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Evaluation of stand level hybrid PipeQual-model with permanent sample plot data of Norway spruce

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Abstract

The evaluation of process-based models (PBM) includes ascertaining their ability to produce results consistent with forest growth in the past. In this study, we parameterized and evaluated the hybrid model, PipeQual, with datasets containing traditional mensuration variables collected from permanent sample plots (PSP) of even-aged Norway spruce (*Picea abies* (L.) Karst) stands in Finland. To initialize the model in middle of stand development and reproduce observed changes in Norway spruce crown structure, the built-in empirical relationships of crown characteristics were made explicitly dependent of light environment. After these modifications, the model accuracy at the whole dataset level was high, slope values of linear regressions between the observations and simulations ranging from 0.77 to 0.99 depending on the variable. The average bias in stand dominant height ranged between -0.72 – 0.07 m, -0.68 – 0.57 cm in stand mean diameter, -2.62 – 1.92 m^2 in stand basal area and 20 - 29 m^3 in stand total stem volume. Stand dynamics after thinning also followed reasonable closely the observed patterns. Accurate predictions illustrate the potential of model for predicting forest stand growth and forest management effects in changing environmental conditions.

Keywords

Picea abies, growth simulation model, validation, forest management effect, growth response

Introduction

The importance of forests as resources of raw material is growing due to increasing pressure to reduce the use of fossil fuels and fossil based materials. At the same time, the environmental change driven by climate change challenges traditional silvicultural practices, creating an increasing demand for tools capable of predicting forest responses to both climate and management. Empirical growth models are generally thought to be of limited usefulness under changing conditions since their representation of environmental effects is, at its best, implicit and derived from past data. (Monserud 2003; Cuddington et al. 2013; Lonsdale et al. 2015). Process-based forest growth models (PBM) are based on a mechanistic description of processes which in principle allows for projections into the future once the driving variables and process parameters have been determined. In practice, however, no model is fully mechanistic and some degree of model calibration against data on predicted variables is always required (Korzhukin et al. 1996; Mäkelä et al. 2000; Robinson and Ek 2003; Monserud 2003; Fontes et al. 2010 Cuddington et al. 2013). This adds an empirical dimension to PBMs, making them "hybrid" to a lesser or greater degree (Korzhukin et al. 1996; Mäkelä et al. 2000), and emphasizes the need for thorough evaluation of such models against available data as a prerequisite for any future predictions (e.g. Vanclay and Skoovsgard 1997; Bokalo et al. 2013). The evaluation should quantitatively assess how useful the model is for the specific purpose it has been constructed.

Evaluation of process-based or hybrid models is far from simple. There are two main challenges in the evaluation. Firstly, many of these models do not incorporate variables describing explicit tree and stand structure which could be evaluated against empirical stand data. Secondly, strict testing demands proper datasets which are scarce. Yield tables and inventory data have been used in PBM evaluation (e.g., Lonsdale et al. 2015; Mäkelä et al. 2016). However, permanent sample plots (PSPs) provide more rigorous data for the evaluation. To date, a few studies exist that have evaluated process-based or hybrid forest growth models against data from PSPs (Robinson and Ek 2003; Raulier et al. 2003; Zhou et al. 2005; Pinjuv et al. 2006; Fontes et al. 2006; Minunno et al. 2010). From the viewpoint of evaluating PBMs and hybrid models with PSP data, a specific challenge is that most of the PSPs have been established after juvenile stage in stands of pole or mature stage. The PBMs usually contain a large number of state variables to be initialized, but only a subset of these is available in the PSP data. The PBMs are therefore usually initialized at the seedling or sapling stage where forest management has not yet affected tree or stand structure (e.g., Pérez-Cruzado et al. 2011) and required state variables are easier to attain. If stand management prior to the first PSP measurement has been recorded, the initial state can be estimated through simulation from stand establishment to the first measurement, possibly combined with some calibration (e.g. Kantola et al. 2007). However, this method is problematic for model applications as the management history of forest stands is usually unknown and actual management pathways vary considerably.

In the hybrid stand growth model PipeQual (Mäkelä et al. 1997; Mäkelä and Mäkinen 2003; Kantola et al. 2007), the initial data requirements are low because the model uses structural constraints that connect standard forestry variables with each other and functional biomasses. In addition to these constraints, we hypothesized here that connecting the tree and crown structure more tightly to stand light conditions would allow us to account for the adaptation of tree structure occurring from sapling to subsequent developmental stages and solve this way the initialization problem in the middle of stand development.

The objective of this study was to test the PipeQual model for spruce against PSP data in southern and central Finland, with special focus on requirements outlined below. In particular, we aimed at modifying the model to make it applicable from any initial state measured in the field, regardless of stand age. In case the results deviate from the measurements, our aim was to interpret the causes of this in terms of model assumptions. Finally, we interpreted the results from the perspective of evaluating PBMs against PSP data in general.

In our evaluation, we thus concentrated on the tree and stand characteristics easily measurable in the field and which are of importance in forestry practice. To pass the evaluation successfully, PipeQual should fulfill the following requirements:

REQ1: The model must be initializable at any time during the rotation.

REQ2: The model must be unbiased with respect to annual volume increment.

REQ3: Simulated growth responses to forestry operations, e.g. thinning, must be qualitatively and quantitatively reasonable .

REQ4: Tree form and growth allocation to different compartments must behave logically over time and in response to forestry operations.

Material and methods

Description of the model

The PipeQual model is based on ecological theory and describes stand and tree growth as a result of carbon acquisition and allocation (Mäkelä 1997, 2002). The model consists of four modules, STAND, TREE, WHORL and BRANCH, through which tree metabolism, tree structure and stand dynamics are interconnected in the framework of carbon balance at an annual time resolution (Fig. 1 Structure of model, Supplementary material). The Norway spruce version of the model is described in detail in Kantola et al. (2007), and subsequent modifications reported in Niinimäki et al. (2012, 2013) and Mäkelä et al. (2016). Here, we describe the key characteristics of the model, as well as outline some further modifications made in this study.

The stand is described as a distribution of tree size classes. Each class is represented by its mean tree and stocking density. Annual photosynthetic production is first computed for the whole stand and then allocated to trees using a modified Lambert-Beer equation (Duursma and Mäkelä 2007). This is input to the TREE module where the growth of trees is derived from the carbon balance of the mean tree of the size class. The mean tree acquires carbon, respires, and loses biomass through turnover. Growth is allocated to foliage, branches, stem, coarse roots and fine roots to maintain a regular structure derived from the pipe model (Shinozaki et al. 1964), profile theory (Chiba et al. 1988) and fractal crown allometry (Mäkelä and Sievänen 1992; Duursma et al. 2010). These regularities allow for tracking the development of dimensional variables in addition to the biomass variables.

Climate and site impacts enter the model through (1) tissue-specific rates of carbon fluxes and (2) carbon allocation coefficients. Through modularity of model structure, different submodels may be chosen to describe these processes. Here, we use the approach introduced by Mäkelä et al. (2016) who proposed to incorporate these effects in PipeQual under current climate by means of effective temperature sum (ETS) and site type (as defined by Cajander 1949). Potential gross primary production depends on ETS because temperature, radiation (photosynthetically active radiation, PAR) and vapour pressure deficit (VPD) correlate with each other while soil water availability only plays a minor role in Norway spruce in Finland under current climate (Härkönen et al. 2010; Minunno et al. 2016). Growth respiration in the model is proportional to net production while maintenance respiration depends on the biomass of different compartments, air temperature and nitrogen concentration of tissue (through site type). Tissue life span is also related to climate and nitrogen content. Mäkelä et al. (2016) demonstrated that the consequent climate and soil driven geographic trends of forest carbon balance components yielded accurate estimates of the productivity of Norway spruce stands in Fennoscandian conditions.

Modifications to model structure

In the original PipeQual model (Mäkelä et al. 1997, 2000), stand density effects on tree structure were described on the basis of crown coverage which mediated both crown rise and mortality. No other density impacts on tree and stand structure were included. In order to improve the description of tree interactions in the model, here foliage density and crown width were made responsive to the competitive position of the tree. We made these explicitly dependent on the light availability to the trees instead of crown coverage.

The proportion of photosynthetically active light reaching height x in the canopy is calculated in the model as

$$f(x) = \exp\left[-\int_{H}^{x} \sum_{i} k_{i,\mathrm{eff}}\, l_i(y)\, dy\right] \qquad (1)$$

where H is canopy height, l_i is the vertical leaf area distribution of tree class i, $k_{i,\mathrm{eff}}$ is the effective extinction coefficient of tree class i (Duursma and Mäkelä 2007). The mean light environment experienced by tree class i is characterised as

$$f_{\mathrm{M}i} = \frac{1}{2}\left[f(H_i) + f(H_{\mathrm{C}i})\right] \qquad (2)$$

where H_i and $H_{\mathrm{C}i}$ are the height and crown base height of tree class i, respectively.

Using these definitions, crown rise was made dependent on the light conditions at the base of the crown. Firstly, we assumed the rise of the crown to follow the height growth as suggested by Valentine and Mäkelä (2005):

$$\frac{dH_{\mathrm{C}}}{dt} = s_{\mathrm{C}} \frac{dH}{dt} \tag{3}$$

and secondly, we made the coefficient s_{C} dependent on the proportion of light reaching the base of the crown of the tree class in a ramp-like manner as follows:

$$s_{\mathrm{C}} = 1 - \frac{1}{1 + e^{-a(f(H_{\mathrm{C}}) - f_0)}} \tag{4}$$

Here, a and f_0 are parameters (Table S1). In other words, crown rise occurs if the light level below the crown goes below a threshold, then rapidly accelerates to match height growth as the light levels fall (Figure S1).

In addition, plasticity of the crowns was assumed in two parameters. The foliage density parameter ξ was allowed to decline in trees in very poor light as follows:

$$\xi = \min\left\{\xi_0, \xi_0 \frac{f_{\mathrm{M}}}{f_1}\right\} \tag{5}$$

where ξ_0 is the value of this parameter in good and moderate light conditions and f_1 is the relative light level below which foliage density declines (Table S1).

Secondly, the growth of branch length was assumed to be regulated by the stand crown coverage A_{tot}; in sparser stands crowns were assumed to grow wider than in denser stands:

$$\gamma_b = \min\left\{\gamma_{b0}, \gamma_{b0}\frac{A_{\mathrm{tot},0}}{A_{\mathrm{tot}}}\right\} \quad (6)$$

where γ_b is the steady-state crown radius to crown length ratio, γ_{b0} is that ratio in a sparse stand, and $A_{\mathrm{tot},0}$ is a parameter (Table S1). When changes occur in A_{tot} the model changes γ_b gradually, tracking the effect of increased carbon demand of the accelerated growth of branches. This new formulation replaced the dependence of γ_b on tree age assumed by Niinimäki et al. (2012).

Description of permanent sample plots

The *Harkas* dataset of Natural Resources Institute Finland used in model evaluation consisted of 19 stands containing altogether 126 PSPs. These PSPs included 30800 sample trees of which 20576 Norway spruce were used in this evaluation (Table 1, Mäkinen and Isomäki 2004a, b). Temparature sum (ETS) of sites ranged from 1033 to 1275 d.d. and forest site type of 18 stands was fertile (*Oxalis-Myrtillus*) and one stand was classified as medium fertile (*Myrtillus*) site type according to the Finnish classification system (Cajander 1949). The stands were even-aged, almost pure Norway spruce stands. Measurements were taken 3 - 8 times, the longest measurement period being 37 years. In each measurement, tree species, stem diameter at 1.3 m (D1.3) and possible damage were measured in each tree. Tree height, height of the crown base and stem diameter at 6 m were measured, on average, from 54 sample trees in each plot. However, crown base heights had not been measured in the first measurement in any of the PSPs. Stand age at the first measurement ranged from 26 to 57 yrs, stand density from 935 to 3335 ha^{-1}, and dominant height (average height of the hundred thickest trees in the stand) from 9.8 to 24.3 m. In the last measurement, stand dominant height ranged from 29 to 34.5 m.

