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Analysis of carbon and water fluxes from the NOPEX boreal forest: comparison of measurements with FOREST-BGC simulations

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Abstract

The ecosystem process model, FOREST-BGC, was applied on a stand in the NOPEX region in central Sweden. It was compared with measured data of net ecosystem carbon flux (F_n) and transpiration (E_0) on a daily basis. Using the parameterized model, yearly budgets of carbon and water were constructed. F_n was obtained from eddy correlation measurements on a tower at heights of 35 and 100 m. E_0 was obtained from sap flow measurements using a heat balance method. The model predictions were generally good, considering the relatively low requirements for input parameters. The explained variability of E_0 was high (95%), particularly relative to the presence of large water deficit conditions on the site. The explained variability of F_n was lower: it was 50% and 66% when compared to the measurements at 35 and 100 m, respectively. These results reflect the large spatial variability of F_n and the quantitative differences of measured F_n at the two heights over a patchy forest consisting of small stands of different age, density and pine/spruce composition (the validation was made prior to a detailed footprint analysis). The model performed differently for various periods during a year, which demonstrates the value of long-term measurements for model validations. The simulated yearly net carbon ecosystem uptake for the 50-year-old stand with a high leaf area index was 1.99 t ha⁻¹, with a range of 0.55–2.04 t ha⁻¹ for leaf area index of 3–6 observed at the NOPEX site. The model analysis of controls for mass fluxes showed that soil water shortage was the main limiting factor on the NOPEX site in the year studied. The comparative model run for the northern BOREAS site in central Canada indicated that a high atmospheric drought and plant resistance to water flow frequently limited fluxes there. A more maritime climate of NOPEX site permits a larger gross production; however, larger respiration and decomposition rates reduce the quantitative differences of net ecosystem carbon uptake relative to the BOREAS site with a continental climate. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

Boreal forests play an important role in the global hydrological and biogeochemical cycles (Thomas and Rowntree, 1992), but changes in controls in fluxes of water, heat and carbon in boreal areas are not well known. Therefore, two major projects have recently been initiated in boreal forest zones: BOREAS (The Boreal Ecosystem Atmosphere Study; Sellers et al., 1995), targeting the continental interior of Canada, and NOPEX (The Northern

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Hemisphere Climate-Processes Land-Surface Experiment; Lundin and Halldin, 1994a, 1994b), located in the southern Scandinavian boreal zone in central Sweden. It is expected that the greatest amounts and effects of global warming due to increased CO₂ concentration will occur at higher latitudes, dominated by boreal forests (e.g., Schlesinger and Mitchell, 1987). There is also evidence that a large terrestrial carbon sink exists in mid-latitudes of the northern hemisphere (Tans et al., 1990; Ciais et al., 1995; Denning et al., 1995). This could help to close the global carbon budget, with a currently estimated "missing" sink of about 1.4 Gt C year⁻¹ (Schimel, 1995). Global warming is likely to shift present biome boundaries, which will have considerable socio-economic effects and climate feedbacks (Bonan et al., 1992; Amthor, 1995). Hence, similarly to BOREAS, the ultimate goal of NOPEX is to increase our understanding of the effects of climate change on boreal forests. This is to be achieved. among others, by providing parameterization schemes of exchange of water, carbon and energy between land and atmosphere using models operating on different spatial scales (Lundin and Halldin, 1994a, 1994b). Modelling is the main scientific tool to provide predictions of anticipated changes. Prior to solving the global issues, a sound parameterization of processes on local scales must be accomplished. Properly tested and parameterized process models provide a basis to attack methods of aggregation and dissagregation of parameters among the different spatial scales, and provide links between satellite, airborne and ground observations.

This paper is an application of the ecosystem process model FOREST-BGC (Running and Coughlan, 1988; Running and Gower, 1991) on forests in the NOPEX region. The model was designed to integrate with surface climate and distribution of vegetation in order to map ecosystem processes over landscapes (see, for example, Ford et al., 1994). Much work in this direction has already been accomplished: FOREST-BGC and its generalized clone BIOME-BGC, applicable for a range of ecosystems, have already been implemented in systems for simulations on regional to global scales (see, for example, Running and Hunt, 1993). FOREST-BGC represents a reasonable generalization of ecological processes and minimizes requirements of site-specific data. It is particularly sensitive to leaf area index (LAI) as the most important single variable describing the vegetation cover that can be estimated by satellite sensors over large areas (Running and Gower, 1991). In its spatial representation, FOREST-BGC represents a point model. Its validity over larger areas is determined by the homogeneity of the modelled ecosystem and its driving variables. For application to multiple landscape units, FOREST-BGC was linked with a terrain-sensitive generator of microclimate, MT-CLIM (Running et al., 1987), producing the Regional Ecological Simulation System (RESSys; Running et al., 1989). The system was also tested in combination with an advanced hydrological model for topographically-specific routing and deep water storage (Band et al., 1993; Ford et al., 1994; White and Running, 1994).

The sub-boreal and boreal forests in Scandinavia differ compared to those found on the American and Asian continents. They have been mostly managed in a planned way for up to hundreds of years and presently contain more woody biomass than ever before. There is generally more biomass, larger LAI and smaller specific leaf area in the intensively managed European forests as compared to the mostly natural sub-boreal and boreal forests in Russia and Canada. Therefore, this parameterization was a necessary step before using the model to provide regional estimates of fluxes in the NOPEX area. For global ecology issues, it is also vital to explore how representative is the NOPEX site of global boreal forest. Most of the forests in the boreal zone grow under a pronounced continental climate, whereas the NOPEX site is situated near the sea, with a more maritime climate and smaller temperature extremes. It is hence desirable to provide a comparative analysis of boreal stands growing under these contrasting climatic conditions.

