Sensitivity and uncertainty analysis from a coupled 3-PG and soil organic matter decomposition model

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ABSTRACT

3-PG [Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecol. Manage. 95, 209–228] is a process-based model using simplified physiological concepts such as light use efficiency, a constant ratio between net and gross primary production and a simple stand nutritional status parameter. This last parameter is commonly adjusted manually to fit observations, based on data from field surveys. It has been shown that nutritional status has a significant effect on estimated gross and net productivity and it has been suggested that the introduction of a soil sub-model could overcome such problems. This paper introduces a soil organic matter decomposition model within the routines of 3-PG. ICBM/2N (Introductory Carbon Balance Model [Andrén, O., Kätterer, T., 1997. ICBM: the introductory carbon balance model for exploration of soil carbon balance. Ecol. Appl. 7, 1226–1236]) was chosen because it operates at a level of complexity similar to 3-PG. The new model 3-PGN (3-PG Nitrogen) includes three soil carbon and three soil nitrogen pools with eleven additional parameters. This approach provides a new way to account for soil nutritional status within 3-PGN by introducing a fertility rating that varies over the life of a stand. We present the integrated model and describe the basic concepts of the integration. The model has been calibrated and tested for commercial plantations of Scots pine (*Pinus sylvestris* L.) in Scotland. An uncertainty analysis was performed based on a Bayesian framework using Monte Carlo simulations and a sensitivity analysis to understand the model's feedbacks and interactions between parameters and outputs. The results show that the least uncertain parameters were the most sensitive, having the greatest effect on many of 3-PGN's outputs, including quantum yield efficiency, specific leaf area and foliage:stem biomass partitioning ratio. Although the soil sub-model had no direct effect on productivity, strong non-linear relationships were found between many of the soil parameters and 3-PGN outputs. Root turnover rate was found to be the most uncertain parameter, whereas the ratio of net to gross primary production was the least. Finally, through the validation procedure it was shown that 3-PG's self-thinning routine may cause problems when predicting the number of stems in stands with low fertility.

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1.　Introduction

Process-based models describe the behaviour of a system through a set of functions based on physiological and bio-physical processes occurring over time (Mäkelä, 2003). Forest process-based models simulate the production of a single tree or a stand using meteorological inputs such as mean temperature, rainfall and solar radiation. Photosynthesis, respiration, biomass allocation, nutrient utilisation and uptake, litterfall and root turnover are modelled based on physiological principles (e.g., BIOMASS, McMurtrie et al., 1992) or biochemical principles (e.g., FOREST-BGC, Running and Gower, 1991) at a very fine temporal scale (hours, days). In general, the more complex the model, the smaller is the time step and finer the resolution of processes contained (in the continuum from cells and organs to stands, regions and the globe), which consequently increases the number of parameters requiring parameterisation. Models differ in the way the major processes are represented. To obtain a simple model with high generality, but based on the same physiological principles, one often needs to decrease the modelling resolution and the time step. Such models can be useful not only for research but to inform management decisions (e.g., Johnsen et al., 2001) and the last few years has seen an extensive effort to introduce simplified process-based models for forest management (Landsberg and Waring, 1997; Johnsen et al., 2001; Landsberg et al., 2003; Mäkelä, 2003).

3-PG (Landsberg and Waring, 1997) is one such simplified process-based model based on eco-physiological principles. It has been applied across several species, including Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Scots pine (*Pinus sylvestris* L.), Eucalypt (*Eucalyptus grandis* Hill ex Maiden), Rimu (*Dacrydium cupressinum* Lamb.), Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson), Loblolly pine (*Pinus taeda* L.), Mexican weeping pine (*Pinus patula* Scheide. ex Schldl. & Cham.) and lodgepole pine (*Pinus contorta* Douglas ex Loudon) (Coops et al., 1998; Law et al., 2000; Waring, 2000; White et al., 2000; Dye, 2001; Landsberg et al., 2001; Tickle et al., 2001; Sands and Landsberg, 2002; Whitehead et al., 2002; Hirsch et al., 2004; Stape et al., 2004; Landsberg et al., 2005; Paul et al., 2007). Many of these studies have already highlighted strengths and weaknesses of the model (Sands and Landsberg, 2002; Landsberg et al., 2003; Stape et al., 2004; Landsberg et al., 2005). Additionally, two studies have explored the internal feedbacks between parameters and outputs (Almeida et al., 2004; Esprey et al., 2004).

Some aspects of the model have been criticised, such as the fertility rating (FR) and the thinning routine (Dye, 2001; Landsberg et al., 2001; Whitehead et al., 2002; Landsberg et al., 2003). Landsberg et al. (2003, J.J. Landsberg, personal communication, 2003) suggested the use of soil surveys to estimate FR, but this method has species and site limitations. Landsberg et al. (2003) also suggested that introduction of a dynamic soil organic matter model would be the way forward. Following this suggestion, some studies have integrated 3-PG with soil organic matter decomposition models (Peng et al., 2002; Hirsch et al., 2004; Paul and Polglase, 2004), although none have brought the integration to the point where FR becomes an internal variable estimated through explicit representation of soil processes.

ICBM (Andrén and Kätterer, 1997) is a suitable model to achieve this integration. ICBM was initially developed as a soil carbon balance model for use in agriculture (Kätterer and Andrén, 1999; Andrén et al., 2001; Kätterer and Andrén, 2001). Kätterer and Andrén (2001) presented five other versions of the model with different combinations of carbon, microbial and nitrogen pools. One important feature of the ICBM family of models is the possibility of choosing either a differential or analytically solved format.

The first application of a combined model for forests was a study of the carbon cycle of different forest ecosystems (Magnani et al., 2007). ICBM was integrated with 3-PG as a suitable stand ecosystem carbon dynamics simulator. The model was fitted to observed chronosequence data from a variety of biomes, including Scots pine from Finland and Sweden, Sitka spruce from UK, Maritine pine (*Pinus pinaster* Aiton) from France and Turkey oak (*Quercus cerris* L.) from Italy. This model (3-PG-3) was used to extrapolate observed data across time and to compare carbon fluxes between biomes. The two models were integrated in such a way that 3-PG supplied the litter input for the ICBM routines. However, this work did not incorporate the effects of soil organic matter decomposition on nutrient release and its potential impact on plant growth in 3-PG, and did not remove the requirement for an empirical calibration of FR.

Amongst the criticized limitations of 3-PG is the empirical nature of the fertility rating and lack of representation of the important ecosystem processes of soil organic matter decomposition (Landsberg et al., 2003), The aim of this paper is to provide a description of the integration between 3-PG and ICBM/2N in order to address two of the limitations of 3-PG, namely the empirical nature of the fertility indicator and its manual adjustment and the lack of the nutrient release on tree growth. The model was calibrated using a Bayesian approach and Monte Carlo simulation in order to identify species-specific and site-specific parameters and their uncertainty. Additionally, an investigation was conducted to determine whether changes in site conditions affected the uncertainty of the parameters. A broad range of conditions was included in the calibration process. Finally, a sensitivity analysis was performed to identify a list of parameters crucial to model predictions.

2.　Materials and methods

2.1.　*Model description*

2.1.1.　*The 3-PGN model*

3-PGN follows the conventional structure of a forest process-based model, i.e., photosynthesis and respiration, allocation and senescence, all couple to the major environmental drivers affecting growth. A complete list of all parameters is given in Table 1 , while a more detailed description of the individual models is given by Landsberg and Waring (1997), Sands and Landsberg (2002), Andrén and Kätterer (1997) and Kätterer and Andrén (2001).

3-PGN requires a set of meteorological inputs including mean monthly averages of maximum and minimum temperature, rainfall and solar radiation and site parameters such

Table 1 – Description of 3-PGN parameters and values for Scots pine

Parameter description	3-PGN symbol	Units	*Pinus sylvestris* L.
Allometric relationships partitioning			
Foliage:stem partitioning ratio at $D = 2$ cm	p_{FS_2}	–	0.76
Foliage:stem partitioning ratio at $D = 20$ cm	$p_{FS_{20}}$	–	0.46
Constant in the stem mass versus diam. relationship	a_s	–	0.0572
Power in the stem mass versus diam. relationship	n_s	–	2.4568
Maximum fraction of NPP to roots	n_{Rx}	–	0.48
Minimum fraction of NPP to roots	n_{Rn}	–	0.21
Temperature modifier			
Minimum temperature for growth	T_{min}	°C	−5
Optimum temperature for growth	T_{max}	°C	15
Maximum temperature for growth	T_{max}	°C	35
Frost modifier			
Days production lost per frost day	kF	days	1
Soil water modifier			
Moisture ratio deficit for $fq = 0.5$	SW_{const}	–	Site specific
Power of moisture ratio deficit	SW_{power}	–	Site specific
Fertility effects			
Value of "m" when FR = 0	m_0	–	0
Value of "f_N" when FR = 0	f_{N_0}	–	0.6
Age modifier			
Maximum stand age used in age modifier	F_a	years	120
Power of relative age in function for f_{Age}	n_{age}	–	4
Relative age to give $f_{Age} = 0.5$	r_{Age}	–	0.75
Litterfall and root turnover			
Maximum litterfall rate	γ_{Fx}	month^{-1}	0.024
Litterfall rate at $t = 0$	γ_{F_0}	month^{-1}	0.0022
Age at which litterfall rate has median value	t_{γ_F}	month	60
Average monthly root turnover rate	Rttover	month^{-1}	0.07
Conductance			
Maximum canopy conductance	g_{cx}	m s^{-1}	0.02
Leaf area index for maximum canopy conductance	$L^*_{g_{cx}}$	–	3.33
Defines stomatal response to VPD	CoefCond	mbar^{-1}	0.05
Canopy boundary layer conductance	g_{BL}	m s^{-1}	0.2
Stem numbers			
Max. stem mass per tree at 1000 trees/ha	$w_{Sx_{1000}}$	kg tree^{-1}	255
Power in self-thinning rule	n_m	–	1.5
Fraction mean single-tree foliage biomass lost per dead tree	mF	–	0.2
Fraction mean single-tree root biomass lost per dead tree	mR	–	0.2
Fraction mean single-tree stem biomass lost per dead tree	mS	–	0.2
Canopy structure and processes			
Specific leaf area at age 0	σ_0	m^2 kg^{-1}	6
Specific leaf area for mature leaves	σ_1	m^2 kg^{-1}	4
Age at which specific leaf area $= (\sigma_0 + \sigma_1)/2$	t_σ	years	6
Extinction coefficient for absorption of PAR by canopy	k	–	0.52
Age at canopy cover	fullCanAge	years	18
Maximum proportion of rainfall evaporated from canopy	I_x	–	0.15
LAI for maximum rainfall interception	$L^*_{I_x}$	–	5
Canopy quantum efficiency	α_x	molC molPAR^{-1}	0.05
Branch and bark fraction			
Branch and bark fraction at age 0	p_{BB_0}	–	0.3
Branch and bark fraction for mature stands	p_{BB_1}	–	0.1
Age at which branch and bark fraction $= (p_{BB_0} + p_{BB_1})/2$	t_{BB}	years	10
Various			
Ratio NPP/GPP	Y	–	0.49
Basic density	ρ	t m^{-3}	0.39
Conversion factors			
Intercept of net versus solar radiation relationship	Qa	W m^{-2}	−90
Slope of net versus solar radiation relationship	Qb	–	0.8
Molecular weight of dry matter	gDM_{mol}	gDM mol^{-1}	24
Conversion of solar radiation to PAR	molPAR_MJ	mol MJ^{-1}	2.3
ICBM/2N			
Decomposition rate constant for the young and labile pool	k_{lmax}	month^{-1}	0.0315
Decomposition rate constant for the young and refractory pool	k_{rmax}	month^{-1}	0.0042
Decomposition rate constant for the old pool	k_{omax}	month^{-1}	0.0005