Each stand included plots of different intensity of thinning from below – unthinned, light, moderate, and heavy thinning. The number of plots per stand ranged mostly from 4 to 12, i.e., the four treatments were replicated in a randomized block design. Treatment intensity was defined on the basis of the basal area of the thinned plot relative to that of the unthinned control plot (*c.f.* Mäkinen and Isomäki 2004a). This dataset was utilized for re-calibrating the model after the modifications made to it in this study (see Modifications to model structure).

Another smaller PSP dataset (*Syst*, Table 1, Mäkinen et al. 2006) contained altogether 1565 trees on two experiments representing the fertile *Oxalis-Myrtillus* forest site type. In this dataset, stand age at the first measurement ranged from 38 to 41 yrs, stand density from 2780 to 3500 ha^{-1}, and dominant height from 15.8 to 16.8 m. The experiments were measured five times within a time frame of 17 and 21 years. This dataset was not utilized in model calibration and could thus be regarded as an independent data set.

Initialisation of the model

Because of the structural constraints in PipeQual, the initial state of each tree can be computed from tree height, breast height diameter, crown base height and tree age.The initial values of tree height, D1.3, and tree age were constructed for the size classes of the simulated stands from the first measurement of each PSP. The crown base heights needed for the determination of the crown ratio were not measured in the first measurements of PSPs and were thus determined by an empirical model (see below, eqs. 10 and 11). The diameter distribution of trees in the first measurement of each PSP was formed with two centimeter class width and the mean tree height, crown ratio etc. in each class were computed (SAS 9.4, SAS Institute Inc. 2015). This approach produced 10-20 size classes per plot which were used to describe the stand structure in PipeQual initialization.

Tree height and crown ratio are used for deriving the initial foliage and fine root mass and sapwood areas of the woody components in the TREE module (Mäkelä et al. 1997). The WHORL module (Kantola et al. 2007) is thereafter used for initialising the vertical distribution of variables across whorls, including whorl-mean branch length, branch and stem sapwood area and foliage mass. Initial tree age is needed for setting the initial number of whorls. This information is combined with breast height stem diameter for initialising the stem and branch heartwood both in TREE and WHORL modules. Lengths and diameters of individual branches are generated using empirical, stochastic functions for the number of branches in each whorl and a disaggregation of mean basal area and length to individual branches.

We predicted initial crown base heights by using the empirical model of Petersson (1997) in its original form. We derived model parameter estimates from stand variables obtained from the second, third etc. measurement of PSPs. The crown base height was measured in the field as the height of the lowest living branch above which no more than one dead whorl exists. Petersson's model utilizes both the tree level variables, like tree height, tree diameter and H/D ratio, and stand level variables, like stand density, basal area, volume and age, in the estimation of the crown base height:

$$\ln(y_{ilk}) = b_0 + b_1 \times \ln(x_{ilk}^1) + \ldots b_n \times \ln(x_{ilk}^n) + s_k + p_{lk} + \ln(\varepsilon_{ilk}) \qquad (7)$$

where y_{ilk} is the height of the crown base of tree i in plot l of stand k, b_j and x^j ($j = 1, \ldots n$) are the fixed-effect coefficients and independent variables, respectively, and s_k (stand) and p_{lk} (plot) account for the hierarchical data structure (Table 2). Instead of reducing random variation in stands by taking class means (which were described in terms of size class mean trees), the obtained crown base height estimates of individual trees were smoothed in each stand separately over tree height (*h*) with the Gompertz function (Fig. 2, Huang et al. 1992):

$$y = Ae^{\left[-e^{(\beta-\kappa h)}\right]} \qquad (8)$$

where y is the estimated height of the crown base, and A, β and κ are parameters.

Parameterisation

In this study, we estimated values for the parameters included in the new functions introduced above (see Modifications to model structure). The parameters were estimated through hand-tuning of educated initial guesses, with the *Harkas* data as a qualitative reference (Supplementary material). Other model parameters have been reported in previous studies (Kantola et al. 2007; Niinimäki et al. 2012; Mäkelä et al. 2016).

Model evaluation

We simulated the development of each stand from the initial condition, i.e. from the age of the first measurement of each PSP, until the stand reached the age of 100 years. In the simulations, we applied a thinning routine where the same number of trees was removed as in the field in each thinning. The share of removed trees per size class was based on the proportion of stand basal area contained in each size class.

Test diagnostics were calculated for both *Harkas* and *Syst* datasets. These included absolute model bias (AMB), relative model bias (RMB), and modeling efficiency (EF) to obtain an overall understanding of model behavior (Table 3, Pinjuv et al. 2006). In addition, we evaluated the accuracy of model predictions by plotting the simulated values against the measured values and fitting a linear regression between the observations and simulations. The slope, significance, and coefficient of determination (R^2) of the regressions were used for determining the accuracy of model predictions (Table 3, Fig. 3). Trends in residuals were inspected in order to observe over or underestimation of the model.

Results

Model accuracy at the whole dataset level was acceptable, suggesting that the simulations were able to meet our requirement of initialization at an arbitrary stand age (REQ1). Slope values between simulated and observed values ranged from 0.84 to 0.99 in different variables (Fig. 3). Slopes differed significantly from 1 ($p < 0.001$) in all variables indicating bias in model predictions. However, AMB of stand mean diameter and dominant height were low (Table 3), indicating high overall accuracy. RMB was highest in stand volume ca. 8%.

Stand mean stem diameter was slightly overestimated in stands with dbh < 20 cm, while in stands with larger mean diameter it was generally underestimated (Fig. 3a). Stand dominant height was predicted accurately in most of the stands throughout the observed range (Fig. 3b). Simulated stand density followed the observed (Fig. 3c) as should be expected due to the applied thinning routine where the same number of trees was removed as in the actual thinnings. However, this also indicates the success of the applied mortality function (Reineke 1933). In only a few unthinned or lightly thinned stands, the model predicted a slightly higher mortality rate than the measured one in the PSPs. The simulated diameter distributions of stands were, however, narrower and more peaked than those observed (Fig. 4). Both stand basal area and volume were slightly underestimated (Fig. 3d and e), the AMB being 1.9 m^2 ha^{-1} and 29 m^3 ha^{-1}, respectively (Table 3). Stands with the lowest volume were slightly overestimated while stands with high stem volume were generally underestimated and prediction error increased with increasing stand volume.

The annual volume increment (volume production) residuals were in average under 1 m^3 yr^{-1} (Fig. 5a) which we interpret to be small enough in order for the model to pass REQ2. There was a trend from overestimation in the heavily treated sites to underestimation in the unthinned stands. However, total annual increment also includes drain (harvests and mortality). Separation of these shows that the model tended to underestimate net increment (rate of change of standing volume) and overestimate drain (Fig. 5b and c) but no treatment effect was observed in these terms.

The results illustrated in Fig. 5 indicate that the model was able to meet REQ3, at least partly, since the observed trend in residuals between treatments was reasonably small. In a closer look, the simulated stand dynamics generally followed closely the observed patterns both in the unthinned and thinned plots (Fig. 6). However, in some stands (e.g. in Hauho, Fig. 6) stand basal area was clearly overestimated in the unthinned and lightly thinned plots. A similar pattern could be seen in stand volume.

For testing the REQ4, we analyzed the simulated height to diameter ratio (H/D), crown base heights and stand leaf area index (LAI). Both simulated H/D and crown base height showed a moderate correspondence with the observations (Fig. 7a and 8a). The development of simulated H/D over stand age followed a logical pattern, responding to thinning as expected although not quite as strongly as observed (Fig. 7b). This deviation was especially clear in heavily treated plots. The height to crown base was generally overestimated at the initialization, the error being largest in the trees with low crown base heights (Fig. 8). The simulated rise of the crown base and thinning response seemed generally to follow closely the observed (Fig. 8b) and no treatment effect was observed in the residuals (data not shown).

The stand leaf area index (LAI) estimate was not included in the PSP dataset. Thus, we evaluated the LAI prediction of PipeQual by estimating the foliage mass of simulated trees with empirical biomass models (Marklund 1988; Repola et al. 2009) and converting those values to LAI with the mean specific leaf area value used in PipeQual. PipeQual generally predicted higher stand LAI than these two empirical models (Fig. 9a). In most of the stands, PipeQual and Repola's model predicted similar thinning responses while in Marklund's model the development of LAI after thinning deviated from the other models (Fig. 9b).

In the comparison against the smaller independent dataset (*Syst*), the model showed similar accuracy as in the larger *Harkas* PSP dataset (Table 3). The level of stand mean diameter, predicted dominant height and stand basal area did not deviate from the observations ($p > 0.05$) while the level of stand volume was underestimated ($p = 0.006$). In stand mean diameter and stand volume, the residuals had a significant trend with stand age ($p = 0.048$ and 0.026, respectively).

Discussion

In this study, our main focus was on evaluating the PipeQual model for applications in forestry practice, where data on standard forest mensuration variables are available from stands at an arbitrary measurement age, and the aim is to make predictions about forest growth and yield under different thinning schedules. While most empirical forest growth models have been planned for precisely this type of use, process-based models are prone to face a challenge because of their detailed input requirements and lack of variables relevant to forest mensuration (Cuddington et al. 2013). However, there is a need for models capable of projecting the potential impact of climate change on long-term patterns of forest growth and development while being reasonably accessible to forest managers. Most importantly, such models should be able to represent the effects of climate change on forest productivity, to simulate a variety of forest management options for creation of adaptive management strategies and be relatively straightforward to calibrate (Seely et al. 2015). Hybrid models, like PipeQual here, could be seen as a bridge between traditional statistical forest growth and yield models and overly complex PBMs called for the support in forest management decision-making in changing environmental conditions (Valentine and Mäkelä 2005; Fontes et al. 2010; Cuddington et al. 2013). Climatic envelope models are too simplistic for predicting changes in tree growth at stand level which is the meaningful scale for forest management (Kimmins et al. 2008). Stand level hybrid models are founded in ecological theory and incorporate key ecophysiological processes involved in tree growth rates to deal adequately with the increasing uncertainty of future tree growth and climate change effects on forests (Lo et al. 2010). We see model evaluation as a prerequisite for using any model in forest management decision making or scenario modeling. Model evaluation aims at assessing how well a model performs in the types of application it was planned for (Bokalo et al. 2013).

In our evaluation, we combined several metrics in order to get a robust idea of the strengths and weaknesses of the model. The low AMB values (Table 3) are indicative of coherence of model predictions over the whole dataset. The high efficiency values indicate that there is little variation in the residual errors, i.e., the predictions had high precision (but not necessarily good accuracy, *c.f.* Bokalo et al 2013). The prediction error in the annual volume increment was at an acceptable level (on average ca. 1 m^3), thinning responses were logical and quantitatively reasonable, and the simulated tree form in terms of height to diameter ratio (H/D) showed a fair correspondence with the observations. These results support the robustness of the model and its applicability to assess the effects of forest management activities, while Mäkelä et al. (2016) have shown that PipeQual is also able to reproduce the geographic variation of tree growth within forests of Finland.

That an arbitrary age and stand structure could be used for model initialization, was primarily due to the inclusion of structural constraints (e.g. the ratio between leaf mass and sapwood area, see Supplementary material) in the model which allowed us to derive all key state variables from a small subset of inputs. However, the new components of the model accounting for acclimation of foliage density and crown width to light conditions further improved model performance especially with regard to the initial state. The model bias was not, however, stable over time since residuals of the examined variables had a trend, with increasing bias over stand age. This trend was the strongest in stand-mean diameter and weakest in stand volume, suggesting that while total stem increment was reasonably well estimated, there may have been problems in the allocation of growth between stem height and diameter.

