SILVA FENNICA
Silva Fennica 46(4) research articles
www.metla.fi/silvafennica · ISSN 0037-5330
The Finnish Society of Forest Science · The Finnish Forest Research Institute

Forest Stand Modelling As a Tool to Predict Performance of the Understory Herb *Cornus suecica*

Eivind Meen, Anders Nielsen and Mikael Ohlson

Meen, E., Nielsen, A. & Ohlson, M. 2012. Forest stand modelling as a tool to predict performance of the understory herb *Cornus suecica*. Silva Fennica 46(4): 479–499.

Forest simulation models have been widely used to predict future stand structure. Generally these models do not include the understory vegetation and its response on stand structure change or other environmental factors. Previous simulation studies have shown that stand structure related variables, e.g. basal area, can explain diversity of the forest floor vegetation in boreal forests. We hypothesise that such variables also can be used to explain the performance of understory species and we conceptualise how plant ecology and forest modelling can be combined to predict the performance of understory plants in Norwegian boreal forests. We predict the performance of an understory plant species (*Cornus suecica*) over time using simulated values of forest variables as input to models expressing the relationship between forest environment variables and plant performance variables (viz. plant height, plant dry weight, number of flowers, number of branches and number of leaves). We also present relationships between plant performance and explanatory variables commonly used in basic ecological research, variables that currently not are readily compatible with forest simulators (e.g. soil chemical variables).We found basal area of canopy trees being the most important explanatory variable explaining *C. suecica* performance. The performance variable dry weight was predicted by one single model whereas the other performance variables were best predicted by model averaging. Forest simulations for 150 years showed values of plant performance of *C. suecica* to be reduced during forest succession.

Keywords stand structure dynamics, forest simulator, composite models, field layer, canopy layer, Akaike's information criterion

Addresses Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management, P.O. Box 5003, NO-1432 Ås, Norway **E-mail** eivind.meen@umb.no

Received 27 February 2012 **Revised** 9 July 2012 **Accepted** 10 July 2012
Available at http://www.metla.fi/silvafennica/full/sf46/sf464479.pdf

1 Introduction

Loss of biodiversity is seen as one of the major negative consequence of current forest management practices (Ohlson et al. 1997, Bengtsson et al. 2000, Wolfslehner and Vacik 2008). Most of the plant biodiversity in boreal forests is located in the understory (Gilliam and Roberts 2003, Halpern and Spies 1995, Økland and Eilertsen 1996) and the dynamics of the understory vegetation is greatly influenced by the structure and dynamics of the tree canopy layer (Klinka et al. 1996, McKenzie et al. 2000, Miina et al. 2009). Understanding the relationship between forest canopy structure and understory dynamics is therefore important for sustainable forest management and biodiversity conservation (Hart and Chen 2006, Miina et al. 2010). In particular, the species composition and primary production in the understory respond to changes in the availability of photosynthetically active radiation (PAR) at the forest floor, determined by the structure of the canopy layer (Kellomäki and Väisänen 1991, Van Couwenberghe et al. 2011). In addition, the tree canopy layer affect the understory vegetation through root competition and changed nutrient and water availability (Coomes and Grubb 2000, Légaré et al. 2001). Conversely, the understory community also affects tree growth and canopy succession through a broad range of interference mechanisms that impact tree seed germination and seedling establishment success (Zackrisson et al. 1995, Hörnberg et al. 1997) and nutrient availability (Zavitkovski 1976, Carleton and Read 1991).

Monitoring the relationship between stand structure succession and changes in the understory vegetation is labour intensive and time-consuming. In principle a combination of models predicting plant performance, viz. a measure of plant growth and reproduction which determine plant viability, and simulations of the forest environment provided by a forest model can potentially be used as a supplement to vegetation monitoring in the field. Forest simulation models are models quantifying annual tree growth, tree establishment and death (Shugart and West 1980), providing information on the structural premises for forest dwelling species. However, Weisberg et al. (2003) point at a common lack of link between mathematical models of understory vegetation dynamics and forest simulation models. Changes in the understory vegetation can be simulated by gap models (see Peng 2000 for classifications of forest models) in the same way as for the tree canopy, but as stated by McKenzie et al. (2009) this has rarely been done. An operational framework of canopy-understory models may facilitate other ecological modelling issues. Current predictive habitat distribution models relate geographical distribution of species or communities to the present environment, hence, such models are static (Guisan and Zimmermann 2000). Forest simulation models linked to understory plant performance can make predictions of habitat distribution more dynamic by also including forest succession. McKenzie et al. (2009) suggest including empirical models for understory components in forest models until an explicit mechanistic framework is developed. A quantification of plant performance variables is thus important to understand how the understory vegetation is affected by changes in the tree canopy layer. There is also a need for more knowledge about the relationships between understory plant performance and stand structure dynamics in order to develop forest management strategies that can sustain the biodiversity in the understory vegetation.

Based on one focal species, an understory forest plant, the aim for this study is to conceptualize how forest simulations and plant ecology can be combined to predict performance of understory vegetation in boreal forests. We use two types of model selection approaches to increase the understanding of the relationship between variables describing the forest environment and variables describing the performance of the focal species. The first approach (approach I) is based on a small number of explanatory variables, corresponding to variables derived from the results generated by a chosen forest simulator. The selected plant performance models are connected with the derived variables from the forest simulations, predicting plant performance during 150 year of stand dynamics. The second approach (approach II) is based on all registered field variables, i.e. not only variables corresponding to the forest simulator results. Assessed on previous simulation studies where stand structure related variables have been found to explain diversity of ground vegetation in boreal forests (Kolström and Pitkänen 1999) we state the a priori hypothesis (Thompson III 2010) that stand structure related variables can be sufficient for explaining performance of a plant in the understory.

Our focal understory plant species is the Lapland Cornel *Cornus suecica* (L.), which is widespread in NW European boreal forests (Hultén and Fries 1986). The general biology of *C. suecica* is reviewed by Taylor (1999), but surprisingly few studies have targeted the species and our knowledge about its ecology in relation to forest dynamics and management is very modest. Actually we know of only a few studies of *C. suecica* with a forest ecological perspective. In Finland, Kujala (1964) found tree felling not to negatively affect the appearance of *C. suecica* and in Norway Nygaard and Ødegaard (1999) reported that the occurrence declined with increasing forest stand age. Consequently, by selecting *C. suecica* as focal species, we will also add to our knowledge about a forest species that has been only little studied so far.

2 Materials and Methods

2.1 Study Species

Cornus suecica has two separate distributions areas, one North Atlantic and one Pacific (Hultén and Fries 1986). In Europe it is mainly found in Scandinavia with extensions into Northern British Isles (mainly Scotland) and arctic and subarctic regions of Russia and Iceland. Outlying populations extend southwards to the coastal region of Estonia and Poland, Schleswig-Holstein in north-west Germany and the Netherlands. Outside Europe, the species occurs in western Greenland, Baffin Island, Quebec, Labrador, Newfoundland, north-eastern and north-western United States, Yukon, Alaska, Aleutian Islands and in far eastern Russia (after Hultén and Fries 1986 and Taylor 1999).

In Scandinavia *C. suecica* is common throughout the boreal zone, especially on relatively nutrient poor soils (Lid et al. 2005). In Norway the species is widespread in *Vaccinium myrtillus* forests and is a sub-dominant character species in the oceanic influenced *Vaccinium myrtillus-Cornus suecica* forest type (Fremstad 1997, Moen 1998). In Finland *C. suecica* occurs mainly in northern Finland and at the sea coasts in western Finland (Kujala 1964) and is registered to be more frequent and abundant on herb-rich heath sites (*V. myrtillus* type) than on mesic ones (Lehtelä et al. 1996).

Cornus suecica is a rhizomatous herb with erect, annual stems growing 6–30 cm tall. Inflorescences are terminal umbel-like with 8–25 dark purple flowers, each with a short stalk 1–2 mm, surrounded by 4 white ovate involucral bracts (Taylor 1999). Stems and leaves die off in autumn and new shoots develop from buds next year. In the study area flowers of *C. suecica* are frequently visited by insects, mainly dipterans of the families Muscidae and Empididae (A. Nielsen unpublished data).

2.2 Study Area and Collection of Stand Structure Data

To assess relationships between the performance of *C. suecica* and variables describing the structure of the forest canopy and other aspects of the forest environment (viz. soil chemistry and elevation) we used a study area situated (59°21´N, 9°45´E) in a boreal forest landscape in Telemark County, South Eastern Norway. The study area represents a typical intensively driven Norwegian boreal forest landscape with even aged forest stands consisting mainly of Norway spruce *Picea abies* (L.) Karst.

