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Evaluation of six process-based forest growth models using eddy-covariance measurements of CO_2 and H_2O fluxes at six forest sites in Europe

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Abstract

Reliable models are required to assess the impacts of climate change on forest ecosystems. Precise and independent data are essential to assess this accuracy. The flux measurements collected by the EUROFLUX project over a wide range of forest types and climatic regions in Europe allow a critical testing of the process-based models which were developed in the LTEEF project. The ECOCRAFT project complements this with a wealth of independent plant physiological measurements. Thus, it was aimed in this study to test six process-based forest growth models against the flux measurements of six European forest types, taking advantage of a large database with plant physiological parameters.

The reliability of both the flux data and parameter values itself was not under discussion in this study. The data provided by the researchers of the EUROFLUX sites, possibly with local corrections, were used with a minor gap-filling procedure to avoid the loss of many days with observations.

The model performance is discussed based on their accuracy, generality and realism. Accuracy was evaluated based on the goodness-of-fit with observed values of daily net ecosystem exchange, gross primary production and ecosystem respiration ($gC\,m^{-2}\,d^{-1}$), and transpiration ($kg\,H_2O\,m^{-2}\,d^{-1}$). Moreover, accuracy was also evaluated based on systematic and unsystematic errors. Generality was characterized by the applicability of the models to different European forest ecosystems. Reality was evaluated by comparing the modelled and observed responses of gross primary production, ecosystem respiration to radiation and temperature. The results indicated that:

***Accuracy*. All models showed similar high correlation with the measured carbon flux data, and also low systematic and unsystematic prediction errors at one or more sites of flux measurements. The results were similar in the case of several models when the water fluxes were considered. Most models fulfilled the criteria of sufficient accuracy for the ability to predict the carbon and water exchange between forests and the atmosphere.**

***Generality*. Three models of six could be applied for both deciduous and coniferous forests. Furthermore, four models were applied both for boreal and temperate conditions. However, no severe water-limited conditions were encountered, and no year-to-year variability could be tested.**

***Realism*. Most models fulfil the criterion of realism that the relationships between the modelled phenomena (carbon and water exchange) and environment are described causally. Again several of the models were able to reproduce the responses of measurable variables such as gross primary production (GPP), ecosystem respiration and transpiration to environmental driving factors such as radiation and temperature. Stomatal**

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conductance appears to be the most critical process causing differences in predicted fluxes of carbon and water between those models that accurately describe the annual totals of GPP, ecosystem respiration and transpiration.

As a conclusion, several process-based models are available that produce accurate estimates of carbon and water fluxes at several forest sites of Europe. This considerable accuracy fulfils one requirement of models to be able to predict the impacts of climate change on the carbon balance of European forests. However, the generality of the models should be further evaluated by expanding the range of testing over both time and space. In addition, differences in behaviour between models at the process level indicate requirement of further model testing, with special emphasis on modelling stomatal conductance realistically.

Keywords: accuracy, climate change, generality, process models, realism, water and carbon fluxes

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Introduction

It is increasingly agreed that the rise in the concentrations of atmospheric CO_2 and other greenhouse gases are likely to result in a globally changed climate, possibly in the coming decades (Houghton *et al*. 1996). Terrestrial ecosystems are an important component in the global carbon cycle, especially forests, because of the large pools and long-term storage of carbon in the vegetation and forest soils that can be manipulated by management. Growth of vegetation and carbon storage of forests will be affected by changes in the climate and atmospheric CO_2 concentration. This in turn affects the CO_2 concentration in the atmosphere. The Kyoto conference (UNFCCC 1997a,b) recognized the potential of forests to store carbon, thereby possibly reducing the rate of increase in atmospheric CO_2. Therefore it is now important to quantify the current and future sink strength of forests at the regional scale, e.g. for different (regions and) countries in Europe.

Carbon and water flux data issued from a regional and global flux network allow reducing the uncertainty about the net carbon exchange from different types of vegetation canopies. However, a central question is raised concerning the partitioning of the carbon stored by a forest between harvestable and nonharvestable biomass compartments and soil organic matter. Unfortunately, short-term changes in the amount of carbon stored in those compartments cannot be easily measured. These short-term changes need to be known to assess the potential of forests to store carbon on a short-term and on a long-term basis, since wood products, leaves and branches, roots and soil organic matter have quite different turnaround times. Combining both flux data and process-based models, predictions in terms of GPP, net primary production (NPP), respiration and net ecosystem exchange (NEE) could help to reduce the uncertainty about the partitioning of carbon flux between storage pools. A prerequisite is that process-based forest growth models should be able to describe the carbon flux measured with an acceptable accuracy both in terms of daily and annual balances and climate sensitivity.

Three European projects made it possible to test the accuracy of the models with detailed quantitative observations at the stand scale and thus analyse the contribution of different processes to the forest CO_2 - and H_2O-exchange:

1. In the LTEEF-project (Mohren & Kramer 1997; Mohren 1999) a suite of forest growth models have been developed, describing the exchange of CO_2 and water between forests and atmosphere at the daily level. Many of these models were developed to simulate primarily the long-term (decades to century) stand development rather than the short-term (daily to annual) carbon exchange. Detailed canopy transport models would be more suitable for the analysis of the half-hourly fluxes that are available. Nevertheless, the LTEEF models should be able to give an unbiased estimate of the correct magnitude for the daily and seasonal variation in carbon and water fluxes. In addition, comparison of models should show the applicability of various models to the analyses of CO_2 and H_2O fluxes in different European forests.
2. The EUROFLUX project (Valentini 1929) provides a unique database of short-term CO_2 and H_2O fluxes over a wide range of sites and tree species.
3. The ECOCRAFT project provides a database containing many of the parameter values required by the models. The first phase of this project focused on quantification of the response of tree species to elevated CO_2 concentration and temperature by means of controlled experiments (Medlyn & Jarvis 1997, 1999).