Tree form is a measure of the trade-off between accumulating height and accumulating diameter (Robinson and Ek 2003). Trees grown in high stocking have different stem form from those grown in sparse stands (Assman 1970, Fontes et al. 2006). PipeQual produced underestimates in high H/D values (Fig. 7a) due to simulated small trees being shorter than those observed relative to their diameter, whereas simulated large trees were taller than those observed relative to their diameter resulting in overestimation of low H/D values. Nevertheless, the fact that the model explicitly considers stem form as part of the carbon allocation routine is crucial for converting the carbon fluxes into meaningful forest mensuration variables. Most of the PBMs either ignore stem dimensions (e.g., Landsberg and Waring 1997, Pietritsch et al. 2007) or assume a prescribed H/D ratio (Thornley and Cannell 2000). In PipeQual, the allocation between height and diameter growth is linked to crown ratio and crown rise according to the profile theory (Chiba et al. 1988), and the model does not make any *a priori* assumptions about the height growth pattern. With no crown rise, more growth is allocated to increasing the size of the crown. This results in a demand of basal area growth through the pipe model assumption. In contrast, when crown recession occurs, more photosynthates are needed for the replacement of the dead branches and the corresponding woody "pipes" as well as for the height increment, whereas crown size and therefore basal area growth remain low (Valentine and Mäkelä 2005).

Despite the causal structure of this allocation pattern, there are still problems in actually quantifying it. As demonstrated in the present parameter estimation (see also Supplementary material), the resulting H/D ratio is sensitive to the assumptions about crown rise. Similarly, changes in crown shape and the demand of photosynthates to branch growth affect the pattern. The new model features implemented here about the impact of the light climate on foliage density and branch length amplified the effects of crown rise by increasing the photosynthate demand of foliage and branches in high relative to low light availability. Nevertheless, the simulated crown rise was faster than the observed. This could partly be caused by the model of Pettersson (1997) used for predicting initial height of crown base, in some cases, produced initial crown base heights that were higher than the actual heights in the subsequent measurements, although part of the effect evidently came from the model dynamics.

Our results suggest that the physiological foundation of PipeQual was sufficient for producing plausible growth responses to thinnings. According to ecological theory and forestry experience, tree populations respond to thinning by increased diameter increment, maintained or reduced height increment and reduced crown recession (Assmann 1970; Vuokila and Väliaho 1980; Pretzsch 2002; however, see Raulier et al. 2003). From the carbon balance modeling perspective this is indicative of changes in carbon allocation after thinning between diameter and height increment on one hand, and between crown rise and crown extension on the other hand. (Mäkelä 1997; Valentine and Mäkelä 2005). Thinning slowed down the simulated crown rise, however, the effect was modest compared with the observations on the heavily treated plots. Heavy thinning yielded a clear halt in the observed crown rise for several years, whereas in the simulations the plateau was clearly shorter. One reason behind this could be that the model overestimates production after heavy thinning (Fig. 5a) since the photosynthesis model does not take into account the clustering of foliage enough (Duursma and Mäkelä 2007).

The basic carbon balance modeling approach in PipeQual follows the general convention used in many models with different species and conditions (Thornley and Cannell 2000, Fontes et al. 2006). On the other hand, it differs from many models in the way it translates the carbon balance into structural growth. Here, the key components are the assumptions made on conservative structures, such as the pipe model, and on plastic structures, such as crown ratio. Valentine and Mäkelä (2005) presented an explicit derivation of dimensional growth from the carbon flux rates (Bridging Model) under assumptions virtually identical with the CROBAS module of PipeQual. The Bridging Model has been succesfully parameterised for stand mean trees using statistical fitting in spacing experiments (Valentine et al. 2012, 2013) and Bayesian calibration in national inventory data (Van Oijen et al. 2013). The PipeQual model has also been previously parameterised for Scots pine (Mäkelä and Mäkinen 2003). These results suggest that the structural assumptions of PipeQual are realistic and generic, but adjustment to actual parameter values will nevertheless be required when moving from one ecosystem to another. Our on-going work in this respect is focusing on deciduous stands, old growth forests and continuous cover management.

Like in any carbon balance model, the responses to a changing environment are accounted for through the corresponding responses in the carbon flux rates, including the relative allocation of carbon to below-ground components (Mäkelä et al. 2016). The relatively simple description of the metabolic processes compared with many PBMs (Medlyn et al. 2011) and the modular structure of PipeQual ensure its flexible application to different conditions. For example, the module for deriving potential photosynthetic production from effective temperature sum can easily be replaced by a module responsive to a number of environmental drivers (Minunno et al. 2016) that may be of importance under climate change. A more challenging question is that of nitrogen availability in relation to photosynthetic potential (e.g. Mäkipää et al. 2015). As Cuddington et al. (2013) point out climate change may alter the processes which operate at different scales than decision-making and are still critical for model predictions e.g. global atmospheric CO_2 concentration. In addition, there remains uncertainty about how an ecological process will interact with new global change conditions. This challenges the scale and scope of models developed for answering forest management questions. It is evident that continuous evaluation of models will be required as data gradually becomes available from changing environments.

Conclusions

Process-based simulation model predictions should be evaluated before their use as a tool for depicting the growth and development of forest stands in a changing environment. In this evaluation, we showed that the hybrid model, PipeQual, was able to describe forest management effects on Norway spruce in terms of traditional stand mensuration variables at an acceptable level of error. Low AMB and RMB values along with sensible thinning responses demonstrate that PipeQual was reliable enough for tasks usually performed by empirical forest models. The structural constraints coupled with underlying processes form a foundation of the model which ensures applicability in different conditions. The new functions connecting tree crown characteristics explicitly to stand light conditions further improved this flexibility. This approach enabled more stringent evaluation of the model with PSP data but it will also enhance the applicability of the model to real life situations where the prediction of stand development from random initial conditions is of interest. The approach provides both forecasts and insights into the underlying processes that drive changes in forest growth, thus helping us answer forest management related questions in scenario modeling of future climate conditions.

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Figure captions

Fig. 1. The structure of PipeQual model.

Fig. 2. An example of the estimation of the crown base height for the initial stage of PipeQual model by empirical model of Petersson (1997). Dots are the observed crown base heights and squares the predictions of model. Line is the result of smoothing (eq. 8). In this specific stand and plot (located in Keuruu, ID = Vh002, plot = 2), parameter values of Gompertz function were $A = 4.2129$, $\beta = 1.0740$ and $\kappa = 0.1559$.

Fig. 3. The tree and stand level relationships between simulated and observed variables. a) stem diameter at breast height (cm), b) dominant height (m), c) stand density (stems ha^{-1}) d) basal area (m^2 ha^{-1}), e) stand volume (m^3 ha^{-1}). Each dot represents one permanent sample plot (PSP) and different colors specify different stands. Continuous line is 1:1 line and dashed line the linear regression curve obtained with coefficients in subfigures.

Fig. 4. Simulated vs observed diameter distribution. The average of all stand distributions in the last measurement.

Fig. 5. Residuals (observation - simulation) of a) annual volume increment (volume production), b) annual net increment (rate of change of standing volume), and c) annual drain (harvested + mortality).

Fig. 6. Dynamics of stand basal area (a-c) and stand volume (d-f) over stand age in three stands (top row Heinola, ID = Vh012, middle Hauho, ID = Ha001, bottom Punkaharju, ID = Pu041). Continuous lines with symbols are the observations, dashed lines with symbols are the PipeQual predictions. Symbols depict the treatment intensities of the experiments.

Fig 7. Stem form (height to diameter ratio, H/D). a) The relationship between simulated and observed H/D in the whole dataset. Each dot represents one permanent sample plot (PSP) and different colors specify different stands. Continuous line is 1:1 line and the dashed line the linear regression curve obtained with coefficients in the figure. b) The change of H/D over stand age in one stand (located in Hauho, ID = Ha001) with different treatments. Continuous lines with symbols are the observations and the dashed lines with symbols are the PipeQual predictions. Symbols depict the treatment intensities of the experiment.

Fig.8. Height to crown base. a) The relationship between simulated and observed height to crown base in the whole dataset. Each dot represents one permanent sample plot (PSP) and different colors specify different stands. Continuous line is 1:1 line and the dashed line the linear regression curve obtained with coefficients in the figure. b) Height to crown base over stand age in one stand (located in Heinola, ID = Nyn3). Continuous lines with symbols are the observations and the dashed lines with symbols are the PipeQual predictions. Symbols depict the treatment intensities of the experiment.

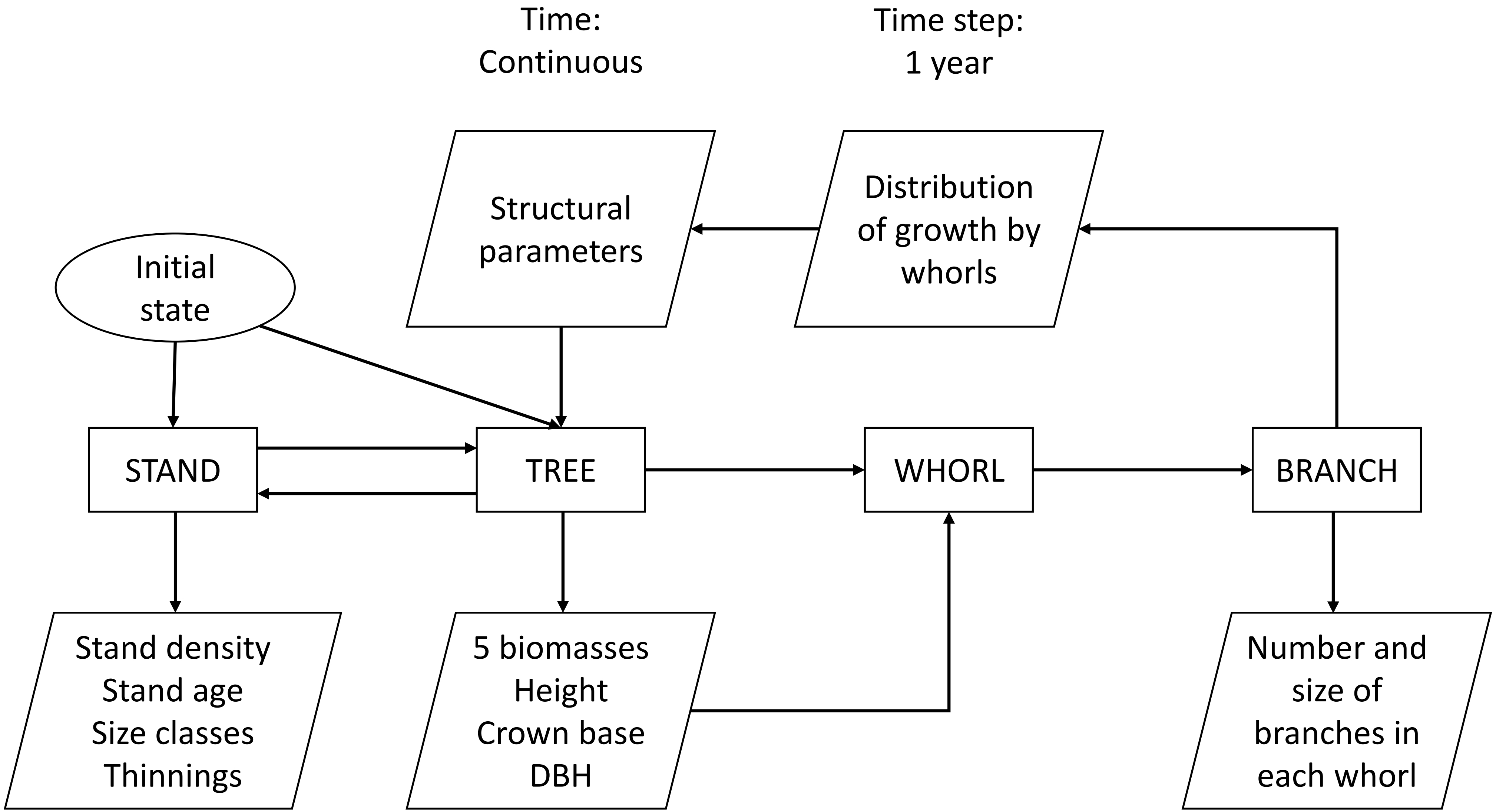
Fig. 9. Stand leaf area index (LAI) over stand age. a) Lines represent the means of different models over all stands in the PSP dataset. Bands are ± 1 standard deviation. b) foliage dynamics in one stand on the unthinned plot (located in Heinola, ID = Vh001) predicted by different models.