Within an area of approximately 3.5 × 2.5 km in size, we selected 25 forest stands, located approximately 440 to 530 meters above sea level, representing the full span in forest maturity classes found in the area; from clear cuts to old growth forest (> 100 years). The stands encapsulated a span in site index from 8 to 17, with the majority of plots in site index 14. The site index on each site was retrieved from stand maps made available by the forest owner (Fritzøe Skoger). Site index is the common productivity measure in Norwegian forestry and is defined as mean height at breast height of the dominant trees in a stand at 40 years of age at breast height, ranging from 8 to 26 meters for *P. abies* in Norway (Tveite 1977, Braastad 1980). The tree ages for the different maturity classes are (for site index 11, with site index 14 in brackets): Maturity class 1 equals newly logged stands, with no trees of diameter >5 cm at breast height (1.3 m above ground); maturity class 2: 15–35 (13–30) years; maturity class 3: 35–70 (30–60) years; maturity class 4: 70–100 (60–90) years; maturity class 5: >100 (>90) years.

Within each forest stand we selected a sampling plot based on the presence of three plant species, namely *Vaccinium myrtillus* (L.), *Cornus suecica* and *Melampyrum pratense* (L.). If a forest stand contained more than one appropriate study plot, one study plot was randomly selected. The forest surrounding the sampling plot was measured in two separate ways. First, the number of trees within a radius of 5.6 meters (100 m^2) was counted to quantify the density of the forest on a small scale. Second, the number of trees per species and their basal area on a 10 000 m^2 scale was registered using a relascope (Bitterlich 1984). The trees selected by the relascope were also used to calculate average height weighted by basal area. At both scales only trees with diameter larger than 5 cm at 1.3 m breast height (dbh) were included. All sampling and measurements were done during the summer of 2003. See Nielsen et al. (2007) for further details on the study area.

Picea abies was present in 24 out 25 stands, ranging from 33 percent to 100 percent in stem number of all trees, and ranging from 50 to 100 percent of total basal area (appendix A). In 18 stands *P. abies* counted for two thirds of the basal area. *Pinus sylvestris* (L.) was present in 9 plots with relatively higher proportion of basal area than number of trees. *Betula* sp. (*B. pendula* (L.) and *B. pubescens* (Ehrh.)) did not show a consistent pattern of high abundance in young stands. For instance, in 2 of 5 plots of maturity class 3 (young production forest) *Betula* sp. were not present. The heterogeneity in tree species composition was considered to be too small to be included as a biological meaningful variable in the data analysis.

2.3 Quantifying Plant Performance

Performance variables were measured by sampling 10 flowering stalks of *C. suecica* per study site, selected at regular intervals along a 10 meter line. The line was laid out with approximately 5 m to each side of the plot, in the direction of the slope surrounding the plot. On each flowering stalk vegetative performance variables, i.e. number of branches, number of leaves, plant height and plant dry weight, and generative performance variables, i.e. number of flowers and number of berries, were registered. Only above ground plant parts were measured. Average values over the 10 flowering stalks were used for all estimates of plant performance within each plot. See Nielsen et al. (2007) for details on the sampling protocol.

2.4 Soil Analyses

Soil samples were collected for chemical analysis in October 2003. The samples included the whole organic topsoil down to the underlying mineral soil. A metal tube (5.5 cm in diameter) was used to collect 10 samples of soil along the 10 meter line used in the plant sampling. Living green plant parts (mainly bryophytes) and larger root and rhizome fragments were removed prior to analysis. The soil samples were analysed for loss-on-ignition (LOI), total carbon (C), total nitrogen (N), pH and extractable ammonium (NH_4^+) and nitrate (NO_3^-) at the Soil Science Laboratory at the Swedish University of Agricultural Sciences, Umeå, Sweden, using standard methods following Emteryd (1989).

2.5 Data Analysis

To establish the relationship between measurements of plant performance and forest environment variables we used multiple linear regression. As explanatory variables describing the stand structure we used maturity class, number of trees on the 100 m^2 scale, basal area of trees per hectare (basal area), basal area based mean tree height, basal area mean tree diameter (mean of diameters of trees registered by the relascope, hereafter termed diameter at breast height or dbh), site index (SI), stand density index (SDI) and the GINI coefficient. SDI is calculated as (basal area * number of trees)$^{0.5}$ sensu Weisberg et al. (2003). The GINI coefficient is a measure of heterogeneity quantifying the deviation from perfect equality (Gini 1912) and has been recommended as an objective measure to compare tree size diversity in different stands (Lexerød and Eid 2006). We used tree size expressed as diameter at breast height given by

$$\mathrm{GINI} = \frac{\sum_{j=1}^{n}(2\mathrm{j}-n-1)\,ba_j}{\sum_{j=1}^{n} ba_j\,(n-1)} \tag{1}$$

where j is the rank of a tree by diameter class in ascending order from 1, …, n; *n is* total number of trees, ba_j is basal area for tree with rank j ($\mathrm{m}^2\ \mathrm{ha}^{-1}$). At the minimum value zero all trees are of equal size. At the theoretical maximum of one all trees except one have a value of zero (after Lexerød and Eid 2006).

In addition to variables describing stand structure and soil properties, altitude (meters above sea level) was included as explanatory variable. We did not find interpretable biological reasons for including interactions among the independent variables in our candidate models. Pearson's correlation test revealed loos-on-ignition and total carbon, and basal area weighted tree height and dbh to be highly correlated ($r=0.98$ and $r=0.94$, respectively). Because basal area weighted tree height is calculated from dbh, dbh was considered the most relevant variable. Among total carbon and LOI, the latter was excluded from all analysis. Correlated variables (Pearson $r>0.5$ with $P<0.05$) were discounted.

We used visual inspection and numerical methods provided by the Capability procedure in SAS 9.2 (SAS 2008) to assess whether the plant performance response variables followed a normal distribution. The vegetative performance variables (plant dry weight, number of leaves, plant height and number of branches) were considered to be normally distributed, except for number of berries. Number of berries was therefore not included in the ordinary least square regression analysis. Model selection was performed by Akaike's information criterion (Akaike 1974). Because the ratio of sample size ($n=25$) and number of parameters is low (<40) the models were ranked by second order AIC, named AICc (Sugiura 1978).

According to the two approaches described in the introduction, each response variable was explained by two sets of AICc-ranged models. Approach I includes models with explanatory variables being compatible with the output variables given by the forest simulator (see section 2.6). Here, each variable is a priori assumed to affect plant performance in the understory. Basal area and dbh of trees express continuity of the canopy and light conditions, stand density index express light conditions, site index reflects nutrient, moisture and climatic conditions and altitude is interpreted as a temperature gradient, affecting the start and extent of the of growing season. Approach II comprises models explaining the variation in *C. suecica* based on all 14 available parameters.

When the aim of AIC-ranked models is prediction, model averaging is recommended to increase precision and to reduce bias (Burnham 2002). For the model sets used with the forest simulator, where the objective was prediction of plant performance (approach I), models within $\Delta\mathrm{AICc} \leq 2$ were included in a composite model, calculated by model averaging. The cut-off level for inclusion in the composite model was set where the ΔAICc value equals an evidence ratio of approximately 2.7. As the ΔAICc value exceeds two units the ratio augments rapidly. The evidence ratio between the highest ranked model and the *i*th model is given as

$$E_{high.i} = w_{high} / w_i = e^{(-(1/2)\Delta_i)} \tag{2}$$

where w_{high} is the weight (Akaike weights) for the highest ranked model, w_i is the weight for the *i*th model and Δ_i is the difference in ΔAICc value (Anderson 2008). The Akaike weight, estimate of the probability of model *i* being the Kullback-Leibler best model given the data and the model set (i.e. the set of models included in the composite model) is

$$w_i = \frac{\exp\left(-\tfrac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\tfrac{1}{2}\Delta_r\right)} \tag{3}$$

where Δ_i and Δ_r are ΔAICc values for model i and all models in the model set, respectively (Anderson 2008).

Precision of estimators in the composite models was estimated by an unconditional variance estimator incorporating both sampling variance, dependent on a given model, and a variance component for model selection uncertainty, expressed as

$$var\left(\hat{\hat{\theta}}\right) = \sum_{i=1}^{R} w_i \quad \mathrm{var}\left(\hat{\theta} \mid g_i\right) + \left(\hat{\theta}_i - \hat{\hat{\theta}}\right)^2 \qquad (4)$$

where R is the number of models included in the composite model, $\hat{\theta}$ is the model estimate given g_i, where g_i is the ith model, $\hat{\theta}_i$ is the estimate for model i, and $\hat{\hat{\theta}}$ is the model averaged estimate and w_i are the Akaike weights (Anderson 2008).

Analysis of covariance (ANCOVA) was used to assess whether plant height of *C. suecica* should be interpreted as normal growth or induced by reduced light availability. SAS version 9.2 (SAS 2008) was used for statistical analysis and model selection, while figures were generated in R 2.10.0 (R-Development Core Team 2010).