The aim of this paper is to: (a) provide parameterization for coniferous forest in the NOPEX area; (b) explore the abilities of a simple ecosystem model to track the measured processes; (c) construct carbon and water budgets and give feasible predictions of the processes that were not measured or were not measurable; (d) analyse the carbon and water fluxes and their controls using the parameterized model on NOPEX and BOREAS sites to assess the effect of contrasting climate on boreal forest ecology.



Fig. 1. Climatic variables for the NOPEX site; also included is air temperature for the BOREAS site to demonstrate a more maritime NOPEX climate relative to a continental BOREAS climate. Top: 3-day mean values of short-wave radiation (R_g) and vapour pressure deficit (δe). Middle: 3-day mean of minimum and maximum daily air temperature (T_a) (solid and dashed line shading for NOPEX and BOREAS sites, respectively). Bottom: daily and cumulative values of precipitation (P, P_{cum}).

2. Materials and methods

2.1. Description of the region and measurement site

The NOPEX region is situated in the southern Swedish boreal forest zone. It is located about 50 km from the sea and in its southern part includes the town of Uppsala. The landscape of the region is topographically very flat, with clay soils and moraines dominating in the area. Most of the region is confined between 30 and 70 m above sea level. Forests occupy about 60% of the land cover. They consist mostly of coniferous tree species (85%): these are Scots pine (Pinus sylvestris, L.) and Norway spruce (Picea abies, L. Karst.). Deciduous tree species, representing only a small fraction of total forested area, occupy south-facing slopes in the southern part of the region. The main measurement site, with the stand used for parameterization, was situated in mature pine/spruce forest. It was a patchy mixture of mostly 25- to 110year-old stands with a mean height of 25 m, basal area of about $32 \text{ m}^2 \text{ ha}^{-1}$ and LAI (projected) varying between 3 and 6. The site was chosen carefully using both land and airborne observations to represent a typical forested area of the region and to comply with requirements for maximum available homogeneity for tower (100 m high) flux measurements.

Climate is influenced by the sea and can be characterized as more maritime, with less pronounced temperature extremes than in other boreal regions (Fig. 1). Mean annual air temperature is about 5.5 (5.4)°C, mean annual precipitation about 550 (460) mm; values in parentheses are for the year 1994, when the measurements of validation data were performed. Seasonal courses of climatic variables for the year 1994 are shown in Fig. 1.

2.2. Validation data

2.2.1. Canopy transpiration

Canopy transpiration (E_Q) was obtained on the basis of sap flow measurements. The trunk–tissue heat balance method (Cermak et al., 1973; Kucera et al., 1977) was used by applying standard equipment from Ecological Measuring Systems (EMS, Brno, Czech Republic) on 12 trees (24 channels) in the studied stand. Sampling strategy, scaling and actual measurements have been described elsewhere (Cermak et al., 1995). The stand where the measurements were performed was fairly typical of the region. It was a medium-age (50-year-old) stand falling between the usual rotation period of 100-120 years. Its height was 24 m and basal area 29.3 m^2 , with a pine and spruce share of 67% and 32%, respectively. Transpiration was previously compared to water vapour flux measured by an eddy correlation system on the tower: for dry cases, there was a tight relationship, both qualitatively and quantitatively (Cienciala et al., 1997). Due to the high LAI of the stand (4.5-5.0; projected), evaporation from the sparse ground vegetation was considered negligible. Available data covered most of the growth season in 1994.

2.2.2. Canopy conductance

Canopy conductance (g_c) was obtained by rearranging the Penman (1953) combination equation in the form given by Monteith (1965) with a known transpiration term (E_0) and unknown canopy conductance term (e.g., Cienciala et al., 1992; Bréda et al., 1993; Granier and Loustau, 1994). The length of the light period involved in the computation was reduced by a factor of 0.85 in order to comply with the logic of the FOREST-BGC model, which uses this reduction to represent an "effective day length". Note that g_c estimated this way does not involve any fluxes of understory vegetation and evaporation of dew on the surface. For the study site, the maximum values of g_c and those of the ecosystem surface conductance may be expected to differ by less than 10% (Schulze et al., 1994). The radiation term in the Penman-Monteith equation was represented by net radiation absorbed by the canopy following Beer's law. Due to a high LAI, the canopy received more than 95% of the net radiation incoming above the canopy.

2.2.3. Ecosystem carbon flux and evapotranspiration

The fluxes of CO_2 and evapotranspiration were measured by an eddy correlation system on a tower at heights of 35 and 100 m. The system consisted of a sonic anemometer (Solent) and an infrared gas analyser (LI-COR LI-6262), which measured the components with a frequency of 10 Hz (Grelle and Lindroth, 1994, 1996). The tower was located about 600 m from the chosen 50-year-old reference stand. Available CO_2 data included the period from June to December 1994. The CO_2 data were expressed in weight units of carbon per hectare as the net ecosystem carbon flux (F_n) .

2.2.4. Stem, root and foliage carbon and increment

Marklund (1988) biomass functions were used to obtain dry mass for tree components. These functions relate tree diameter over bark, height and other parameters to dry weight of various tree components. The input data for the functions were inventory data of the 50-year-old stand measured at the beginning of the growth season. As FOREST-BGC distinguishes only three compartments, the mass of stump and living branches without foliage was added into the pool of the stem. A fraction of 48% was used to convert dry weight biomass into carbon.