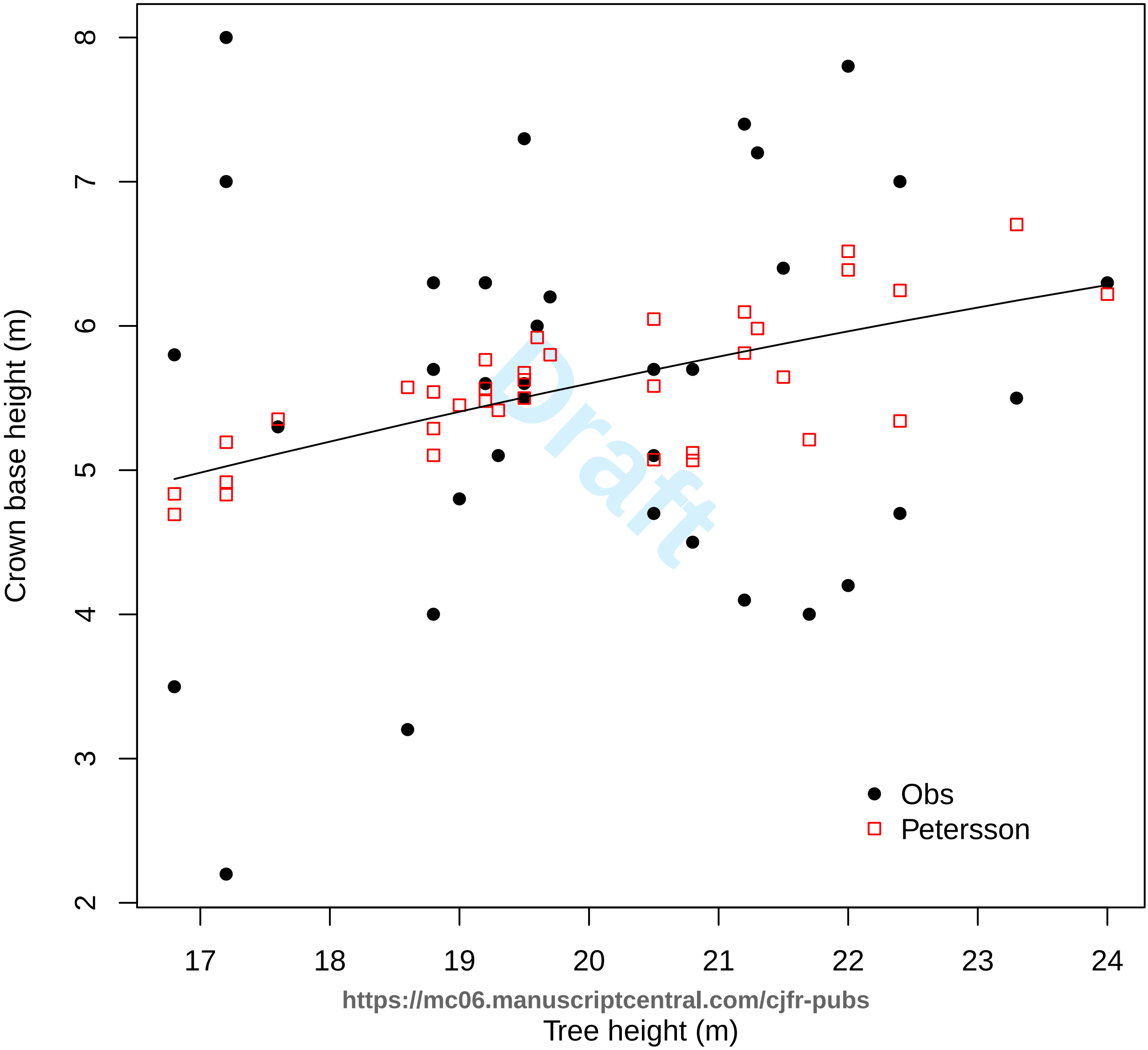
Table legends

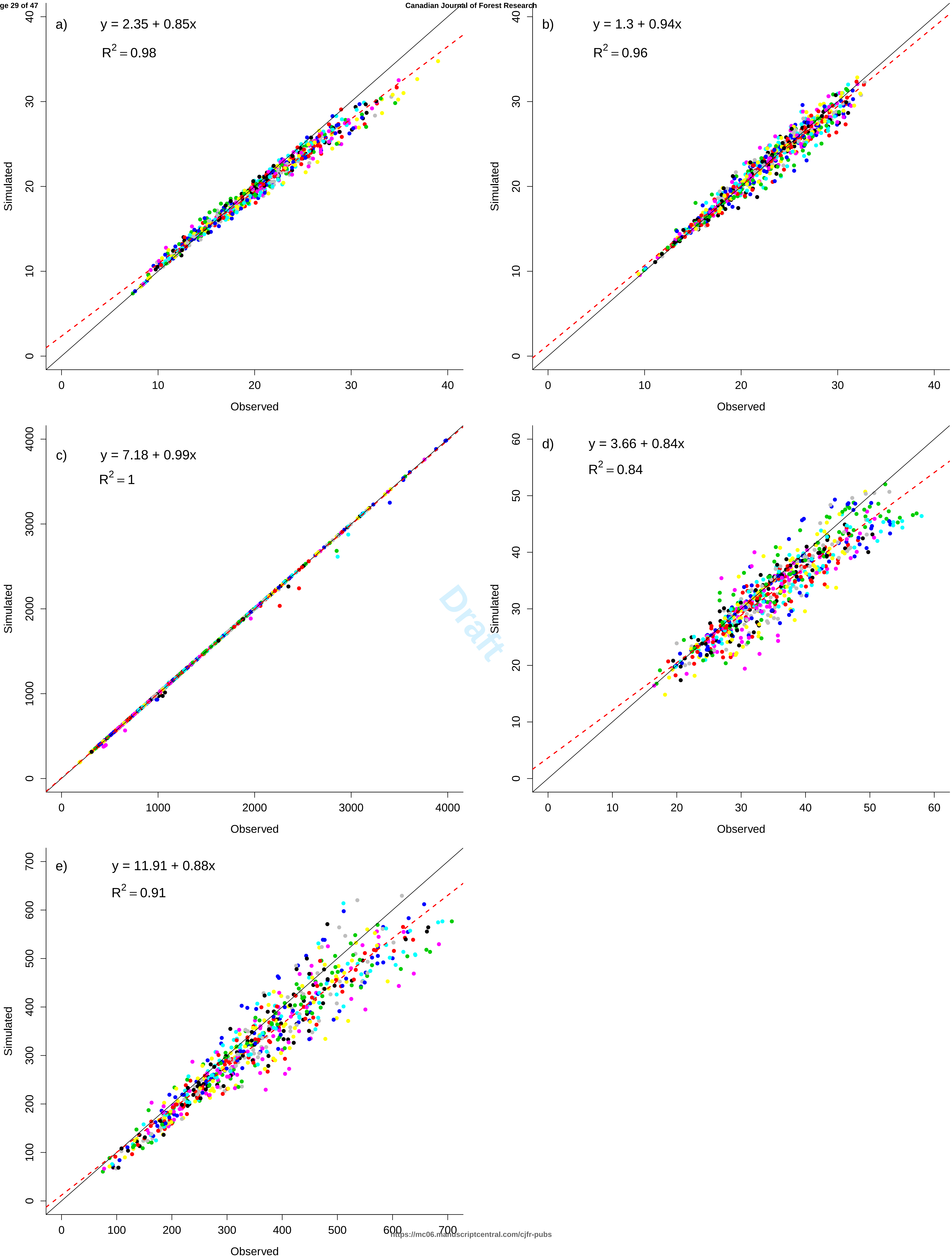
Table 1. Stand characteristics of the permanent sample plot (PSP) datasets.

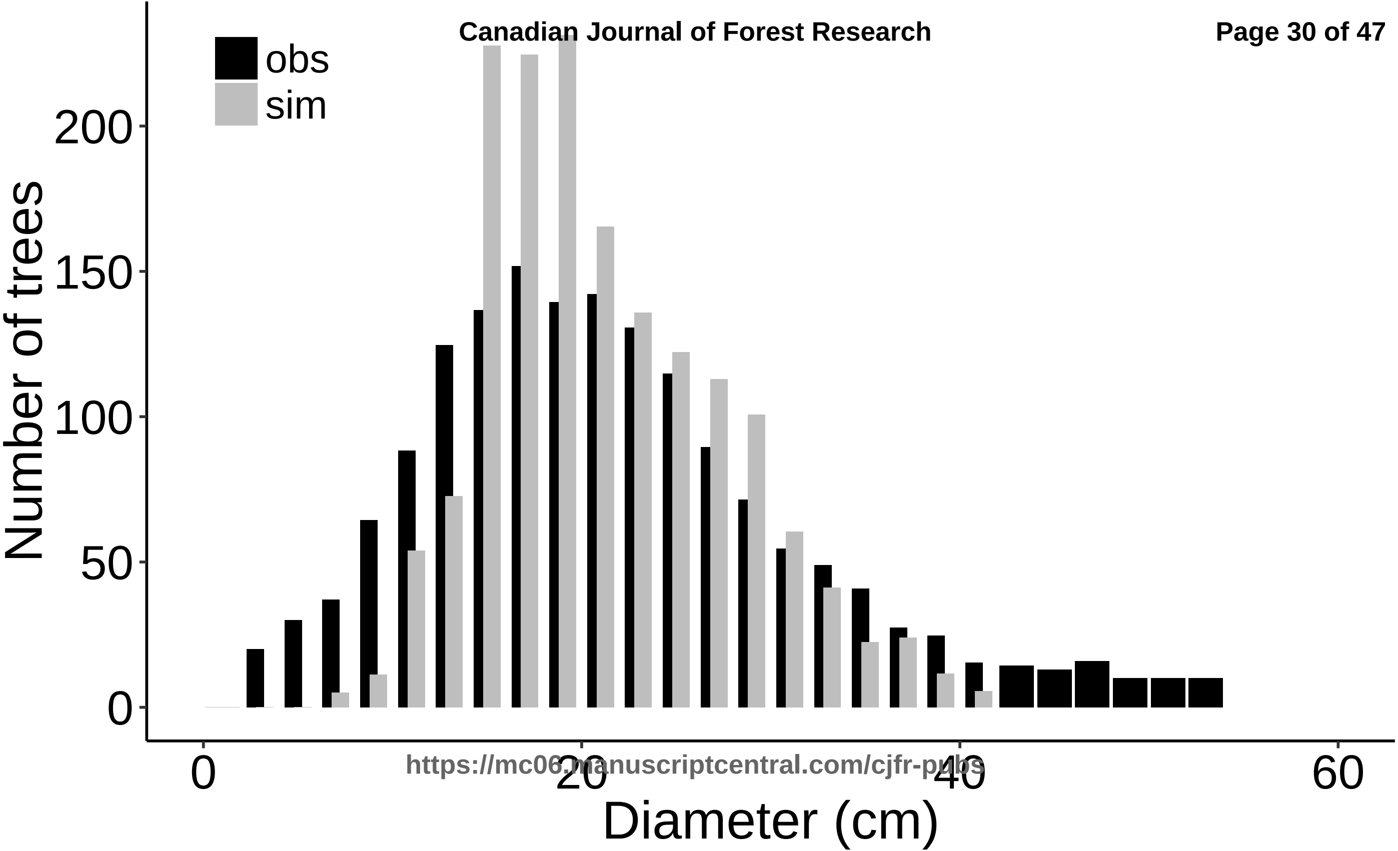
Table 2. Independent variables and the parameter estimates used in the prediction of crown base height (Eq. 7).

