

Analysis of biomass accumulation and stem size distributions over long periods in managed stands of *Pinus sylvestris* in Finland using the 3-PG model

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Summary We tested the performance of a process-based model (PBM) in relation to long-term mensuration data from two sites in Finland where the stands were up to 90 years old and had been thinned at approximately 5-year intervals over the last 50 years. The PBM used was based on the 3-PG (Physiological Principles to Predict Growth) model developed by Landsberg and Waring (1997), with modifications in the biomass allocation routine, for which we used data and calculations by Vanninen (2003) to estimate the allocation coefficients and turnover rates. Site fertility was estimated in terms of known site-type characteristics. The model was evaluated in terms of stand development and its ability to simulate responses to thinning; stem numbers after thinning were specified at the dates when the thinning took place. Stand development in terms of basal area, volume and mean diameter at breast height, closely followed the measured characteristics of all stands. Foliage mass predictions were close to estimates obtained by an empirical method.

The analysis shows that, under normal thinning regimes, a range of different thinning intensities can be adequately described using a simple multiplicative model relating the proportion of volume and foliage mass removed to the corresponding proportion of stem numbers. This model, together with stem allometry data, described the “growth” in mean diameter after thinning, which simply reflected the removal of the smaller trees. These results indicate that, with a single set of parameter values, 3-PG can provide good descriptions of the growth patterns of trees—in this case *Pinus sylvestris* L. —over long periods, including growth after repeated thinning. One of the outputs from the 3-PG model is mean stem diameter (B): we show that it is feasible to estimate stem size distributions, which changed considerably over the life of these stands, from B using the Weibull function. This shows that, given information about the Weibull parameters for particular species and cultural systems, it should be possible to use stem numbers and the B obtained from the 3-PG model to produce information about stem size distributions from simulated data.

Keywords: biomass growth, process-based model, thinning.

Introduction

The Finnish Forest Research Institute has excellent measurements covering all forest types in Finland, from which site productivity curves have been produced for all regions (Koivisto 1959). Nevertheless, it would be of considerable value if stand growth could be accurately simulated using process-based models (PBMs); these are not only useful as research tools, but have considerable potential practical value as aids for management and policy decision-making. There is a developing view (Mäkelä et al. 2000, Landsberg 2003) that hybrid models, combining empirical relationships with models based on causal processes, will be the best tools for predicting the behavior of forest stands and their responses to perturbation. If these models are to be adopted by industry, it will be necessary to show that they perform better than the currently widespread statistical approach to growth and yield estimation, and that the claims made for PBMs—that they offer greater flexibility, generality and predictive power, as well as having the capacity to lead to increased understanding—are supported by the results of rigorous tests.

In this paper, we present such test results, based on a single PBM evaluated in relation to long-term mensuration data from two well-managed sites in Finland. The mensuration data cover a period of more than 60 years. The stands were up to 95 years old when the last of the data analyzed here were collected, and were managed by careful thinning at approximately 5-year intervals over the last 50 years, with the aim of maintaining high growth rates and a (relatively) constant basal area over the last 50 years of the cycle. The PBM used was based on the 3-PG (Physiological Principles to Predict Growth) model developed by Landsberg and Waring (1997), with modifications in the biomass allocation routine. Outputs from this model include biomass and stand volume, foliage mass and leaf area index, mean stem diameter at breast height

(B ; cm) at each time step, stand basal area and mean stem volume.

The 3-PG model has been extensively tested in recent years (Coops et al. 1988a, 1988b, Landsberg et al. 2000, Waring 2000, White et al. 2000, Coops and Waring 2001, Tickle et al. 2001, Sands and Landsberg 2002); the results confirm that the principles underlying the model are sound and hold for a wide range of evergreen forests. A key question in new applications of the model is to what extent parameters can be estimated from independent data generally available for the species and region of application, and what part of the model needs to be calibrated against the actual test data. The objective of this paper was to determine the parameter values as independently as possible of the data from the sites where the simulations were carried out. We therefore paid special attention to defining the structural parameters and the allocation routine using data from other sources than the stands simulated. We evaluated the performance of the 3-PG model in terms of its ability to simulate responses to thinning and characterized the observed stem size distributions by analysis in terms of the Weibull distribution. To evaluate the feasibility of providing stem size distributions from simulated values of B , the parameter values for the Weibull distribution, obtained from each set of measurements, were analyzed by regression analysis against B .

Outline of the 3-PG model

The 3-PG model is a simple stand model requiring few parameter values and only readily available data as inputs that was developed in an attempt to bridge the gap between conventional mensuration-based growth and yield models and process-based carbon balance models. In 3-PG, the basic unit of calculation is the whole stand described in terms of biomass and stocking density. The model consists of two sets of calculations: those that lead to biomass increments and those that allocate the increments among the various components of the stand. The model dynamically follows four independent state variables: foliage, fine root and stem mass of the stand, and stocking density.

The model uses a time step of a month and the output variables it produces are those of interest to forest managers. It is not site- or species-specific, but needs to be parameterized for individual species in plantations or even-aged, relatively homogeneous forests. Beside the description in the original paper, 3-PG has been described in detail in several recent publications (e.g., Landsberg et al. 2000, Waring 2000, Coops and Waring 2001, Sands and Landsberg 2002), but the key processes are briefly reviewed below.

Net primary production

Net primary production (NPP) is calculated from gross primary production (GPP) based on the assumption that total respiration is a fixed proportion of GPP. To calculate GPP, the model uses the idea of radiation-use efficiency: intercepted (absorbed) photosynthetically active radiation (APAR) is converted to photosynthates through a canopy quantum efficiency

(radiation-use efficiency) factor (α), constrained by sub-optimal temperatures, nutrition and stomatal conductance. Stomatal conductance is affected by vapor pressure deficit, soil water availability and stand age. The constraints are specified by semi-empirical modifying functions, some parameters of which need to be adjusted for the area and species in question. The driving variables of the model mainly affect this module.

Allocation of NPP

The biomass state variables (stem, foliage and fine root mass) are incremented at each time step by allocation of NPP. Key features of 3-GP are that (1) the ratio of allocation to foliage and stems decreases with increasing mean tree diameter, and (2) allocation to roots depends on site quality (Landsberg and Waring 1997, Sands and Landsberg 2002). The present application modifies some aspects of the allocation routine on the basis of recent empirical results on Scots pine (Vanninen 2003, Vanninen and Mäkelä 2005), while retaining these basic characteristics of 3-PG.