Parameter description	3-PGN symbol	Units	*Pinus sylvestris* L.
Table 1 (*Continued*)			
Humification coefficient	h_c	–	0.2308
Quality, C:N ratio of refractory litter input	q_{i_r}	–	334.29
Quality, C:N ratio of labile litter input	q_{i_l}	–	49.08
C:N ratio of humification	q_{h_c}	–	23.63
C:N ratio of soil organism biomass	q_{b_c}	–	2.21
Efficiency of labile pool	e_l	–	0.25
Efficiency of refractory pool	e_r	–	0.56
Foliage nitrogen concentration	N_{c_f}	–	1.48

Calibration procedure included the exploration of the posterior distribution of 32 dimension parameter space using Bayes' theorem and Monte Carlo Markov Chain simulation. Parameters which were not included in the procedure were chosen from literature.

as planting year and soil texture. Gross primary production (P_G) is the product of intercepted photosynthetically active radiation and quantum yield efficiency. Environmental limitations on growth are simulated by multipliers (modifiers) taking values between 0 and 1. Net primary production (P_N) is derived from gross production using a constant ratio (0.45 Landsberg and Waring, 1997; Waring et al., 1998) to account for respiration losses. Net primary production is then allocated to the three structural compartments of stem, roots and foliage, through a series of allocation coefficients estimated from allometric relationships (Landsberg, 1986; Landsberg and Waring, 1997). All carbohydrates are allocated on a single-tree basis. Allocation occurs firstly to the root compartment, the value of which is directly affected by site fertility and water availability. Stem allocation is then estimated from a foliage:stem ratio using an allometric relationship with diameter at breast height, whereas the remaining carbohydrate is allocated to foliage.

Soil water balance is derived by subtracting from rainfall the canopy interception and transpiration losses calculated using the Penman–Monteith formula (Landsberg and Waring, 1997). The model assumes loss of water by run-off when soil water holding capacity is exceeded. Leaf area index (L^*) is the product of an age-dependent specific leaf area and current foliage biomass. Litterfall reduces foliage biomass monthly, based on a time-dependent litterfall rate (Sands and Landsberg, 2002). Natural mortality is described by the self-thinning law, which is applied when the above ground biomass of the mean single tree exceeds a maximum value, for a fixed stand density.

Standard model outputs include a wide range of variables, including annual and monthly values of stem, foliage and root biomass, stand timber volume, diameter at breast height, stand basal area, mean annual increment, total litterfall, net and gross primary production, total evapotranspiration and leaf area index.

ICBM/2N was chosen as the most appropriate version for coupling to 3-PG as it allows different tree components (e.g., root and leaf detritus) to have different decomposition rates (Berg and Ekbohm, 1993; Titus and Malcolm, 1999; Hyvönen et al., 2000; Mäkelä and Vanninen, 2000; Janssens et al., 2002; Laiho and Prescott, 2004). The model has two pools for "young" carbon, one "labile", which includes the small-sized detritus (litterfall and fine root turnover) and a "refractory" pool, which includes coarse woody detritus (coarse roots and branches). There is also an old pool, which represents the humified organic matter. Each pool has a constant decomposition rate with a fixed external response (r_e). Finally, the humification coefficient applied to both young pools, represents the rate at which carbon turns into humus. Each carbon pool has a respiratory loss due to decomposition, which is also affected by external (mainly environmental) conditions.

A similar representation of initial state variables exists for nitrogen stocks. ICBM/2N simulates nitrogen based on the fluxes and stocks of carbon and through C:N ratios. Two additional parameters represent the microbial efficiency for labile and refractory pool, i.e., the fraction of C flux from the pool allocated to microbial growth.

Each young pool has inputs from above and below ground litter, which is divided by the equivalent C:N ratio. Both young nitrogen stocks "release" nitrogen depending linearly on the decomposition rate and on external influence. An input of nitrogen is added to each young pool by the microbial activity during humification process.

The new 3-PGN model has incorporated all the main features of 3-PG and ICBM/2N with a two-way dynamic integration, in such a way that both soil organic matter (SOM) and nutrient dynamics affect growth. This was achieved by implementing a new method of estimating fertility rating (FR), removing the need for manual adjustment.

The first integration step involved partitioning the supply of litter to carbon and nitrogen pools within ICBM/2N. Monthly losses of roots, foliage and stem predicted by 3-PG, were separated into labile and refractory carbon pools. Each pool was updated at a monthly time step.

The second integration step involved the estimation of plant and soil nutritional status and their effect on productivity. The FR parameter is derived by using the ratio in Eq. (1):

$$FR = \frac{N_{av}}{U_n} \tag{1}$$

where N_{av} is the soil "plant available" nitrogen and U_n is the stand "nitrogen uptake". Although nutrients such as phosphorus (P) and potassium (K) have significant effects on growth (e.g., Oleksyn et al., 2003; Ladanai and Ågren, 2004; Vestgarden et al., 2004), nitrogen was assumed to be the most limiting nutrient (Flaig and Mohr, 1992; Vollbrecht and Kasemir, 1992; Ingacio Rangel-Castro et al., 2002; Öhlund and Näsholm, 2004) in order to maintain a low level of complexity.

The "plant available" nitrogen term describes the mineral form of nitrogen available to the plant roots, dissolved in soil solution. This quantity is estimated by ICBM/2N using Eq. (2):

$$N_{av} = k_{Y_l}\left(\frac{1-h_c}{1-e_l}\right)Y_{N_l} - e_l\frac{Y_l}{q_{b_c}} + k_{Y_r}\left(\frac{1-h_c}{1-e_r}\right)Y_{N_r}$$
$$- e_r\frac{Y_r}{q_{b_c}} + k_O O_N \tag{2}$$

where Y_l and Y_r are the young labile and young refractory carbon pools, respectively and Y_{N_l}, Y_{N_r} and O_N are the young labile, young refractory and old nitrogen pools, respectively. For explanations of the other symbols, see Table 1. The three nitrogen pools of the model have three outfluxes dependent on decomposition rates. We assumed that no nitrogen is lost through leaching and the sum of all three quantities gives the plant available nitrogen.

The uptake rate of nitrogen is estimated as described by Landsberg (1986), in which the plant uptake rate (U_i) is proportional to its concentration ($[M_i]$) in the structural tissues (foliage, stem and roots) and the growth rate of that tissue (Eq. (3)).

$$U_i = \sum_{i=F,S,R} [M_i]\frac{dW_i}{dt} \tag{3}$$

Since nitrogen is more important in the foliage, we ignored concentrations of stem and root nitrogen. Additionally, we assumed that nitrogen concentrations of Scots pine needles remained constant with age (Mencuccini and Grace, 1996; Korakaki, 2003). Thus, uptake of nitrogen from the soil is necessary during canopy growth.

Following the estimation of the nitrogen uptake rate and nitrogen availability, the ratio of FR is estimated (see Eq. (1)). The ratio takes values between 0 and 1. A value of one indicates that the availability of nitrogen exceeds the uptake rate and so the site is fertile. In such circumstances, 3-PG will allocate less biomass to roots and more to foliage and stem, which will increase the foliage growth rate. This causes an increase in nitrogen uptake and a decrease in FR. Additionally, the model does not explicitly remove nitrogen from the soil. FR is determined to provide an indication of the site fertility and is estimated for each time step according to the current soil and stand growth conditions. As in 3-PG, FR affects the root allocation coefficient and the environmental modifier affecting quantum yield efficiency. The initialisation of FR is through ICBM/2N state variables of nitrogen pools, although the possibility of manually adjusting FR based on soil survey data is retained as an option.

$$k_{Y_l} = k_{l_{max}} f_T f_\theta \tag{4}$$

$$k_{Y_r} = k_{r_{max}} f_T f_\theta \tag{5}$$

$$k_O = k_{o_{max}} f_T f_\theta \tag{6}$$

The equations of ICBM/2N were modified to include the effects of climate on the decomposition of SOM and nutrient release. More specifically, we removed the user-defined parameter r_e and made decomposition a function of air temperature and soil moisture using the environmental modifiers of 3-PG (f_T and f_θ, respectively). The maximum values of decomposition rates for labile young, refractory young and old carbon pools ($k_{l_{max}}$, $k_{r_{max}}$ and $k_{o_{max}}$, respectively) were reduced by the estimated f_T and f_θ of 3-PG (see Eqs. (4)–(6)). This approach is consistent with other well-established models (Running and Gower, 1991; Aber and Federer, 1992; Parton et al., 1993).

2.2. Data sources

2.2.1. Stand level data
Stands of Scots pine are found across Scotland, covering an area of 219,438 ha of commercial plantation stands, 73,421 ha of which are under Forestry Commission ownership (Forestry Commission, National Inventory of Woodlands and Trees, 2003). Almost half of the total area of Scots pine is in native woodlands (Mason et al., 2004). Sites across the country were selected to explore differences in productivity and to produce a parameter set which captured those differences.

The data for calibration and validation of 3-PGN came from 51 experimental plots of Scots pine, receiving different silvicultural treatments that were part of the UK Forestry Commission permanent sample plot (PSP) data base. The data base included control plots, stands with low, "neutral" and crown thinning and provided information about mean diameter, top height, basal area, stocking and standing volume as a time series for each plot. Stem, foliage and root biomass was calculated for each stand with pooled allometric equations developed using data for Scots pine from five studies across Europe (Ovington, 1957; Albrektson, 1980; Vanninen et al., 1996; Oleksyn et al., 1999; Xiao et al., 2003) with the methodology described by Zianis and Mencuccini (2005). From the database, six control plots were used for calibration and three control plots for validation.

Of the three validation plots, plot 1, growing on clay soil, had a general yield class 14 and so was considered a very fertile plot. Plot 2, also growing in clay soil, was less fertile and had a general yield class 12. Plot 3, on a sandy soil, had also a general yield class 12, but was considered the least fertile plot.

In addition to the PSP data set, an extensive field survey of 45 plots was carried out across Scotland, sampling productive stands of Scots pine experiencing different climate, elevations and soil types. The measurements included top height, stocking, standing volume, volume increment and soil information such as soil texture, water content and carbon and nitrogen stocks. Eight plots were extracted from this data set to represent a range of elevations and latitudes and were included in the calibration analysis. All calibration and validation plots had an elevation range between 3 and 364 m a.s.l., with latitude between 55°05.1′ and 58°27.7′ N and longitude between 3°06.3′ and 4°30.8′W.