2.6 Ecological Forest Simulation Model

The ecological forest simulation model SIMA (Kellomäki et al. 1992a, 1992b) was used to simulate future stand structure. SIMA was chosen as it is one of few gap models that satisfactory predicts basal area and volume increment of *P. abies* (Kolström 1998, Perry and Millington 2008). Tree data are entered into the model as diameter at breast height for single trees. Temperature and precipitation are entered as monthly means with standard deviations and the output of the model is given as yearly number of trees per diameter class (one cm intervals).

Transformation of tree data obtained in the field (relascope measurements on one hectare scale) into the input format required by the forest simulator (whole trees per diameter class on a 100 m^2 scale) resulted in unwanted deviations from the original field data. Therefore, we decided not to use the tree data representing the plots. Hence, tree data and climate variables to the forest simulator were obtained from the permanent sample plots of the Norwegian National Forest Inventory (NFI, Tomter et al. 2010), collected by The Norwegian Forest and Landscape Institute, round 6 (year 1990). Among NFI stands in South Eastern Norway, where site index, vegetation type, tree species composition and altitude closely correspond to the plots in the field study, six *P. abies* dominated stands were selected. The stands had intermediate production capacity (site index 14) with age around 35–40 years, i.e. younger production forest (maturity class 3). The development of the stands was simulated without any forest activity, e.g. cuttings or fertilization, for 150 years. The stands were assumed to be naturally regenerated. From the output given by the forest simulator, yearly values of relevant explanatory variables were calculated and implemented in the selected regression models, enabling predictions of plant performance over a period of 150 years.

3 Results

3.1 Selection of Models Corresponding to the Forest Simulator (Approach I)

This approach is based on explanatory variables that correspond to variables produced by the forest simulator and variables that are constant for a given site (i.e. altitude and site index). The models were ranked by the AICc-scores (AIC-ranking is shown in appendix B). The highest ranked model explaining plant dry weight contained the variables altitude, number of trees and basal area (Table 1), and reasoned in the ΔAICc value of 2.34, model averaging was not performed (see section 2.5). Plant dry weight was the response variable being clearest predicted by one single model whereas the other response variables were predicted by composite models.

Number of leaves was explained by a composite model based on three models within $\Delta \mathrm{AICc} \le 2$ and an accumulated $\mathrm{AICc}_{\mathrm{weight}}$ of 0.567 (see section 2.5 for calculation of Akaike weights). A composite model of four models explained the variation in number of flowers ($\mathrm{AICc}_{\mathrm{weight}} = 0.441$), number of branches ($\mathrm{AICc}_{\mathrm{weight}} = 0.544$) and plant height ($\mathrm{AICc}_{\mathrm{weight}} = 0.489$).

In all selected models (highest ranked or composite models) where the variables were present the variables diameter at breast height, stand density index and site index had negative effects. On the contrary, number of trees had positive effect in all models the variable was present. Increased basal area of trees per hectare had negative impact

Table 1. Model selection of models explaining plant performance in *Cornus suecica*. Explanatory variables are compatible with the forest simulator Sima.

	Plant dry weight	Averaged models based on models ≤2 ΔAICc of the highest ranked model			
		Number of branches	Number of leaves	Plant height	Number of flowers
Parameter estimates					
Intercept	0.2915	1.3667	14.1943	26.0706	6.5015
Dbh		–0.0128			–0.0772
Basal area	–0.0015	–0.0181	–0.1029	0.0503	
Number of trees	0.0013		0.0222	0.1535	
Stand density index		–0.0030			–0.0278
Site index		–0.0286	–0.1317	–0.2374	–0.2229
Altitude	–0.0004	0.0022		–0.0359	0.0123
Standard errors					
Intercept	0.0708	0.4305	0.6747	5.0113	1.5633
Dbh		0.0005			0.0131
Basal area	0.0005	0.0016	0.0114	0.0044	
Number of trees	0.0005		0.0025	0.0298	
Stand density index		0.0001			0.0022
Site index		0.0061	0.0284	0.0223	0.0329
Altitude	0.0002	0.0003		0.0069	0.0010
95% CI$_{\mathbf{low}}$					
Intercept	0.1444	0.4656	12.8720	15.6170	3.2405
Dbh		–0.0138			–0.1046
Basal area	–0.0024	–0.0216	–0.1254	0.0412	
Number of trees	0.0002		0.0173	0.0913	
Stand density index		–0.0032			–0.0325
Site index		–0.0414	–0.1874	–0.2839	–0.2916
Altitude	–0.0007	0.0015		–0.0502	0.0102
95% CI$_{\mathbf{high}}$					
Intercept	0.4387	2.2677	15.5167	36.5241	9.7626
Dbh		–0.0118			–0.0498
Basal area	–0.0005	–0.0147	–0.0805	0.0595	
Number of trees	0.0023		0.0271	0.2157	
Stand density index		–0.0029			–0.0232
Site index		–0.0158	–0.0760	–0.1909	–0.1542
Altitude	–0.0001	0.0029		–0.0215	0.0144

Table 2. Covariance analysis on the effect light availability has on the relationship between plant dry weight and plant height among plots with different light availability, expressed as forest maturity class.

Response variable	Explanatory variable	Slope	P	F-value
Weight	Plant height	Plant height*Maturity class	0.3767	1.06
Weight/height ratio	Plant height	Plant height*Maturity class	0.4048	1.01

on plant dry weight, number of branches and number of leafs, but not on the plant height. Altitude had negative effect on plant dry weight and plant height, and positive effect on number of branches and number of flowers.

Analysis of covariance (ANCOVA) was used to declare whether the plant height of *C. suecica* should be interpreted as being promoted by reduced light availability to the expense of plant dry weight (Morgan and Smith 1979) or to be interpreted as elongation growth relative to the plant dry weight. The ANCOVA did not reveal significant dissimilarities in the effect light availability has on the relationship between plant dry weight or the plant dry weight/plant height ratio and plant height among plots with different light availability, expressed as forest maturity class (Table 2).

3.2 Forest Simulations and Implementation of Plant Performance Models

The ecological forest simulation model SIMA (Kellomäki et al. 1992a, 1992b) was used to simulate stand structure in six stands with site index 14 and 35–40 years stand age (maturity class 3). All the simulated stands had for the first approximately 100 years of stand age similar patterns in the development of basal area, number of trees, mean diameter at breast height and stand density index. From around 110 years more deviation was seen in the development of basal area. The simulated values for basal area, number of trees and stand density index were mainly within maximum values registered in NFI stands from South Eastern Norway with similar forest type and site index, irrespective of stand age, whereas

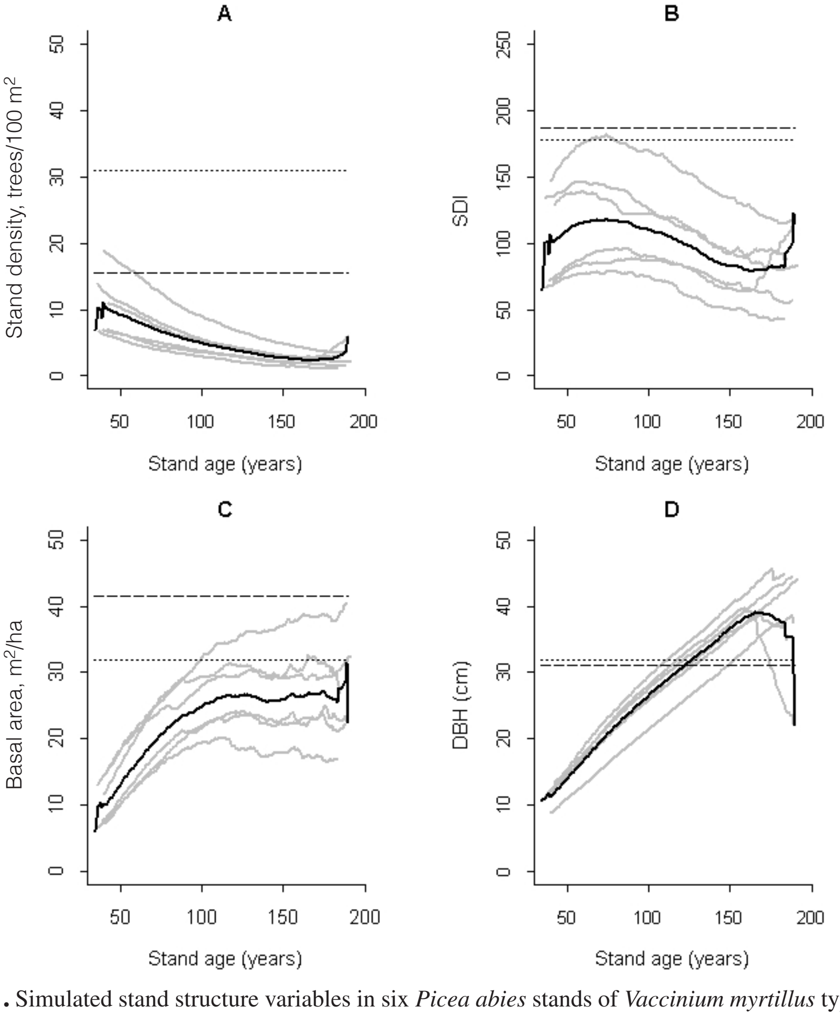

Fig. 1. Simulated stand structure variables in six *Picea abies* stands of *Vaccinium myrtillus* type with intermediate productivity (site index 14), by stand age. Individual stands (grey curves) and mean of the stands (black curve). Horizontal lines are maximum performance values registered on the field plots (small dotted line) and maximum values registered on NFI plots from South Eastern Norway on the given vegetation type, independently of stand age and maturity class (slashed line). Stand density index (SDI) = (basal area * number of trees)$^{0.5}$, see Weisberg et al. (2003). DBH = basal area mean tree diameter.

diameter at breast height (basal area mean tree diameter) exceeded maximum registered NFI and field values when the simulated stands reached 100–150 years (Fig. 1).