The present modified version of the 3-PG model allocates the biomass (NPP) produced by the canopy among wood, foliage and fine roots. Wood consists of stems, branches, bark and coarse roots. Allocation to fine roots (η_r) is assumed constant over time and depends on site fertility (Vanninen 2003). Allocation to foliage relative to wood ($p_{f,w}$) is assumed to decrease with increasing mean breast height diameter (B) as follows:

$$p_{f,w} = aB^n \quad (1)$$

where $n < 0$ and a is a coefficient. Equation 1 is derived from the allometric equations describing the relationships between B and stem mass (Equation 3, below) and between B and foliage mass (see Sands 2001, Equations 15 and 16; and Sands and Landsberg 2002, Equation A8). To calculate stem growth it is assumed, in addition, that a fraction ξ_s of biomass allocated to wood is directed to stems, whereas $1 - \xi_s$ is directed to branches and coarse roots. The carbon allocation coefficients for foliage (η_f), wood (η_w) and fine roots (η_r) must sum to unity, so the coefficients for wood and foliage are obtained from the relationships:

$$\eta_w = \frac{1 - \eta_r}{p_{f,w} + 1} \quad (2a)$$

and

$$\eta_f = 1 - \eta_r - \eta_w \quad (2b)$$

Allocation to stem growth is obtained from allocation to wood growth as $\eta_s = \xi_s \eta_w$.

The above carbon allocation routine requires values of individual tree B at each moment of time. The model uses mean stand B , which is calculated from the mean mass of individual stems with an allometric equation between mean stem mass, W_s , and B :

$$W_s = a_s B^{n_s} \quad (3)$$

where a_s and n_s are empirical coefficients. Mean stem mass is obtained from the state variables, total stem mass and stocking density. The relationship between B and W_s combined with stocking density determines stand basal area at any time. The carbon allocation procedure allows leaf area index to vary with growing conditions.

Litter fall and mortality

Another crucial component of stand dynamics consists of litter fall and mortality. State variables (foliage mass, stem number, stem mass and fine root mass) are reduced at each time step by litter fall, stem mortality and fine root turnover, respectively. Stem numbers in 3-PG may be determined by a mortality function, based on the $-3/2$ power law, or by specifying the stem numbers at any time—the procedure used to simulate thinning. In this study, the latter method was used. When stems are removed (in the model), the appropriate foliage and stem masses are also removed. The relative removal of foliage and stem mass is generally less than the relative decrease in stocking, as smaller than average stems are usually removed in thinnings. This reduction is denoted m_f and m_s for foliage and stems, respectively. The same relative amount of fine roots is removed as foliage. However, there is no feedback between root mass and water uptake or nutrition; the root turnover term leads to root mass values that can be compared with observed values, where these exist, and are useful when the model is used to make carbon balance calculations (Landsberg and Waring 2004).

Summary of stand dynamics in the model

The dynamics of stem number are calculated from removal during thinnings as follows:

$$\Delta N(t) = -T(t) \quad (4)$$

where $T(t)$ is stem number removed during thinnings at time step t . No additional mortality is assumed; however, measured values of removal in our test sites include a small component of natural mortality.

The biomass state variables, W_i ($\text{kg}_{\text{DM}} \text{ha}^{-1}$) ($i = s$ for stem mass, $i = f$ for foliage mass and $i = r$ for fine root mass) are calculated from three dynamic equations of the following form:

$$\Delta W_i(t) = \eta_i(t) \text{NPP}(t) - s_i(t) W_i(t) - m_i(t) \frac{T(t)}{N(t)} W_i(t) \quad (5)$$

where η_i is allocation to component i , s_i is turnover in i , and m_i is a coefficient dependent on the size distribution of the stand, relating the proportion of removed stem number to the proportion of removed mass of component i . We determined m_i from data. The value of $\text{NPP}(t)$ was calculated monthly as indicated above.

Data available

Model predictions were compared with long-term measurements of tree and stand growth in Scots pine experiments in southern Finland, namely Punkaharju ($61^\circ 48' \text{ N}$, $29^\circ 19' \text{ E}$, 90 m a.s.l., annual effective temperature sum 1229 degree days (dd)) and Ruotsinkylä ($60^\circ 21' \text{ N}$, $25^\circ 00' \text{ E}$, 60 m a.s.l., annual effective temperature sum 1301 dd). In Punkaharju, the site is fertile (site index 21.5 m at base age 50 years) and classified as *Oxalis–Majanthemum* type (OMT) in the standard Finnish site classification system (Cajander 1949). The forest was established in 1892 by sowing. Three plots with different thinning regimes were created in 1924 and 10 sets of measurements were made in two plots from 1924 to 1987 (stand ages 32–95 years) and eight sets in one plot from 1934 to 1987 (stand ages 42–95 years). The Ruotsinkylä experiment consists of one plot that was established in 1931 in a stand started by sowing in 1918 on a medium fertile *Vaccinium* type site (VT, site index 18.4 m at base age 50 years); nine sets of measurements were made from 1931 to 1989 (stand ages 14–71 years).

The data include stem diameters (B), height, number of stems in each stem size class (class intervals were approximately 1 cm), stem mass and wood density. All plots were thinned periodically, and information about removed individuals was available for the Punkaharju plots. The thinnings were light; usually less than 10% of basal area was removed; maximum removal was 35%.

All the necessary weather variables (solar radiation, maximum and minimum temperatures, vapor pressure deficit and frost days) were available from stations near the sites. For Punkaharju, data were available for the period 1961–1990, and for Ruotsinkylä, for 1964–1990.

Estimation of model parameters

Net primary productivity

Most of the parameter values required in calculating NPP are derived from knowledge of the behavior of the species in question, or are default values that have been found suitable for a wide range of tree species (Table 1).

The temperature limits ($T_{\min} = -2^\circ \text{C}$, $T_{\text{opt}} = 15^\circ \text{C}$ and $T_{\max} = 25^\circ \text{C}$) are “best guess” values for the minimum, optimum and maximum temperatures for the growth of *Pinus sylvestris* L. based on knowledge of the geographical distribution and climatic requirements of this species (these are not the same as the temperatures determining physiological processes with short response times). The fertility effects, which determine the effect of soil fertility on the efficiency with which photosynthetically active radiation (PAR) is used by trees to produce biomass (the canopy quantum efficiency, α) and influence the proportion of NPP allocated to roots, are general (default) values. Soil fertility is characterized by the fertility rating (FR) specified in the initial conditions for any model run. The relationship between FR and α is assumed to be linear (the slope is determined by the fertility effects parameter; see Sands 2001, Landsberg et al. 2003). Because we lacked direct empirical information for the plots under study, FR was adjusted to a value

Table 1. Parameter values used in the simulations with the 3-PG model.