2.2.2. Climate
Climatic inputs for the model for any geographical location in Scotland were developed by spatial interpolation from data set obtained from the Climate Research Unit of the University of East Anglia (CRU) (Hulme et al., 1999). The dataset is a 10 km point-grid including mean monthly averages of maximum and minimum temperature, precipitation, rain days,

frost days, sunshine hours and relative humidity for the period 1961–1997 across Great Britain.

We created surfaces of latitude, frost days and relative humidity. The first two variables were used as input to 3-PGN. The digital layers were masked for Scotland at a 1 km resolution.

Incoming solar radiation was estimated using the algorithm by Nikolov and Zeller (1992), which is based on monthly average temperature, total precipitation and relative humidity. It applies corrections for topography by using latitude, elevation, slope and aspect. We ran the algorithm within ArcInfo workstation (ESRI, Redland California) using our spatial dataset of monthly climatic inputs and the topographic variables extracted from a DEM (Ordnance Survey, UK).

The resulting 1 km grid surfaces of solar radiation were validated using independent data from two meteorological stations. The model showed very good prediction over the winter and spring months, but it slightly overestimated values during June, July and August at both sites. The difference was not statistically significant for either site ($P > 0.05$ using a two sample t-test).

2.3. Model calibration

We used a calibration approach based on Bayesian theorem (Gertner et al., 1999; Radtke et al., 2002; Van Oijen et al., 2005;

Svensson et al., 2008). This approach is not new (Reckhow, 1990; Ellison, 1996, 2004). Modern computer capabilities however, allow the procedure to be implemented in complex ecological process-based models.

The technique has already been used to parameterise 3-PG for Corsican pine in the UK (Patenaude et al., 2008) providing estimates of the uncertainty and a sensitivity analysis of the parameters. We expanded on that study by including the soil sub-model in the Bayesian calibration.

2.3.1. Bayesian approach

Bayesian statistics require the uncertainty of a parameter θ to be defined by its prior probability distribution $P(\theta)$. This represents the existing knowledge of the parameter. No prior information exists for the distribution of 3-PGN parameters and so a uniform distribution providing maximum and minimum limits was assumed (Van Oijen et al., 2005). The limits were obtained from existing literature on Scots pine and pines in general (Table 2). Some parameters were kept constant, such as the maximum proportion of rainfall evaporated from the canopy, the leaf area for maximum rainfall interception, slope and intercept for the relationship between net and global radiation and the conversion factor for radiation to photosynthetically active radiation. Soil parameters where chosen to match the soil texture conditions estimated during an extensive field survey of the calibration sites.

Table 2 – Upper and lower limits of the uniform prior parameter distribution			
Parameter	Upper	Lower	Reference
p_{FS_2}	1	0.4	Landsberg and Waring (1997) and Landsberg et al. (2003)
$p_{FS_{20}}$	1	0.2	Landsberg and Waring (1997) and Landsberg et al. (2003)
n_{Rx}	1	0.4	Waring and McDowell (2002)
n_{Rn}	0.40	0.2	Waring and McDowell (2002) and Janssens et al. (2002)
f_{N_0}	1	0.1	–
γ_{Fx}	0.03	0.02	Schoettle and Fahey (1994), Mäkelä and Vanninen (2000) and Jalkanen and Aalto (1994)
γ_{r_0}	0.0025	0.0005	–
Rttover	0.16	0.003	Vanninen and Mäkelä (2005), Mäkelä and Vanninen (2000), Janssens et al. (2002) and Schoettle and Fahey (1994)
g_{cx}	0.03	0.02	Beadle et al. (1985)
$L^*_{g_{cx}}$	4	2.5	–
$w_{Sx_{1000}}$	600	100	–
mF	0.5	0.1	–
mR	0.5	0.1	–
mS	0.5	0.1	–
σ_0	9	4	Mencuccini and Bonosi (2001)
σ_1	6	3	Mencuccini and Bonosi (2001)
k	0.6	0.2	Law et al. (2000) and Waring and McDowell (2002)
fullCanAge	25	15	–
α_x	0.06	0.03	Law et al. (2000) and Landsberg et al. (2003)
Y	0.49	0.43	Waring et al. (1998)
ρ	0.45	0.3	–
$k_{l_{max}}$	0.1	0.009	Berg and Ekbohm (1993), Titus and Malcolm (1999) and Hyvönen et al. (2000)
$k_{r_{max}}$	0.005	0.001	Laiho and Prescott (2004)
$k_{o_{max}}$	0.001	0.0001	Peltoniemi et al. (2004)
h_c	0.4	0.1	Peltoniemi et al. (2004)
q_{i_r}	600	90	Krankina et al. (1999)
q_{i_l}	60	10	Hyvönen et al. (2000)
q_{h_c}	50	10	Kätterer (personal communication)
q_{b_c}	20	1	Kätterer (personal communication)
e_l	0.6	0.1	Hart et al. (1994) and Hyvönen et al. (2000)
e_r	0.6	0.1	Hart et al. (1994) and Hyvönen et al. (2000)
N_{c_f}	2	1	Vestgarden et al. (2004) and Korakaki (2003)

The prior information was updated using the distribution of a dataset given a specific parameter vector, denoted as $P(\text{Data}|\theta)$. The updated information is the posterior distribution of the parameter θ given the existing data, denoted as $P(\theta|\text{Data})$ (Eq. (7)).

$$P(\theta|\text{Data}) = \frac{P(\theta)P(\text{Data}|\theta)}{P(\text{Data})} \qquad (7)$$

In most cases it was not necessary to compute the probability of the data ($P(\text{Data})$) because of the method of computation or when the data are constant and it could be ignored, so that $P(\theta|\text{Data}) \propto P(\theta)P(\text{Data}|\theta)$. $P(\text{Data}|\theta)$ is also known as the likelihood function of the parameter θ. To estimate the likelihood of the data given the specific model parameter vector an indication of the measurement error is needed by assuming a Gaussian function φ_g with a mean of zero and a given standard deviation (S.D., Eq. (8))

$$P(\text{Data}|\theta) = \prod_i^n \varphi_g(\text{Data}_i - f_i(\theta); 0, \text{S.D.}_i) \qquad (8)$$

where n is the number of data points used and $f_i(\theta)$ is the model's output. In our case n differed from site to site depending on the number of available data. Because no information about the distribution of the data was available we assumed a constant standard deviation of 5 t/ha for biomass and 5 $m^3\,ha^{-1}$ for stand volume.

Because of the complexity of the model, applying Bayes' theorem for a 32-dimensional parameter space is computational intensive. To speed up computational time we randomly sampled each parameter from its prior distribution and evaluated its the likelihood by using the Metropolis-Hastings algorithm for Markov Chain Monte Carlo (MCMC) simulations as described by Van Oijen et al. (2005) and Robert and Casella (2004), allowing a large number of iterations until the Markov chain "burns in" (Van Oijen et al., 2005).

2.3.2. Procedure

The calibration procedure had two objectives; to quantify the uncertainty of parameters within 3-PGN and to provide a parameter set representative of the climate and soil conditions of Scots pine stands across Scotland. In addition the approach was used to determine the differences in parameter uncertainty by comparing the Bayesian calibration results across sites.

The first objective was achieved by running MCMC for six sites across Scotland using the PSP data. 40,000 iterations were run for each site, this being a sufficient number to allow the chain to "burn in". This could be verified by visually inspecting MCMC trace plots. The posterior distributions for the 32 parameters were estimated for each site together with some of the major outputs of the model, such as stem biomass and stand volume. Climatic inputs were extracted from the spatial database whereas initial values for 3-PGN's state variables such as biomass of foliage, roots and stems were set as 0.01, 0.1 and 0.1, respectively. Soil state variables were also considered following a steady state condition (Peltoniemi et al., 2004). Soil texture information was used to estimate soil water retention parameters from our field survey and max-

imum soil water capacity was assumed constant at 300 mm (Waring, 2000).

With regard to the second objective, a strategy was devised to allow the parameter set to vary across site. To do so, we ran another set of MCMC for eight of the 45 sites across Scotland. The "most likely" parameter vectors were extracted for the eight sites and also for the initial six PSP sites used to quantify uncertainty. The means and standard deviation were estimated for each parameter for the combined fourteen sites and the coefficient of variation (CV) was calculated. A CV of 20% was taken as the upper limit below which parameters were considered not uncertain within and across sites. The parameters with a CV > 20% were used for further MCMC simulations. Before proceeding, the resulting parameter vector was compared with an independent validation PSP data set, for stands with different initial stocking and with no thinning. Since the fit was not good, we proceeded with several cycles of Bayesian calibration. After the simulation the "most likely" parameter vector for the three sites was extracted and averaged. The CV was checked and the set was tested again against the observed data. If the fit was still not good, some parameters were manually changed to give reasonable fits based on the literature data for pine species. This process was repeated five times by progressively reducing the size of the parameter vector and increasing the goodness of fit against observations, ending up with the best parameter set for the different growing conditions of Scots pine. The resulting parameter vector was finally validated using the PSP validation dataset, which includes eight plots with different initial stocking and without any thinning.

2.4. Uncertainty analysis

To summarize the uncertainty of the parameter vector from the posterior distributions of each parameter, we calculated the mean vector and the matrix of coefficients of variation for each of the 32 parameters, for each of the six sites. Additionally, we produced pdf graphs to explore graphically within-sites and between-sites uncertainty. We also estimated the mean and the coefficient of variation of the "most likely" parameters and the standard deviations for the six sites as indicators of the between-site uncertainty.

2.5. Sensitivity analysis

A sensitivity analysis was performed to identify the effect of each parameter on the outputs of both 3-PG and ICBM/2N. Patenaude et al. (2008) used the resulting posterior distributions to produce partial correlation coefficients between the parameters and the model outputs and also amongst the parameters. This methodology provides useful information about the relationships of the parameters with the model outputs, although it has the limitation of assuming linearity. For our model such information was unknown. Additionally, because of the lack of posterior information for the main soil carbon outputs, we performed a sensitivity analysis based on the technique presented by Esprey et al. (2004). This method explores the likely effect of each parameter on the main outputs of both 3-PG and ICBM/2N and explores any non-linear relationship between parameters and outputs.