The usefulness and hence the criteria for refutation of a model depends on the purpose for which the model was

designed. The models considered in this study are explanatory models aimed to analyse long-term growth (decades to centuries) of forest stands. The models include formal descriptions of the causal relationships that are assumed to be relevant for forest growth. Conceptual differences between models are therefore the result of different hypotheses for these causal relationships. Such models are typically refuted based on realism of the model behaviour based on expert judgement. The generality and realism of these models make them good candidates to make projections under future conditions. In the case of impact assessment of climate change another model evaluation criterion is added, which is the accuracy of a model to simulate independent data. Hence, there are three criteria to evaluate a model, including generality, realism and accuracy (Levins 1966; Sharpe 1990). Levins (1966) stated that at the most two of these partly contrasting criteria could be maximized but not all three. The requirements for climate change assessment are a wide range of application in space and time (general); including all significant future causal relationships (realistic); and quantitatively correct (accurate). Hence a successful model needs to find an optimal solution for all three criteria.

Generality can be evaluated over space or time. For the models considered, a general model can be proved to be useful for different sites. Alternatively, a general model will produce reliable (nonbiased) estimates over long time periods (decades) and under various climatic conditions. If this is the case, then absolute short-term accuracy may not be necessary.

Realism can be evaluated when all causal relationships are included that are significant for the examined phenomenon. This criterion cannot be derived directly from accuracy or generality. Amongst the models considered, the same processes might be described based on different theories considering the underlying mechanisms. Due to the complexity of such models it is then difficult to determine an objective refutation criterion. According to the definition, an empirical model may also be realistic if the independent variables are the actual driving forces of the dependent variable. However, the application of an empirical model outside its tested range is more uncertain than the application of a mechanistic model if it can be assumed that the same mechanisms are important in the untested conditions and that no new significant causal relationships need to be included.

Accuracy can be evaluated in terms of goodness-of-fit of the model results. In the case of the models considered in this study, this has been done by using independent values of daily carbon and water fluxes of a single site. Although a model can be found accurate according to this procedure, it does not guarantee its generality or realism. For example, traditional growth and yield models tend to be very accurate but lack realism and generality and hence are neither directly applicable to future climatic conditions nor at other sites.

The aims of this study were: (1) to analyse the generality and accuracy of the different models in producing the carbon and water fluxes of different forests, and (2) to analyse the environmental determinants in the daily fluxes of carbon and water between different European forests and the atmosphere, indicating possible differences in model realism. This was done by comparing the results of 6 LTEEF models to the independent EUROFLUX data of CO_2 and H_2O fluxes of six forest sites in Europe, and by taking advantage of the values of parameters compiled in the ECOCRAFT database.

Materials and methods

Definition of carbon and water fluxes

For the analysis of the carbon fluxes (all in $gC\,m^{-2}$ ground d^{-1}) the following definitions were used, with the convention that assimilation has a negative sign, and respiration positive:

$$GPP = A + R_d$$

$$NPP = A + R_f + R_w + R_r = \Delta W + d_l + d_r + c_{II}$$

$$NEE = A + R_f + R_w + R_r + R_h = \Delta W + \Delta S$$

Where:

Symbol	Explanation
ΔS	rate of change in soil carbon content
ΔW	rate of change in plant carbon content
A	net assimilation rate per unit ground area (=gross assimilation − daytime leaf respiration)
C_{II}	rate of consumption by secondary producers
d_l	rate of litter production
D_r	rate of root turnover
GPP	gross primary production
NEE	net ecosystem exchange (= NEP: net ecosystem production): net exchange of carbon between ecosystem and the atmosphere per unit ground area
NPP	net primary production assimilation rate per unit ground area
R_d	daytime leaf respiration
R_f	night-time leaf respiration rate per unit ground area
R_h	heterotrophic respiration
R_r	respiration of the root tissues
R_w	respiration of the other aerial plant tissues, e.g. branch stem and reproductive organs

The water fluxes include transpiration ($kg\,H_2O\,m^{-2}\,y^{-1}$) only.

CO_2 and H_2O flux data

EUROFLUX: a uniform measuring approach for all sites In the EUROFLUX project emphasis was laid on a unified protocol and instrumentation to obtain CO_2 and H_2O fluxes of 14 sites in Europe (Valentini 1999). In the following, a brief qualitative description of this approach is presented. Moncrieff *et al*. (1997) and Aubinet *et al*. (2000) give a full description of the system. See Table 1 for an overview of the characteristics of the EUROFLUX sites. Figure 1 presents the location of the sites that are used in this study.

The eddy-correlation technique is used to obtain the turbulent fluxes. The measurements system is based on a 3D ultrasonic anemometer in combination with a fast infrared gas analyser placed on top of a tower reaching 10–20 m above the forest. Additionally, profiles of CO_2 and H_2O concentrations as well as wind speed and temperature were measured. To determine net radiation, the four components of the radiation balance were measured simultaneously using a net radiometer. Both incoming and reflected short wave radiation was measured with pyranometers. The long wave components were estimated as the difference between global and net radiation.

At the top of the tower, standard meteorological measurements of precipitation, horizontal wind speed, wind-direction, relative humidity and air temperature were made. The soil heat flux was measured using heat flux sensors under the litter layer in the mineral soil. Soil moisture and temperature were measured in one or more vertical profiles at several depths.

In the EUROFLUX data, transpiration values were not separated from the total water fluxes. However, during dry days, interception and soil evaporation will be negligible in forest stands. Therefore, the model output was analysed for data during the growing season at days without precipitation.

Gap-filling of missing flux data The flux data consist of half-hourly values of the exchange of CO_2 and H_2O between the vegetation and the atmosphere. The output interval of the models is typically one day, although the smallest time interval for the calculations is also one hour for most models (see Table 2). To compare the measurements to the simulated values, the half-hourly values thus need to be accumulated to a daily value. In case of missing measurements, a linear interpolation between adjacent observations is used based on the following criteria: maximally two consecutive values are missing during daytime, or maximally four consecutive values are missing during night-time. If more than four consecutive values are missing, then this day is not used for the comparison with the simulated fluxes. No other adjustments than these were performed on the data as provided by the principal investigator of the EUROFLUX site. See the references for each of the sites (Table 1) for the correction of the night-time fluxes.

Fig. 1 Location of the EUROFLUX sites. 1-Hyytiälä; 2-Loobos; 3-Hesse; 4-Bray; 5-Collelongo; 6-Tharandt.