Based on the output given by the forest simulator yearly values of explanatory variables were calculated and implemented into the selected regression models (section 3.1), enabling predictions of the performance in *C. suecica* over a period of time. For the first 50–60 years of simulation (i.e. approximately 90–100 years stand age) the development in stand structure implied generally a reduction in plant dry weight, number of leaves, number of branches and number of flowers.The following 50–60 years, i.e. up to stand age of approximately 190 years, the performance values generally fluctuated around a relatively stable level (Fig. 2). The uncertainty of predicted performance values, measured as confidence intervals on the mean, increased by simulation time (Fig. 3).

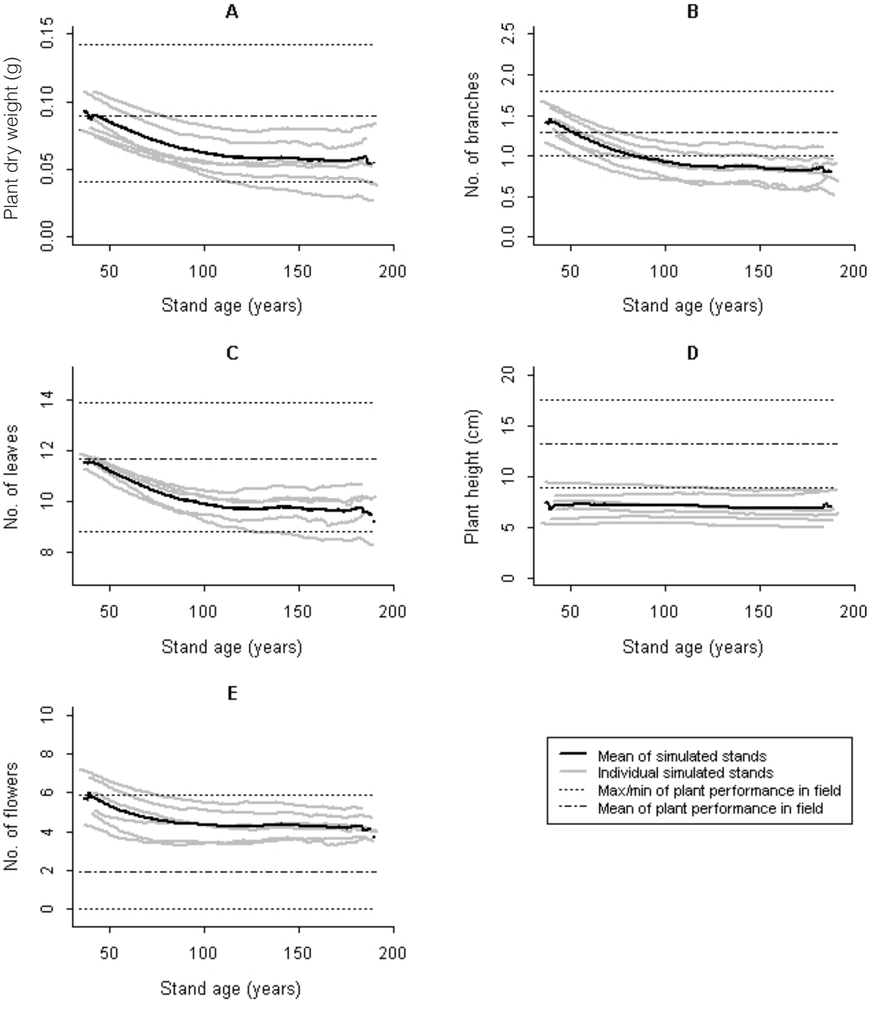

Fig. 2. Predicted development of five plant performance measures of *Cornus suecica* in six simulated *Picea abies* stands of *Vaccinium myrtillus* type with intermediate productivity (site index 14), by stand age.

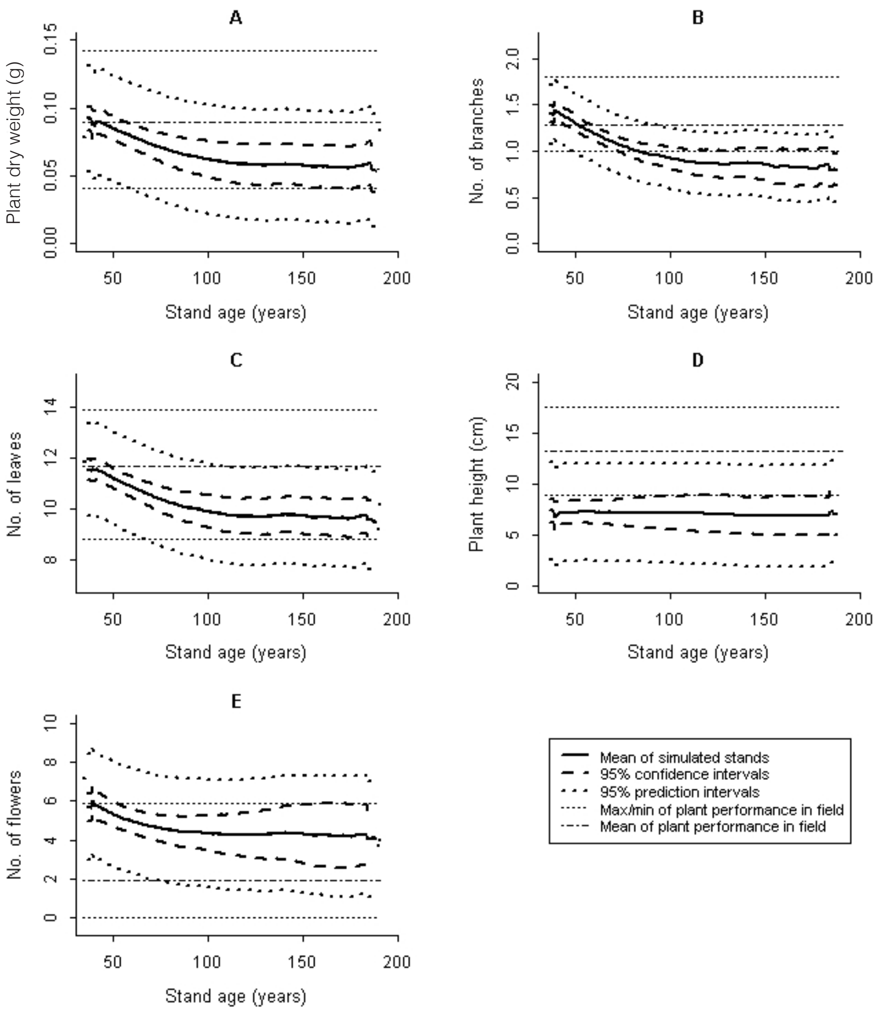

Fig. 3. Predicted mean of five plant performance measures of *Cornus suecica* in six simulated *Picea abies* stands of *Vaccinium myrtillus* type with intermediate productivity (site index 14), by stand age.

3.3 Model Selection on all Registered Field Variables (Approach II)

This approach is based on all 14 explanatory variables registered in field, not only those corresponding to parameters produced by the forest simulator. Also in this approach, plant dry weight was the performance variable to have the least number of models within two ΔAICc units. The best model to explain plant dry weight consisted of altitude, number of trees, basal area and pH, and the second best model was the same as the selected model related to the forest simulation model (section 3.1).

Variables present in the highest ranked models (ΔAICc ≤ 2) in approach I (see section 3.1) were also dominant when all variables were included (AIC-ranking in appendix C), i.e. basal area was present in 16 out 25 of the highest ranked models (Table 3). The GINI coefficient and maturity class, stand structure variables not included in the forest simulation model, were present in

Table 3. Model selection on all ecologically relevant variables (approach II). Frequency of explanatory variables in regression models ≤ 2 ΔAICc in bold and ranking number of models where the variables occur in brackets.