Table 3 – Coefficients of determinations (R^2) and slope for the comparison between predicted (x-axis) and observed (y-axis) values and significance levels for the slope of the regression, for stem number (N, ha^{-1}), stand volume (V, m^3 ha^{-1}), mean diameter at breast height (D, cm), aboveground tree biomass (W$_{AB}$, tDM ha^{-1}) and stem biomass (W$_S$, tDM ha^{-1}) for the three validation plots (number of observations, respectively = 12, 10 and 10)

	Plot 1			Plot 2			Plot 3		
	R^2	Slope	P	R^2	Slope	P	R^2	Slope	P
N	0.85	1.05	<0.01	0.95	0.77	<0.01	0.49	0.67	<0.01
V	0.98	1.12	<0.01	0.81	1.06	<0.01	0.99	0.99	<0.01
D	0.93	0.98	<0.01	0.99	1.04	<0.01	0.84	1.11	<0.01
W$_{AB}$	0.81	1.31	<0.01	0.84	1.31	<0.01	0.98	1.25	<0.01
W$_S$	0.63	0.98	<0.01	0.88	0.94	<0.01	0.96	0.91	<0.01

Regression line was forced through origin.

We ran the model at a monthly time step, for a specific site, increasing and decreasing the parameter values and the soil state variables by 10% and 40% and explored the major outputs of the model including tree and soil carbon pools, stand volume, litterfall production and leaf area index and finally nitrogen availability and uptake. The relative sensitivity and the relative non-linearity of a certain output X to a parameter or input p was estimated with Eqs. (9) and (10), respectively.

$$\lambda_1(X, p) = \frac{p}{X}\frac{\partial X}{\partial p} \tag{9}$$

$$\lambda_2(X, p) = \frac{p^2}{X}\frac{\partial^2 X}{\partial p^2} \tag{10}$$

where p is the parameter's value, X is the model's output and ∂p and ∂X is the relative change of the parameter and the model's output, respectively. Calculations were performed for each point in time and the results were averaged for the whole simulation period. Greater values indicated higher sensitivity or non-linearity. The analysis did not include differences in sensitivity across sites. The parameter vector used for the analysis included the 11 parameters of the soil sub-model and all the major parameters of 3-PG.

3. Results

3.1. Performance of 3-PGN

The performance of 3-PGN was tested using five of the major outputs of the model, i.e., aboveground and stem biomass, stand volume, diameter at breast height and total number of stems per hectare. No soil data were available for comparison. Table 3 illustrates the coefficients of determination and the slopes of the relationships between model predictions and observations for the three validation plots. The model successfully predicted the patterns of stand volume (R^2 = 0.98, R^2 = 0.81 and R^2 = 0.99 for plots 1, 2 and 3, respectively), diameter at breast height (R^2 = 0.93, R^2 = 0.99 and R^2 = 0.84 for plots 1, 2 and 3, respectively) and stem biomass (R^2 = 0.88 and R^2 = 0.91 for plots 2 and 3, respectively). Stem biomass for plot 1 had an R^2 of 0.63 with the model slightly underestimating for the first 40 years of the simulation. Stem number was adequately predicted for plots 1 and 2 (R^2 = 0.85 and R^2 = 0.95, respectively) but not for plot 3 (R^2 = 0.49), the least fertile stand

of all validation plots. Aboveground biomass was underestimated (slope greater than 1) for all tree validation plots due to underestimation of foliage biomass.

Fig. 1 shows the development of the new fertility rating as predicted by the model for the first 80 years of the simulation. At the time of planting (age 0) FR is 0 for all three plots. Two years after planting, FR increased to 0.45 for plot 1, whereas for plot 2 it increased to 0.47, 4 years after planting. Maximum FR was reached by year 3 for plot 1 and year 5 for plot 2. FR was then decreased for both plots 1 and 2 to less than 0.2 approximately by the age of 20. After that fertility increased
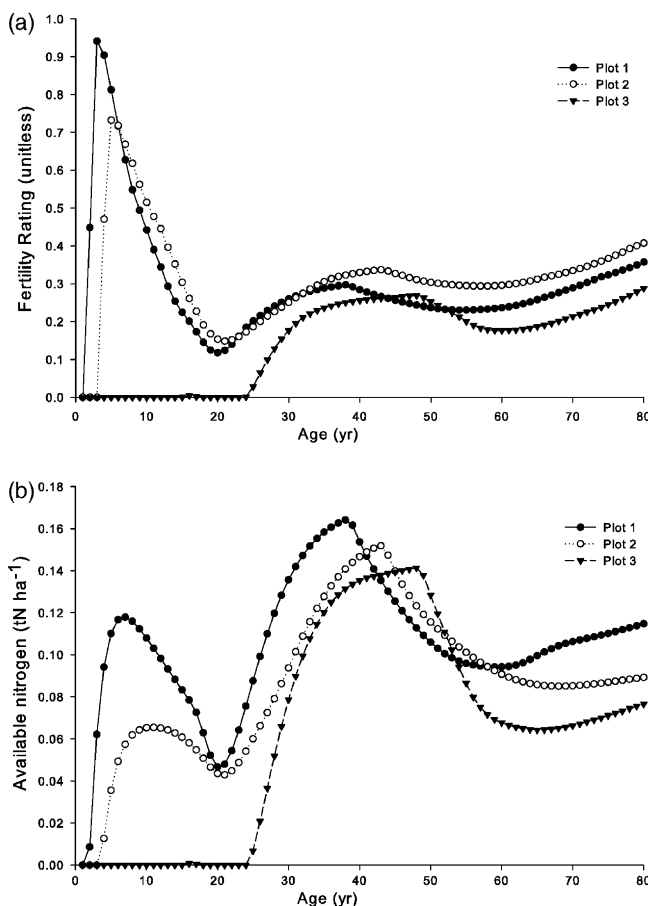
Fig. 1 – (a) Fertility rating (FR) and (b) plant available nitrogen (N$_{av}$ tN ha^{-1}) predictions for plot 1 (filled circles), plot 2 (empty circles) and plot 3 (filled triangles).
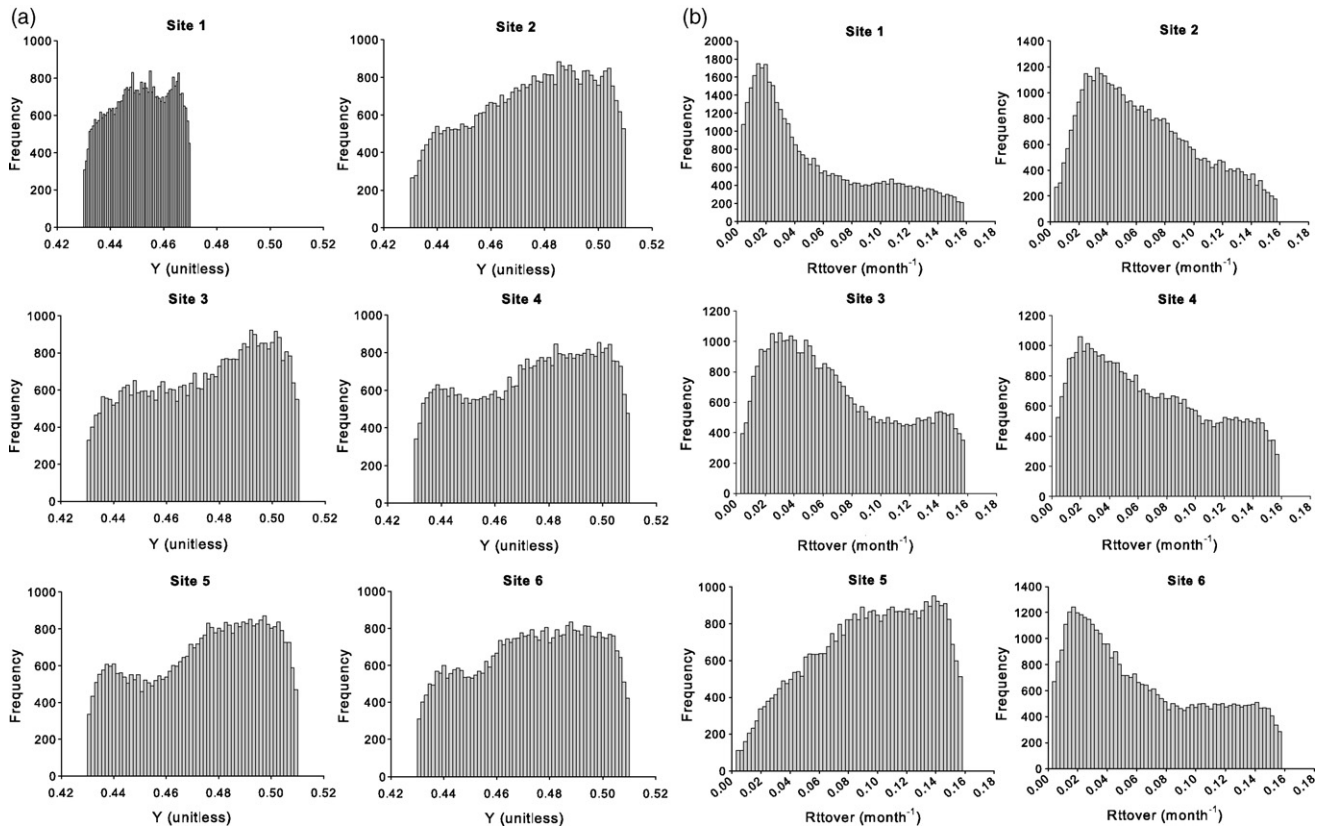
(a)

(b)

Fig. 2 – Posterior distributions for (a) the ratio between net and gross primary production and (b) root turnover rate. The shapes of the distributions of the net to gross primary production ratio are similar for all sites supporting the contention that values are not site-specific. On the other hand, difference in the shape of the distributions for the root turnover rate indicates a difference in the most likely values for which the model fits the observations. This is likely to be due to differences in site characteristics such as soil texture, soil moisture and soil density. Site 1 is the less fertile whereas site 5 is more fertile.

at similar rates, but for plot 2 it lasted for 5 more years. Then for both plots FR was stable between 0.2 and 0.3 for plot 1 and 0.3 for plot 2. Fertility in plot 3 on the other hand, appears to have a different trajectory from the other two plots. Fertility was 0 until the age of 23 and then started to increase, reaching a maximum value at the age of 48. Fig. 1 also shows the predicted nitrogen availability. Nitrogen became available for the plants within the first 10 years for both plots 1 and 2, while it was limited for plot 3 until the age of 23. Both plots 1 and 2 showed a decrease in available nitrogen by the age of 20.

3.2. Uncertainty

Fig. 2 shows pdf graphs for Y and Rttover. Rttover showed high but variable uncertainty at all of the six sites (Fig. 3). Site 1 had the highest uncertainty with 76.8% variation and a mean value of 0.055, whereas site 2 had a variation of 57.6% and a mean value of 0.067. Overall, the mean coefficient of variation for this parameter among sites was 61.0% with a mean of 0.070. On the other hand, the ratio between P_N and P_G was the least uncertain parameter for each site, whilst also not variable across sites. Site 1 had the lowest uncertainty with 2.4% and a mean of 0.451, whereas site 3 had the highest variation

of 4.8% with a mean 0.474. The variation between sites was still very low at 4.3%. $w_{Sx_{1000}}$ was characterised by moderate levels of uncertainty but high across-site variability, with site 2 having a CV of 16.9% and a mean of 130.624, and site 4 a CV of 42.6% with a mean of 581.591.