Model description

The models considered are process-based models aiming to assess the long-term dynamics of tree growth of managed forest stands. Stand characteristics include tree density, stem volume, tree height, stem diameter at breast height, canopy dimensions, biomass of foliage, branches, stem (hardwood and sapwood), coarse roots and fine roots. The stand characteristics are based either on individual trees, cohorts of trees of different diameter classes, or average trees (i.e. all trees of a species in the stand are identical), depending on the model. Forest management strategies affect these features by thinning or harvesting.

The models describe the physical environment (light, temperature, and water content) above ground and in the soil in detail. Figure 2 gives a general scheme on how the processes are interrelated for the model GOTILWA, which is representative of the models used in this study. Table 2 gives an overview of the features of each model. Much effort is put on the interception and attenuation of light in the canopy because of the nonlinear relationship between photosynthesis and light. Because photosynthesis is strongly affected by temperature most models also include a leaf energy balance and describe a vertical temperature gradient. None of the models include vertical gradients in either CO_2 or water vapour concentration. Maintenance respiration is proportional to the amount of respiring biomass and increases exponentially

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Table 1 Characteristics of EUROFLUX sites

Site/stand/climate	Bray	Collelongo	Hesse	Hytiälä	Loobos	Tharandt
Location	44°46′N, + 0°42′E	41°52′N, 13°38′E	48°40′N, 7°05′E	61°51′N, 24°18′E	52°10′N, 5°44′E	50°58′N, 13°38′E
Elevation (m)	62.5	1550	305	170	25	380
Species	Pinus pinaster	Fagus sylvatica	Fagus sylvatica	Pinus sylvestris	Pinus sylvestris	Picea abies
Understorey	Molinia caerulea	Herbs, cf. Gallium	Carpinus betulus	Calluna vulgaris Vaccinium vitis-idaea Vaccinium myrtillus	Deschampsia flexuosa	Deschampsia flexuosa
Soil type	sandy podzol	Calcareous brown earth		Haplic podzol	Podzol	Podzol brown earth
Age (in 1996)	27	100	25–30	34 (30–35)	100	95
Height (m)	18.0	22	13	13	15	25
Tree density (n ha^{-1})	526	890	4000	2500	362	783
Basal area (m^2 ha^{-1})	31.8	32.1		21.9	24.8	33.9
LAI (m^2 m^{-2}) (projected)	2.6–3.1	3.5	5.5	5	3.0	7.2
Wood biomass (kg m^{-2})	12.3	21.1	8.0	5.4	7.3	20.1
Mean temperature (°C)	13.5	7	9.2	3	12	7.5
Precipitation (mm y^{-1})	930	1180	820	700	800	820
Data used						
period	30-6-96/30-6-97	1-1-97/31-12-97	1–1-97/31-12-97	1-1-97/31-12-97	1-1-97/31-12-97	1–1-97/31–12–97
site responsible	Berbigier	Matteucci	Granier	Vesala 1998;	Dolman	Bernhofer
reference	Aubinet *et al*. (1999); Berbigier (submitted) Diawara *et al*. (1991) Lamaud *et al*. (1996) Porté *et al*. Loustau *et al*.	Valentini *et al*. (1996); Matteucci (1998) Cutini *et al*. (1998)	Granier *et al*.(1999a,b); Epron *et al*. (1999) Granier *et al*. (2000)	Vesala *et al*. (1999) Rannik (1998a,b)		Bernhofer *et al*. (1998); Grünwald & Bernhofer (1998)
Measurements						
Radiation balance*	Rn, Rg, PAR (i, r, d/d)	Rn, Rg, PAR (i, r, d/d)	Rn, Rg, PAR (i, r)	Rn, Rg	Rn, Rg, PAR (i, r, d/d)	Rn, Rg, PAR (i, r, d/d)
Scalar fluxes	CO_2, H_2O; Heat	CO_2, H_2O; Heat	CO_2, H_2O; Heat	CO_2, H_2O; Heat	CO_2, H_2O; Heat	CO_2, H_2O; Heat
Soil moisture	y	y	y	y	y	y

*Abbreviations used: *Rn*: net radiation, *Rg*: global radiation, PAR: visible radiation, NIR: near infra red, FIR: far infra red, i:incident, r: reflected, d/d: direct/diffuse

Table 2 Characteristics of the models

	COCA/FEF	FINNFOR	FORGRO	GOTILWA	HYDRALL	TREEDYN
Range of applicability in Europe						
Species	coniferous	coniferous	coniferous/deciduous	coniferous/deciduous	coniferous	coniferous/deciduous
Climate	boreal	boreal	boreal/temperate/ Mediterranean	boreal/temperate/ Mediterranean	boreal/temperate/ Mediterranean	boreal/not water-stressed temparature
Canopy structure						
Vertical	needle distribution	Homogeneous, ellipsoid leaf density	LAI layers. Homogeneous or ellipsoid leaf density	Two LAI layers (sun and shade). Ellipsoid leaf density	Different leaf density per layer dependent on diameter class	LAI layers
Horizontal	Homogeneous	Homogeneous	Homogeneous	Homogeneous	Homogeneous	Homogeneous
Architecture	size classes of trees; description of tree structure in each class	Cohorts of trees; description of tree structure in each class	identical trees	size classes of trees	identical trees	individual
Clumping	y	n	y	n	y	n
Radiation interception						
Direct/diffuse	y	y	y	y	y	y
Scattering	y	y	y	y	y	n
Photosynthesis						
Model	Solution of optimum stomal control problem	Biochemical (Farquhar type)	Biochemical (Farquhar type)	Biochemical (Farquhar type)	Biochemical (Farquhar type)	Biochemical (Farquhar type)
Control variables	I, T	I, T, CO_2	I, T, CO_2	I, T, CO_2	I, T, CO_2	I, T, CO_2, RH
Conductance						
Model	Optimal stomatal control	Jarvis-type stomatal control	Ball & Berry	Leuning (1995)	Optimal stomatal conductance	Ball & Berry
Control variables*	–	T, VPD	RH	VPD	T, VPD	RH
Phenology	Pelkonen & Hari (1980)	Pelkonen & Hari (1980)	Hänninen (1990); Kramer (1994); Leinonen (1996)	Pelkonen & Hari (1980)		Sonntag (1998); Kramer (1994); Leinonen (1996)