Stem diameter increment was measured using dendrometer bands made of a thin metal sheet. They were placed at a height of about 1.5-2 m on the trees where sap flow was measured. The increment of basal area was used to calculate the total carbon stand allocation for the period of 10 May to 12 October, using the functions of Marklund (1988). This carbon pool estimate served as an additional constraint for building the carbon budget by the model.

2.3. Model description

Briefly, FOREST-BGC (Running and Coughlan, 1988; Running and Gower, 1991) is a process model which estimates cycling of water, carbon and nitrogen through a forest ecosystem. It requires data of daily microclimatic conditions: minimum and maximum air temperature, relative humidity (or dew point), incident solar radiation and precipitation. It also requires some key site and vegetation variables for initialization. For the water cycle, FOREST-BGC calculates transpiration, interception and evaporation from the canopy, soil water content, snowmelt and outflow from the soil. For carbon cycles, the model calculates photosynthesis, growth respiration, maintenance respiration, allocation, litterfall and decomposition. Finally, nitrogen cycling is represented by deposition, uptake, litterfall and mineralization. FOREST-BGC has a dual time step, where water and most carbon variables are calculated on a daily basis, whereas



Fig. 2. A compartment flow diagram of FOREST-BGC, showing the daily and yearly components of the model (Running and Coughlan, 1988). Compartments include symbols for the concerned elements of water (H₂O), carbon (C) and nitrogen (N).

nitrogen and some carbon variables are calculated yearly (Fig. 2).

function:

2.4. Changes made to the default version of the FOREST-BGC model

There were few changes made to the default version of the model (Running and Coughlan, 1988; Running and Gower, 1991). Three changes were made in the form of canopy and mesophyll conductances (g_c and g_m , respectively). Firstly, the original scalar function of absolute humidity deficit was replaced by a new scalar function of vapour pressure deficit ($f_{gc}(\delta e)$) in the form:

$$f_{\rm gc}(\delta e) = \exp(-B24 \cdot \delta e), \tag{1}$$

where *B*24 (kPa⁻¹) is a parameter specifying the slope of the function and δe (kPa) is vapour pressure deficit.

Secondly, the symmetric parabolic scalar function of air temperature was replaced by an asymmetric

$$f_{\rm gm}(T_{\rm a}) = \frac{T_{\rm a} - B17}{B22 - B17} \bigg[B18 - \frac{T_{\rm a}}{B18 - B22} \bigg]^{\frac{B18 - B22}{B22 - B17}},$$
(2)

where T_a is air/leaf temperature, and *B*17, *B*18 and *B*22 are parameters specifying minimum, maximum and optimum temperature (°C) for photosynthesis, respectively (e.g., Jarvis, 1976; Massman and Kaufmann, 1991; Bonan, 1991).

Thirdly, a parameter (*B*50) was added to reduce g_c for wet conditions (default value 0.8), which may be understood as a factor expressing the reduction of the free surface for stomatal gas exchange due to the intercepted water on the foliage.

Finally, a constant of 0.2 involved in the computation of pre-dawn leaf water potential (ψ_p) in Running and Coughlan (1988) was altered to 0.3, which mimics a relatively smaller proportion of sand in the soil by shifting the relation of ψ_p to the actual soil water content. Table 1

Initial state variables and parameters for FOREST-BGC runs for medium-aged coniferous stand at the NOPEX site. The values altered from the default FOREST-BGC version are identified by bold face. The values altered from the default FOREST-BGC version are identified by bold face.

Code	Value	Description	Unit	
State variab	les			
X1	5.0	Snowpack	m ³	
X2	800.0	Soil water content	m ³	
X3	0.0	Water outflow	m ³	
<i>X</i> 4	0.0	Transpiration	m ³	
X5	0.0	Evaporation	m ³	
X6	0.0	PSN	kg	
X7	0.0	Respiration, autotrophic	kg	
X8	5.93E + 3	Leaf carbon	kg	
X9	64.6E + 3	Stem carbon	kg	
X10	13.8E + 3	Root carbon	kg	
X11	9.0E + 3	Leaf/root litter carbon	kg	
X12	000	Respiration decomp., C	kg	
X13	40.0E + 3	Soil carbon	kg	
X14	50.0	Available nitrogen	kg	
X15	89	Leaf nitrogen (1.5% of X8)	kg	
X16	64.6	Stem nitrogen (1% of X9)	kg	
X17	104	Root nitrogen $(0.75\% \text{ of } X10)$	kg	
X18	900.0	Leaf/root litter nitrogen (1% of X11)	kg	
X19	3000	Soil nitrogen	kg	
X20	000	Nitrogen loss	kg	
Parameter v	ariables			
<i>B</i> 1	19.0	Specific leaf area	$m^2 kg^{-1} C$	
<i>B</i> 2	- 0.5	Canopy light extinction coefficient		
B3	1800	Soil water capacity	m^3	
<i>B</i> 4	0.00025	Interception coefficient	m LAI^{-1} day ⁻¹	
B5	1.0E4	Ground surface area	$m^2 ha^{-1}$	
<i>B</i> 6	0.0007	Snowmelt coefficient	$m \circ C^{-1} day^{-1}$	
<i>B</i> 7	60	Latitude	0	
<i>B</i> 8	0.92	One-surface albedo*		
B9	0.5	Spring min. leaf water potential	MPa	
B10	4500	Rad. red. LC threshold	kJ m ^{-2} day ^{-1}	
B11	0.0011	Max. canopy ave. LC	$\mathrm{m \ s}^{-1}$	
B12	2.00	LWP at stomatal closure	MPa	
B13	0.5	Slope of g_c reduction by δe	kPa ⁻¹	
B14	432	PSN light comp. PT	kJ m ^{-2} day ^{-1}	
B15	9720	PSN I	kJ m ^{-2} day ^{-1}	
B16	0.00055	Max. $LC(CO_2)$	$m s^{-1}$	
B17	- 5	Min. temp. PSN	°C	
B18	40	Max. temp. PSN	°C	
B19	0.00015	Leaf respiration coefficient		
<i>B</i> 20	0.0020	Stem respiration coefficient		
B21	0.0002	Root respiration coefficient		
B22	12	Optimum temp. PSN	с	
B23	0.7	Temp. effect mesophyll cond.		
5.9.4		adjustment coefficient		
B24				
B25	0.085	$Q_{10} = 2.3$, constant for exponential respiration surface		