While only a few of the 3-PG parameters appeared to have uncertainty at or above 40%, a high uncertainty was associated with many of the ICBM/2N parameters. Some of the most uncertain were q_{b_c} and all three decomposition rates $k_{l_{max}}$, $k_{r_{max}}$ and $k_{o_{max}}$. All of the soil carbon parameters had an uncertainty of more than 30%. In addition, the lack of any soil carbon data increased the uncertainty of the parameters. However, most of the soil parameters appeared to vary little across sites, except from $k_{o_{max}}$ and q_{b_c}.

The less uncertain parameters also included n_{Rx}, n_{Rn}, f_{N_0}, γ_{Fx}, g_{c_x}, $L^*_{gc_x}$, σ_1, fullCanAge and ρ, all of which having a CV lower than 20% at each site.

3.3. Sensitivity analysis and non-linearity

An investigation was conducted on the relationships between parameters and outputs of 3-PGN, the most important results of which are given in Figs. 4 and 5. Fig. 4 illustrates the effect of 3-PG parameters on soil carbon stocks and nitrogen
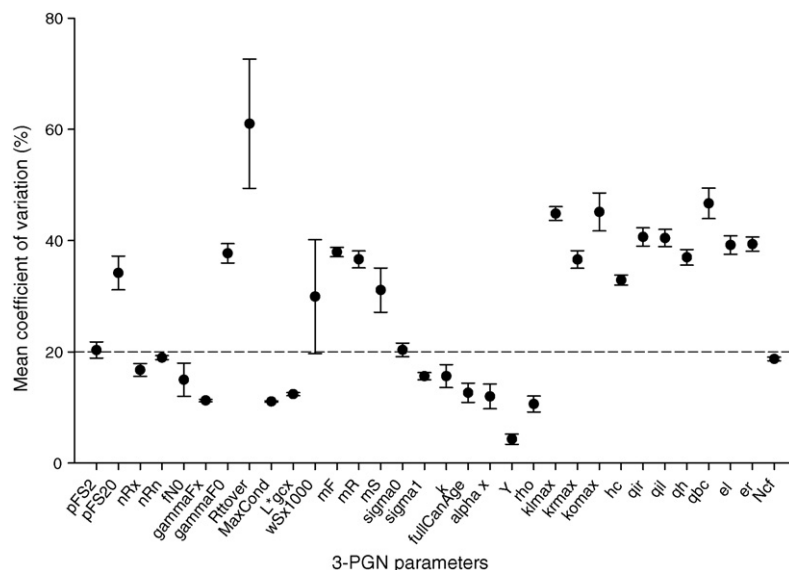
Fig. 3 – Mean coefficient of variation ($\overline{\text{CV}}$) for the 32 parameters of 3-PGN estimated from the six uncertainty sites. Bars represent standard deviations (S.D.$_{\overline{\text{CV}}}$) of the estimated $\overline{\text{CV}}$. Larger error bars indicate variable uncertainty between sites and thus site specific parameters.

availability and uptake, while Fig. 5 shows the effects of ICBM/2N parameters on biomass predictions. Table 4 summarises the results of the first comprehensive sensitivity analysis of ICBM/2N.

Young labile carbon stocks were found to be highly sensitive to Y, α_x, k, σ_1, f_{N_0}, $p_{FS_{20}}$, n_s and γ_{F_x} (Fig. 4). Refractory carbon stocks on the other hand were highly sensitive to Y, α_x, k, σ_1, fullCanAge, f_{N_0}, n_s, n_{Rx}, γ_{F_x}, T_{opt} and $w_{Sx_{1000}}$. Humified carbon stocks were also sensitive to the same parameter set. Nitrogen availability was highly sensitive to Y, α_x, k, f_{N_0}, n_s, and γ_{F_x}, while nitrogen uptake was sensitive to a similar parameter set including $p_{FS_{20}}$. Root turnover rate appeared to have no effect on carbon stocks, not even availability and uptake of nitrogen. Hence, parameters to which 3-PGN was sensitive to (e.g., Y and α_x) were also those with the lowest uncertainty in their estimation. Conversely, root turnover, whose values were very uncertain, appeared to have a non-significant effect on the model predictions.

Biomass predictions of 3-PGN were also not affected by changes in the soil sub-model parameters (Fig. 5), although a strong non-linearity existed (data not shown). Non-linearity in most occasions was high with a 10% change of the parameters, but disappeared with a 40% change.

The sensitivity analysis conducted for ICBM/2N showed that nitrogen availability was highly sensitive to $k_{l_{max}}$, q_{b_c} and e_l, while nitrogen uptake was sensitive only to N_{c_f}. Finally, the sensitivity analysis of 3-PG's outputs on model parameters showed that stem biomass was sensitive to n_{Rx}, γ_{F_x}, fullCanAge, T_{opt}, f_{N_0}, σ_1, k, α_x and Y. On the other hand foliage biomass is sensitive to γ_{F_x}, $p_{FS_{20}}$, f_{N_0}, σ_1, k, α_x, Y and n_s. Finally root biomass was sensitive to γ_{F_x}, Rttover, $p_{FS_{20}}$, n_{Rx}, f_{N_0}, σ_1, k, α_x, Y and n_s. Non-linearity again was an issue, causing similar extreme variations between small and large changes in the parameter's value (data not shown), especially with some of the ICBM/2N parameters and initial state variables.

Table 4 – Results of the first sensitivity analysis performed on the ICBM/2N model

	Y_{N_l}		Y_{N_r}		Y_l		Y_r		O		N_{av}		U_N	
	10%	40%	10%	40%	10%	40%	10%	40%	10%	40%	10%	40%	10%	40%
$k_{l_{max}}$	−0.798	−0.895	–	–	−0.976	−1.124	–	–	–	–	−0.736	−0.565	–	–
$k_{r_{max}}$	–	–	–	–	–	–	−0.543	−0.570	–	–	–	–	–	–
h_c	–	–	–	–	–	–	–	–	0.586	0.586	–	–	–	–
q_{b_c}	−0.808	−0.956	−0.928	−1.098	–	–	–	–	–	–	−1.003	−1.167	–	–
e_l	0.820	0.821	–	–	–	–	–	–	–	–	1.000	0.997	–	–
e_r	–	–	1.282	1.336	–	–	–	–	–	–	–	–	–	–
N_{c_f}	–	–	–	–	–	–	–	–	–	–	–	–	0.832	0.839

Only highly significant results are presented. Y_{N_l} and Y_{N_r}, labile and refractory pool for nitrogen (tC ha^{-1}); Y_l and Y_r, equivalent pools for carbon (tC ha^{-1}); O, humified poll for carbon (tC ha^{-1}); N_{av} and U_N available nitrogen and nitrogen uptake (tN ha^{-1}), respectively.
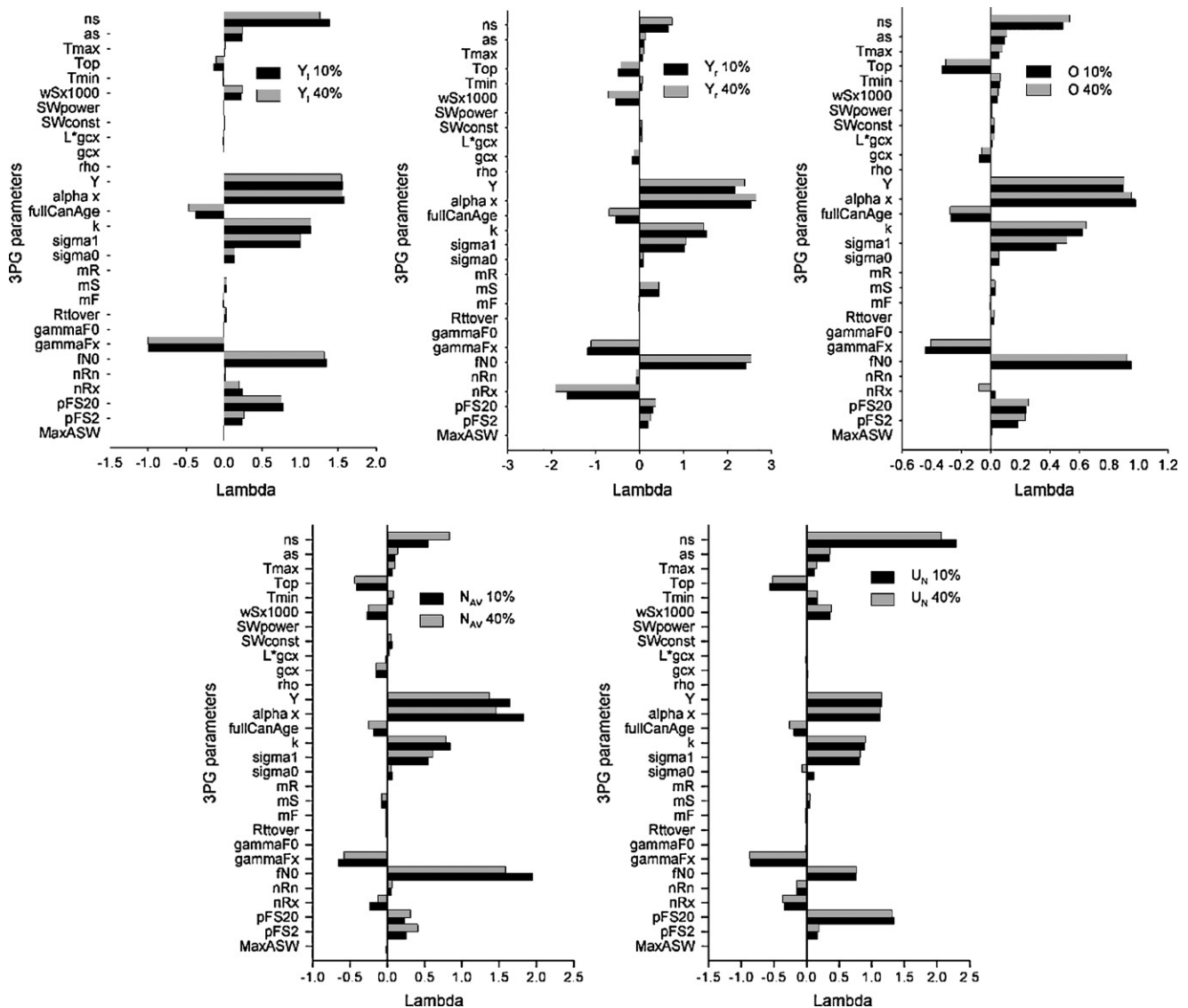
Fig. 4 – Sensitivity (λ_1) of (a) young labile, (b) young refractory, (c) old soil carbon stocks, (d) nitrogen availability and (d) nitrogen uptake to the 3-PG parameter vector for a change of 10% and 40%.