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Energy balance/water flux						
Canopy temperature	n	n	y	y	y	n
Transpiration	n	y	y	y	y	n
Rainfall interception	n	y	y	y	y	n
Soil evaporation	n	y	n	n	n	n
Soil water balance	n	n	y	y	y	n
Respiration	Foliage, fine roots, sapwood, soil	Foliage, fine & coarse roots, branches, sapwood, soil	Foliage, fine root, sapwood, soil	Leaves, fine & coarse roots, live xylem, soil	Foliage, fine roots, sapwood, soil	Leaf, fruit, fine root, sapwood, soil
Autotroph	y	y	y	y	y	y
Growth/Maintenance	y	y	y	y	y	y
Temperature dependency	Q10	Q10	Q10	Q10	Exponential	Quadratic
Heterotroph						
Temperature dependency	Q10	Q10	Exponential	Q10	Q10	Quadratic
Smallest time step	COCA: seconds FEF:years	hours	hours	hours	half hour	hours
Principal literature	Hari *et al*. (1999); Vesala *et al*. (1999)	Këllomaki & Väisänen (1997); Kellomäki *et al*. (1993)	Mohren (1987); Kramer (1996)	Gracia *et al*. (1997, 1999)	Magnani *et al*. (2000a,b,c)	Sonntag (1998); Bossel (1996)

*abbreviations used: T: temperature; I: radiation, CO_2: CO_2 concentration, RH: relative humidity, VPD: water vapour pressure deficit

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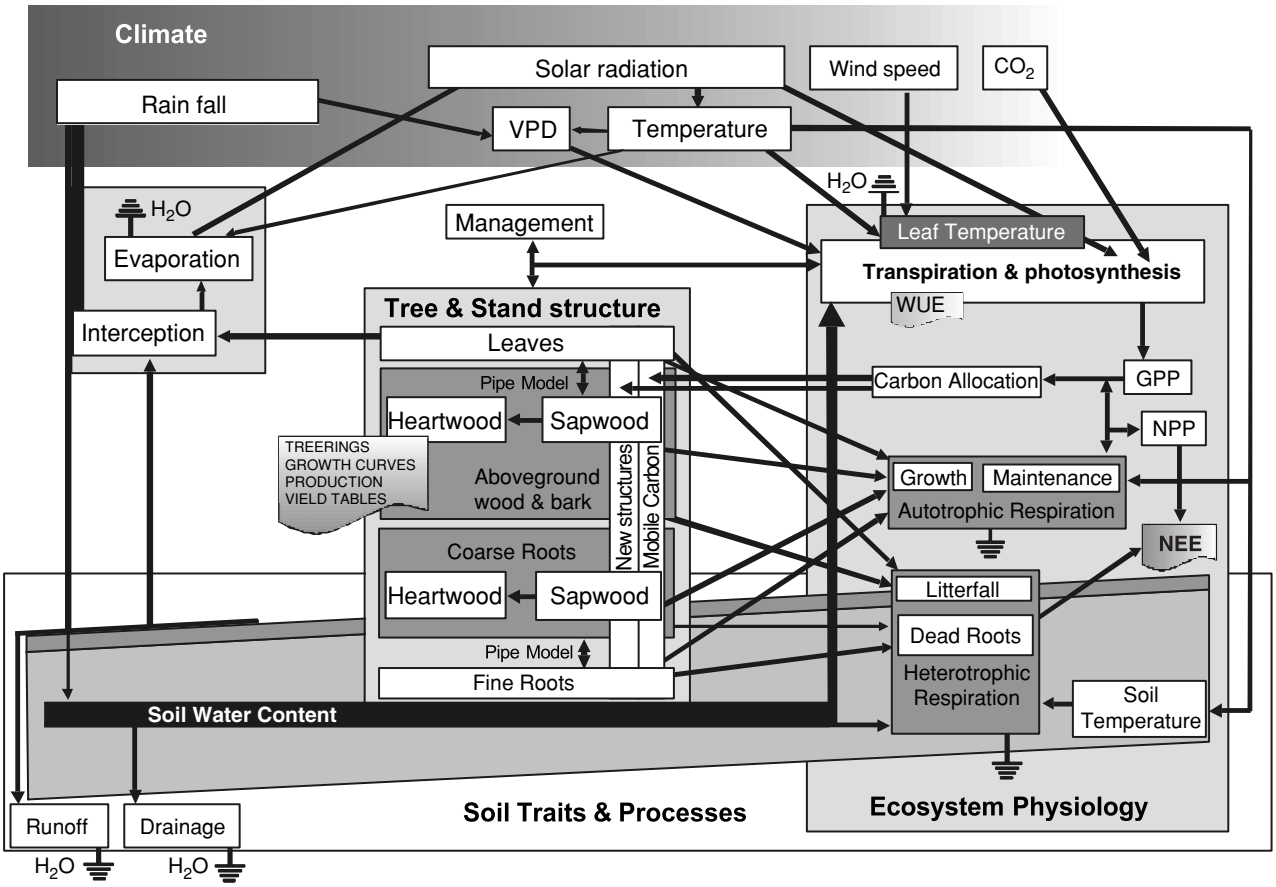

Fig. 2 General scheme of processes and their interrelationships for the models considered in this study (courtesy A. Sanchez).

with increasing tissue temperature. In many models maintenance respiration depends on the nitrogen concentration in the plant tissue. Growth respiration is proportional to growth of each tissue but is not as temperature dependent. Phenology, i.e. the timing of bud burst and foliage loss, is usually described as temperature dependent. Also root turnover depends on temperature and in some models also on water availability. The models use different approaches for the allocation of assimilates to plant components (e.g. pipe model, allometric relationships, hydraulic constrains). Allocation is especially important to simulate long-term dynamics of forest growth, but it is not so important in the modelling of short-term exchange of CO_2 and H_2O. The models differ in the degree of detail in which the dynamics of soil carbon and temperature and hence heterotrophic respiration are described.

The hydrological aspect of most models includes interception and evaporation of rain by the canopy and transpiration of water through the vegetation taken from the soil. Some models describe evaporation from the soil. The links between carbon and water cycles in the soil and the vegetation are through the effects of soil moisture on conductance. Either directly using an empirical relationship, or through the effect of soil water potential on leaf water potential based on a series of resistances for the transport of water through the tree from the soil to the atmosphere.