Explanatory variable	Response variables						% of all models ≤ 2 ΔAICc
	Plant dry weight	Number of branches	Number of leaves	Plant height	Number of flowers	Total	
Dbh	-	**2**(3,5)	-	**6**(1,2,3,4,5,6)	**5**(1,2,3,4,5)	**13**	52
Basal area	**2**(1,2)	**6**(2,3,4,5,6,7)	**5**(1,2,3,4,5)	**3**(2,3,4)	-	**16**	64
Number of trees	**2**(1,2)	**1**(1)	**1**(4)	-	-	**4**	16
Stand density index	-	**1**(7)	-	**6**(1,2,3,4,5,6)	**5**(1,2,3,4,5)	**12**	48
Site index		**1**(1)	**4**(1,3,4,5)	**2**(1,5)	**2**(1,2,3,4,5)	**9**	36
Altitude	**2**(1,2)	**5**(2,3,4,5)	-	**1**(3)	**2**(3,5)	**10**	40
Gini	-	**1**(1)	-	-	-	**1**	4
Maturity class	-	-	-	-	**1**(2)	**1**	4
CN-ratio	-	-	**1**(3)	**3**(2,3,5)	-	**4**	16
NH_4^+	-	**4**(2,5,6,7)	-	**6**(1,2,3,4,5,6)	-	**10**	40
NO_3^-	-	-	-	-	-	**-**	-
LOI %	-	-	-	-	-	**-**	-
N %	-	-	-	-	-	**-**	-
pH	**1**(1)	-	**1**(5)	**6**(1,2,3,4,5,6)	-	**8**	32
Number of models ≤ 2 ΔAICc	**2**	**7**	**5**	**6**	**5**	**-**	-

one model each, namely number of leaves and number of flowers, respectively. The soil chemical variables NH_4^+, pH and the carbon-nitrogen ratio (CN ratio) were present least once in the models explaining vegetative performance. No soil chemical variables were present in the models explaining number of flowers.

4 Discussion

4.1 Importance of Explanatory Variables

We found stand structure related variables and proxies for abiotic factors (site index and altitude) rather than soil chemical variables to best describe the variation in plant performance in the focal species *C. suecica*. The findings support our a priori assumption in which stand structure, here quantified as e.g. number of trees and basal area, is important for understory plant performance. Because the proxy variables for abiotic factors are constant for a given stand we assess the impact of structure related variables to be the most important variables for predicting the changes in performance of *C. Suecica* as a response to forest succession. However, the importance of structural variables vs. soil variables on plant performance in general is not clear cut. For *Vaccinium myrtillus* measured within the same field plots, variables representing soil chemistry were shown to be of greater importance for explaining performance than we found for *C. suecica* (Nielsen et al. 2007), whereas Miina et al. (2009) elaborated sound models for predicting cover and production of *V. myrtillus* in Finland without including soil variables. Finally, Lehtelä et al. (1996) found both stage of development of the tree stand and variables representing soil chemistry properties to determine the variation in the vegetation, including *C. suecica*, on different Finnish heath sites.

We believe the importance of stand structure variables to be related to competition for above ground environmental resources (i.e. light). However, we are aware that stand structure variables not always capture the variation in light availability. For instance, given the same basal area an old stand might be found to have more available sunlight for the understory than a middle-aged stand. Also, common forest inventory procedures may have limitations in describing all stand structure aspects important for ecological interpretation. In our field study and in the data used for the stand simulations the tree structure variables dbh and basal area were registered according to the protocol for the National Forest Inventory in Norway, where trees ≥ 5 cm dbh are measured and registered by species (Tomter 2010). The total number of trees per species might have been underreported and the common pattern of a higher fraction of deciduous trees in the early phases of succession is not clearly seen. For instance, all stands in the early succession stages (maturity class 2) were registered with only *P. sylvestris* and *P. abies*. Also two out of five stands in maturity class 3 had no presence of deciduous trees (appendix A). Because of generally low measured variation in tree species between stands tree species were not used as an explanatory variable. However, for this conceptual study we believe the stand structure variables have the quality to give basal information on performance of a little studied understory species.

4.2 Simulated Stand Structure

We have shown how temporal change in plant performance in an understory species, *C. suecica*, can be estimated through time by supplying models on plant performance with yearly site specific parameter values, produced by a forest simulator. The general reduction in measured plant performance (except for plant height) in spruce dominated stands, up to the stand age of around 100 years, is mainly driven by a decrease in number of trees and increase in basal area and mean dbh.

The simulated values for number of trees, site density index and basal area were mainly within maximum registered NFI and field values, whereas dbh (basal area mean tree diameter) exceeded the registered values after 100–150 years stand age. One reason for the deviations between simulated values and maximum registered NFI and field values might be because the simulations were performed with natural generation and without forest management, such as tree planting, thinning or cutting whereas forest stands registered in NFI and in the field are subject to forest management. In addition, imperfections in the forest simulator may have contributed to the observed deviations. However, validation of the forest modelling performance per se has not been focused in this study. Based on published model validation and simulation studies of this model (Kellomäki 1992a, 1992b, Kolström 1998, Kellomäki et al. 2006) we conclude that the simulated values are realistic for the purpose of this study and therefore applicable for assessing the performance of an understory species in a Norwegian boreal forest ecosystem.

4.3 The Ecology of *Cornus suecica*

Increased basal area leads to denser crown cover and reduced light availability in the understory. The negative impact of basal area on the performance *C. suecica* found in this study is in line with Nygaard and Ødegaard (1999) who found the frequency of *C. suecica* to decrease by increasing living stem biomass of *P. abies*. We therefore conclude that basal area is an important measure of the ecological impact canopy trees have on the performance of *C. suecica*. Our results correspond also to those of Nielsen et al. (2007) on *V. myrtillus* in the same area, showing that most measures of performance peaked in early stages of forest succession. For *V. myrtillus*, the performance responses are however, ambiguous. Kardell and Erikson (1995) found optimal performance of *V. myrtillus* to increase with forest maturity in Swedish boreal forests and Parlane et al. (2006) found the same in *Pinus sylvestris* forests in Scotland, In Finland and Sweden Palviainen et al. (2005) found biomass of *V. myrtillus* to decrease rapidly after clear-cutting, whereas Miina et al. (2009) found the coverage of *V. myrtillus* to increase with increased basal area and stand age up to the age of 191 years and density of 25 $m^2 ha^{-1}$, after which the coverage gradually decreased. Because of few studies focusing on *C. suecica* related to stand structure the standard of reference is limited and similar specific reports as on *V. myrtillus* are not known.

Few available studies limit also the comparison of soil chemical parameters and we have only found references for pH. The measured range of pH 4.19–5.03 in our study is in line with Taylor (1999) where *C. suecica* usually was found on soils with $pH < 4.5$ whereas Sonesson (1974) measured pH to 4.0–5.1.

Cornus suecica has both vegetative and sexual propagation (Taylor 1999) and population survival is not depending solely on seed production. Hence, we assess measures of vegetative performance to be as important indicators of the species' performance as measures of sexual reproduction, as has been shown also for other plant species e.g. (Nielsen et al. 2007). We also assess measures of sexual production, particularly number of fruits, to be more affected by casual climate effects such as cold or rainy conditions. Because increased plant weight comes prior to branching we assess plant dry weight to be the performance variable with the most straight forward biological interpretation. Contrary, variation in plant height in understory species should generally be interpreted with care, as reduced light availability may promote elongation growth to the expense of plant dry weight (Morgan and Smith 1979). However, forest maturity class, used as a proxy for crown cover and light availability, did not explain variations in plant dry weight or plant weight/height ratio with respect to plant height. We conclude that the measured plant height is not an artefact of elongation induced by reduced light availability but rather is an adequate measure of plant performance. Measured plant height is thus interpreted to be elongation growth accompanied by stable dry mass content and not elongation accompanied by relatively less dry mass.

In Norwegian forestry, *P. abies* stands with site index of 14, like the sites we have modelled, will likely be cut at around 100 years stand age. The subsequent increase in light availability, i.e. low basal area of trees, will lead to higher values of plant performance variables. Hofgaard et al. (1991) reported *C. suecica* to disappear from a permanent plot in an old growth forest in northern Sweden between 1938 and 1983 because of insufficient light availability. The plots in our study are however, chosen on the presence of *C. suecica*, and hence we do not have appropriate data for predicting when the canopy is too dense for the presence of *C. suecica.*

5 Concluding Remarks

We draw four main conclusions from the results. First, we conclude that for our system models consisting only of stand structure related variables suffice to explain and predict variation in the performance of forest floor species *C. suecica*. Second, we found evidence for reduced plant performance of *C. suecica* during forest succession, simulated for 150 years. Third, the negative impact of basal area on the performance *C. suecica* found in this study is in line with a previous study on *C. suecica*. Fourth, traditional ecology and forest simulations can be combined to produce sound predictions on how plant performance might change as a response to changes in the overstory. To develop the concept further also data on species performance specifically related to measured stand structure specified by tree species <5 cm dbh is recommended. A further step will be to include forest management strategies in the forest simulations, as has been done with biodiversity indices (Kolström and Pitkänen 1999) and abundance and berry yields of *V. myrtillus* (Miina et al. 2009, Miina et al. 2010).