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Code	Value	Description	Unit	
B26	0.044	Maximum canopy ave. leaf		
		nitrogen conc., $\% \times 2.2$ C/CH ₂ O		
B27	0.0132	Minimum canopy ave. leaf		
		nitrogen conc.		
B28	0.50	Max. leaf nitrogen		
		retranslocation fraction		
B29	1.0	Soil water decomp. rate factor		
		(0-1)		
B30	0.5	N/C decomp. release fraction		
B31	15.0	Maximum leaf area index, all		
		sides		
B32	4.0	Leaf turnover rate	year	
B33	0.25	Leaf lignin fraction	%/100	
B34	0			
B35	1.0	Nitrogen avail. leaf/root		
		allocation factor		
B36	0	Date of spring leaf growth	year/day	
B37	365	Date of fall leaf drop	year/day	
B38	20.0	Mobile N retention time	year	
B39	5.0	Atmospheric deposition N	kg ha ⁻¹ year ⁻¹	
B40	0.0	Biological fixation N	kg ha ^{-1} year ^{-1}	
B41	0.02	Stem turnover coefficient		
B42	0.80	Root turnover coefficient		
B43	0.35	Leaf growth resp.		
B44	0.30	Stem growth resp.		
B45	0.35	Root growth resp.		
B46	50.0	Decomposition temperature	°C	
		optimum		
B47	0.03	Soil/litter C decomp. fraction		
B48	0.4	Decomposition rate, scalar		
B49	0.0			
B50	0.8	Reduction of g_c for rainy days		

2.5. Model parameterization and runs

The model was applied for the entire year of 1994. Daily outputs were regressed to their corresponding measured values, and both slope and coefficient of determination were used to assess the correctness of the altered parameters in the model. This way, the site parameters, which were estimated with a large error or variability, or which were not directly measured, were modified. The final parameterization is itemized in Table 1, with parameters changed from standard FOREST-BGC values identified.

In the water budget, the modified parameters included: soil water capacity, interception coefficient, maximum g_c , parameter for reduction of g_c by vapour pressure deficit term, leaf water potential at stomatal

closure and the reduction parameter for g_c under wet conditions. The estimation of soil water holding capacity (SWC) may vary because of uncertain volume of soil penetrated by roots. The estimate of 1000– 1500 m³ accessible water (Jansson, P.-E., personal communication) was used as the initial boundaries. As discussed by Running (1994), SWC is by far the most difficult important parameter to be defined in the model. Defining a correct value of SWC remains a problem for all range of different models solving the water balance. In FOREST-BGC, SWC also influences the daily uptake rate, because SWC defines together with actual water content (AWC)—the average daily canopy water potential. This makes the assessment of SWC crucial to correctly simulate



Fig. 3. Measured (filled symbols) and simulated (solid line) values of canopy transpiration (E_Q) and canopy conductance (g_c) during the growth season.

both daily fluxes and yearly budget of water. We have finally put SWC equal to 180 mm, which permitted large enough variations in AWC to reproduce the seasonal extremes in the water budget.

The interception coefficient was adjusted according to previous experience with a SVAT-model SPAC with an hourly/minute temporal resolution (Eckersten, 1991a, 1991b; Cienciala et al., 1994). Similarly, the introduction of the reduction parameter B50 for $g_{\rm c}$ during wet conditions was based on the above investigations and the default value was found in analysis of variation between measured and modelled canopy conductance (g_c) . The default value of the maximum $g_{\rm c}$ given in Running and Coughlan (1988) for Douglas fir in temperate forests was changed to represent boreal forests. The curvilinear reduction of g_c by vapour pressure deficit was implemented on the basis of previous findings from other Swedish coniferous forests (Lindroth, 1985; Bringfelt and Lindroth, 1987; Cienciala et al., 1992) and elsewhere (e.g., Granier and Loustau, 1994).

In the carbon budget, most of the default literature parameters related to photosynthesis were preserved (Running and Coughlan, 1988). Some parameters, however, remained uncertain, e.g., the respiration coefficients and factors determining the rate of decomposition, and these should be validated by complimentary measurements. The temperature parameters involved in Eq. (2) were set similarly as used in Bonan (1991). The maximum mesophyll conductance (g_m) was derived using the relation of g_c to g_m as applied previously by Running and Coughlan (1988) after Jarvis (1981). Note that, during the year, the ratio of conductances varies depending on actual meteorological and site conditions.