The required climatic variables, expressed as daily values, include global radiation, minimum and maximum temperature, relative humidity or early morning water vapour pressure, wind speed and rainfall.

Model evaluation

Goodness-of-fit To meet the first aim: *to analyse the generality and accuracy of the different models in producing the carbon and water fluxes of different forests*, the results of each of the models for different EUROFLUX sites are presented. However, it was not possible, to apply all models to all sites. The goodness-of-fit of each of the models was evaluated first by comparing the modelled annual fluxes of GPP and ecosystem respiration to observed values, and secondly by calculating the r^2, MSE_s and MSE_u for both the carbon and water fluxes.

The models were evaluated based on r^2, MSE_s and MSE_u because Wallach & Goffinet (1987, 1989) conclude that the evaluation of two models should not be based on R^2 values alone, but also on the analysis of mean squared errors (MSE):

$$MSE = \frac{\sum(y_o - y_p)^2}{N}$$

Where y_o and y_p are the observed and predicted values of the dependent variable, and N is the total number of observations. The use of MSE makes it possible to discriminate between systematic (MSE_s) and unsystematic error (MSE_u). If predicted values are linearly regressed on observed values, let the equation of the regression line be: $\hat{y} = a + by_o$. In the case of a perfect model fit it would be: $a = 0;\ b = 1;\ y_p = \hat{y}$.

In the case of an unsystematic error, the modelled points would be scattered around the regression line, while a systematic error would result in values of the parameters that are different from those above. The systematic and unsystematic error can thus be quantified as:

$$MSE_s = \frac{\sum(\hat{y} - y_o)^2}{N}, \quad MSE_u = \frac{\sum(\hat{y} - y_p)^2}{N},$$

respectively. In case of a perfect model fit both $MSE_s = 0$ and $MSE_u = 0$.

The results of r^2, MSE_s and MSE_u were presented for NEE for all models and all sites where they were applied. Furthermore, these statistics were evaluated for GPP, ecosystem respiration and transpiration during the growing season for both a coniferous and a deciduous site where most of the models could be applied. The coniferous site was Hyytiälä (Scots pine) in the boreal zone in Finland, and the deciduous site was Hesse (Beech) in the temperate zone in France.

Environmental responses To meet the second aim: *to analyse the environmental determinants in the daily fluxes of carbon and water between different European forests and the atmosphere*, the results were analysed for the same two sites, Hyytiälä and Hesse. For this analysis, the modelled response of GPP, ecosystem respiration and transpiration to climatic variables during the growing season were compared with the measured responses. The daily modelled output and observed data were plotted against both incoming global radiation and temperature during the period May 1 until September 30.

Results

Goodness-of-fit

A visual comparison of the model output and the data over time showed that all models accurately predicted the beginning of carbon uptake in spring and the seasonal patterns in NEE. Figure 3 presents these results for both Scots pine in Hyytiälä and beech in Hesse. The highest differences between measured and modelled daily values of NEE occurred in summertime. Nevertheless, there was a good correlation between the measured NEE fluxes and the daily predictions of most of the models (Table 3). The r^2 varied between 0.29 (TREEDYN for Tharand) and 0.93 (FORGRO for Collelongo). However, for some models and sites, there were considerable systematic errors between the model predictions and the EUROFLUX estimates (Table 3). This leads either to underestimation or to overestimation of the annual fluxes.

To better understand the differences between models, the model predictions were analysed in more detail for the Scots pine forest in Hyytiälä and the beech forest in Hesse. This analysis includes the disaggregation of the annual NEE into gross primary production and ecosystem respiration. The daily values of gross primary production and ecosystem respiration predicted by the models were compared to the estimations from the EUROFLUX data (Valentini *et al*. 2000). Figure 4(A) shows that for Hyytiälä, COCA/FEF, FORGRO and HYDRALL predicted accurately the annual GPP, while GOTILWA gave a slight overestimate (13%) and FINNFOR and TREEDYN underestimated the EUROFLUX results (30% and 34%, respectively). For Hesse, the most precise prediction for GPP was given by GOTILWA (Fig. 4B). For this site, FORGRO underestimated GPP by 11% and TREEDYN by 26% The major differences between the model output occurred in their predictions of ecosystem respiration. For Hyytiälä, HYDRALL and COCA predicted the annual respiration accurately compared to the EUROFLUX estimate (Fig. 4A). GOTILWA overestimated the respiration by 26% and FORGRO, TREEDYN and FINNFOR underestimated by 14%, 57% and 58%, respectively. For Hesse, GOTILWA predicted the annual respiration accurately and both FORGRO and TREEDYN underestimated it by 18% and 29%, respectively (Fig. 4B).

The goodness-of-fit of the predicted daily values of GPP and ecosystem respiration were determined for Hyytiälä. For this site daily estimates for these variables were available. Hyytiälä was also the only site where all models were applied. Generally, the models showed a higher goodness-of-fit for the separate processes compared to the total net ecosystem exchange (cf. r^2 in Table 3 and Table 4 for Hyytiälä). However, those models that simultaneously under- or overestimated both GPP and respiration showed systematic errors of single processes that were considerably higher compared to the errors in NEE (cf. MSE_s in Table 3 and Table 4 for Hytiälä).

Since transpiration and carbon sequestration are linked through stomatal conductance, the comparison of measured and predicted transpiration can be used to analyse the modelled carbon fluxes. This was done