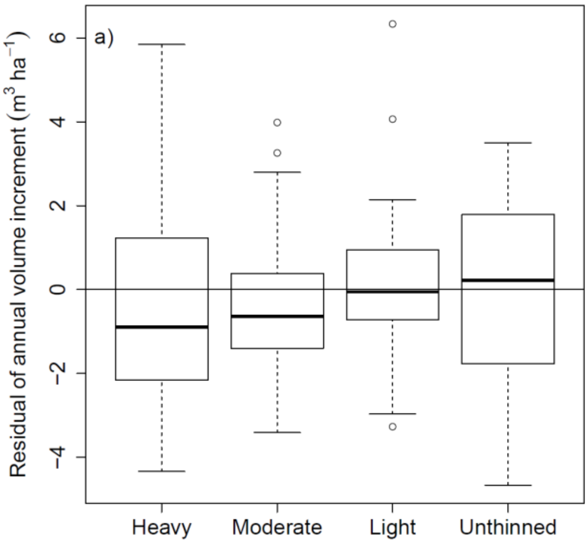
Table 3. Validation metrics. AMB = absolute model bias (negative values are overestimates, positive underestimates, cm in diameter, m in dominant height, m^2 ha^{-1} in basal area, and m^3 ha^{-1} in stand volume), RMB = relative model bias, EF = modeling efficiency.

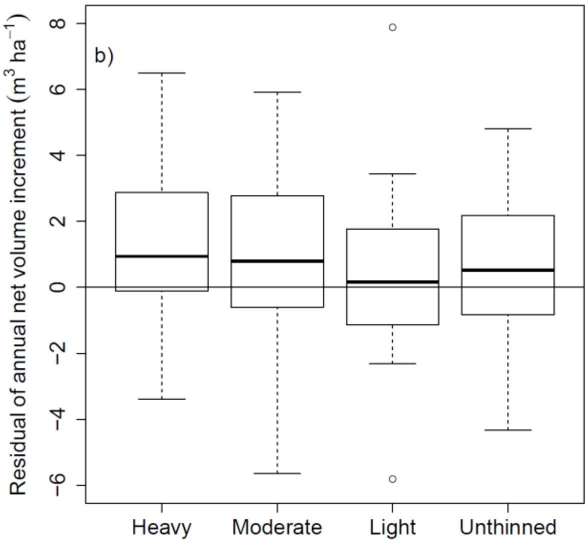

Time:
Continuous
Time step:
1 year
Structural parameters
Distribution of growth by whorls
Initial state
STAND
TREE
WHORL
BRANCH
Stand density
Stand age
Size classes
Thinnings
5 biomasses
Height
Crown base
DBH
Number and size of branches in each whorl

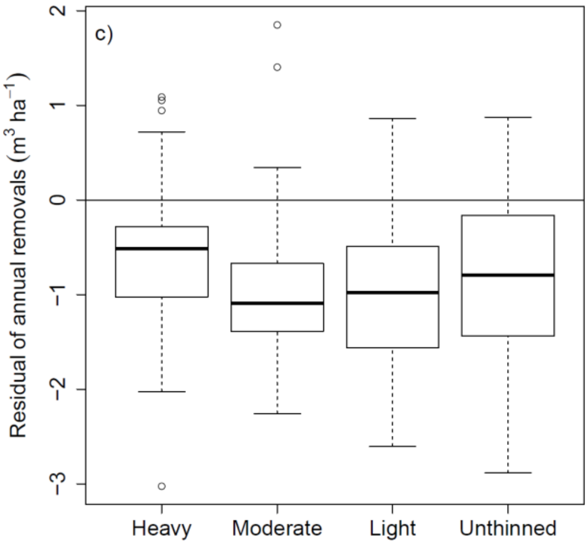

Crown base height (m)
8
7
6
5
4
3
2
17
18
19
20
21
22
23
24
Tree height (m)
● Obs
□ Petersson

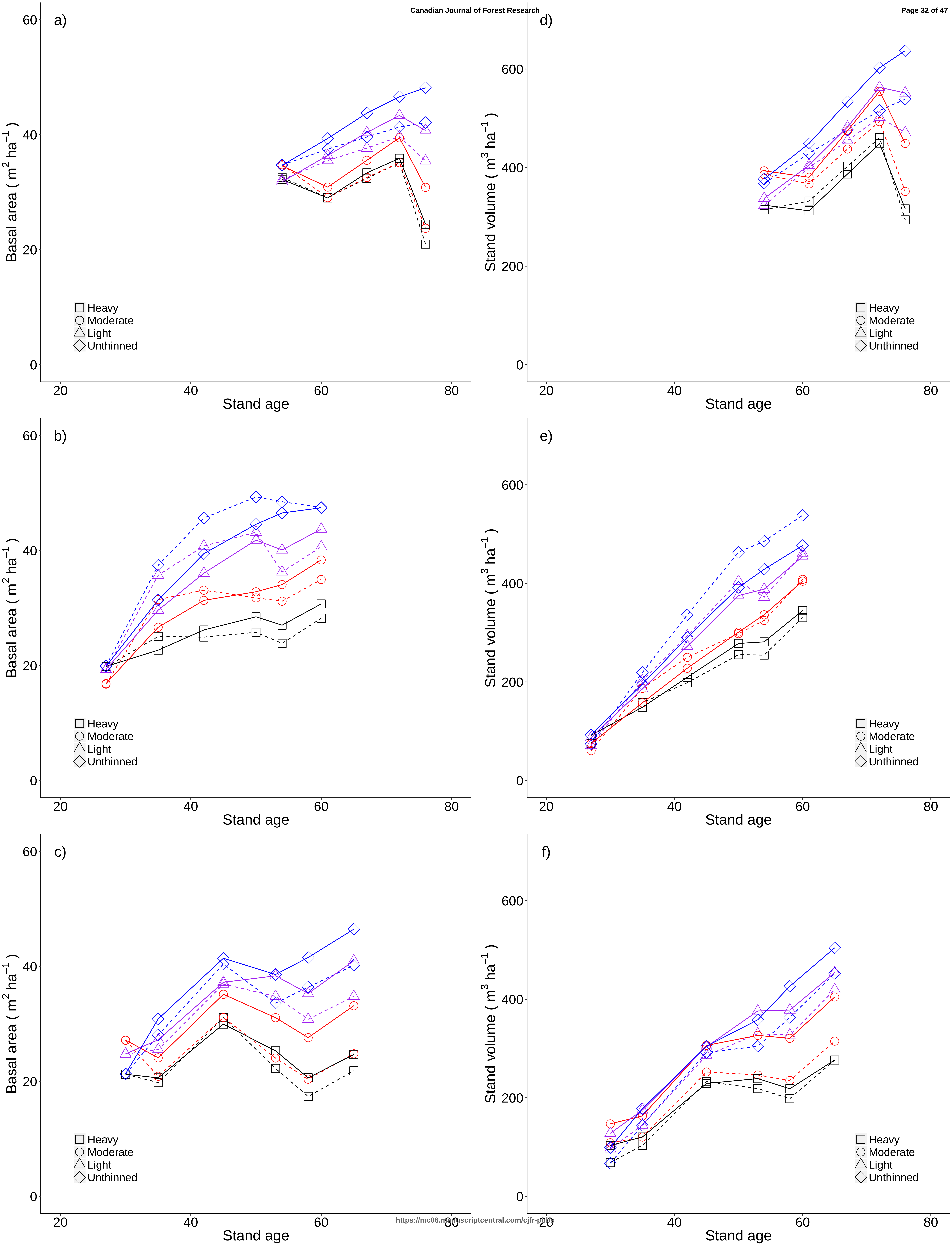

a)
y = 2.35 + 0.85x
$R^2 = 0.98$
Simulated
Observed
0
10
20
30
40
b)
y = 1.3 + 0.94x
$R^2 = 0.96$
Simulated
Observed
0
10
20
30
40
c)
y = 7.18 + 0.99x
$R^2 = 1$
Simulated
Observed
0
1000
2000
3000
4000
d)
y = 3.66 + 0.84x
$R^2 = 0.84$
Simulated
Observed
0
10
20
30
40
50
60
e)
y = 11.91 + 0.88x
$R^2 = 0.91$
Simulated
Observed
0
100
200
300
400
500
600
700

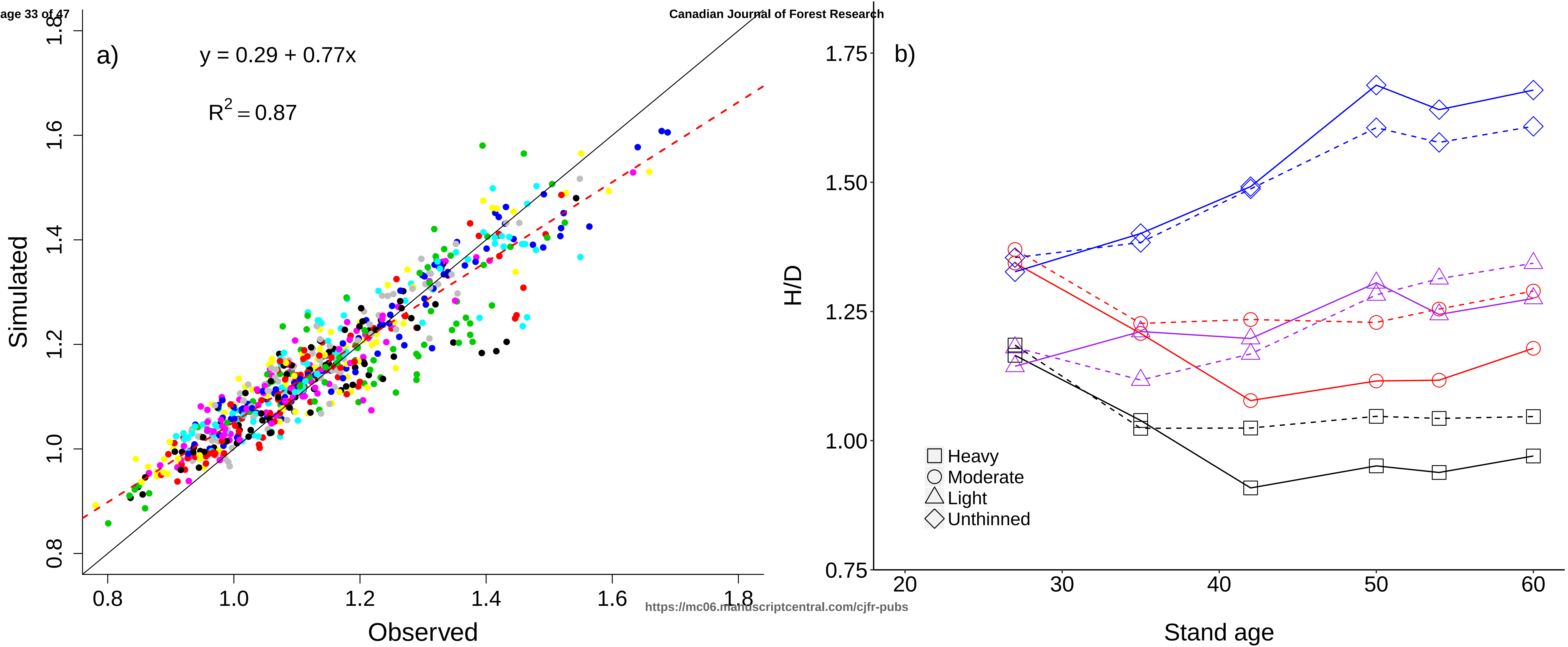

obs
sim
Number of trees
0
50
100
150
200
0
20
40
60
Diameter (cm)