The construction of the carbon budget was based upon the comparison of measured and modelled daily values of ecosystem net carbon flux (F_n) . F_n is given as net photosynthesis minus plant maintenance and construction respiration and decomposition. FOREST-BGC subtracts the construction respiration only at the end of a yearly iteration. Therefore, for model calculation of F_n on a daily basis, we subtracted a 20% fraction of the net carbon fixation, representing the construction respiration (Ryan, 1991). Additionally, an estimate of the net carbon allocation calculated on the basis of stem increment for the period of 10 May to 12 October served as an independent constraint for the modelled carbon fluxes.

2.6. Reference data from the BOREAS site

Some comparative runs were made using the climatic variables from the BOREAS (Sellers et al., 1995) northern old jack pine (OJP) site. The runs were made using the parameterization scheme from the NOPEX site, but with changed pools of carbon to represent the local BOREAS stand. These new input parameters were leaf and stem carbon values of 1.88 and $23.6 \text{ th} a^{-1}$, respectively; the latter value also contains branch carbon (Gower, S.T., unpublished

results). The remaining pools of root and leaf/litter carbon were derived so as to correspond to the ratio of carbon pools from the NOPEX site. Specific leaf area was set to $24 \text{ m}^2 \text{ kg}^{-1} \text{ C}$, which was given by the known LAI (2.0) and leaf carbon. Foliar nitrogen concentration was set as 0.84% (Gower, S.T., unpublished results). Soil water content and soil water capacity were not changed. Finally, a latitude value of 56° was used. The climatic variables were taken from the tower measurements at the OJP site in 1994 (BOREAS project database).

3. Results and discussion

3.1. Water budget

The daily values of measured transpiration (E_Q) were largely explained by the model, for both the variation and quantitative agreement ($r^2 = 0.95$, slope of the regression = 0.92, P < 001; Fig. 3Fig. 4). Canopy conductance (g_c) was predicted with a larger variation, with some values being somewhat overestimated ($r^2 = 59\%$, slope of the regression = 0.79, P < 0.001; Figs. 3 and 5), especially for the wet cases and for the days with a low evaporative demand.

Since the seasonal run contains all the variety of weather conditions and a large summer soil water deficit, the overall good correlation of the modelled and measured transpiration gives credibility to both the model philosophy and to the consistency of sap flow measurements: the basis of E_0 . However,



Fig. 4. Scatter of daily measured and modelled values of transpiration (E_0) .

attention must be paid to the quantitative estimations. The error in estimation of E_Q from sap flow measurements with given sampling density may be expected to be about 10–15% and up to 15–20% during conditions of water deficit (Cermak et al., 1995). Also, local variations in soil water storage increase the uncertainty of flux estimations. Since the year 1994 was dry relative to the long-term average, a large soil water deficit developed on the site (Cienciala et al., 1997). Therefore, the parameterization scheme of the model should also be tested on a hydrologically contrasting year to gain confidence in quantitative estimations.

Interestingly, the prediction of g_c by the model was less good relative to the successful simulation of E_Q . Parameterization and validation of g_c is a crucial task for correct predictions of water and carbon fluxes by models. This is valid especially for a coniferous ecosystem, where the stomatal control over exerted water is large (e.g., Jarvis and McNaughton, 1986). It was obvious that the simulated g_c departed mostly for wet conditions, i.e. for the days with high relative humidity and moisture on the foliage. For those days, vapour pressure deficit was low and thus the occasional over-prediction of g_c was not pronounced in the calculation of transpiration, which remained low.

The default value of maximum g_c was reduced from 1.6 to 1.1 mm s⁻¹. This is similar to the conclusion of Running (1994), who applied FOREST-BGC on forests across a climatic gradient in Oregon. Running



Fig. 5. Scatter of daily "measured" and modelled values of canopy conductance (g_c) ; the regression is shown (solid line).

(1994) explained that, primarily, the age of the trees and decreased hydraulic conductance might be the reason for lower g_c values. This also corresponds to the previous observations from this site, when two stands with a different age were compared (Cienciala et al., 1997). There is a considerable uncertainty in these estimations of g_c , which are scaled to canopy from chamber or porometer measurements: as demonstrated by Leverenz et al. (1982), extrapolation of stomatal conductance even to the nearest hierarchical level (tree) is practically impossible. The same is valid for estimations on the basis of cuvettes for gas exchange: outputs from small chambers must be scaled, whereas big whole-tree chambers considerably alter the natural microclimate (e.g., Denmead et al., 1993). A more appropriate approach to obtain conductance data is to rearrange the Penman-Monteith equation and estimate g_c using either known evapotranspiration (e.g., Lindroth and Halldin, 1986; also see Kelliher et al., 1995, for summary of field studies) or transpiration flux density (e.g., Cienciala et al., 1992, 1994; Bréda et al., 1993; Granier and Loustau, 1994). This yields either total surface or canopy conductance. The latter has the advantage of being directly related to the main canopy and data are not limited to dry cases, as was the case here. The relations between maximum stomatal, canopy and surface conductance have recently been summarized by Schulze et al. (1994) and Kelliher et al. (1995). Though g_c is usually estimated with a relatively large scatter, it is a good basis for parameterization of approximate functions.