Parameters	Abbreviation/symbol	Units	Values for <i>P. sylvestris</i>
<i>Temperature modifier (fT)</i>			
Minimum temperature for growth	T_{\min}	°C	−2
Optimum temperature for growth	T_{opt}	°C	15
Maximum temperature for growth	T_{\max}	°C	25
<i>Frost modifier (fFrost)</i>			
Days of production lost per frost day	kF	day	1
<i>Soil water modifier (fSW)</i>			
Moisture ratio deficit for $f_0 = 0.5$	SW_{const}	—	0.7
Power of moisture ratio deficit	SW_{power}	—	9
<i>Fertility effects</i>			
Value of “m” when fertility rating (FR) = 0	m_0	—	0
Value of “fNutr” when FR = 0	fN_0	—	0.6
<i>Age modifier (fAge)</i>			
Maximum stand age used in age modifier	MaxAge	year	500
Power of relative age in function for fAge	n_{age}	—	4
Relative age to give fAge = 0.5	r_{age}	—	0.95
<i>Litter fall and fine root turnover</i>			
Maximum litter fall rate	gammaF_x	month^{-1}	0.0255
Litter fall rate at $t = 0$	gammaF_0	month^{-1}	0.0255
Age at which litter fall rate has median value	tgammaF	month	60
Average monthly root turnover rate	R_{tturn}	month^{-1}	0.07
<i>Conductance</i>			
Maximum canopy conductance	Max_{cond}	m s^{-1}	0.02
Leaf area index (LAI) for maximum canopy conductance	LAI_{gex}	—	3.333
Defines stomatal response to vapor pressure deficit	$\text{Coeff}_{\text{cond}}$	mBar^{-1}	0.05
Canopy boundary layer conductance	BL_{cond}	m s^{-1}	0.2
<i>Stem numbers</i>			
Fraction mean single-tree foliage dry mass lost per dead tree	m_f	—	0.64
Fraction mean single-tree root biomass lost per dead tree	m_r	—	0.64
Fraction mean single-tree stem biomass lost per dead tree	m_s	—	0.61
<i>Canopy structure and processes</i>			
Specific leaf area at age 0	SLA0	$\text{m}^2 \text{kg}^{-1}$	9
Specific leaf area for mature leaves	SLA1	$\text{m}^2 \text{kg}^{-1}$	6
Age at which specific leaf area = (SLA0 + SLA1)/2	tSLA	year	10
Extinction coefficient for absorption of PAR by canopy	k	—	0.6
Age at canopy cover	fullCanAge	year	5
Maximum proportion of rainfall evaporated from canopy	MaxIntcptn	—	0.15
Leaf area index for maximum rainfall interception	$\text{LAI}_{\text{maxIntcptn}}$	—	5
Canopy quantum efficiency	α	$\text{mol C mol}^{-1} \text{PAR}$	0.055
<i>Various</i>			
Ratio net primary productivity/gross primary productivity	Y	—	0.47
Basic density	Density	t m^{-3}	0.4
<i>Conversion factors</i>			
Intercept of net versus solar radiation relationship	Q_a	W m^{-2}	−90
Slope of net versus solar radiation relationship	Q_b	—	0.8
Molecular weight of dry matter	gDM_{mol}	gDM mol^{-1}	24
Conversion of solar radiation to PAR	$\text{molPAR}_{\text{MJ}}$	mol MJ^{-1}	2.3
<i>Allocation and allometry</i>			
Coefficient for the ratio of foliage to wood allocation	a	—	0.46
Exponent for the ratio of foliage to wood allocation	n	—	−0.279
Fraction of wood allocation directed to stems	ξ	—	0.6
Fine root allocation, Punkaharju	η_r	—	0.1
Coefficient in stem allometric equation, Punkaharju	a_s	—	0.0571
Exponent in stem allometric equation, Punkaharju	n_s	—	2.5698
Fine root allocation, Ruotsinkylä	η_r	—	0.2
Coefficient in stem allometric equation, Ruotsinkylä	a_s	—	0.046
Exponent in stem allometric equation, Ruotsinkylä	n_s	—	2.6496

that gave satisfactory model performance; we found that $FR = 1$ was required to produce the growth rates observed at Punkaharju, which implies, in terms of the assumptions incorporated into 3-PG, that fertility is not a factor limiting α at that site. To fit the Ruotsinkylä data, it was necessary to reduce FR to 0.6. This is consistent with the classification of the Punkaharju site as very fertile (OMT) (Cajander 1949) and the Ruotsinkylä site as only moderately fertile (VT).

Only a single soil type is assumed for soil water calculations. The conductance parameters are default values, specific leaf area (SLA) values are essentially the default values for conifers, and the wood density value used is a mean for the data. We used an extinction coefficient (in Beer's Law, describing the absorption of PAR) of 0.6 to account for the decreased efficiency that can be expected as a consequence of the clumped nature of the foliage. Canopy quantum efficiency was taken as $0.055 \text{ mol C mol}^{-1} \text{ PAR}$, the default value for conifers. (For detailed discussions of these parameters see Landsberg and Waring 1997, Sands 2001, Sands and Landsberg 2002, Landsberg et al. 2003.)

Boreal pines grow much more slowly, and hence reach maturity and "old age" more slowly, than pines in temperate, mediterranean and sub-tropical climates. For example, at the age of 30 years, *Pinus radiata* D. Don stands in New Zealand resemble *Pinus sylvestris* L. stands at the age of about 100 years in Finland (e.g., Garcia 1984, Koivisto 1959). We therefore set the maximum age parameter related to photosynthetic efficiency and stomatal conductance to 500 years, compared with the 100 years used for pines, e.g., in Australia. Consistent with empirical results (Vanninen 2003), this led to virtually no age effects on GPP within the age range considered.

Allocation of NPP

We used data and calculations by Vanninen (2003) and Vanninen and Mäkelä (2005) to estimate the allocation coefficients. They used the method of allometric equations combined with estimates of turnover to derive estimates of allocation of growth in individual Scots pine trees sampled from stands of variable age, density and site quality. According to their results, growth allocation to foliage relative to wood changes from about $p_{f:w} = 0.30$ in small trees to about $p_{f:w} = 0.15$ in mature trees. According to the same results, the share of total allocation to wood that goes to stems remains approximately constant at about 60% throughout the rotation (Vanninen and Mäkelä 2005). We used $a = 0.46$ and $n = -0.279$ in Equation 1, and $\xi_s = 0.6$. Allocation to fine roots was relatively constant over stand age at $\eta_R = 0.15$ for the fairly fertile *Myrtillus* site type (MT) and $\eta_R = 0.30$ for the poor *Calluna* site type (CT) (site types according to Cajander 1949). Because the Punkaharju site was more fertile than MT, we set $\eta_R = 0.10$. The Ruotsinkylä site was between MT and CT, so we used $\eta_R = 0.20$.

Litter fall and mortality

Foliage litter fall rates are estimated on the assumption that *P. sylvestris* in Finland holds its foliage for about 3–4 years.

Default values were used for other parameters related to litter fall and root turnover. No natural tree mortality was assumed (Table 1).

Relationship between stem volume and basal area

Because the allometric Equation 3 is defined between mean tree basal area and mean tree volume as they develop over time, the appropriate data for fitting the equation are mean tree characteristics obtained from a time-series of stand development such as growth and yield data. Different (and biased) results will usually be obtained if the allometry is derived from a sample of trees in any one stand (e.g., Zeide and Pfeifer 1991). We calculated mean tree volume and basal area from stand volume, stand basal area and stocking density given by growth and yield tables for Scots pine in Finland (Koivisto 1959) to fit the parameters of Equation 3. We used the corresponding site types for each stand (VT for Ruotsinkylä and OMT for Punkaharju), but the relationship was rather conservative between different site types (Figure 1).