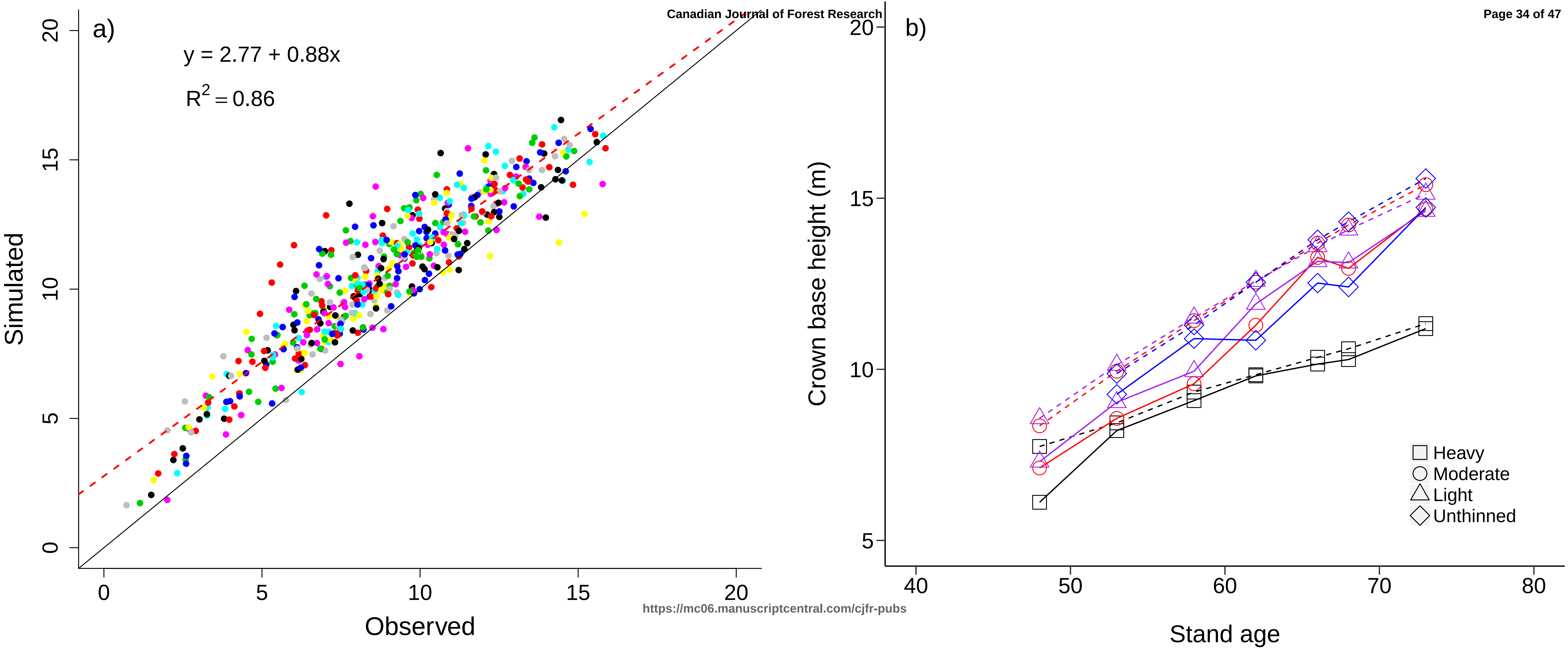

a)
Residual of annual volume increment (m^3 ha^{-1})
6
4
2
0
−2
−4
Heavy
Moderate
Light
Unthinned


b)
Residual of annual net volume increment (m^3 ha^{-1})
8
6
4
2
0
−2
−4
−6
Heavy
Moderate
Light
Unthinned


c)
Residual of annual removals (m^3 ha^{-1})
2
1
0
−1
−2
−3
Heavy
Moderate
Light
Unthinned


a)
b)
c)
d)
e)
f)
Basal area (m^2 ha^{-1})
Stand volume (m^3 ha^{-1})
Stand age
0
20
40
60
0
200
400
600
20
40
60
80
Heavy
Moderate
Light
Unthinned


a)
y = 0.29 + 0.77x
$R^2 = 0.87$
Simulated
Observed
0.8
1.0
1.2
1.4
1.6
1.8
b)
H/D
1.75
1.50
1.25
1.00
0.75
20
30
40
50
60
Stand age
Heavy
Moderate
Light
Unthinned


a)
y = 2.77 + 0.88x
R2 = 0.86
Simulated
0
5
10
15
20
Observed
0
5
10
15
20
b)
Crown base height (m)
5
10
15
20
Stand age
40
50
60
70
80
Heavy
Moderate
Light
Unthinned

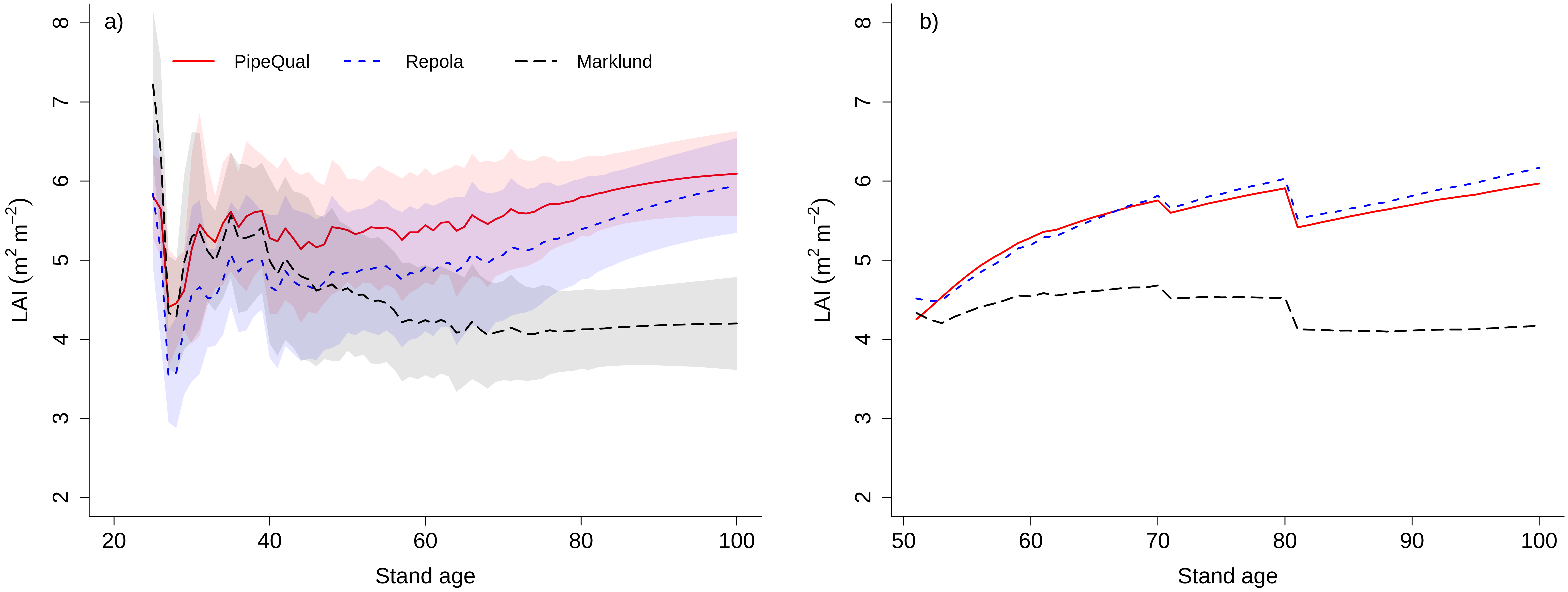

a)
PipeQual
Repola
Marklund
LAI (m^2 m^{-2})
2
3
4
5
6
7
8
20
40
60
80
100
Stand age
b)
LAI (m^2 m^{-2})
50
60
70
80
90
100
Stand age

Table 1. Stand characteristics of the permanent sample plot (PSP) datasets.

								At establishment	
Experiment	ID	N of plots	Forest type	H_{100}	Year of planting	Establishment of plots	Last measured	H_{dom} (m)	N of stems
Harkas									
1	Vh001	6	OMT	34.4	1918	1970	1998	24.3	1072
2	Vh002	3	OMT	31.6	1925	1979	1998	16.9	1404
3	Vh005	10	MT	28.9	1931	1971	1994	13.5	2212
4	Vh009	4	OMT	31.1	1931	1973	1998	17.0	1856
5	Vh011	8	OMT	30.2	1914	1970	1999	22.4	1114
6	Vh012	10	OMT	32.4	1916	1970	1998	23.4	1042
7	Vh013	8	OMT	32.9	1932	1970	1998	18.1	2013
8	Vh014	8	OMT	32.7	1918	1971	1998	23.1	935
9	Vh017	4	OMT	32.9	1936	1971	1985	16.3	2932
10	Vh048	8	OMT	31.0	1934	1977	2001	16.9	2137
11	Vh097	12	OMT	34.0	1955	1981	1994	12.5	2973
12	Ha001	5	OMT	30.2	1938	1965	1998	9.8	3335
13	Pu041	4	OMT	33.0	1934	1964	1999	12.1	1689
14	Pu042	4	OMT	33.0	1924	1964	1999	17.4	1168
15	Nyn1	12	OMT	30.0	1922	1961	1998	14.2	2055
16	Nyn2	4	OMT	34.5	1931	1962	1998	14.7	3247
17	Nyn3	8	OMT	34.7	1926	1962	1999	16.0	2394
18	Nyn4	4	OMT	33.0	1925	1962	1988	15.6	2295
19	Nyn5	4	OMT	33.0	1930	1962	1992	14.3	3402
Syst									
1	102	2	OMT	28.6	1933	1974	1995	15.4	2768
2	107	3	OMT	32.0	1940	1977	1994	16.0	3290

Table 2. Independent variables and the parameter estimates used in the prediction of crown base height (Eq. 7).

Variable	Parameter estimate	Standard error
Fixed effects		
Intercept	-3.2697	0.5169
Tree height (m)	0.4125	0.0865
Stem diameter (cm)	0.3769	0.0841
Height/Diameter	-0.7335	0.0745
Stand density (n ha^{-1})	0.1117	0.0539
Stand basal area (m^2 ha^{-1})	-0.1052	0.2646
Stand volume (m^3 ha^{-1})	0.4796	0.1849
Stand age (a)	0.1568	0.1299
Random effects		
Stand	-3.14E-12	0.0143
Plot	-7.07E-13	0.0060

Table 3. Validation metrics. AMB = absolute model bias (negative values are overestimates, positive underestimates, cm in diameter, m in dominant height, m^2 ha^{-1} in basal area, and m^3 ha^{-1} in stand volume), RMB = relative model bias, EF = modeling efficiency.

Experiment	Variable	AMB	RMB (%)	EF
Harkas	Mean stem diameter	0.57	2.9	0.95
	Dominant height	0.07	0.3	0.96
	Stand basal area	1.92	5.5	0.79
	Stand volume	29	8.2	0.86
Syst	Mean stem diameter	-0.68	-3.8	0.91
	Dominant height	-0.72	-3.7	0.86
	Stand basal area	-2.62	-7.0	0.86
	Stand volume	20	6.3	0.82

Supplementary material

S1. Model description

In the TREE module, trees are described in terms of 16 state variables which are bound together through structural rules, such that only a few fully independent variables remain (Table S1). These include tree height, height to the crown base, stem basal area at breast height, and mass of branch heartwood. Temporary deviations of the structural rules may occur due to, e.g, defoliation or abrupt changes in the environment, such as those caused by thinning (Mäkelä 1999). The most important structural rules are the following:

1) foliage mass, W_f, is related to crown length, $H - H_\mathrm{C}$, through an allometric relationship (Mäkelä and Sievänen 1992):

$$W_\mathrm{f} = \xi (H - H_\mathrm{C})^z \qquad \text{(S1)}$$

where H is tree height, H_C is height to the crown base and ξ and z are parameters.