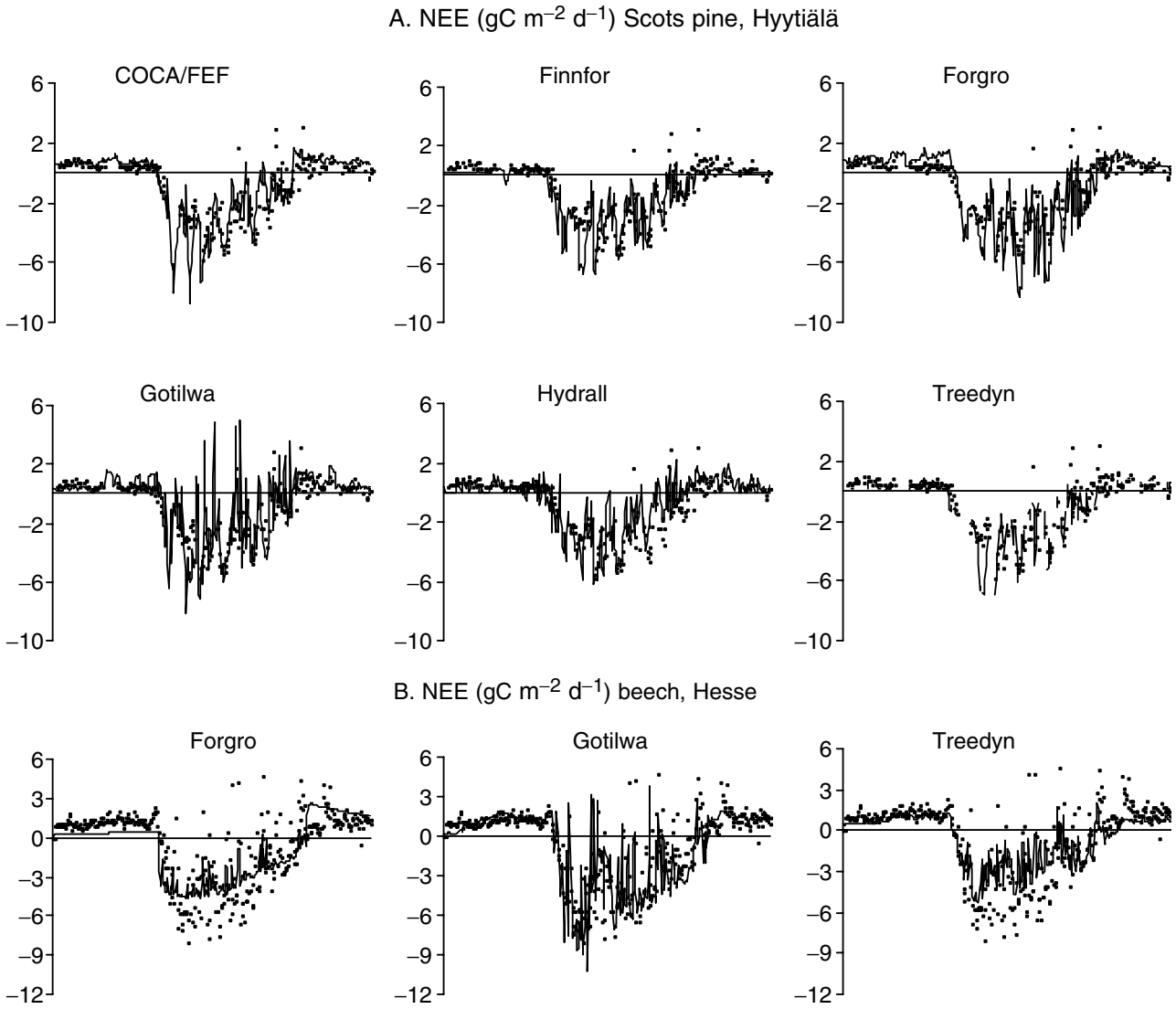

Fig. 3 Seasonal patterns of fluxes of NEE in 1997 of Scots pine in Hyytiälä (A), and beech in Hesse (B). Lines – model prediction; dots – observed values.

for two sites, Hyytiälä and Hesse, and for four models (FINNFOR, FORGRO, GOTILWA and HYDRALL), all of which provide daily transpiration as an output.

For Hyytiälä, the transpiration predicted by HYDRALL fitted the data most closely (Table 5). Also FORGRO and GOTILWA showed low systematic error but more unsystematic variation. FINNFOR systematically underestimated the transpiration for values exceeding one millimeter per day. This may be due to the fact that in this model transpiration is calculated based on the amount of water available in the upper soil-layer only. Only the models FORGRO and GOTILWA were applied to the beech forest at Hesse. Both models gave accurate estimates of transpiration, but FORGRO gave a larger systematic error (Table 5).

Responses to environmental driving variables

The realism of models can be investigated by comparing the modelled response to environmental driving variables with the observed responses. In this section the results of this approach for both the carbon and water fluxes are presented. For the carbon fluxes, this was done for the model output for the Hyytiälä site by plotting the predicted daily values of GPP vs. temperature and radiation, and ecosystem respiration vs. temperature (Fig. 5). Whereas for the water fluxes, the modelled response of transpiration to both radiation and temperature was compared with the observed response for the Scots pine site in Hyytiälä and the beech site in Hesse (Fig. 6).

Table 3 Goodness-of-fit of the model predictions expressed as explained variance (r^2), systematic mean square error (MSE_s) total mean square error (MSE) of Net Ecosystem Exchange (both in gC m^{-2} d^{-1}) compared to estimates based on EUROFLUX measurements at different sites

	COCA/FEF	FINNFOR	FORGRO	GOTILWA	HYDRALL	TREEDYN
Bray ($n = 259$)						
r^2			0.37	0.48	0.56	0.58
MSE_s			4.43	0.90	0.56	0.95
MSE			10.56	2.40	2.07	2.03
Collelongo ($n = 319$)						
r^2			0.93	0.91		
MSE_s			0.81	0.34		
MSE			1.59	1.73		
Hesse ($n = 365$)						
r^2			0.71	0.74		0.81
MSE_s			0.69	0.05		1.24
MSE			2.14	2.34		1.82
Hyytiälä ($n = 357$)						
r^2	0.77	0.86	0.83	0.68	0.81	0.80
MSE_s	0.07	0.15	0.40	0.05	0.00	0.07
MSE	1.08	0.62	1.43	1.61	0.61	0.83
Loobos ($n = 282$)						
r^2			0.46	0.62	0.67	0.66
MSE_s			1.95	0.61	0.34	0.56
MSE			3.99	1.29	1.18	1.18
Tharandt ($n = 282$)						
r^2			0.47			0.29
MSE_s			3.91			3.43
MSE			5.86			8.44

Carbon fluxes Figure 5(A) shows the temperature response of the GPP predicted by the models during days with high radiation level (above 20 MJ m^{-2} d^{-1}). All models showed a similar pattern at low temperatures. However, at high temperatures (> 15 °C), FINNFOR and TREEDYN showed a stronger reduction of GPP compared to both the other models and the EUROFLUX data. GOTILWA predicted higher level of GPP and showed also a higher temperature optimum.