The new scalar function of vapour pressure deficit $(f_{gc}(\delta e); \text{ Eq. (1)})$ improved the prediction of g_c by about 8–13%. This range was given by either concurrently re-adjusting other parameters in the water budget or by a run with unchanged parameters but a former $f_{gc}(\delta e)$ function. The introduced parameter *B*50, which reduces g_c during wet conditions (reflecting the reduction of free foliage surface available for stomatal gas exchange due to the intercepted water) improved the model prediction of g_c by about 8%.

The model was sensitive to the altered parameters in the water budget part, i.e. to soil water capacity, interception coefficient, maximum g_c , parameter for reduction of g_c by vapour pressure deficit (δe) term, leaf water potential at stomatal closure and the reduction parameter for g_c under wet conditions. Their influence may be roughly demonstrated by the following example: decreasing the parameter value by only 10%, the explained variability of transpiration was reduced by each of them, except the interception coefficient. That influence was strongest for the slope parameter in $f_{gc}(\delta e)$ (Eq. 1) (- 1.0%) and maximum $g_{\rm c}$ (-0.8%), whereas the effects of the other tuned parameters were 0.5% or less. The 10% reduction of the interception coefficient did not decrease the correlation of the modelled and measured transpiration, but it reduced the slope parameter of the linear regression, indicating an over-prediction of transpiration relative to a default run. However, it must be understood that this example is a simplification of real conditions, with multiple and mutual effects of the particular variables and parameters.

Mean daily rates of transpiration and evapotranspiration for the period of the growth season (n =178 days from 21 April to 15 October) were 1.08 and 1.69 mm. These values are lower than those estimated for temperate forests (e.g., Roberts, 1983; Verma et al., 1986). Also, the preliminary results from the BOREAS sites reveal similarly low seasonal means (Sellers et al., 1995). The seasonal transpiration sum reached 207 mm with the given parameterization; evaporation and water outflow were 136 and 16 mm, respectively. These components balance the vearly sum of precipitation (456 mm) for 1994 with a surplus of 97 mm that was allocated into the soil water content term. These results support observations from the site during the installation of sap flow measurements: in spring 1994, soil was much drier as compared to the early spring of 1995, when there was standing water on several places within the site.

In the previous study from the site, the period of water shortage was shown to affect transpiration during practically the whole summer of 1994, and it was hypothesized that this effect may have been extended even during the spring months that year (Cienciala et al., 1997). The precipitation pattern during the growth season of the following year also contrasted sharply compared to that in 1994 (unpublished results). Although the NOPEX area is a humid region, it is evident that the production of the forest ecosystems is water limited there, because of an uneven annual and seasonal distribution of precipitation, with considerable dry spells during summer.



Fig. 6. Simulated flux of net ecosystem carbon flux in comparison with measured data from 35 and 100 m for six months of 1994 for which the validation data were available; the simulation is identical in both figures. Sensitivity runs for LAI values of 3-6 are shown by shading (top figure only).

3.2. Carbon budget

The simulated and measured daily values of the net carbon ecosystem flux (F_n) for the season are shown in Fig. 6. The two reference measurements of F_n at the two heights, 35 and 100 m, respectively, differed considerably. Overall, there was a closer relative relationship to the F_n measured at the height of 100 m ($r^2 = 0.66$, slope of the regression = 0.72; Fig. 7),



Fig. 7. Scatter of daily measured (at 35 and 100 m) and modelled values of net ecosystem carbon flux (F_n) ; the 1:1 line is shown.

whereas F_n from 35 m was captured by the model with a larger scatter ($r^2 = 0.50$, slope of the regression = 0.52). The model under-estimated F_n relative to the measurements for about 3 weeks in June-July, especially with respect to the measurements taken at 35 m. During the period of August to October, there was a close correspondence of model prediction and measurements, with $r^2 = 0.63$ and 0.72 for F_n measured at 35 and 100 m, respectively. During this period, the modelled values were mostly approximating the span between the two measured signals, and the quantitative correspondence was better relative to the measurements at 35 m (Eq. 6). At the end of the year-outside the period of the growth season in November and December-the model was generally over-predicting F_n relative to the measured values.

Apart from the uncertain period at the beginning of the eddy correlation measurements in June/July, the simulation of F_n for the rest of the growth period must be considered as satisfactory. The modelled F_n agreed with respect to both variation and slope relative to the measured fluxes: the slope parameter of the regression line was 1.24 and 0.79 for the F_n measured at 100 and 35 m, respectively. It can be expected that the correlation of simulated to measured values may increase when data are screened after a detailed flux footprint



Fig. 8. Components of the annual carbon budget simulated by FOREST-BGC. Top: courses of gross carbon assimilation (GPP), maintenance respiration (MR), decomposition (D) and net carbon flux into stand (F_n) 3-day mean values. Bottom: the composition of annual carbon budget with GPP, MR, growth respiration (GR), D and net accumulated carbon (Net C).

analysis. However, the model performance outside the growth period was less good: at that time, the importance of respiration functions increases dramatically. It also reveals a weak handling of decomposition in FOREST-BGC, which should be preferably parameterized by local data, if available (Running and Coughlan, 1988). The daily decomposition rate is principally derived from a total leaf and root litter carbon pool divided into a daily fraction by 365. Therefore, the daily decomposition rate is a likely source of error, contributing to a weaker correlation of daily modelled and measured F_n values. This is especially pronounced outside the growth period, but also during the growth season, when air/soil temperature is high and soil is wet.

