* shelterwood stands in northern Sweden. Scandinavian Journal of Forest Research, ***18***: 163–167.

Hynynen J., Ojansuu R., Hökkä H., Salminen H., Siipilehto J., Haapala P. (2002): Models for predicting stand development in MELA System. Vantaa, Research Papers, ***835***: 116.

Jönnson A.M., Lagergren F. (2012): Climate change and the risk of forest damage. Mistra-Swecia, Annual report 2011: 13–15.

Kimmins H., Blanco J.A., Seely B., Welham C., Scoullar K. (2010): Forecasting Forest Futures: A Hybrid Modelling Approach to the Assessment of Sustainability of Forest Ecosystems and their Values Earthscan. London, Washington, Routledge: 304.

Kint V., Geudens G., Mohren G.M.J., Lust N. (2006): Silvicultural interpretation of natural vegetation dynamics in ageing Scots pine stands for their conversion into mixed broadleaved stands. Forest Ecology and Management, ***223***: 363–370.

Kolström T. (1993): Modelling the development of an uneven-aged stand of *Picea abies*. Scandinavian Journal of Forest Science, ***8***: 373–383.

Lähde E., Laiho O., Norokorpi Y., Saksa T. (2002): Development of Norway spruce dominated stands after single-tree selection and low thinning. Canadian Journal of Forestry Research, ***32***: 1577–1584.

Laiho O., Lähde E., Pukkala T. (2011): Uneven- vs even-aged management in Finnish boreal forests. Forestry, ***84***: 547–556.

Larsen J.B. (2005): Naturnær skovdrift. [Natural Forest Management.] København, Dansk Skovforening: 400.

Linder P. (1998): Stand structure and successional trends in forest reserves in boreal Sweden. Acta Universitatis agriculturae Sueciae, Silvestria, ***72***: 17–33.

Lundqvist L. (1989): Blädning i granskog - strukturförändringar, volymtillväxt, inväxning och föryngring på försöksytor skötta med stamvis blädning. [Changes in the Stand Structure on Experimental Plots Managed with Single-Tree Selection.] [Ph.D. Thesis.] Umeå, Swedish University of Agricultural Sciences: 25.

Lundqvist L., Chrimes D., Elfving B., Mörling T., Valinger E. (2007): Stand development after different thinnings in two uneven-aged *Picea abies* forests in Sweden. Forest Ecology and Management, ***238***: 141–146.

Lundqvist L., Cedergren J., Eliasson L. (2009): Blädningsbruk. [Selection cutting.] Skogsskötselserien, ***11***: 4–13.

Lundström A. (2008): Regional Analyses of Old-Growth Forests and Continuous Cover Forestry. Jönköping, Skogsstyrelsen: 15

Mård H. (1996): The influence of a birch shelter (*Betula* spp) on the growth of young stands of Picea abies. Scandinavian Journal of Forest Research, ***11***: 343–350

Matala J., Hynynen J., Miina J., Ojansuu R., Peltola H., Sievänen R., Väisänen H., Kellomäki S. (2003): Comparison of a physiological model and a statistical model for prediction of growth and yield in boreal forests. Ecological Modelling, ***161***: 95–116.

Nagel J., Duda H., Hansen J. (2006): Forest Simulator BWINPro7. Forst und Holz, ***61***: 427–429.

Nilsson U., 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.

Pinjuv G., Mason E.G, Watt M.S. (2006): Quantitative validation and comparison of a range of forest growth models, Forest Ecology and Management, ***236***: 37–46.

Pretzsch H., Grote R., Reineking B., Rötzer T., Seifert S. (2008): Models for forest ecosystem management: A European perspective. Annals of Botany, ***101***: 1065–1087.

Pukkala T., Lähde E., Laiho O. (2009): Growth and yield for uneven-sized forest stands in Finland. Forest Ecology and Management, ***258***: 207–216.

Pukkala T., von Gadow K. (2012): Continuous Cover Forestry. Dordrecht, Heidelberg, London, New York, Springer: 296.

Ranneby B., Cruse T., Hägglund B., Jonasson H., Swärd J. (1987): Designing a new national forest inventory for Sweden. Studia Forestalis Suecica, ***177***: 29.

Schmidt M., Hansen J. (2007): Validierung der Durchmesserzuwachsprognose des Wachstumssimulators BWINPRO 7.0 für Fichte und Buche für den Bereich der alten Bundesländer. In: Proceeding of the annual DVFFA meeting Sektion Ertragskunde. Alsfeld-Eudorf, 21.–23. May 2007. Göttingen, Nordwestdeutsche Forstliche Versuchsanstalt: 164–179.

Söderberg U. (1986): Functions for Forecasting Timber Yield: Increment and Form Height of Individual Trees of Native Tree Species in Sweden. Umeå, Swedish University of Agricultural Sciences: 251.

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

Tahvonen O., Pukkala T., Laiho O., Lähde E., Sami N. (2010): Optimal management of uneven-aged Norway spruce stands. Forest ecology and management, ***260***: 106–115.

Thurnher C., Klopf M., Hasenauer H. (2011): Forests in transition: a harvesting model for uneven-aged mixed species forests in Austria. Forestry, ***84***: 517–526.

Vanclay J.K. (1994): Modelling Forest Growth and Yield. Wallingford, CAB International: 286.

von Gadow K. (2005): Forsteinrichtung. Analyse und Entwurf der Waldentwicklung. Göttingen, Universitätsverlag Göttingen: 246.

Weiskittel A.R., Hann D.W., Kershaw J.A., Vanclay J.K. (2011): Forest Growth and Yield Modeling. Chicester, Wiley-Blackwell: 415.

Wikström P. (2007): Economics and Productivity in Selection Harvesting in Norway Spruce Stands in Sweden – Summary of Results from a Simulation Study. Umeå, Swedish University of Agricultural Sciences: 10.

Wikström P., Edenius L., Elfving B., Eriksson L.O., Lämås T., Sonesson J., Öhman K., Wallerman J., Waller C., Klintebäck F. (2011): The Heureka Forestry Decision Support System: An Overview. Mathematical and Computational Forestry and Natural-Resource Sciences, ***3***: 87–94.

Wikberg P.E. (2004): Occurrence, Morphology and Growth of Understory Saplings in Swedish Forests. [Ph.D. Thesis.] Acta Universitatis Agriculturae Sueciae. Silvestria, ***322***: 25.

Yue C., Kohnle U., Hein S. (2008): Combining tree- and stand-level growth models: a new approach to growth prediction. Forest Science, ***54***: 553–566.

Received for publication June 12, 2013
Accepted after corrections November 5, 2013

Corresponding author:

Dr. Lars Drösser, Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences,
Rörsjövägen 1, SE-23053 Alnarp, Sweden
e-mail: Lars.drossler@slu.se