The current version of SIMA simulates growth of the understory as three aggregated groups, categorized by succession appearance (Kellomäki et al. 1992a, 1992b). This ensures that some of the competition between the trees and understory is accounted for, but not on a per species basis. Ideally, to improve the accuracy of simulations feedback mechanisms between understory species and the trees forming the canopy should be implemented in simulation models.

References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control AC 19(6): 716–723.

Anderson, D.R. 2008. Model based inference in the life sciences: a primer on evidence. Springer Verlag, New York.

Bengtsson, J., Nilsson, S.G., Franc, A. & Menozzi, P. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132(1): 39–50.

Bitterlich, W. 1984. The relascope idea: relative measurements in forestry. Commonwealth Agricultural Bureaux, Farnham.

Braastad, H. 1980. Growth model computer program for Pinus sylvestris. Meddelelser fra Norsk institutt for skogforskning 35(5): 272–359.

Burnham, K.P. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York. 488 p.

Carleton, T.J. & Read, D.J. 1991. Ectomycorrhizas and nutrient transfer in conifer-feather moss ecosystems. Canadian Journal of Botany 69(4): 778–785.

Coomes, D.A. & Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70(2): 171–207.

Emteryd, O. 1989. Chemical and physical analysis of inorganic nutrients in plant, soil, water and air. Swedish University of Agricultural Sciences, Department of Forest Site Research, Umeå.

Fremstad, E. 1997. Vegetasjonstyper i Norge. Vol. 12. NINA temahefte.

Gilliam, F.S. & Roberts, M.R. (eds.). 2003. The herbaceous layer in forests of eastern North America. Oxford University Press, Oxford, United Kingdom.

Gini, C. 1912. Variabilità e mutabilità. Reprinted in: Pizetti, E. & Salvemini, T. (eds.). 1955. Memorie di metodologica statistica.

Guisan, A. & Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135(2–3): 147–186.

Halpern, C.B. & Spies, T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5(4): 913–934.

Hart, S. & Chen, H. 2006. Understory vegetation dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25(4): 381–397.

Hofgaard, A., Kullman, L. & Alexandersson, H. 1991. Response of old-growth montane Picea abies (L.) Karst. forest to climatic variability in Northern Sweden. New Phytologist 119(4): 585–594.

Hörnberg, G., Ohlson, M. & Zackrisson, O. 1997. Influence of bryophytes and microrelief conditions on Picea abies seed regeneration patterns in boreal old-growth swamp forests. Canadian Journal of Forest Research 27(7): 1015–1023.

Hultén, E. & Fries, M. 1986. Atlas of North European vascular plants north of the Tropic of Cancer. Koeltz Scientific Books, Königstein.

Kardell, L. & Eriksson, L. 1995. Bärproduktion och markvegetation. Effekter av kvävegödsling och slutavverkning under en 15-årsperiod. Swedish University of Agricultural Sciences, Department of Environmental Forestry, SLU Rapport 60. (In Swedish).

Kellomäki, S. & Väisänen, H. 1991. Application of a gap model for the simulation of forest ground vegetation in boreal conditions. Forest Ecology and Management 42(1–2): 35–47.

— , Strandman, H., Nuutinen, T., Peltola, H., Korhonen, K.T. & Väisänen, H. 2006. SYKEmo334 Adaptation of forest ecosystems, forests and forestry to climate change. Finnish Environment 1: 10.

— , Väisänen, H., Hänninen, H., Kolström, T., Lauhanen, R., Mattila, U. & Pajari, B. 1992a. SIMA: a model for forest succession based on the carbon and nitrogen cycles with application to silvicultural management of the forest ecosystem. Silva Carelica 22: 185.

— , Väisänen, H., Hänninen, H. Kolström, T. Lauhanen, R. Mattila, U. & Pajari, B. 1992b. A simulation model for the succession of the boreal forest ecosystem. Silva Fennica 26: 1–18.

Klinka, K., Chen, H.Y., Wang, Q. & DeMontigny, L. 1996. Forest canopies and their influence on understory vegetation in early-seral stands on west Vancouver Island. Northwest Science 70: 193–200.

Kolström, M. 1998. Ecological simulation model for studying diversity of stand structure in boreal forests. Ecological Modelling 111(1): 17–36.

— & Pitkänen, S. 1999. Effect of forest management on alpha diversity of ground vegetation in boreal forests: a model approach. Boreal environment research 4(1): 45–54.

Kujala, V. 1964. Metsä-ja suokasvilajien levinneisyysja yleisyyssuhteista Suomessa: vuosina 1951–1953 suoritetun valtakunnan metsien III linja-arvioinnin tuloksiaMetsä-ja suokasvilajien levinneisyysja yleisyyssuhteista Suomessa: vuosina 1951–1953 suoritetun valtakunnan metsien III linja-arvioinnin tuloksia. Referat: Über die Frequenzverthältnisse der Wald-und Moorpflanzen in Finnland – Ergebnisse der III. Reichswaldabschätzung 1951–1953. Communicationes Instituti Forestalis Fenniae 59(1). 137 p. + 134 app.

Légaré, S., Bergeron, Y., Leduc, A. & Pare, D. 2001. Comparison of the understory vegetation in boreal forest types of southwest Quebec. Canadian Journal of Botany 79(9): 1019–1027.

Lehtelä, M., Hotanen, J.P. & Sepponen, P. 1996. Understorey vegetation in fresh and herb-rich upland forests in southwest Lapland. Silva Fennica 30(1): 11–29.

Lexerød, N.L. & Eid, T. 2006. An evaluation of different diameter diversity indices based on criteria related to forest management planning. Forest Ecology and Management 222(1–3): 17–28.

Lid, J., Lid, D., Elven, R. & Alm, T. 2005. Norsk flora. Samlaget, Oslo.

McKenzie, D., Halpern, C.B. & Nelson, C.R. 2000. Overstory influences on herb and shrub communities in mature forests of western Washington, USA. Canadian Journal of Forest Research 30(10): 1655–1666.

— , Raymond, C.L. & Cushman, S.A. 2009. Modeling understory vegetation and its response to fire. In: Millspaugh, J.J & Thompson, F.R. (eds.). Models for planning wildlife conservation in large landscapes. Elsevier. p. 391–414.

Miina, J., Hotanen, J.P. & Salo, K. 2009. Modelling the abundance and temporal variation in the production of bilberry (Vaccinium myrtillus L.) in Finnish mineral soil forests. Silva Fennica 43(4): 577–593.

— , Pukkala, T., Hotanen, J.P. & Salo, K. 2010. Optimizing the joint production of timber and bilberries. Forest Ecology and Management 259(10): 2065–2071.

Moen, A. 1998. Nasjonalatlas for Norge: Vegetasjon. Statens Kartverk, Hønefoss. 199 p.

Morgan, D. & Smith, H. 1979. A systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. Planta 145(3): 253–258.

Nielsen, A., Totland, Ø. & Ohlson, M. 2007. The effect of forest management operations on population performance of Vaccinium myrtillus on a landscape-scale. Basic and Applied Ecology 8(3): 231–241.

Nygaard, P.H. & Ødegaard, T. 1999. Sixty years of vegetation dynamics in a south boreal coniferous forest in southern Norway. Journal of Vegetation Science 10(1): 5–16.

Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biological conservation 81(3): 221–231.

Økland, R.H. & Eilertsen, O. 1996. Dynamics of understory vegetation in an old-growth boreal coniferous forest, 1988–1993. Journal of Vegetation Science 7(5): 747–762.

Palviainen, M., Finér, L., Mannerkoski, H., Piirainen, S. & Starr, M. 2005. Responses of ground vegetation species to clear-cutting in a boreal forest: aboveground biomass and nutrient contents during the first 7 years. Ecological Research 20(6): 652–660.

Peng, C. 2000. Understanding the role of forest simulation models in sustainable forest management. Environmental Impact Assessment Review 20(4): 481–501.

Perry, G.L.W. & Millington, J.D.A. 2008. Spatial modelling of succession-disturbance dynamics in forest ecosystems: Concepts and examples. Perspectives in Plant Ecology, Evolution and Systematics 9(3–4): 191–210.

SAS. 2008. SAS OnlineDoc (R), Version 9.2. SAS Institute Inc. Cary, NC.

Shugart, H.H. & West, D.C. 1980. Forest succession models. Bioscience: 308–313.

Sonesson, M. 1974. Late Quaternary forest development of the Torneträsk area, North Sweden. 2. Pollen Analytical Evidence. Oikos 25(3): 288–307.