2) sapwood cross-sectional areas of stem (A_s), branches (A_b), and coarse roots (A_c), are related to foliage mass according to the pipe model:

$$W_\mathrm{f} = \eta_i A_i \qquad \text{(S2)}$$

where η_i $(i = s, b, c)$ are parameters.

3) fine root mass, W_r, is related to foliage mass

$$W_\mathrm{r} = \alpha_\mathrm{r} W_\mathrm{f} \qquad \text{(S3)}$$

where the parameter α_r depends on site fertility.

4) sapwood biomasses are related to sapwood area and mean length, L_i $(i = s, b, c)$:

$$W_i = \phi_i A_i L_i \qquad \text{(S4)}$$

where ϕ_i $(i = s, b, c)$ are empirical form factors.

5) the mean lengths of the branch and coarse root systems are proportional to crown length and tree height, respectively.

The WHORL module takes in the information from the TREE module and distributes the organ biomasses to whorls on the basis of empirical information about the vertical distributions of biomass in the tree (Mäkelä and Mäkinen 2003; Kantola et al. 2007). Importantly, the foliage biomass is assumed to follow a β-function which moves upward as tree height and crown base rise. This distribution gives rise to sapwood area in whorls, which turns into heartwood as the foliage reduces in the lower whorls. At the same time, stem heartwood accumulates when the wood loses its connection to live foliage.

Detailed stem and branch structure is described in the WHORL module which contains the sapwood and heartwood area and section length as state variables for each whorl. The growth of the whorls is driven by the TREE module, and changes in structure are fed back to the TREE module in the form of aggregated parameter values updated each year (Mäkelä et al. 1997).

The BRANCH module further divides the branch sapwood into individual branches. It computes the number of branches and their size distribution in the new whorls, then keeps track of the sizes of all branches and finally induces branch mortality and shedding. The BRANCH module is fully statistical and has no feedback effect on the rest of the model components.

S2. Parameter estimation

To estimate the parameters of new equations, the model was simulated with a range of plausible values, and a set of parameters providing a qualitatively reasonable output was selected. This was done prior to the quantitative model testing against the PSP data.

The initial values of the parameter ranges were either derived from the literature or set in such a way that the model produced logical responses at the stand level. In general, different combinations of the parameters could produce virtually the same stand-level responses. As the equations are semi-empirical or phenomenological, the actual values of the parameters are largely unknown and model calibration is needed in order to fix the parameter values. Here, we show the results of stand-level model sensitivity analysis which was used to select the parameter values. These parameters were related to the interactions of tree size classes, and the main influence of the present data was through the initialization procedure. Other model parameters have been reported in previous studies (Kantola et al. 2007; Niinimäki et al. 2012; Mäkelä et al. 2016).

Figure S1 illustrates the Eqn 6 of study. Crown rise occurs if the light level below the crown goes below a threshold, then rapidly accelerates to match height growth as the light levels fall.

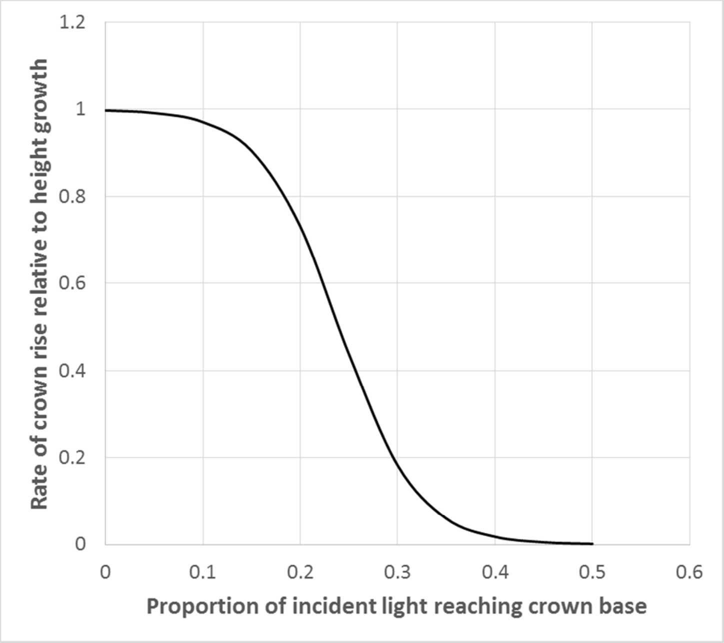


Fig. S1. The vertical axis shows s_C as a function of $f(H_C)$ when $a = 25$ and $f_0 = 0.24$ (default values in simulations).

Table S1. Parameters related to structural acclimation to light

Parameter	Value	Units	Equation
a	25	-	(S3)
f_0	0.24	-	(S3)
ξ_0	0.112	-	(S4)
f_1	0.55	-	(S4)
γ_{b0}	0.20	-	(S5)
A_{tot}	0.7	-	(S5)

The foliage density parameter ξ_0 relates foliage mass to crown length in good and moderate light (Fig. S2), while f_1 is the mean relative light level of the crown that causes the foliage density to decline (Fig. S3). The parameter ξ_0 was allowed to decline in trees in very poor light. Height growth response is very sensitive to the changes of this parameter (Fig. S2).

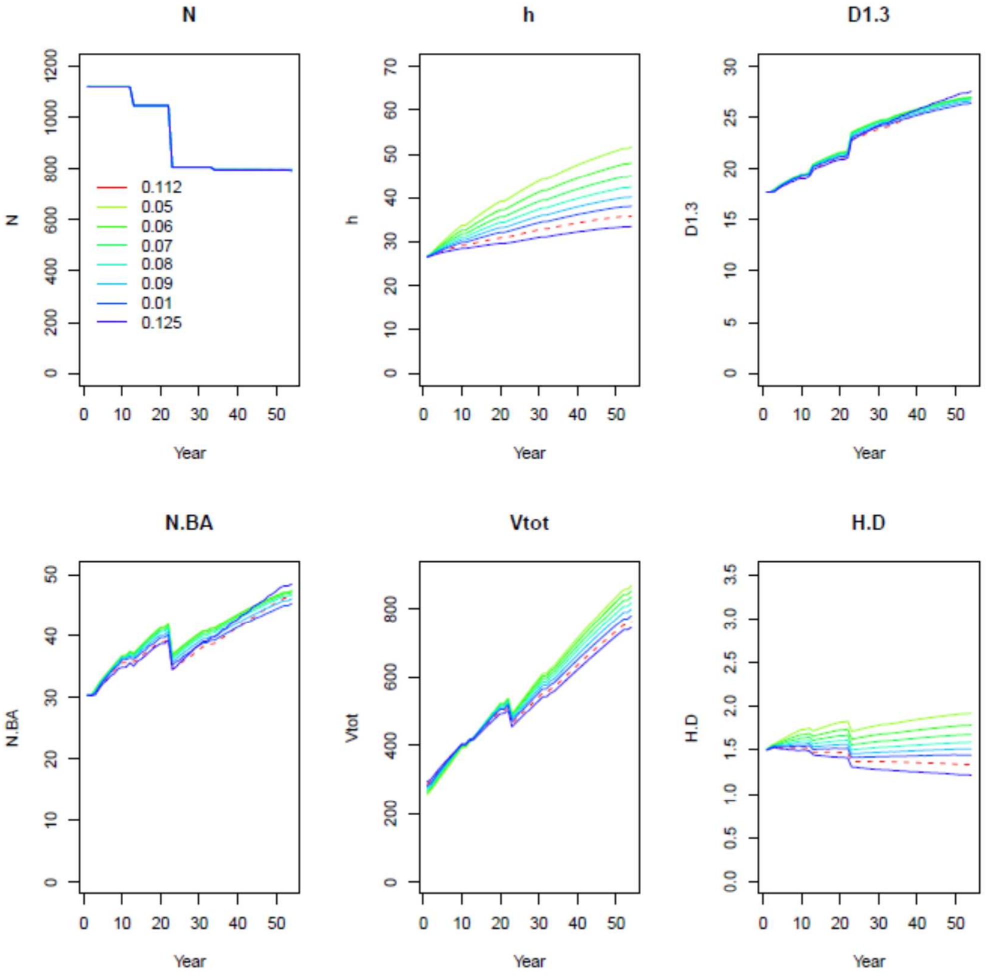


Fig. S2. The effect of ξ parameter to stand variables. Dashed line represents the original value used in simulations. N is stand density (number of trees ha^{-1}), h stand maximum height (m), D1.3 stand mean diameter (cm), N.BA stand basal area (m^{2} ha^{-1}), Vtot stand volume (m^{3} ha^{-1}) and H.D height to diameter ratio.

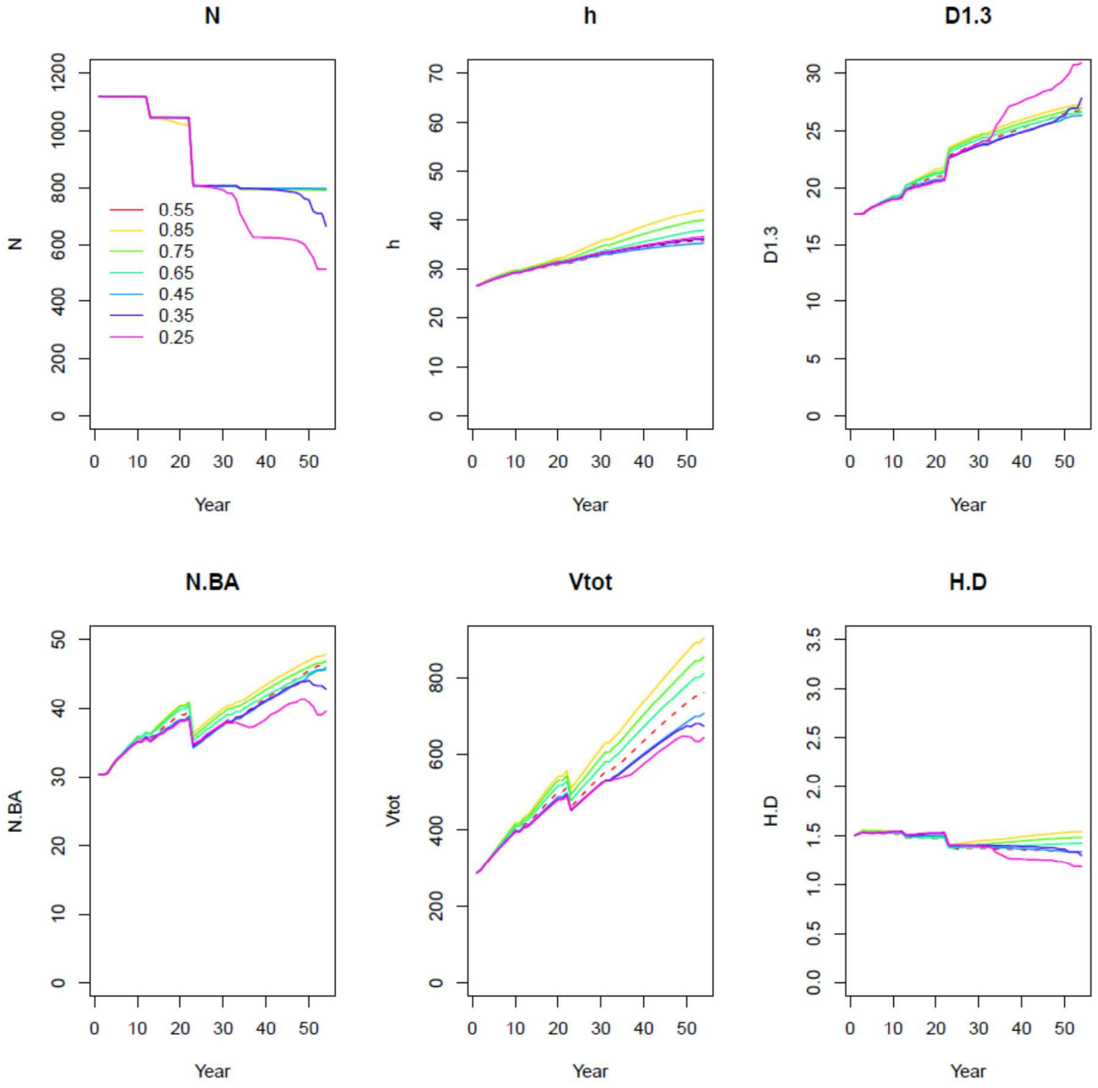


Fig. S3. The effect of $f1$ parameter to stand variables. Dashed line represents the original value used in simulations. N is stand density (number of trees ha^{-1}), h stand maximum height (m), D1.3 stand mean diameter (cm), N.BA stand basal area (m^{2} ha^{-1}), Vtot stand volume (m^{3} ha^{-1}) and H.D height to diameter ratio.