Effect of size distribution on removals

The permanent sample plot data were detailed in the description of tree sizes in both the remaining population and trees removed, implying that accurate information about volumes and basal areas removed at each thinning could have been utilized. However, to obtain a more robust and more generally applicable method for estimating biomass removals from stem numbers, we postulated that the coefficients m_i in Equation 5 were constant for each i . We assumed that m_f could be approximated by the proportion of removed basal area, and we found best-fit estimates for m_s and m_f from the data by comparing the proportion of removed basal area and volume to the proportion of removed stem number. This gave $m_f = 0.64$ and $m_s = 0.61$ (Figure 2).

Procedure

We ran the model with the mean monthly weather data appropriate for the region. Simulations were started with the stem numbers on the plots at the first measurement on the Punkaharju plots (1924, when the trees were 32 years old) and at the 1953 measurement on the Ruotsinkylä plots (when the trees were 33 years old). We did not attempt to simulate the earlier measurements on this plot, when regenerating tree numbers were of the order 13,000–17,000. The stem numbers on each plot after thinning were specified at the dates when the thinning took place. Starting values of stem mass (Mg ha^{-1}) were estimated from stand volume measurements and initial leaf mass was given a "reasonable" value based on the literature (but the initial leaf mass does not affect the results for more than about 1 or 2 years).

Results

Stand development

Because there was no age effect on GPP or NPP during the simulation period, the potential productivity (achieved when

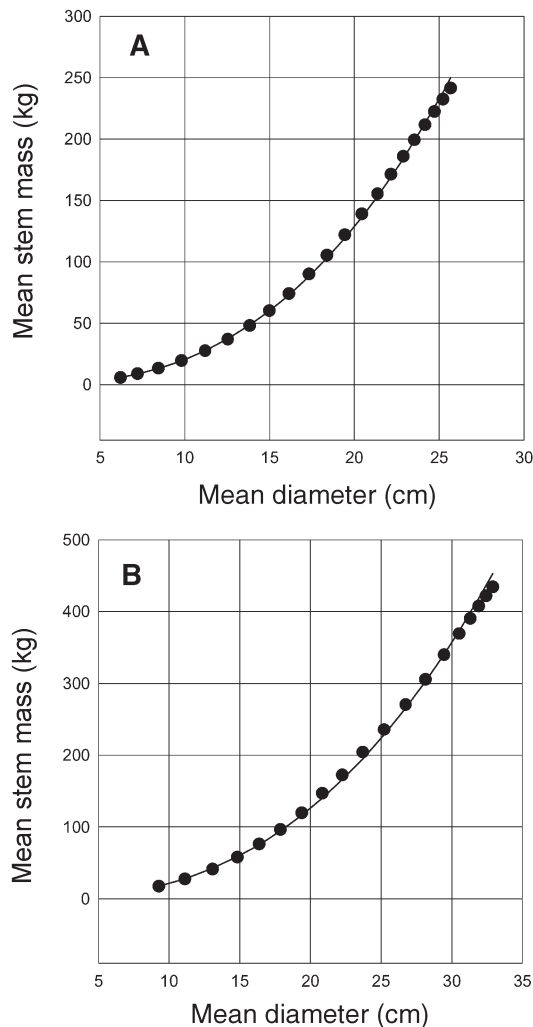


Figure 1. Allometric relationships between stand mean diameter at breast height (B) and stand mean stem biomass (W_s), calculated by fitting an exponential function (solid line) to values obtained from growth and yield tables (filled circles) (Koivisto 1959). Stem volume was converted to stem biomass assuming that wood density was 400 kg m^{-3} . (A) *Vaccinium* site type, $W_s = 0.046\exp(2.65B)$, $r^2 = 0.98$; and (B) *Oxalis-Majanthemum* site type, $W_s = 0.057\exp(2.57B)$, $r^2 = 0.99$.

the age modifier = 1 and leaf area is not limiting) of both sites depended only on the mean annual weather conditions and hence remained constant over time in the simulations. The annual potential GPP was estimated at $2.82 \text{ kg}_{\text{DM}} \text{ m}^{-2} \text{ year}^{-1}$ in Punkaharju and at $2.52 \text{ kg}_{\text{DM}} \text{ m}^{-2} \text{ year}^{-1}$ in Ruotsinkylä. Actual GPP and NPP varied according to current leaf area, NPP attaining values between 8 and $10 \text{ kg}_{\text{DM}} \text{ m}^{-2} \text{ year}^{-1}$ in Ruotsinkylä and between 10 and $12 \text{ kg}_{\text{DM}} \text{ m}^{-2} \text{ year}^{-1}$ in Punkaharju (Figure 3).

Stand development in terms of basal area, volume and mean B closely followed the measured stand characteristics in all stands (Figures 4–6). The fit was closest for mean diameter development for all stands, where the largest deviation from measurements was an overestimation of mean diameter in Punkaharju Site 2 from age 70 to 95 years (Figure 4). Basal area was somewhat underestimated in Punkaharju for Sites 1 and 3, whereas the overestimation of diameter at the later stages in Punkaharju 2 was again apparent for basal area. For the Ruotsinkylä site, simulated and measured data were in good agreement (Figure 5).

For volume development, the agreement was best for Punkaharju 3, whereas for Ruotsinkylä, volume was slightly overestimated (Figure 6). The discrepancy between basal area and volume suggests that the allometry derived from the yield tables did not accurately describe the Ruotsinkylä stand. Also, the stem volume removals appeared to be somewhat underestimated at this site. In contrast, volume and basal area growth were consistent for all sites at Punkaharju, suggesting that this site closely followed the allometry derived from the yield tables for this fertile site type.

Measurements of basal area at crown base were also available at the later measurement times for all sites and for most measurement times in Ruotsinkylä. Estimates of stand foliage mass were obtained from these measurements by multiplying the crown basal area by a mean foliage mass to sapwood area ratio (450 kg m^{-2}) measured in southern Finland (Lehtonen 2004, Berninger et al. 2005). These estimates are considered robust; the standard deviation of the ratio between several stands in southern Finland was only about 10% (Berninger et al. 2005). The foliage mass predictions from the model, although tending toward lower values than the empirical esti-

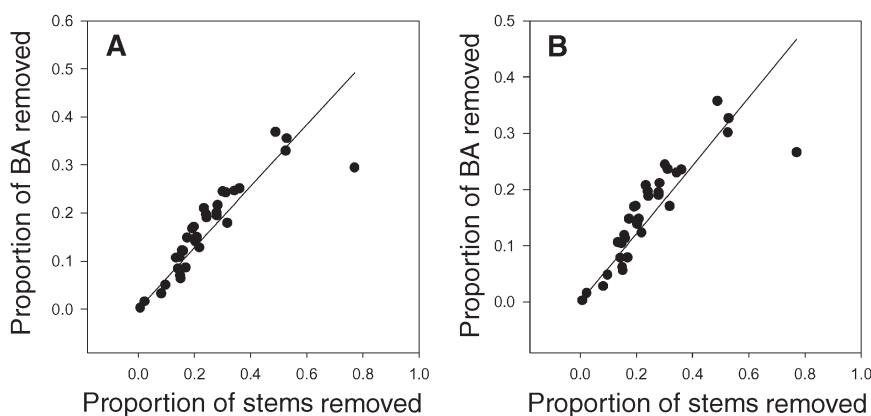


Figure 2. The proportion of basal area (BA) and volume removed in thinnings as a function of the proportion of stems removed. Data from all four plots were pooled. (A) Basal area: $\Delta \text{BA}/\text{BA} = 0.639\Delta N/N$, $r^2 = 0.78$, $n = 35$. (B) Volume: $\Delta V/V = 0.606\Delta N/N$, $r^2 = 0.73$, $n = 35$. The regressions were forced through zero because removal of stem mass and basal area have to vanish for no thinnings.