Sugiura, N. 1978. Further analysts of the data by Akaike's information criterion and the finite corrections. Communications in Statistics – Theory and Methods 7(1): 13–26.

Taylor, K. 1999. Cornus suecica L. (Chamaepericlymenum suecicum (L.) Ascherson & Graebner). Journal of Ecology 87(6): 1068–1077.

Thompson III, F.R. 2010. Application and presentation of statistics. Journal of Wildlife Management 74(4): 617–619.

Tomter, S.M., Hylen, G. & Nilsen, J.-E. 2010. Development of Norway's National Forest Inventory. In: Tomppo, E., Gschwantner, T., Lawrence, M. & McRoberts, R.E. (eds.). National Forest Inventories. Pathways for common reporting. Springer Verlag, Heidelberg. p. 411–424.

Tveite, B. 1977. Site index curves for Norway spruce (Picea abies (L.) Karst.). Meddelelser fra Norsk institutt for skogforskning 33(1). 84 p.

Van Couwenberghe, R., Collet, C., Lacombe, E. & Gégout, J.C. 2011. Abundance response of western European forest species along canopy openness and soil pH gradients. Forest Ecology and Management 262(8): 1483–1490.

Weisberg, P.J., Hadorn, C. & Bugmann, H. 2003. Predicting understorey vegetation cover from overstorey attributes in two temperate mountain forests. Forstwissenschaftliches Centralblatt 122(5): 273–286.

Wolfslehner, B. & Vacik, H. 2008. Evaluating sustainable forest management strategies with the Analytic Network Process in a Pressure-State-Response framework. Journal of Environmental Management 88(1): 1–10.

Zackrisson, O., Nilsson, M.C., Steijlen, I. & Hörnberg,

G. 1995. Regeneration pulses and climate-vegetation interactions in nonpyrogenic boreal Scots pine stands. Journal of Ecology 83: 469–483.

Zavitkovski, J. 1976. Ground vegetation biomass, production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems. Ecology 57(4): 694–706.

Total of 57 references

Appendix A

Tree species composition and basal area of each stand.

Plot	Number of stems				Basal area				Maturity class
	Total ha^{-1}	percent			Total m^2 ha^{-1}	percent			
		Pinus sylvestris	*Picea abies*	*Betula* sp.		*Pinus sylvestris*	*Picea abies*	*Betula* sp.	
1	632	0.0	32.8	67.2	12	0	58.3	41.7	4
2	1031	2.9	61.4	35.6	21	4.8	66.7	28.6	3
3	55	0.0	100.0	0.0	2	0.0	100.0	0.0	1
4	289	0.0	96.7	3.3	23	0.0	95.7	4.3	4
5	698	0.0	100.0	0.0	17	0.0	100.0	0.0	3
6	403	0.0	91.9	8.1	17	0.0	94.1	5.9	5
7	872	39.2	60.8	0.0	2	50.0	50.0	0.0	2
8	572	0.0	94.7	5.3	29	0.0	96.6	3.4	5
9	432	3.8	96.2	0.0	18	11.1	88.9	0.0	5
10	255	5.5	74.9	19.5	7	14.3	71.4	14.3	5
11	286	3.9	96.1	0.0	10	20.0	80.0	0.0	3
12	1409	0.0	100.0	0.0	7	0.0	100.0	0.0	2
13	2134	0.3	87.3	12.4	9	11.1	66.7	22.2	3
14	14	0.0	100.0	0.0	1	0.0	100.0	0.0	1
15	1055	0.0	61.8	38.2	22	0.0	90.9	9.1	4
16	1661	0.0	100.0	0.0	6	0.0	100.0	0.0	2
17	1187	100.0	0.0	0.0	4	100.0	0.0	0.0	2
18	737	1.0	99.0	0.0	17	5.9	94.1	0.0	5
19	980	0.0	100.0	0.0	11	0.0	100.0	0.0	2
20	426	0.0	100.0	0.0	17	0.0	100.0	0.0	4
21	505	20.7	79.3	0.0	18	44.4	55.6	0.0	5
22	510	0.0	77.4	22.6	25	0.0	96.0	4.0	5
23	104	7.4	92.6	0.0	2	50.0	50.0	0.0	1
24	995	0.0	95.6	4.4	32	0.0	96.9	3.1	4
25	995	0.0	35.3	64.7	12	0.0	50.0	50.0	3

Appendix B

Models explaining performance in *Cornus suecica* where the explanatory variables are compatible with the forest simulator Sima (approach I). Model 1 is the best model and the other models are ranked by ΔAIC. For each plant performance variable all models within 2 ΔAICc and the next model exceeding 2 ΔAICc are given.

Table B.1. Plant dry weight (approach I).

	Models ranked by ΔAIC	
	1	2
DF	21	20
RMSE	0.0182	0.0184
SSE	0.007	0.0067
Log(L_i)	102.309	102.719
R^2_{adj}	0.571	0.564
AICc	–194.617	–192.279
ΔAICc	0	2.338
$AICc_{weight}$	0.413	0.128
Parameters	-	-
Intercept	0.2915	0.3217
Dbh	-	-
Basal area	–0.0015	–0.0014
Tree number	0.0013	0.0013
Stand density index	-	-
Site index	-	–0.0014
Altitude	–0.0004	–0.0004

Table B.2. Number of branches (approach I).

	Models ranked by ΔAIC				
	1	2	3	4	5
DF	21	22	21	22	21
RMSE	0.1427	0.1491	0.1460	0.1528	0.1505
SSE	0.4275	0.4891	0.4475	0.5135	0.4758
Log(L_i)	50.859	49.177	50.288	48.566	49.52
R^2_{adj}	0.570	0.531	0.550	0.507	0.522
AICc	–91.719	–91.21	–90.576	–89.99	–89.04
ΔAICc	0	0.508	1.143	1.729	2.678
$AICc_{weight}$	0.197	0.153	0.111	0.083	0.052
Parameters	-	-	-	-	-
Intercept	0.9134	1.9327	2.1632	0.3325	1.8862
Dbh	-	-	–0.0030	-	-
Basal area	-	-	-	-	0.0031
Tree number	-	-	–0.0128	-	-
Stand density index	–0.0267	–0.0312	–0.0282	-	–0.0310
Site index	–0.0188	–0.0165	-	–0.0196	–0.0160
Altitude	0.0020	-	-	0.0025	-

Table B.3. Number of leaves (approach I).

	Models ranked by ΔAIC 1	2	3	4
DF	22	23	21	22
RMSE	0.8480	0.8850	0.8491	0.8863
SSE	15.8190	18.0148	15.1404	17.2831
$Log(L_i)$	5.721	4.096	6.269	4.614
R^2_{adj}	0.549	0.509	0.548	0.507
AICc	–4.299	–3.647	–2.538	–2.086
ΔAICc	0	0.652	1.761	2.213
$AICc_{weight}$	0.265	0.192	0.110	0.088
Parameters	-	-	-	-
Intercept	14.8501	13.1004	14.5169	12.7762
Dbh	-	-	-	-
Basal area	–0.1031	–0.1047	–0.0994	–0.1008
Tree number	-	-	0.0222	0.0230
Stand density index	-	-	-	-
Site index	–0.1321	-	–0.1306	-
Altitude	-	-	-	-

Table B.4. Plant height (approach I).

	Models ranked by ΔAIC 1	2	3	4	5
DF	22	21	23	21	21
RMSE	2.1892	2.1663	2.3264	2.2004	2.2137
SSE	105.4392	98.5472	124.4836	101.6813	102.9109
$Log(L_i)$	–17.991	–17.146	–20.066	–17.537	–17.687
R^2_{adj}	0.230	0.246	0.130	0.222	0.212
AICc	43.124	44.291	44.678	45.074	45.375
ΔAICc	0	1.167	1.554	1.950	2.250
$AICc_{weight}$	0.204	0.114	0.094	0.077	0.066
Parameters	-	-	-	-	-
Intercept	27.6398	32.4965	11.635	30.0057	28.3012
Dbh	-	-	-	-	-
Basal area	-	-	-	0.0503	-
Tree number	0.1555	0.1559	0.1317	0.1712	0.1469
Stand density index	-	-	-	-	0.0077
Site index	-	–0.2374	-	-	-
Altitude	–0.0336	–0.037	-	–0.0402	–0.0361

Table B.5. Number of flowers (approach I).