In the model, crown rise follows the height growth as shown in Eqns S2 and S3 and Figure S1. The parameter f_0 in s_C function defines the light level at which the rate of crown rise is half of the height growth rate (Fig. S4) while the parameter a determines the steepness of the curve: if a is large, the switch from no crown rise to maximum crown rise is abrupt, whereas for small a the effect of declining light is gradual (Fig. S5).

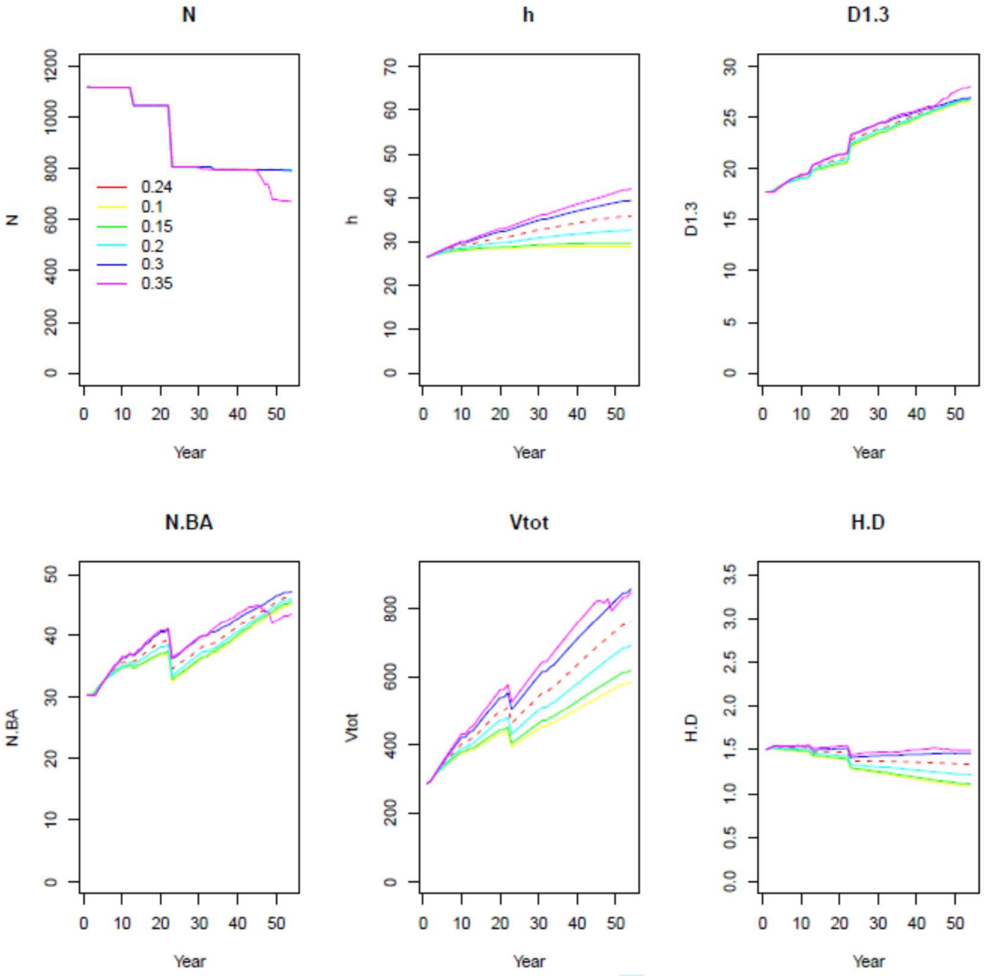


Fig. S4. The effect of f_0 parameter to stand variables. Dashed line represents the original value used in simulations. N is stand density (number of trees ha^{-1}), h stand maximum height (m), D1.3 stand mean diameter (cm), N.BA stand basal area (m^2 ha^{-1}), Vtot stand volume (m^3 ha^{-1}) and H.D height to diameter ratio.

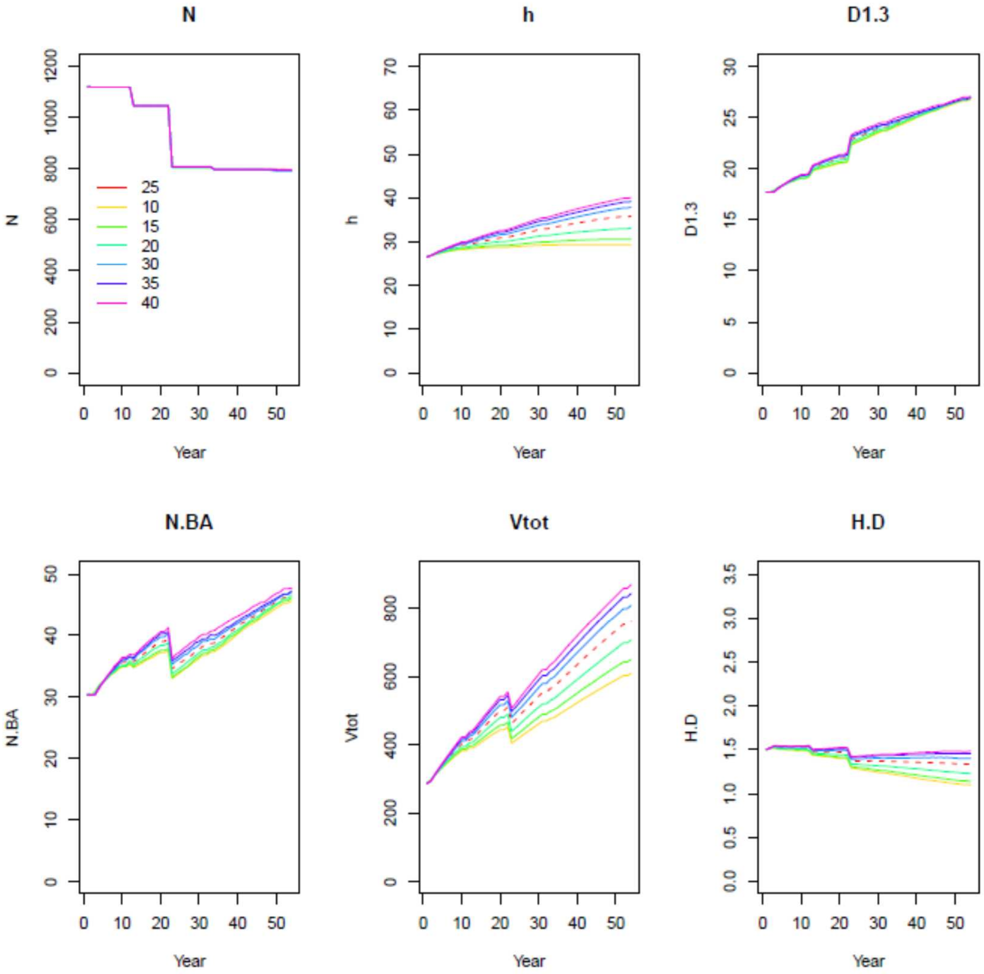


Fig. S5. The effect of *a* parameter to stand variables. Dashed line represents the original value used in simulations. N is stand density (number of trees ha^{-1}), h stand maximum height (m), D1.3 stand mean diameter (cm), N.BA stand basal area (m^2 ha^{-1}), Vtot stand volume (m^3 ha^{-1}) and H.D height to diameter ratio.

The growth of branch length was assumed to be regulated by the stand crown coverage A_{tot}. Parameter $A_{\text{tot},0}$ describes the crown ratio above which average branch length relative to crown length starts to decline. As shown in Fig. S6 the model response to $A_{\text{tot},0}$ is conservative especially in height growth. Only very low values cause drastic changes in model response.

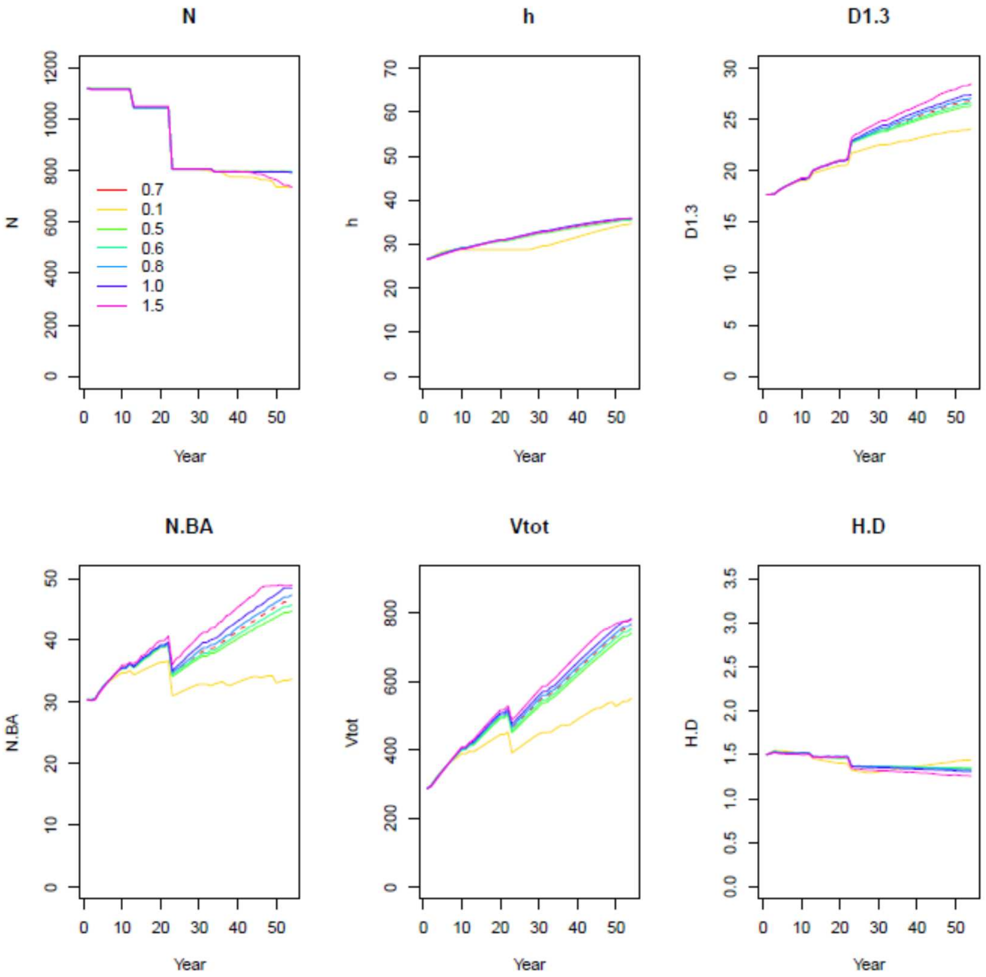


Fig. S5. The effect of $A_{tot,0}$ parameter to stand variables. Dashed line represents the original value used in simulations. N is stand density (number of trees ha^{-1}), h stand maximum height (m), D1.3 stand mean diameter (cm), N.BA stand basal area (m^{2} ha^{-1}), Vtot stand volume (m^{3} ha^{-1}) and H.D height to diameter ratio.