The varying success of F_n predictions by FOREST-BGC for the different periods may also be attributed to the fact that the model does not distribute the assimilated carbohydrates into individual compartments on a daily basis. Therefore, it cannot track the changes associated with seasonal dynamics of specific leaf area (SLA), which may vary up to 40% between April and October in Swedish conditions (Ellis, J.F., personal communication). The dynamic allocation of carbon is provided only on a yearly basis in FOREST-BGC, but a new version of the model is being developed which unifies the dual time step of the model. Also, the LAI of conifers changes during the year as the foliage biomass becomes reduced during winter and spring. Since these data were not available, no attempt was made to redefine the LAI during the season as the model input. Obviously, a temperature-based routine for seasonal readjustment of LAI would additionally improve the prediction of both carbon and water fluxes.

The differences between the fluxes measured at the different heights above the forest demonstrate the difficulties in validating models for carbon fluxes. It must be understood that the measured data of CO_2 from the eddy correlation system cannot be an absolutely representative reference for validation. There was a large directional variability observed for CO_2 fluxes at the site. The measurements reflect the very patchy structure of the forest in the region, with many small stands of different age and density. The tower was placed about 600 m from the investigated stand. Therefore, the comparison of modelled and measured F_n must be considered as approximate and not conclusive prior to a detailed analysis of the flux footprint of the eddy correlation system.

However, the effect of varying canopy foliage density (patchiness of the forest in the area) may be roughly assessed by modelling F_n using a range of LAI values. LAI ranged from 3 to 6 for the stands in the area. The extent of F_n with limits given by model runs with LAI values of 3 and 6 could explain



Fig. 9. Seasonal course of simulated transpiration (E_Q ; A), canopy conductance (g_c ; B) and net carbon assimilation (F_n ; C) for control parameterization (control), decoupled limitation of g_c by vapour pressure deficit (δe) and unlimited soil water (SW), respectively. All values in A–C are means of five days. (D) Seasonal course of soil water content for the three scenarios above (daily values).

some of the discrepancy relative to the measured $F_{\rm n}$ (Fig. 6). For example, most of the measured values of $F_{\rm n}$ at 100 m would fit well into the modelled range in June. Later, the modelled range of F_n corresponds more closely with the measurements at 35 m. Note that there are several processes which partly compensate the differences in the modelled F_n for the different LAI values. Therefore, the effect of LAI on F_n is not straightforward. Firstly, there are differences in water use: under water-limiting conditions, the stand with lower LAI will benefit relative to that with higher LAI. Tree water status is linked to photosynthesis via g_c , and this narrows the differences in absolute values of F_n in the dry period of July and August. Secondly, a larger gross photosynthesis is accompanied by a larger respiration for a canopy with a higher LAI. Therefore, a larger LAI gives a larger F_n , particularly for high rates of photosynthesis, whereas for low rates of photosynthesis the LAI effect on F_n is small (Fig. 7).

The simulated seasonal courses of gross primary production, maintenance respiration, decomposition and ecosystem net carbon assimilation are shown in Fig. 8. The predicted yearly gross photosynthesis was $9.71 \text{ th} \text{ a}^{-1}$. With maintenance and growth respiration of 4.66 and 1.71 t ha⁻¹, respectively, and decomposition of 1.35 t ha⁻¹, the yearly F_n was 1.99 t ha⁻¹ (Fig. 8). The modelled range of yearly F_n , given by LAI values of 3 and 6 (see above), was $0.55-2.05 \text{ th} \text{ a}^{-1}$.

The carbon accumulation for a control period of 10 May to 12 October, for which total carbon accumulation was estimated on the basis of stem increments, was over-predicted by 13.6%. This is acceptable, considering that the stand was exposed to water deficit conditions for most of the growth season (Cienciala et al., 1997). Therefore, an estimate of net carbon flux based on stem increment may be biased due to preferential root growth (e.g., Rook et al., 1977; Schulze, 1986).

For yearly integrals, the respiratory losses (growth and maintenance) were high compared to the gross primary production (about 65%). For a temperate mixed deciduous forest, the ecosystem respiration was estimated as 67% of the gross ecosystem production and the annual net uptake was 3.7 t carbon per hectare (Wofsy et al., 1993). The mean value of carbon accumulation found for Polish forest ecosystems was similarly high (Galinski and Küppers, 1994). For young dense monospecific Norway spruce forest in southern Sweden, Nilsson (1993) reported a yearly accumulation of 4.7 t carbon per hectare. For boreal conifer ecosystems at Fairbanks, Alaska, the model estimations of Bonan (1991), 1993) ranged from 0.2 t ha^{-1} (unproductive Black spruce stands) to about 4.3 t ha⁻¹ (productive White spruce stands); the observations for the two forest types were 0.88 and 2.56 t ha⁻¹, respectively (Bonan, 1993). Relative to these examples, the above estimate of FOREST-BGC for forest in the NOPEX region seems to be realistic. However, to gain confidence in the annual carbon budget, more sensitivity analyses must be done on stands with different tree densities and age; particular attention must be paid to the decomposition and respiration processes, which should also be validated by independent measurements.