4.   Discussion

Our study represents the first attempt to parameterise the complete ecosystem model 3-PGN and is only the second parameterisation of 3-PG for Scots pine (Landsberg et al., 2005). Our results showed that 3-PGN can reliably represent patterns of stand volume, stem biomass and diameter at breast height. However predictions of foliage and root biomass were less successful. For all three validation plots the model has underestimated aboveground biomass. A further investigation in the model's output showed that 3-PGN underestimated foliage biomass for older trees. We are unable to reach any safe conclusions on the reasons behind this failure, however, a possible explanation is that the model overestimates litterfall because of the time dependent litterfall rate, causing a rapid decrease in both foliage biomass and leaf area index (data not shown). On the other hand, our foliage and root "obser-

vations" were estimated from allometric relationships with breast-height diameter, which might have caused an overestimation of foliage for older trees because of the small number of old trees used in developing the equations. A more complete parameterisation of 3-PGN needs to include a calibration data set with information about foliage and root biomass, carbon and nitrogen stocks in a chronosequence and nitrogen availability.

The validation process showed that 3-PGN was not able to adequately predict stem numbers as fertility decreases and in particular for plot 3, which is the least fertile validation plot with trees growing on sandy soils (Table 3). In the log–log function of the self-thinning rule between the logarithm of biomass per unit area versus the logarithm of density of the surviving population the intercept is known to be affected by site fertility and intensity of shading and initial spacing (Westoby, 1984). We believe that 3-PG's failure to match the observed stem numbers for all three validation plots was
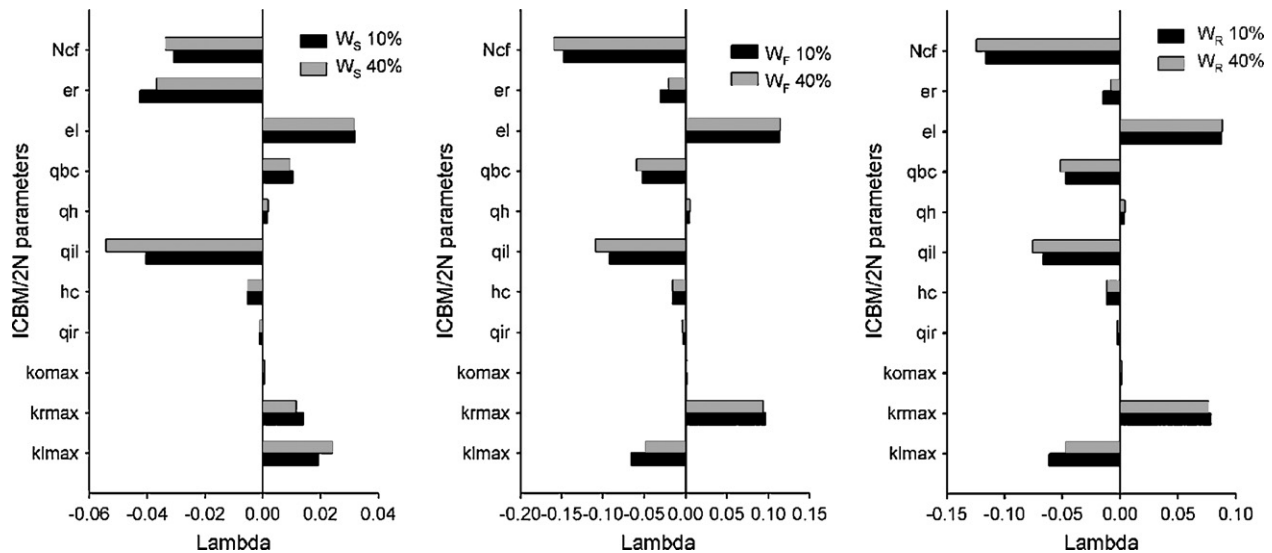
Fig. 5 – Sensitivity (λ_1) of (a) stem, (b) foliage and (c) root biomass to the ICBM/2N parameter vector for a change of 10% and 40%.

due to the inability of the self-thinning routine to adequately adjust the intercept of the relationship according to differences in site fertility and light competition. The robustness of the self-thinning routine is once more criticised (Dye, 2001; Landsberg et al., 2001, 2005) and future development of the model should consider the improvement of the natural mortality function including a more direct effect of fertility. The introduction of a gap-type model (Seidl et al., 2005) could provide a partial solution, but even such integration has the limitation of a stochastic mortality function. Further experimentation and modelling is necessary on the physiological causes of stem mortality.

Fig. 1 illustrates the new site fertility indicator and nitrogen availability as it was predicted by 3-PGN. The model showed that the litter input of the newly planted trees builds up the fertility of the site by realising nutrients (Fig. 1). Depending on soil characteristics and in particular temperature and soil water status, the release can be either high (plot 1), medium (plot 2) or low (plot 3). 3-PGN was able to predict that plot 1 as the most productive stand had a greater capacity to grow trees because nutrients were in abundance whereas, plot 3, on a sandy soil with low water table was infertile for a long period (Fig. 1). 3-PGN was also able to predict the need for nutrients until the canopy is closed, which for Scots pine is at approximately 18–20 years. Until then competition between trees for light and nutrients is high, increasing the demand for nitrogen thus increasing nitrogen uptake and reducing nitrogen availability and fertility of the site (Fig. 1).

The dynamic site fertility classification of 3-PGN showed that plot 1, which has the highest yield class was not always the most fertile. From age 38 to 80 plot 2 appeared to be slightly more fertile than plot 1. This is because of the high demand for nutrients to maintain the high rates of production between age 38 and 57 for plot 1 (Fig. 1). Although nutrient availability started to increase again after age 57, that was not enough to satisfy the high demand of the trees. Despite the fact that plot 2 is more fertile for almost 40 years, other climatic factors

must have had a more significant effect on growth to keep the stands to a lower yield class.

The results from the first sensitivity analysis performed on ICBM/2N showed the importance of labile and refractory decomposition rates of carbon accumulation (Table 4) with the size of young pools decreasing at higher rates of decomposition. Young carbon pools represent the first decomposition stage where the input litter is beginning to decompose and large respiratory losses lead to losses of large quantities of carbon. The old pool represents more stable carbon storage where carbon is "locked" and respiratory losses are much lower, changes in the values of the humification coefficient (h_c) have a much lower impact on the size of the young carbon pools. The humification coefficient is very important in affecting the size of the old carbon pool, which is frequently the largest store of carbon in the soil.

Nitrogen cycling follows slightly different dynamics from carbon cycling. The efficiency and C:N ratios of microbial activity also affect nitrogen stocks. Greater efficiency helps the break down of complex substances (e.g., lignin) into simpler, easily available forms such as nitrate and ammonium. The process was successfully captured by the model as efficiency of microbial activity (e_l) increased nitrogen stocks and availability. The model also showed that the decomposition rates of foliage labile pools and roots are among the most important factors influencing the availability and the uptake of nitrogen.

The results of the sensitivity analysis on 3-PGN were in good agreement with those from previous studies performed on 3-PG (Almeida et al., 2004; Esprey et al., 2004; Patenaude et al., 2008). We found that Y, $p_{FS_{20}}$, α_x, n_{Rx}, f_{N_0} and T_{opt} were important for biomass and for stand volume (data not shown) and Y, $p_{FS_{20}}$, γ_{Fx}, σ_1 and α_x were important for L^* (Esprey et al., 2004), whereas we did not find that g_{cx} significantly affected any of the outputs (cf. Esprey et al., 2004). Root turnover was found to affect only root biomass. We did not find any relationship between root turnover and soil carbon storage, a result also observed by Paul et al. (2003) in their evaluation of 3-PG

with the integrated GRC3 model. The optimum temperature for growth (Patenaude et al., 2008) and rate of uptake of nitrogen were the important parameters affecting stem and root biomass growth (Fig. 4). Temperature can limit photosynthesis as high air temperatures will increase vapour pressure deficit and cause the stomata to close. Specific leaf area was also significant for soil carbon accumulation, as it affected foliage biomass production and litter input (Paul et al., 2003). One of the most important parameters was f_{N_0}, which affected almost every output. Because of the way FR has been modelled, the probability of getting a minimum value of nutrient availability at the precise time of maximum stand development increased, then the accurate estimation of f_{N_0} became increasingly important. Finally, the proportion of net to gross primary production is a parameter to which the model outputs are very sensitive (Almeida et al., 2004; Esprey et al., 2004; Patenaude et al., 2008). Our results are supported by the similar study on Corsican pine (Patenaude et al., 2008) which found that specific leaf area parameters (σ_1), litterfall rate, light extinction coefficient, maximum quantum yield efficiency and fertility rating were among the critical parameters affecting model outputs.

Overall ICBM/2N did not change the internal relationships between 3-PG's parameters and its outputs, as it did not affect productivity (Fig. 5). A similar result was observed in a recent integration of 3-PG with Roth-C soil carbon model (Hirsch et al., 2004). The sensitivity analysis also showed that the soil model parameters did not affect ecosystem carbon storage. The combination of the fast turnover rates and of a small carbon flux transferred to the soil pools resulted in soil carbon storage being very small and soil parameters unimportant (Hirsch et al., 2004). On the other hand, 3-PG parameters had a more direct impact on the soil outputs. Parameters relating to allometry (such as $p_{FS_{20}}$ and n_s) and those related to canopy development (such as σ_1 and γ_{F_x}) showed a large effect on the development of soil carbon and nitrogen stocks, as they were directly linked to the litterfall inputs.

Comparing our parameter vector with that used by Landsberg et al. (2005) for Scots pine stands in Finland, both studies used well established physiological parameters, with maximum canopy conductance set to 0.02 m s^{-1} (Beadle et al., 1985). Maximum canopy conductance was reached at a leaf area of 3.33 and boundary layer conductance was taken as 0.2 m s^{-1} (Beadle et al., 1985). Good agreement was also found for parameters such as the ratio of net to gross primary production (Waring et al., 1998; Landsberg et al., 2003), f_{N_0} (Landsberg et al., 2005; Patenaude et al., 2008), γ_{F_x} (Patenaude et al., 2008) and Rttover (Landsberg et al., 2005). The constant and the power of the stem allometric relation derived from our pooled regression were close to the previously used values (Landsberg et al., 2005). However, differences were found for important parameters such as maximum stand age, the power of relative age, the relative age to a given $f_{AGE} = 0.5$ and specific leaf area. The first three parameters were fitted to match age-related decline of productivity observed by Magnani et al. (2000), whereas values used for the specific area were 6 m^2 kg^{-1} and 4 m^2 kg^{-1} for mature leaves (Mencuccini and Bonosi, 2001), Landsberg et al. (2005) used 9 m^2 kg^{-1} and 6 m^2 kg^{-1}, whereas Bayesian calibration of 3-PG for Corsican pine in England (Patenaude et al., 2008) gave values of 7.6 m^2 kg^{-1} and 3.5 m^2 kg^{-1}, respectively. Mencuccini and

Bonosi (2001) for the same latitude as the sites used by Landsberg et al. (2005) gave a specific leaf area of 5.5 m^2 kg^{-1}. Our value of 0.5 for the extinction coefficient was different from the 0.6 used by Landsberg et al. (2005) and 0.58 of Patenaude et al. (2008). Finally, the value of maximum quantum yield efficiency was found to be 0.05, slightly lower than the "universal" value for pine species of 0.055 (Landsberg et al., 2003, 2005), which could indicate a relationship with soil fertility, as our stands grow on infertile sandy, podzolic and podzolic brown earth soils.