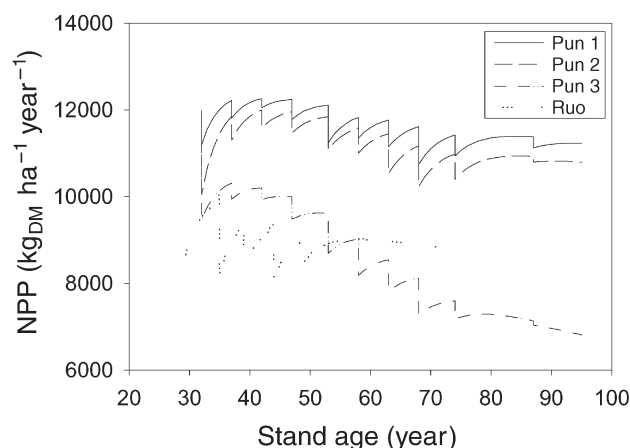


Figure 3. Predicted development of net primary productivity (NPP) at Ruotsinkylä (Ruo) and at the three Punkaharju sites (Pun 1, Pun 2 and Pun 3).

mates, were reasonably close to them (Figure 7).

Analysis of stem size distributions

The 3-PG model produces values of B at each time step, whereas the stem populations in the measured stands are distributed across a number of size classes. To provide a quantitative measure of stem size distribution, we fitted the Weibull probability density function to the stem size distribution data

from each plot at each measurement time, i.e., after the thinning was carried out. Fitting was done using the percentile method, as described by Nanang (1998). For this method, it is necessary to have accurate values of the (probable) diameter of stems at specified numbers N_{pi} and N_{pk} , obtained by multiplying the total number of stems, N , by the probability $p_i = 0.1673$ and $p_k = 0.9737$. These diameters were determined by fitting (cumulative) stem numbers against the diameter classes; this always produced a smooth curve ($N = f(B)$) that could be described accurately by a logistic equation fitted using a statistical software package. The equations were inverted and solved to obtain the precise values of B associated with N_{pi} and N_{pk} .

Management by thinning was not started at Ruotsinkylä until 1953; in 1931, 1940 and 1947 the plot at that location contained between 13,000 and 17,000 trees ha^{-1} . The distribution of stem diameters at these populations was monotonic, with large numbers of small stems and a few larger stems. The data from these years were omitted from the analysis. The Weibull function was fitted to all the other measurements. Examples of the observed and predicted diameter frequencies for a selection of the available data sets are presented in Figure 8. As the stand at Punkaharju aged, there was an increasing tendency for stem size diameter classes to depart from the continuous univariate distributions that can be satisfactorily described by the Weibull distribution. This tendency was not observed in the Ruosinkylä data.

Observed and predicted stem size frequencies for all the measurement sets were compared by regression analysis. Up

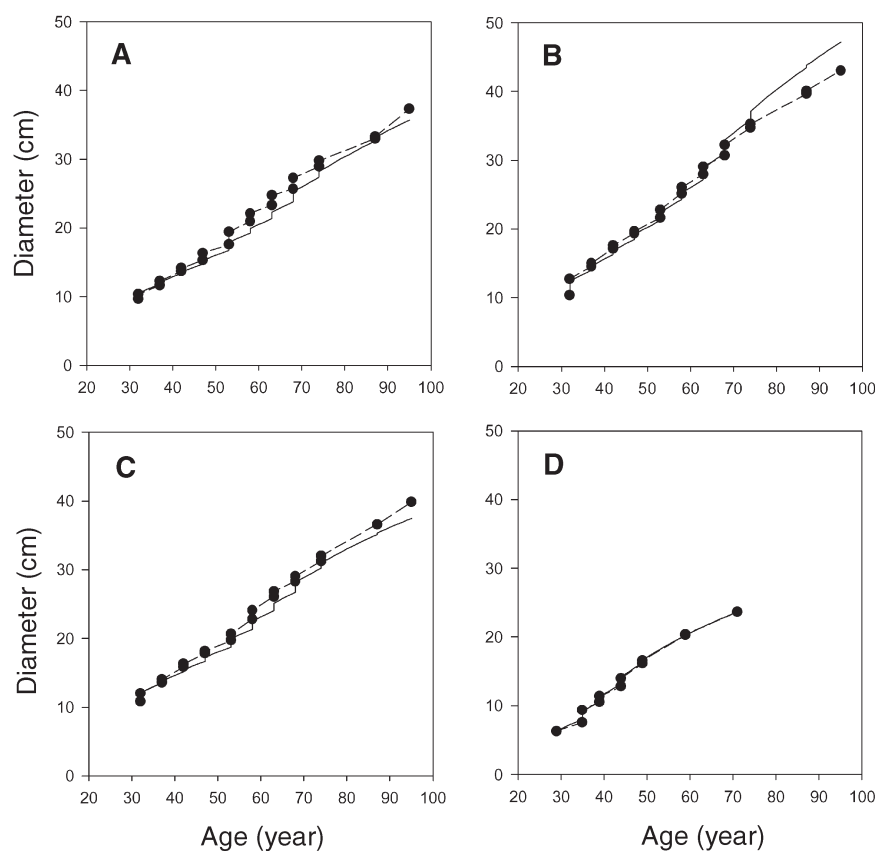


Figure 4. Predictions (solid line) of diameter at breast height compared with measurements (● with dashed line) at Punkaharju 1 (A), Punkaharju 2 (B), Punkaharju 3 (C) and Ruotsinkylä (D).