Figure 5(B) shows the response of GPP to radiation during the Finnish summer time (June–September). The models showed rather similar responses; however, GOTILWA overestimated the GPP at high radiation levels and FINNFOR and TREEDYN underestimated it at low radiation levels. In addition, these two models showed the lowest scatter, which indicates a stricter radiation response compared to other models.

Figure 5(C) shows the differences in the response of ecosystem respiration to air temperature between the models and observations. Two models (COCA/FEF and HYDRALL) have a similar exponential response, which was close to the response estimated from the EUROFLUX data. GOTILWA overestimated respiration when the temperature exceeded 20 °C. FORGRO slightly

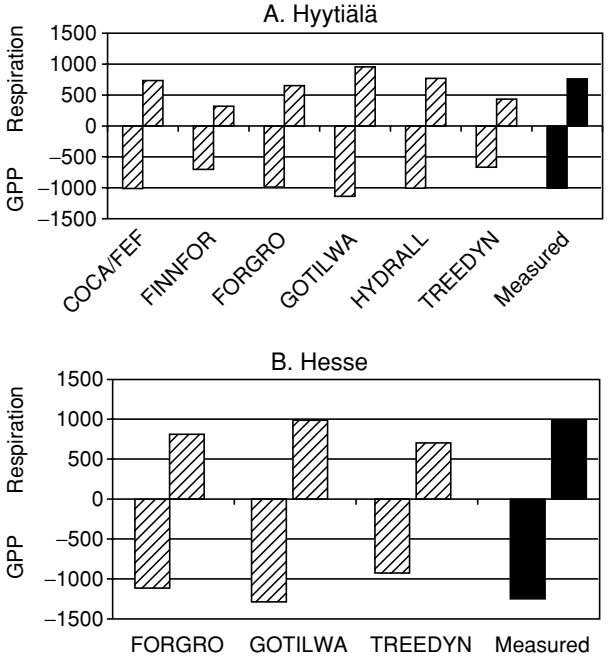

Fig. 4 Annual carbon fluxes (gC m^{-2} y^{-1}) of gross primary production (GPP) and ecosystem respiration for Scots pine in Hyytiälä, Finland (A) and beech in Hesse, France (B).

Table 4 Goodness-of-fit of model prediction expressed as explained variance (r^2), systematic mean square error (MSE_s) total mean square error (MSE) gross primary production (GPP) and ecosystem respiration (both in gC m^{-2} d^{-1}) compared to estimates based on EUROFLUX measurements at Hyytiälä

	COCA/FEF	FINNFOR	FORGRO	GOTILWA	HYDRALL	TREEDYN
GPP ($n = 357$)						
r^2	0.92	0.91	0.94	0.90	0.93	0.85
MSE_s	0.04	1.07	0.02	0.92	0.02	1.30
MSE	0.97	1.66	0.81	2.73	0.75	2.40
Respiration ($n = 357$)						
r^2	0.93	0.94	0.84	0.87	0.86	0.83
MSE_s	0.03	2.27	0.39	0.59	0.02	2.54
MSE	0.26	2.31	0.71	1.41	0.63	2.67

overestimated the respiration at low temperatures (< 0 °C), and underestimated it at high temperature (> 20 °C). Both FINNFOR and TREEDYN showed a nearly linear temperature response, thereby underestimating ecosystem respiration at high temperatures.

Water fluxes Figure 6 shows the responses of transpiration at dry days during the growing season to radiation and temperature. For Hyytiälä (Fig. 6A,B) HYDRALL most closely represents the observed responses. Both FORGRO and GOTILWA show a somewhat wider scatter of the modelled responses, but also accurately represent the observed response. FINNFOR underestimates the higher values of daily transpiration both at high radiation and temperature compared to the EUROFLUX reference.

For Hesse, both FORGRO and GOTILWA represent the observed responses reasonably well (Fig. 6C,D) FORGRO underestimates high transpiration values at high levels of radiation and temperature. GOTILWA somewhat underestimates the transpiration at high radiation levels (Fig. 6C) and at low temperature (Fig. 6D).

Table 5 Goodness-of-fit of predicted transpiration (kg H_2O m^{-2} d^{-1}) at dry days during the growing season compared to estimates based on EUROFLUX measurements at Hyytiälä and Hesse

	FINNFOR	FORGRO	GOTILWA	HYDRALL
Hyytiälä ($n = 43$)				
r^2	0.02	0.57	0.52	0.73
MSE_s	3.33	0.09	0.03	0.01
MSE	3.55	0.37	0.60	0.25
Hesse ($n = 56$)				
r^2		0.75	0.79	
MSE_s		0.24	0.16	
MSE		0.32	0.32	

Discussion

A lack of correspondence between model output and data can be partly due to uncertainties in the flux data. The flux data may contain unsystematic and systematic errors (Wofsy *et al*. 1993; Bernhofer *et al*. 1996; Goulden *et al*. 1996; Moncrieff *et al*. 1996; Lavigne *et al*. 1997; Aubinet *et al*. 2000; Wilson *et al*. 2001). Furthermore, the inevitable gap-filling for missing data points to arrive at annual totals introduces additional sampling uncertainty (Falge *et al*. 2001). Berbigier *et al*. (2001) estimated the unsystematic error of the NEE for the Bray site of ±7%, whereas Goulden *et al*. (1996) estimate a confidence interval of −20 to 0% for Harvard Forest.

According to Berbigier *et al*. (2001), there is no simple way to assess the systematic errors in carbon flux measurements. One estimate of the magnitude of the possible error is given by Anthoni *et al*. (1999), who present a range of ±12%. This error is especially due to a selective underestimation of night-time respiration during calm nights (Goulden *et al*. 1996). As the night-time flux of water vapour is negligible compared to the day-time flux, no significant systematic error of this flux can be expected. The magnitude of systematic errors can be assumed to be similar between the EUROFLUX sites since the same methodology and instrumentation were applied for all EUROFLUX measurements (Aubinet *et al*. 2000), and the sites are all forest sites with adequate measurement height and fetch.