We also estimated the uncertainty associated with the prediction of 3-PGN parameters using Bayesian calibration procedure (Fig. 3). The most uncertain parameters, Rttover, mS, mF, mR and 10 out of 11 soil parameters, were also those to which the productivity outputs were less sensitive. This makes their use more reliable even if their values are very uncertain. On the other hand, an important parameter such as Y was characterised by the lowest uncertainty and a well defined range of likelihood (Fig. 2). However, we observed extreme non-linear relations between most of the parameters and outputs of the model and care is needed in their use since non-linearity can hide potential high sensitivity (Esprey et al., 2004).

Rttover was found to be the most uncertain parameter across sites (Fig. 3). Root turnover is not a species-specific parameter, and it depends on several environmental factors, such as soil temperature, microbial activity, water-logging, frost or nutritional status all of which can differ among sites (Fig. 2). On the other hand, the differences across sites for the foliage:stem ratio at a diameter of 20 cm, were smaller but potentially quite significant. This ratio greatly affects the outputs of foliage biomass, leaf area index, nitrogen availability and uptake, litterfall, nitrogen and carbon pools. This parameter could be affected by many environmental factors such as fertility, light or VPD. Fertile sites have bigger $p_{FS_{20}}$, as they have greater supply of nutrient and greater photosynthetic capabilities (Mencuccini, 2003). VPD can also affect the allocation to foliage in Scots pine (Mencuccini and Grace, 1996; Mencuccini and Bonosi, 2001). $w_{Sx_{1000}}$, $k_{o_{max}}$, q_{b_c}, f_{N_0} and mS are also parameters whose values can vary across sites.

Although we did not include the state variables of soil carbon and nitrogen stocks in our uncertainty analysis, we estimated their sensitivity. We found limited or no sensitivity of tree outputs to the initial values of soil carbon and nitrogen pools, although highly non-linear relations were found for both small and large changes.

Bayesian calibration is a very useful statistical methodology. However, several elements need to be considered before its use. The first is the prior distribution. In our case, no information was available on the prior distribution of the parameters and so a uniform distribution was assumed. It is important to consider prior knowledge of the parameters or the outputs. In our case, information from a literature review was considered as prior knowledge of the limits of the uniform distribution. Since the uncertainty was expected to be very high and no previous information existed, the choice of parameter limits was more relaxed. A second potential problem was the lack of data for some components of the model, particularly the soil dynamics sub-model. Lack of data becomes crucial when relationships between parameters and model outputs exist that are not obvious. The estimation of

the soil parameters from outputs entirely related to productivity is one such example, leading to an additional uncertainty. In such a case a sensitivity analysis provides an indication of whether an underlying relationship exists. On the other hand, Bayesian calibration is applicable even with a small dataset and provides a broad knowledge of the parameters and outputs uncertainty, which would normally be impossible with a manual calibration. Also, automated methods are more efficient in choosing parameters for models with large parameter vectors. Finally, Bayesian calibration does not provide the user with the "optimum fit". We devised a calibration strategy where several cycles of Bayesian calibration applied for a number of sites across a region to produce a mean parameter vector applicable to all situations.

The modelling of the new fertility rating removes the uncertainty derived from its empirical estimation or by its manual adjustment by the user. The new approach makes FR an internal parameter providing an indication of the nutritional status of the stand and how it will affect future production (i.e., it becomes a time integrated "fertility indicator"). As such, comparisons across sites based on this new FR may only be valid if time is also taken under consideration, either by comparing the FR score at a certain stand age or by comparing the absolute difference of FR value between two periods in time (e.g., beginning and end of simulation period). Although the need for manual adjustment of site fertility is no longer present, FR comes with its own uncertainty, and the number of parameters for calibration has increased. Despite this, new parameter values can be more easily estimated by collection of soil samples and the laboratory estimation of carbon and nitrogen stocks and the decomposition rates of various pools of soil organic matter. A further investigation of the relationships between parameters and outputs and of the representation of the major processes in the model would provide a more thorough understanding of the model outputs.

One of the main advantages of the 3-PGN model is that outputs include variables relevant for forest management. The introduction of 3-PGN within a decision support system (DSS) would provide a physiological basis for estimation of forest productivity and aid to management decisions. Integrating 3-PGN with existing DSSs such as Ecological Site Classification (Pyatt et al., 2001; Broadmeadow et al., 2005) and ForestGALES (Gardiner and Quine, 2000) will provide forest managers with a process-based modelling approach to estimate the effect of environmental conditions on forest production for both timber yield and carbon sequestration.

5. Conclusions

For every new model development it is absolutely vital for an uncertainty and sensitivity analysis of the inputs and the parameters to follow. First, it helps the modeller to understand better the processes represented by the model and secondly to identify all the important internal feedbacks and the parameters and highlight those where extra care is needed when choosing their values. For 3-PGN, we were able to identify those parameters that could safely be chosen from the literature (i.e., the non-sensitive) and the parameters whose calibration should be based on field measurements (i.e., highly

sensitive). A calibration procedure based on Bayesian statistics not only offered an automated method for calibration and uncertainty analysis but also contributed significantly to identify which parameters are likely to be site-specific, probably due to underlying relationships with site factors. The use of such parameters for predicting productivity in large spatial scales should be carefully considered. In order to remove one of the highly uncertain parameters of 3-PG a small number of new parameters were necessary. Although the procedure introduces a new source of uncertainty, this is easily quantified. Additionally, this source of uncertainty can be reduced by establishing a series of soil measurements on carbon and nitrogen stocks, fluxes and litter decomposition.

Our results also highlighted the need for further development on the other weak points of 3-PGN such as the modelling of natural mortality and competition. Finally, when a Bayesian calibration with Monte Carlo simulations is carried out, prior knowledge of parameter distributions is crucial. When a uniform distribution is chosen for parameter with no previous prior knowledge, the choice of the upper and lower limits should be wide enough to provide sufficient exploration of their uncertainty.

REFERENCES

Aber, J.D., Federer, C.A., 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. Oecologia 92, 463–474.

Albrektson, A., 1980. Biomass of Scots pine (*Pinus sylvestris* L.). In: Amount – Development – Methods of Mensuration. Swedish University of Agricultural Science, Department of Silviculture, Umea.

Almeida, A.C., Landsberg, J.J., Sands, P.J., 2004. Parameterisation of 3-PG model for fast-growing *Eucalyptus grandis* plantations. Forest Ecol. Manage. 193, 179–195.

Andrén, O., Kätterer, T., 1997. ICBM: the introductory carbon balance model for exploration of soil carbon balance. Ecol. Appl. 7, 1226–1236.

Andrén, O., Kätterer, T., Hyvönen, R., 2001. Projecting soil fauna influence on long-term soil carbon balances from faunal exclusion experiments. Appl. Soil Ecol. 18, 177–186.

Beadle, C.L., Talbot, H., Neilson, R.E., Jarvis, P.G., 1985. Stomatal conductance and photosynthesis in a mature Scots pine forest. 3. Variation in canopy conductance and canopy photosynthesis. J. Appl. Ecol. 22, 587–595.

Berg, B., Ekbohm, G., 1993. Decomposing needle litter in *Pinus contorta* (lodgepole Pine) and *Pinus sylvestris* (Scots pine) monoculture systems—is there a maximum mass loss? Scand. J. Forest Res. 8, 457–465.

Broadmeadow, M.S.J., Ray, D., Samuel, C.J.A., 2005. Climate change and the future for broadleaved tree species in Britain. Forestry 78, 145–161.

Coops, N.C., Waring, R.H., Landsberg, J.J., 1998. Assessing forest productivity in Australia and New Zealand using a physiologically-based model driven with averaged monthly weather data and satellite-derived estimates of canopy photosynthetic capacity. Forest Ecol. Manage. 104, 113–127.

Dye, P.J., 2001. Modelling growth and water use in four *Pinus patula* stands with the 3-PG model. South African For. J. 191, 53–63.

Ellison, A.M., 1996. An introduction to Bayesian inference for ecological research and environmental decision-making. Ecol. Appl. 6, 1036–1046.

Ellison, A.M., 2004. Bayesian inference in ecology. Ecol. Lett. 7, 509–520.

Esprey, L.J., Sands, P.J., Smith, C.W., 2004. Understanding 3-PG using a sensitivity analysis. Forest Ecol. Manage. 193, 235–250.

Flaig, H., Mohr, H., 1992. Assimilation of nitrate and ammonium by the Scots pine (*Pinus sylvestris*) seedling under conditions of high nitrogen supply. Physiol. Plantarum 84, 568–576.

Forestry Commission, 2003. Inventory Report. National Inventory of Woodlands and Trees. Forestry Commission, Edinburgh.

Gardiner, B.A., Quine, C.P., 2000. Management of forests to reduce the risk of abiotic damage—a review with particular reference to the effects of strong winds. Forest Ecol. Manage. 135, 261–277.

Gertner, G.Z., Fang, S.F., Skovsgaard, J.P., 1999. A Bayesian approach for estimating the parameters of a forest process model based on long-term growth data. Ecol. Model. 119, 249–265.

Hart, S.C., Nason, G.E., Myrold, D.D., Perry, D.A., 1994. Dynamics of gross nitrogen transformation in an old-growth forest: the carbon connection. Ecology 74, 880–891.

Hirsch, A.I., Little, W.S., Houghton, R.A., Scott, N.A., White, J.D., 2004. The net carbon flux due to deforestation and forest re-growth in the Brazilian Amazon: analysis using a process-based model. Global Change Biol. 10, 908–924.

Hulme, M., Mitchell, J., Ingram, W., Lowe, J., Johns, T., New, M., Viner, D., 1999. Climate change scenarios for global impacts studies. Global Environ. Change 9, S3–S19.

Hyvönen, R., Olsson, B.A., Lundkvist, H., Staaf, H., 2000. Decomposition and nutrient release from *Picea abies* (L.) Karst. and *Pinus sylvestris* L. logging residues. Forest Ecol. Manage. 126, 97–112.

Ingacio Rangel-Castro, J., Danell, E., Taylor, A.F.S., 2002. Use of different nitrogen sources by the edible ectomycorrhizal mushroom Cantharellus cibarius. Mycorrhiza 12, 131–137.

Jalkanen, R., Aalto, T.O., 1994. Needle retention and needle loss of Scot spine in recent decades at Thefort and Alice Holt, England. Can. J. Forest Res. 24, 862–867.

Janssens, I.A., Sampson, D.A., Curiel-Yuste, J., Carrara, A., Ceulemans, R., 2002. The carbon cost of fine root turnover in a Scots pine forest. Forest Ecol. Manage. 168, 231–240.