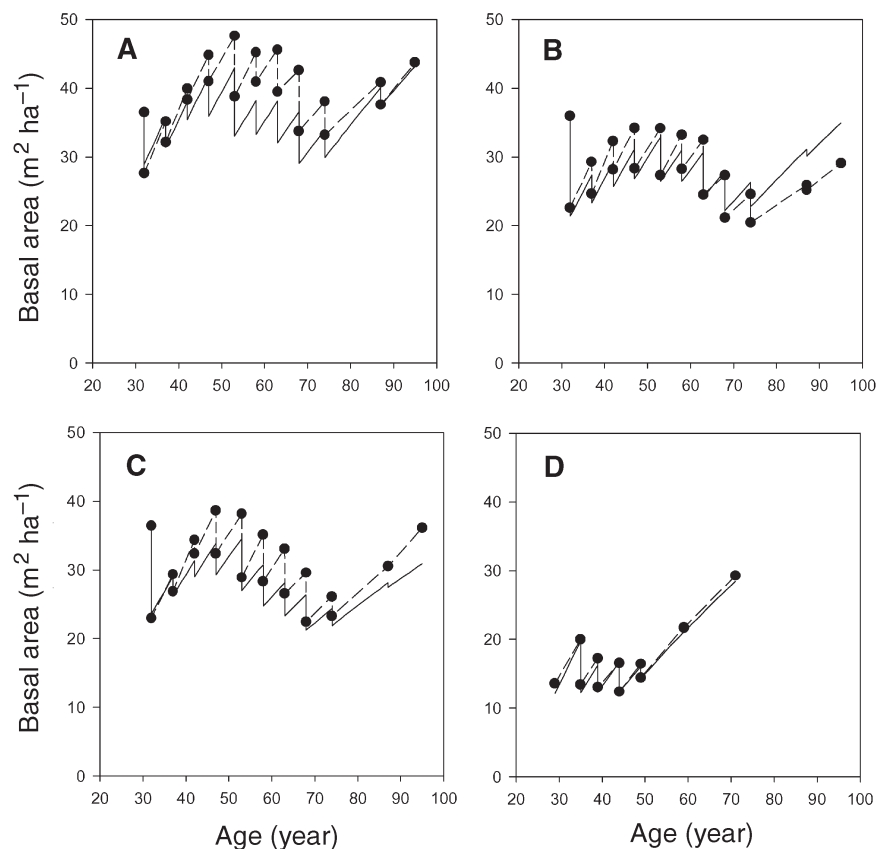


Figure 5. Predictions (solid line) of stand basal area compared with measurements (● with dashed line) at Punkaharju 1 (A), Punkaharju 2 (B), Punkaharju 3 (C) and Ruotsinkylä (D).

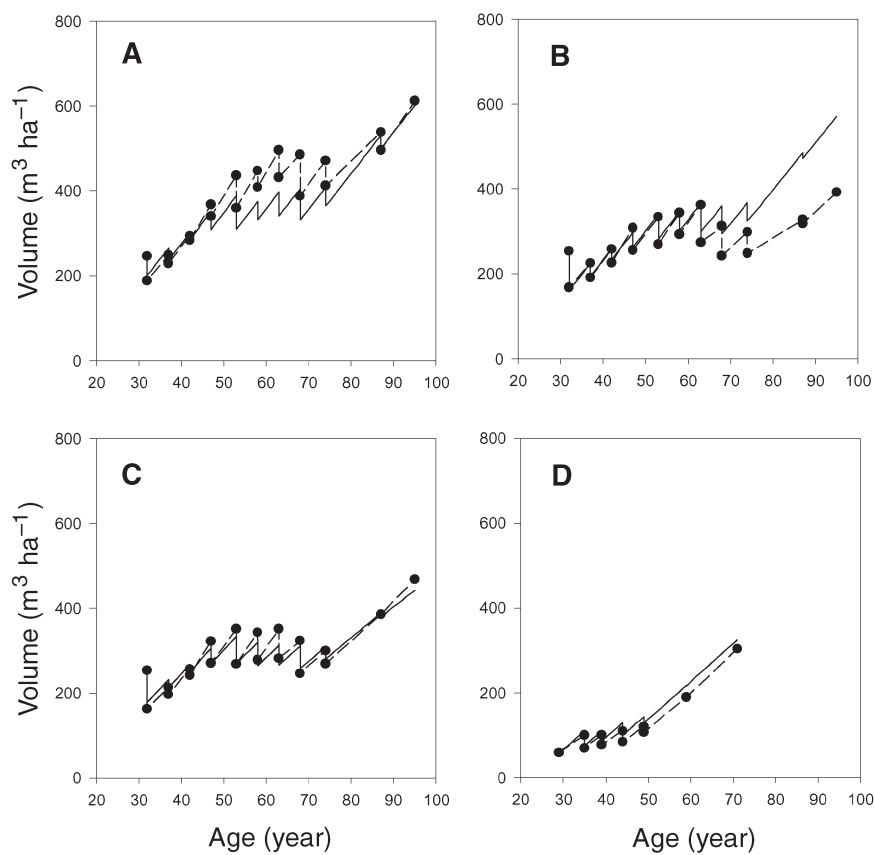


Figure 6. Predictions (solid line) of stand volume compared with measurements (● with dashed line) at Punkaharju 1 (A), Punkaharju 2 (B), Punkaharju 3 (C) and Ruotsinkylä (D).

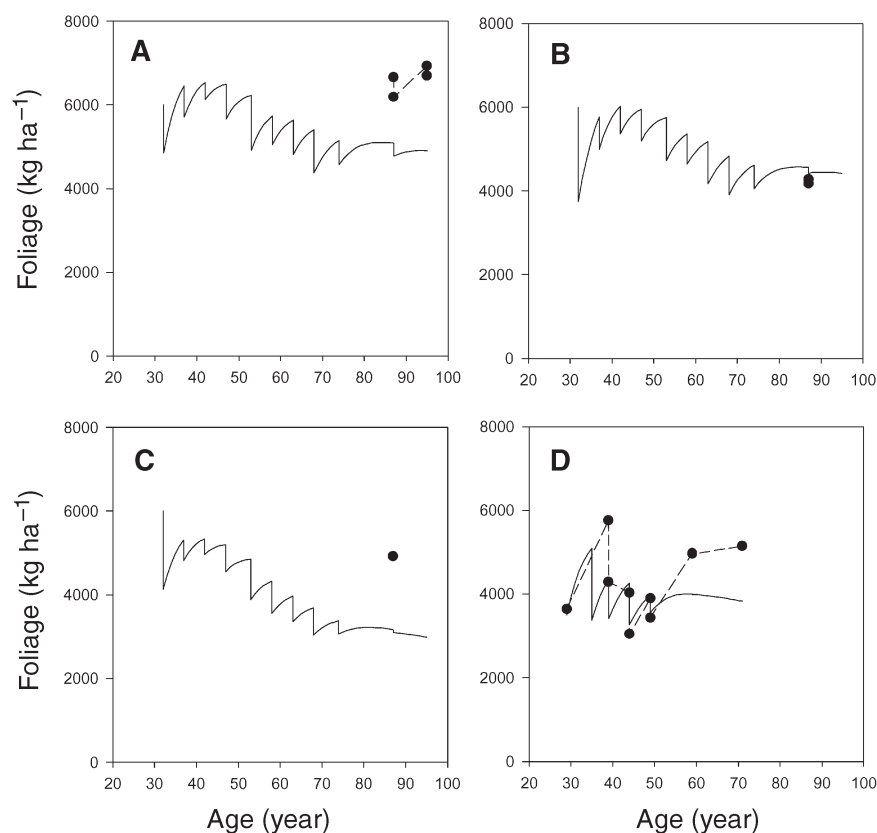


Figure 7. Predictions (solid line) of foliage mass compared with empirical estimates (● with dashed line) at Punkaharju 1 (A), Punkaharju 2 (B), Punkaharju 3 (C) and Ruotsinkylä (D). The estimates were calculated by multiplying stand basal area at the crown base by an empirical coefficient, 450 kg m^{-2} (Vanninen 2003, Lehtonen 2004).