3.3. Model analysis of limitations to E_Q and F_n

Two major, frequent and naturally imposed limitations on mass fluxes are atmospheric and edaphic drought. The effects of atmospheric limitation (high vapour pressure deficit, δe) and hydro-edaphic limitation (soil water deficit) on E_0 and F_n can be illustrated by the following examples: if δe were not a limiting factor, i.e. had no effect on g_c , transpiration rate would increase considerably during the dry month of May, which would cause soil water storage to be depleted faster (Fig. 9). This way, the seasonal sum of E_0 would increase by only about 5%, whereas carbon accumulation would even decrease (-10%), because of the strong limitation of g_c during the productive part of the season in July and August. If soil water were not a limiting factor and were set at SWC, the annual sum of E_0 would increase by 40% and F_n would increase by 10%. Since, in reality, all the limiting factors interact, the partitioning of the joint effects among individual factors is not straightforward. For example, the changes in E_Q and F_n associated with decoupling the δe reduction of g_c were also in this case largely determined by a water shortage, because of the quicker discharge of soil water storage in the late spring (Fig. 9).

The observation of the sole effect of soil water deficit on E_Q was encouraging; in previous work from this site, the limitation of transpiration due to soil drought was assessed on the basis of a simplified canopy conductance parameterization (Cienciala et al., 1997). It was found to be at least one-fifth of the seasonal sum of E_Q . This fits well to the estimate by FOREST-BGC provided here, provided that the assumption of fully saturated soil at the site during the year is very likely exaggerated.

3.4. Comparison of NOPEX and BOREAS sites

It may be concluded that both atmospheric and hydro-edaphic limitation affect the flux rates in the NOPEX region. The preliminary results from BOREAS sites, however, indicate that a combination of plant resistance and atmospheric drought may be the major limiting factor for fluxes (Sellers et al., 1995). We have tested the parameterization scheme from the NOPEX site on the old jack pine (OJP) stand from the northern BOREAS site. The input parameters that were changed were those concerning the actual stand biomass and latitude. The simulated transpiration of the OJP stand was low: maximum daily transpiration reached only 1.5 mm and the yearly total was 137 mm. The simulated daily fluxes of F_n typically reached values of about 20 kg ha^{-1} in the summer. The simulated yearly net carbon uptake reached 0.82 t ha⁻¹.

The analysis of δe effect on E_Q and F_n was made as for the NOPEX site above, i.e. by decoupling the δe reduction of g_c in the model. If the trees were not limited by atmospheric drought, the modelled E_Q of the OJP stand would increase and occasionally reach daily values up to about 3 mm; the yearly sum would increase by 56% to 222 mm. At the same time, the net yearly carbon uptake would increase by 51% to 1.24 t ha⁻¹. These values confirm that, relative to the NOPEX site, the limitation to mass fluxes by atmospheric drought and the effect of plant resistance were stronger at the BOREAS site.

For the carbon budget, the large climate differences between the more maritime NOPEX site and the continental BOREAS site act in two ways. The considerably longer growth period for the NOPEX site (Fig. 1) determines a larger gross production by photosynthesis. On the other hand, a higher temperature-especially outside the growth period-accelerates respiration and decomposition rates. This makes the quantitative differences of annual net ecosystem carbon uptake to be less pronounced than would be indicated by a bare temperature sum for the two sites. The sole effect of BOREAS climate can be checked by imposing it on the NOPEX stand. This would decrease the net annual carbon uptake to 0.88 t ha⁻¹, i.e. by 56%. This is a similar value to that simulated for the OJP BOREAS stand, despite a larger LAI of the NOPEX stand. This shows that trees and stands acclimate to local conditions and develop an appropriate effective growth strategy.

From the global point of view, the results presented only indicate that the boreal forests could possibly act as a sink for carbon. However, the uptake is very low and thus uncertain considering the very large fluxes of assimilation and ecosystem respiration. Even a minor shift in respiration or photosynthesis fluxes could reverse the budget and easily make the boreal forest a source of carbon. Also, the preliminary results of the long-term net ecosystem CO_2 measurements from the NOPEX site the following year (1995) indicate that the forest was a source of carbon. A further application of the model across the full range of stand age, species composition and density will give a better picture of the importance of the boreal forest ecosystem in the carbon cycle on a regional scale.

4. Conclusions and recommendations

 FOREST-BGC is a simple ecosystem process model, yet is capable of producing realistic predictions. The variations of daily values of transpiration, canopy conductance and net carbon flux were generally satisfactorily explained. For water budgets, the problem of defining soil water capacity remains. The next improvements of the model should, however, include a routine accounting for a soil-class-specific shape of pF curve, which affects the chain water potential-canopy conductancetranspiration. Relative to a water budget, the construction of the carbon budget was more uncertain due to difficulties associated with both model routines and data for verification. As for the model. the most uncertain parts of the model version used were respiration and decomposition functions. As for the validation data, the spatial variability of CO₂ measurements and associated sampling problems remain a considerable obstacle to obtaining a truly representative reference for validation. However, the results of both the carbon and water budget parts are good relative to the amount of required input parameters.

- 2. The results showed the immense importance of long-term measurements for parameterization and validation of the model performance. A model may perform successfully for a certain period, but it can also be less successful or fail for another period.
- 3. The more maritime climate of the NOPEX site permits a larger gross production, but this is accompanied by larger respiration and decomposition rates, which reduce the quantitative differences of net ecosystem carbon uptake relative to the BOREAS site with a continental climate.

The model was applied on a selected stand. Boreal forests in the NOPEX region are a heterogeneous mosaic of managed stands with different age and pine/spruce composition. It was found previously that tree age and share of species affected transpiration and its control on local scales (Cienciala et al., 1997). Therefore, the next analytical effort should address the importance of species composition and age for carbon and water fluxes on larger spatial scales. The forest will be categorized into several age classes, with a particular species composition. The next application of FOREST-BGC will target these categories, which will enable regional averaging of fluxes.

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