	Models ranked by ΔAIC				
	1	2	3	4	5
DF	21	20	22	21	22
RMSE	1.2467	1.2296	1.3384	1.2957	1.3443
SSE	32.6393	30.2404	39.4113	35.2556	39.7576
Log(L_i)	–3.333	–2.379	–5.69	–4.297	–5.799
R^2_{adj}	0.531	0.544	0.460	0.494	0.455
AICc	16.666	17.915	18.522	18.594	18.741
ΔAICc	0	1.249	1.856	1.928	2.075
$AICc_{weight}$	0.191	0.102	0.075	0.073	0.068
Parameters	-	-	-	-	-
Intercept	8.8081	2.6867	5.8336	–1.5935	7.4299
Dbh	–0.076	–0.0783	–0.0788	–0.0814	-
Basal area	-	-	-	-	-
Tree number	-	-	-	-	-
Stand density index	–0.0271	–0.0291	–0.0281	–0.0306	–0.0253
Site index	–0.2328	–0.2045	-	-	–0.2419
Altitude	-	0.0123	-	0.0158	-

Appendix C

Models explaining performance in *Cornus suecica* on all relevant ecological explanatory variables. Model 1 is the best model and the other models are ranked by ΔAIC. The 8 highest ranked models for each plant performance variable are shown.

Table C.1. Plant dry weight (approach II).

	Models ranked by ΔAIC		
	1	2	3
DF	20	21	21
RMSE	0.0174	0.0182	0.0189
SSE	0.006	0.007	0.0075
Log(L_i)	104.092	102.309	101.420
R^2_{adj}	0.610	0.571	0.540
AICc	–195.026	–194.617	–192.839
ΔAICc	0	0.409	2.187
$AICc_{weight}$	0.053	0.044	0.018
Parameters	-	-	-
Intercept	0.1294	0.2915	–0.0076
Dbh	-	-	-
Basal area	–0.0013	–0.0015	–0.0018
Tree number	0.0013	0.0013	-
Stand density index	-	-	-
Site index	-	-	-
Altitude	–0.0004	–0.0004	-
Gini	-	-	-
Maturity class	-	-	-
CN-ratio	-	-	–0.002
NH_4^+	-	-	-
NO_3^-	-	-	-
LOI %	-	-	-
N %	-	-	-
pH	0.034	-	0.0401

Table C.2. Number of branches (approach II).

	Models ranked by ΔAIC							
	1	2	3	4	5	6	7	8
DF	21	21	21	22	20	22	20	21
RMSE	0.1400	0.1403	0.1427	0.1491	0.1388	0.1494	0.1400	0.1460
SSE	0.4114	0.4133	0.4275	0.4891	0.3851	0.4913	0.3918	0.4475
Log(L_i)	51.337	51.280	50.859	49.177	52.163	49.121	51.948	50.288
R^2_{adj}	0.587	0.585	0.570	0.531	0.594	0.529	0.587	0.550
AICc	–92.674	–92.56	–91.719	–91.21	–91.167	–91.098	–90.739	–90.576
ΔAICc	0	0.114	0.956	1.464	1.507	1.576	1.935	2.099
$AICc_{weight}$	0.034	0.032	0.021	0.016	0.016	0.016	0.013	0.012
Parameters	-	-	-	-	-	-	-	-
Intercept	1.7971	1.9745	0.9134	1.9327	1.2368	1.6629	1.9173	2.1632
Dbh	-	-	0.002	-	0.0015	-	-	-
Basal area	-	–0.0168	–0.0188	–0.0165	–0.0184	–0.0172	–0.0162	-
Tree number	–0.0201	-	-	-	-	-	-	–0.0128
Stand density index	-	-	-	-	-	-	0.004	-
Site index	–0.0044	-	-	-	-	-	-	–0.003
Altitude	-	–0.0256	–0.0267	–0.0312	–0.0235	-	–0.0249	–0.0282
Gini	0.0732	-	-	-	-	-	-	-
Maturity class	-	-	-	-	-	-	-	-
CN-ratio	-	-	-	-	-	-	-	-
NH_4^+	-	–0.0011	-	-	–0.0009	–0.0013	–0.0012	-
NO_3^-	-	-	-	-	-	-	-	-
LOI %	-	-	-	-	-	-	-	-
N %	-	-	-	-	-	-	-	-
pH	-	-	-	-	-	-	-	-

Table C.3. Number of leaves (approach II).

	Models ranked by ΔAIC					
	1	2	3	4	5	6
DF	22	23	21	21	21	22
RMSE	0.8480	0.8850	0.8351	0.8491	0.8523	0.8863
SSE	15.819	18.0148	14.6468	15.1404	15.2556	17.2831
Log(L_i)	5.721	4.096	6.683	6.269	6.174	4.614
R^2_{adj}	0.549	0.509	0.563	0.548	0.545	0.507
AICc	–4.299	–3.647	–3.366	–2.538	–2.348	–2.086
ΔAICc	0	0.652	0.932	1.761	1.951	2.213
$AICc_{weight}$	0.051	0.036	0.032	0.021	0.019	0.017
Parameters	-	-	-	-	-	-
Intercept	14.8501	13.1004	16.9948	14.5169	10.9646	12.7762
Dbh	-	-	-	-	-	-
Basal area	–0.1031	–0.1047	–0.0987	–0.0994	–0.0992	–0.1008
Tree number	-	-	-	0.0222	-	0.023
Stand density index	-	-	-	-	-	-
Site index	–0.1321	-	–0.1732	–0.1306	–0.1289	-
Altitude	-	-	-	-	-	-
Gini	-	-	-	-	-	-
Maturity class	-	-	-	-	-	-
CN-ratio	-	-	–0.0549	-	-	-
NH_4^+	-	-	-	-	-	-
NO_3^-	-	-	-	-	-	-
LOI %	-	-	-	-	-	-
N %	-	-	-	-	-	-
pH	-	-	-	-	0.8372	-

Table C.4. Plant height (approach II).

	Models ranked by ΔAIC						
	1	2	3	4	5	6	7
DF	19	18	17	19	18	20	19
RMSE	1.8040	1.7184	1.6201	1.8194	1.7676	1.9509	1.8829
SSE	61.8329	53.1526	44.6203	62.8946	56.2385	76.1206	67.3642
Log(L_i)	–11.319	–9.429	–7.241	–11.532	–10.134	–13.918	–12.390
R^2_{adj}	0.477	0.525	0.578	0.468	0.498	0.388	0.430
AICc	39.306	39.446	39.483	39.731	40.856	40.994	41.448
ΔAICc	0	0.140	0.177	0.426	1.551	1.688	2.142
$AICc_{weight}$	0.037	0.034	0.034	0.030	0.017	0.016	0.013
Parameters	-	-	-	-	-	-	-
Intercept	11.4558	14.5157	21.4331	15.1852	11.1808	14.0412	13.3665
Dbh	–0.0534	–0.0533	–0.0546	–0.0591	–0.0475	–0.0443	–0.0382
Basal area	-	0.1023	0.1089	0.0986	-	-	-
Tree number	-	-	-	-	-	-	-
Stand density index	0.1589	0.1720	0.1582	0.2103	0.1304	0.1759	0.1385
Site index	0.0196	-	-	-	0.0176	-	-
Altitude	-	-	–0.2889	-	-	-	-
Gini	-	-	-	-	-	-	-
Maturity class	-	-	-	-	-	-	-
CN-ratio	-	–0.1850	–0.2474	-	–0.1420	-	–0.1752
NH_4^+	–0.0253	–0.0304	–0.0298	–0.0239	–0.0296	–0.0202	–0.0262
NO_3^-	-	-	-	-	-	-	-
LOI %	-	-	-	-	-	-	-
N %	-	-	-	-	-	-	-
pH	5.8892	6.5916	6.4784	5.6025	6.4795	4.5669	5.4668

Table C.5. Number of flowers (approach II).

	Models ranked by ΔAIC					
	1	2	3	4	5	6
DF	21	21	20	22	21	20
RMSE	1.2467	1.2586	1.2296	1.3384	1.2957	1.2496
SSE	32.6393	33.2671	30.2404	39.4113	35.2556	31.2292
Log(L_i)	–3.3330	–3.5712	–2.3788	–5.6897	–4.2969	–2.7810
R^2_{adj}	0.5313	0.5223	0.5441	0.4598	0.4938	0.5292
AICc	16.666	17.1423	17.9154	18.5223	18.5937	18.7198
ΔAICc	0	0.4763	1.2494	1.8563	1.9277	2.0538
$AICc_{weight}$	0.0405	0.0319	0.0217	0.0160	0.0154	0.0145
Parameters	-	-	-	-	-	-
Intercept	8.8081	5.7966	2.6867	5.8336	–1.5935	7.8169
Dbh	–0.076	–0.1256	–0.0783	–0.0788	–0.0814	–0.1045
Basal area	-	-	-	-	-	-
Tree number	-	-	-	-	-	-
Stand density index	–0.0271	–0.0367	–0.0291	–0.0281	–0.0306	–0.0325
Site index	–0.2328	-	–0.2045	-	-	–0.1569
Altitude	-	-	0.0123	-	0.0158	-
Gini	-	-	-	-	-	-
Maturity class	-	0.4927	-	-	-	0.290
CN-ratio	-	-	-	-	-	-
NH_4^+	-	-	-	-	-	-
NO_3^-	-	-	-	-	-	-
LOI %	-	-	-	-	-	-
N %	-	-	-	-	-	-