to age 68 (1966) at Punkaharju, the fitted Weibull distributions accounted for, on average, 67% of the variance in the observed distributions. From age 74 to 95, the variance in the observed

distributions dropped to 21%. At Ruotsinkylä, for stands between 39 and 76 years of age, the fitted Weibull distributions accounted for, on average, 82% of the variance in the observed

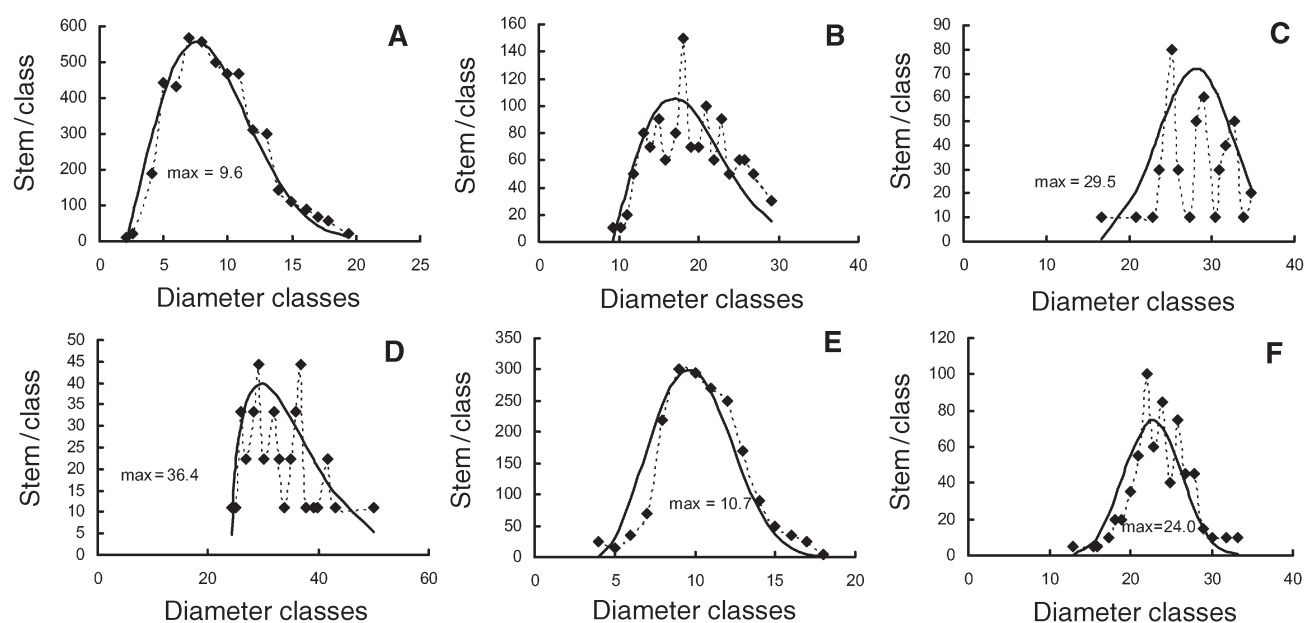


Figure 8. Examples of observed stem size distributions (◆, dotted lines) and distributions calculated using the Weibull distribution (solid lines). The parameters of the Weibull distribution were determined for each set of measurements. (A, B and D): data are from Punkaharju plot 1, stand ages 32, 53 and 87 years; (C): data are from Punkaharju plot 3, stand age 60 years; and (E and F): data are from Ruotsinkylä, stand ages 42 and 69 years.

distributions.

That the observed data can be fitted with the unimodal Weibull function indicates that, given information about the Weibull parameters for particular species and cultural systems, it is possible to use stem numbers and B obtained from the 3-PG model to produce information about stem size distributions from simulated data. Rennolls et al. (1985) estimated the parameters of the Weibull distribution by regression on B , using data from 210 Sitka spruce plots; we investigated the possibilities of this procedure applied to the Punkaharju data, using the Weibull parameters obtained from each of the three plots at each measurement. Polynomial regression of the scale parameter b (which is related to the range of the distribution), on B gave $b = 0.974 + 0.738B - 0.013B^2$ ($r^2 = 0.34$). The location parameter (a), which gives the minimum value of the distribution, was well described in terms of B : $a = 0.0914B^{1.59}$ ($r^2 = 0.96$). But the shape parameter c , which determines the skewness of the distribution, was poorly related to B : $c = 1.0418 + 0.0748B - 0.0014B^2$ ($r^2 = 0.07$). This is similar to the result obtained by Rennolls et al. (1985), who found that B accounted for only 5.1% of the variance in c . Because the Weibull distribution is highly sensitive to the values of its parameters and to the ratio c/b , stem size distributions calculated using the parameter values estimated from these regressions tended to deviate significantly from the observed distributions.

Discussion

The aims of this paper were to evaluate: (1) whether the procedure used in the model for allocating carbohydrates on the basis of B produces accurate results in terms of stem mass for stands growing for long periods; (2) whether significant errors arise from the use of a mean value of stem diameter rather than a parameter that provides a measure of stem size distribution; and (3) whether using the 3-PG model to analyze the growth of stands thinned many times provides insights into the performance of the model in terms of its responses to thinning.

We modified the allocation model from the original 3-PG (Landsberg and Waring 1997) by disconnecting the allocation parameters from the allometric parameters. The allometric parameters (such as in Equation 3) describe the relationships between standing biomass components of trees, which are a result of growth and turnover. Because the turnover of foliage is usually much faster than the turnover of wood, the allocation of growth to foliage must be larger than would be apparent from the observed standing biomass. Allocation coefficients can be derived from allometry and turnover rates, provided that the turnover rates are expressed explicitly (e.g., Mäkelä 1990, Valentine 1999). The 3-PG model does not include variables that could be directly used for the calculation of wood turnover (e.g., branch shedding). Previous model formulations have solved this problem by assuming a given proportion of wood other than stems in standing biomass (Sands and Landsberg 2002). In this study, we used recent empirical work that estimated the temporal development of the allocation coefficients in Scots pine under different growth conditions, us-

ing the method of allometry combined with estimates of turnover (Vanninen 2003, Vanninen and Mäkelä 2005). The results are consistent with the basic assumption of 3-PG that allocation to wood relative to foliage increases exponentially with stem diameter, at least within the age range considered. The age ranges of the present simulations were similar to those of the allocation study.