Johnsen, K.H., Samuelson, L., Teskey, R., McNulty, S., Fox, T., 2001. Process models as tools in forestry research and management. Forest Sci. 47, 2–8.

Kätterer, T., Andrén, O., 1999. Long-term agricultural field experiments in Northern Europe: analysis of the influence of management on soil carbon stocks using the ICBM model. Agr. Ecosyst. Environ. 72, 165–179.

Kätterer, T., Andrén, O., 2001. The ICBM family of analytical solved models of soil carbon, nitrogen and microbial biomass dynamics description and application examples. Ecol. Model. 136, 191–207.

Korakaki, E., 2003. Structural and hydraulic properties of Scots pine (*Pinus sylvestris* L.) branches in a chronosequence. M.Sc. Thesis. University of Edinburgh, Edinburgh.

Krankina, O.N., Harmon, M.E., Griazkin, A.V., 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. Can. J. Forest Res. 29, 20–32.

Ladanai, S., Ågren, G.I., 2004. Temperature sensitivity of nitrogen productivity for Scots pine and Norway spruce. Trees-Struct. Funct. 18, 312–319.

Laiho, O., Prescott, C.E., 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can. J. Forest Res. 34, 762–777.

Landsberg, J.J., 1986. Physiological Ecology of Forest Production. Academic Press, Sidney.

Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecol. Manage. 95, 209–228.

Landsberg, J.J., Johnsen, K.H., Albaugh, T.J., Allen, H.L., McKeand, S.E., 2001. Applying 3-PG, a simple process-based model designed to produce practical results, to data from Loblolly Pine experiments. Forest Sci. 41, 43–51.

Landsberg, J.J., Waring, R.H., Coops, N.C., 2003. Performance of the forest productivity model 3-PG applied to a wide range of forest types. Forest Ecol. Manage. 172, 199–214.

Landsberg, J.J., Mäkelä, A., Sievänen, R., Kukkola, M., 2005. Analysis of biomass accumulation and stem size distributions over long period in managed stands of *Pinus sylvestris* in Finland using the 3-PG model. Tree Physiol. 25, 781–792.

Law, B.E., Waring, R.H., Anthoni, P.M., Aber, J.D., 2000. Measurements of gross and net ecosystem productivity and water vapour exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. Global Change Biol. 6, 155–168.

Magnani, F., Mencuccini, M., Grace, J., 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. Plant Cell Environ. 23, 251–263.

Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S., Grelle, A., Hari, P., Jarvis, P.G., Kolari, P., Kowalski, A.S., Lankreijer, H., Law, B.E., Lindroth, A., Loustau, D., Manca, G., Moncrieff, J.B., Rayment, M., Tedeschi, V., Valentini, R., Grace, J., 2007. The human footprint in the carbon cycle of temperate and boreal forests. Nature 447, 848–850.

Mason, W.L., Hampson, A., Edwards, C., 2004. Managing the Pinewoods of Scotland. Forestry Commission, Edinburgh.

Mäkelä, A., Vanninen, P., 2000. Estimation of fine root mortality and growth from simple measurements: a method based on system dynamics. Trees-Struct. Funct. 14, 316–323.

Mäkelä, A., 2003. Process-based modelling of tree and stand growth: towards a hierarchical treatment of multiscale processes. Can. J. Forest Res. 33, 398–409.

McMurtrie, R.E., Leuning, R., Thompson, W.A., Wheeler, A.M., 1992. A model of canopy photosynthesis and water-use incorporating a mechanistic formulation of leaf CO_2 exchange. Forest Ecol. Manage. 52, 261–278.

Mencuccini, M., 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. Plant Cell Environ. 26, 163–182.

Mencuccini, M., Grace, J., 1996. Hydraulic conductance, light interception and needle nutrient concentration in Scots pine stands and their relations with net primary productivity. Tree Physiol. 16, 459–468.

Mencuccini, M., Bonosi, L., 2001. Leaf/sapwood area ratios in Scots pine show acclimation across Europe. Can. J. Forest Res. 31, 442–456.

Nikolov, N., Zeller, K.F., 1992. A solar radiation algorithm for ecosystem dynamic models. Ecol. Model. 61, 149–168.

Öhlund, J., Näsholm, T., 2004. Regulation of organic and inorganic nitrogen uptake in Scots pine (*Pinus sylvestris*) seedlings. Tree Physiol. 24, 1397–1402.

Oleksyn, J., Reich, P.B., Chalupka, W., Tjoelker, M.G., 1999. Differential above- and below-ground biomass accumulation of European *Pinus sylvestris* populations in a 12-year-old provenance experiment. Scand. J. Forest Res. 14, 7–17.

Oleksyn, J., Reich, P.B., Zytkowiak, R., Karolewski, P., Tjoelker, M.G., 2003. Nutrient conservation increases with latitude of origin in European *Pinus sylvestris* populations. Oecologia 136, 220–235.

Ovington, J.D., 1957. Dry-matter production by *Pinus sylvestris* L. Ann. Bot. 82, 287–313.

Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J.C., Seastedt, T., Moya, E.G., Kamnalrut, A., Kinyamario, J.I., 1993. Observations and modeling of biomass and soil organic-matter dynamics for the grassland biome worldwide. Global Biogeochem. Cy. 7, 785–809.

Patenaude, G.L., Milne, R., Van Oijen, M., Dawson, T.P., 2008. Integrating remote sensing datasets into ecological modelling: a Bayesian approach. Int. J. Remote Sens 29, 1295–1315.

Paul, K.I., Polglase, P.J., 2004. Prediction of decomposition of litter under eucalypts and pines using the FullCAM model. Forest Ecol. Manage. 191, 73–92.

Paul, K.I., Polglase, P.J., Richards, G.P., 2003. Sensitivity analysis of predicted change in soil carbon following afforestation. Ecol. Model. 164, 137–152.

Paul, K.I., Booth, T.H., Jovanovic, T., Sands, P.J., Morris, J., 2007. Calibration of the forest growth model 3-PG to eucalypt plantation growing low rainfall regions in Australia. Forest Ecol. Manage. 243, 237–247.

Peltoniemi, M., Mäkipää, R., Liski, J., Tamminen, P., 2004. Changes in soil carbon with stand age—an evaluation of a modelling method with empirical data. Global Change Biol. 10, 2078–2091.

Peng, C.H., Liu, J., Dang, Q.L., Apps, M., Jiang, H., 2002. TRIPLEX: a generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. Ecol. Model. 153, 109–130.

Pyatt, D.G., Ray, D., Fletcher, J., 2001. An Ecological Site Classification for Forestry in Great Britain. Forestry Commission, Edinburgh.

Radtke, P.J., Burk, T.E., Bolstad, P.V., 2002. Bayesian melding of a forest ecosystem model with correlated inputs. Forest Sci. 48, 701–711.

Reckhow, K.H., 1990. Bayesian inference in non-replicated ecological studies. Ecology 71, 2053–2059.

Robert, C., Casella, G., 2004. Monte Carlo Statistical Methods. Springer, London.

Running, S.W., Gower, S.T., 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications. 2. Dynamic carbon allocation and nitrogen budgets. Tree Physiol. 9, 147–160.

Sands, P.J., Landsberg, J.J., 2002. Parameterisation of 3-PG for plantation grown Eucalyptus globules. Forest Ecol. Manage. 163, 273–292.

Schoettle, A.W., Fahey, T.J., 1994. Foliage and fine root longevity of pines. Ecol. Bull. 43, 136–153.

Seidl, R., Lexer, M.J., Jäger, D., Hönninger, K., 2005. Evaluating the accuracy and generality of a hybrid patch model. Tree Physiol. 25, 939–951.

Stape, J.L., Ryan, M.G., Binkley, D., 2004. Testing the utility of the 3-PG model for growth of *Eucalyptus grandis* × *urophylla* with natural and manipulated supplies of water and nutrients. Forest Ecol. Manage. 193, 219–234.

Svensson, M., Jansson, P.E., Gustafsson, D., Kleja, D.B., Langvall, O., Lindroth, A., 2008. Bayesian calibration of a model describing carbon, water and heat fluxes for a Swedish boreal forest stand. Ecol. Model. 213, 331–344.

Tickle, P.K., Coops, N.C., Hafner, S.D., 2001. Comparison of a forest process model (3-PG) with growth and yield models to predict productivity at Bago State Forest, NSW. Australian For. 64, 111–122.

Titus, B.D., Malcolm, D.C., 1999. The long-term decomposition of Sitka spruce needles in brash. Forestry 72, 207–221.

Van Oijen, M., Rougier, J., Smith, R., 2005. Bayesian calibration of process-based forest models: bridging the gap between models and data. Tree Physiol. 25, 915–927.

Vanninen, P., Mäkelä, A., 2005. Carbon budget for Scots pine trees: effects of size, competition and site fertility on growth allocation and production. Tree Physiol. 25, 17–30.

Vanninen, P., Ylitalo, H., Sievänen, R., Mäkelä, A., 1996. Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L). Trees-Struct. Funct. 10, 231–238.

Vestgarden, L.S., Nilsen, P., Abrahamsen, G., 2004. Nitrogen cycling in *Pinus sylvestris* stands exposed to different nitrogen inputs. Scand. J. Forest Res. 19, 38–47.

Vollbrecht, P., Kasemir, H.I., 1992. Effects of exogenously supplied ammonium on root development of Scots pine (*Pinus sylvestris* L.) seedlings. Botan. Acta 105, 306–312.

Waring, R.H., 2000. A process model analysis of environmental limitations on the growth of Sitka spruce plantations in Great Britain. Forestry 73, 65–79.

Waring, R.H., Landsberg, J.J., Williams, M., 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Physiol. 18, 129–134.

Waring, R.H., McDowell, N., 2002. Use of a physiological process model with forestry yield tables to set limits on annual carbon balance. Tree Physiol. 22, 179–188.

Westoby, M., 1984. The self-thinning rule. Adv. Ecol. Res. 14, 167–225.

White, J.D., Coops, N.C., Scott, N.A., 2000. Estimates of New Zealand forest and scrub biomass from the 3-PG model. Ecol. Model. 131, 175–190.

Whitehead, D., Hall, G.M.J., Walcroft, A.S., Brown, K.J., Landsberg, J.J., Tissue, D.T., Turnbull, M.H., Griffin, K.L., Schuster, W.S.F., Carswell, F.E., Trotter, C.M., James, I.L., Norton, D.A., 2002. Analysis of the growth of rimu (Dacrydium cupressinum) in south westland, New Zealand, using process-based simulation models. Int. J. Biometerol. 46, 66–75.

Xiao, C.W., Yuste, J.C., Janssens, I.A., Roskams, P., Nachtergale, L., Carrara, A., Sanchez, B.Y., Ceulemans, R., 2003. Above- and belowground biomass and net primary production in a 73-year-old Scots pine forest. Tree Physiol. 23, 505–516.

Zianis, D., Mencuccini, M., 2005. Aboveground net primary productivity of a beech (*Fagus moesiaca*) forest: a case study of Naousa forest, northern Greece. Tree Physiol. 25, 713–722.