Although the allocation coefficients are determined without direct connection to tree allometry, the allocation is still driven by B , which is estimated from mean tree volume using an allometric relationship (Equation 3). It is well known in mensuration that the relationship between stem diameter and stem volume is not unique, but depends largely on the height:diameter ratio. This, in turn, varies with tree age, dominance position and stand density (Assman 1970). The allometric relationship derived from trees within one stand will therefore be different from the corresponding relationship for the mean tree of stands of different ages (e.g., Zeide and Pfeifer 1991). It is the latter type of relationship that is of key importance in the model, as the model is concerned with the time development of the mean tree of the stand. Sample trees for determining the allometric relationship should therefore be collected as mean trees of an appropriate age series of stands, rather than as a set of individuals in any one stand.

We could have used data from the measured sample sites to determine mean stem allometry for each site. However, such detailed data are usually unavailable for stands that one intends to simulate. It is desirable to have some more general information for generating the allometric relationships. Our analysis suggests that, when available, growth and yield tables may provide robust estimates of the parameters of mean stem allometry. This relationship was fairly conservative between stands from different site types, and the parameters were close to those calculated from data in the example stands in Ruotsinkylä and Punkaharju (not shown), although stand densities varied considerably.

For simulating thinnings adequately with 3-PG, it is necessary to have information about the reduction of all state variables at each thinning. If the removal of stem numbers is used as input, then a conversion to the corresponding removal of biomass variables is needed. This generally depends on the size distribution of trees in the stand, and on the thinning strategy, i.e., on the size of the removed trees relative to those remaining. As 3-PG does not explicitly describe stem size distributions, it cannot generally simulate all possible thinning situations. Our analysis suggests, however, that under normal thinning regimes, a range of different thinning intensities can be adequately described using a simple multiplicative model relating the proportion of volume and foliage mass removed to the corresponding proportion of stem numbers. This model, together with the stem allometry, also described the "growth" in mean diameter after thinning, a consequence of the removal of the smaller trees (Figure 4).

The simulations were generally in good agreement with the data (Figures 4–7). However, the overestimation of stem growth at the later stage of stand development in Punkaharju 2

(Figure 6B) is accompanied by a foliage mass estimate (Figure 7B) that is closest to the “measured” of all stands. From the time series for Ruotsinkylä (Figure 7D), we may infer that the discrepancy is increasing as the stands age. There is uncertainty in the foliage mass estimates obtained from basal area at the crown base, but according to recent studies, the standard deviation of the related parameter is fairly small (Berninger et al. 2005). This result may therefore indicate that (1) the allocation to foliage is underestimated in older stands and, at the same time, (2) stem growth per unit foliage is overestimated in older stands. However, a small error in the coefficient that determines allocation of NPP to foliage will cause a much larger proportional error in foliage mass than in stem mass. For example, if $NPP = 12 \text{ Mg}_{\text{DM}} \text{ ha}^{-1} \text{ year}^{-1}$, and the fraction allocated to stems is 0.6, with $p_{\text{fw}} = 0.15$, then the increase in stem mass over the year will be $7.2 \text{ Mg}_{\text{DM}} \text{ ha}^{-1}$ and in foliage mass (disregarding litterfall) 1.8 Mg . If, however, the true value of the fraction allocated to stems is 0.61, and $p_{\text{fw}} = 0.14$, then the mass increments will be 7.32 and 1.68 Mg , respectively. The resulting errors in calculated stem and foliage mass increments are 1.7 and 6.7%, respectively.

Before these and similar questions can be subjected to more stringent tests, more data pertaining to the temporal development of GPP and NPP are required, as well as foliage and fine root mass of stands. Our simulation results are consistent, however, with the rather fragmented evidence gathered to date on the magnitude of these variables. The NPP values are close to the range $12\text{--}13 \text{ Mg}_{\text{DM}} \text{ ha}^{-1} \text{ year}^{-1}$ estimated for several pine stands in southern Finland in a carbon budget study (Helmisaari et al. 2002). The GPP values are close to the approximate value of $20 \text{ Mg}_{\text{DM}} \text{ ha}^{-2} \text{ year}^{-1}$ estimated from eddy covariance measurements (Kolari et al. 2004).

These results indicate that, with a single set of parameter values, 3-PG can provide good descriptions of the growth patterns of trees (in this case, *P. sylvestris*) over long periods, including growth after repeated thinning. Furthermore, these parameter values apply equally well at different sites, a point also made by Landsberg et al. (2003). There are a number of parameters that seem to be widely applicable (see Table 1): the canopy quantum efficiency value used ($0.055 \text{ mol C (mol quanta)}^{-1}$, equivalent to $3.04 \text{ g C MJ}^{-1} \text{ APAR}$) has also proved suitable for a wide range of coniferous species (see Landsberg et al. 2003); the SLA values used are typical of coniferous species (Landsberg and Gower 1997, Bond et al. 1999, Stenberg et al. 2001 (Table 1)). As to the allocation and allometry parts of the model, we have used parameters specific to the species and region analyzed. However, the data used for parameter estimation were independent of the test data (Vanninen 2003, Koivisto 1959). It therefore appears that the model is robust and that most of the data needed to use it are readily available.

The matter of fertility remains problematic. The simulation results indicate that nutrient availability was not a limitation on the Punkaharju site ($FR = 1$), but fertility was limiting at Ruotsinkylä: the $FR = 0.6$ value used there to fit the model to the measurements implies that the effective value of α was 0.046 (see Sands and Landsberg 2002, Landsberg et al. 2003).

Short of using complicated nutrient uptake models, with large numbers of parameters, the values of which would be difficult to obtain, there is, as yet, no substitute for estimating site nutrition on the basis of general knowledge about soil type and fertility. However, the results of the fitting seem consistent with knowledge about the site types: the Punkaharju site is classified as the most fertile pine site type in Finland (OMT), whereas the Ruotsinkylä site represents a moderately fertile site type (VT).

A limitation of the 3-PG model as a practical management tool is that it produces, as output, B , whereas the diameters of stems in stands vary. In addition to simulating variable thinning practices, stem size distributions are important determinants of the commercial value of a given volume of timber. Our analysis of the distributions observed in the stands under study in terms of the widely used Weibull distribution was aimed at evaluating the feasibility of providing stem size distributions from simulated values of B . The Weibull distribution provided a good description of stem diameter distributions in the Punkaharju plots in the early years after 1960: the proportion of the variance in observed stem size accounted for by the Weibull curves (r^2) averaged 0.66. When the stand was more than 60 years of age and stem numbers had been reduced to below about $500 \text{ stems ha}^{-1}$, the r^2 values fell to a mean of about 0.2. Stem diameter distributions in the Ruotsinkylä plot, after 1953, were more consistent; stem numbers in that plot were never reduced to less than 650 and the Weibull function provided a reasonable fit to diameter distributions (mean $r^2 = 0.82$). The regressions relating the parameters of the Weibull distribution to B produced results good enough to support the suggestion that, in any commercial assessment of stand productivity, results of this type could be used to provide preliminary indications of likely product quality.

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