The uncertainty related to gap-filling because of lacking data points is quantified by Falge *et al*. (2001) for three gap-filling strategies including mean diurnal variation, look-up tables and nonlinear regression methods. The average errors over the three strategies are 3, 5, 5, 5 and 34% for Tharandt, Loobos, Hyytiälä, Hesse and Bray, respectively (calculated from Table 6 in Falge *et al*. (2001)). See Falge *et al*. (2001) on a more detailed analysis on the sources of these uncertaintes. Goulden *et al*. (1996) estimated a total of unsystematic, systematic and sampling error of the annual NEE of

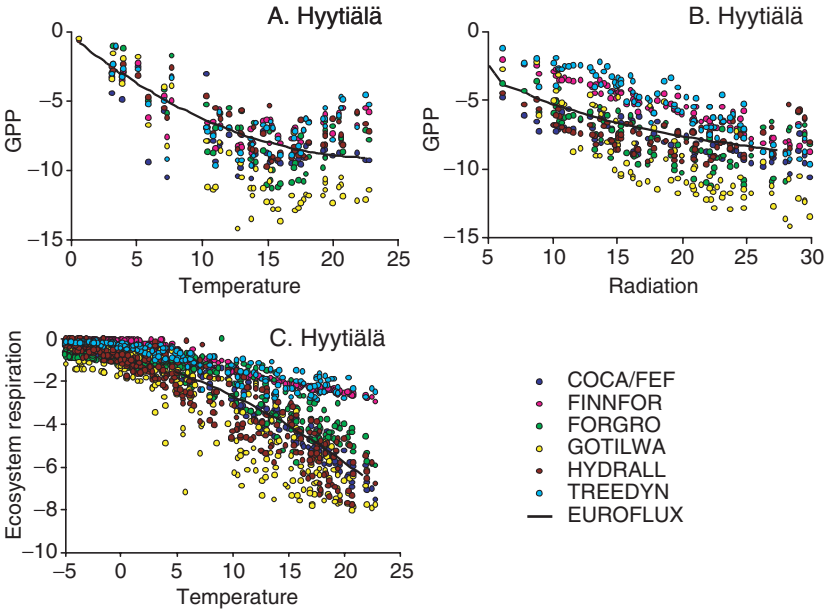

Fig. 5 Responses of gross primary production to temperature (A), radiation (B), and of ecosystem respiration to temperature (C). The EUROFLUX-line is a fitted trend line through the EUROFLUX data.

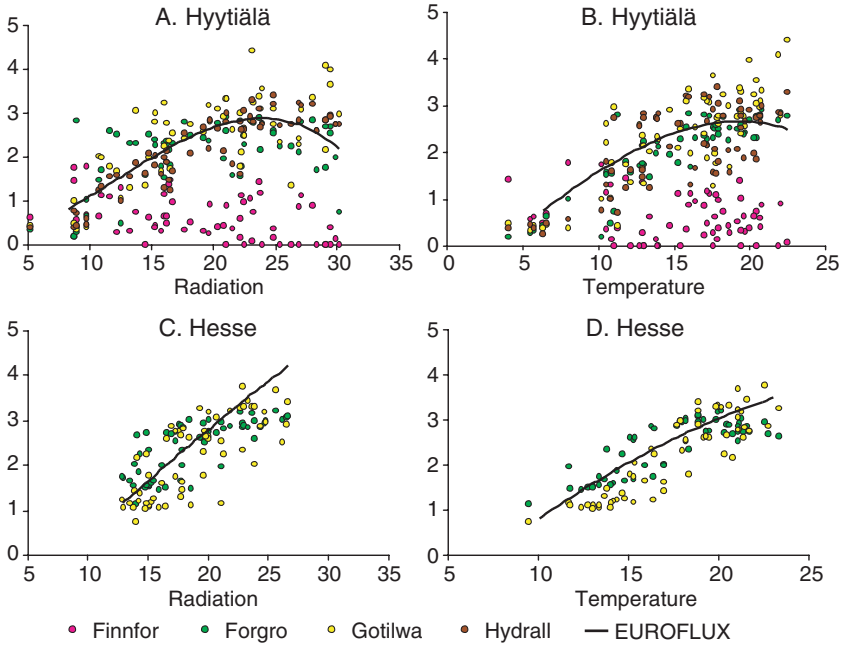

Fig. 6 Responses of transpiration (kg $H_2O\,m^{-2}\,d^{-1}$) at dry days during the growing season to temperature and radiation in Hyytiälä and Hesse. Hyytiälä represents a boreal Scots pine forest site. Hesse represents a temperate beech forest site. The EUROFLUX-line is a fitted trendline through the EUROFLUX data.

$\pm 5\%$, indicating that the long-term precision of the eddy covariance method is very good. The results of this study show much higher differences between the EUROFLUX estimates and the output of some models, especially in the case of disaggregated fluxes (Fig. 4). Thus the inaccuracies of the models cannot be explained by the errors of flux measurements only.

Besides uncertainty in the data, it should furthermore be realized that the flux data sets used in this study are quite limited and do not represent all climatic conditions encountered in Europe. Especially, there was no strong water stress influence in the data sets used. Thus, the conclusion drawn from this exercise is restricted to boreal and northern temperate forests, i.e. not water-stressed conditions. Although some models track the responses of evapotranspiration to global respiration and temperature accurately, the effects of strong water limitation on carbon exchange are not tested in this study.

Nevertheless, at the Bray and possibly the Tharandt site some water stress may occur during summer. This aspect is accurately represented by the models GOTILWA and HYDRALL, that were both originally developed for Mediterranean forests resulting in low systematic errors (Table 3), but should be improved in the model FORGRO.

The process-models were evaluated on a daily basis rather than on an half-hourly time resolution at which the measurements were made. The half-hour data would allow a separation of day and night fluxes, thus enabling an analysis of the accuracy of the models to describe respiration and photosynthesis. This analysis has not been done for the present study because in this study it is aimed at assessing how suitable the process-based models are for long-term impact assessment of climate change, where the focus is on the year-to-year and seasonal variation of exchange of carbon and water vapour, rather than on the diurnal variation. For such an assessment, the models use daily meteorological variables as input. Hourly meteorological information is then generated using general functions of the evolution of incoming radiation and temperature over the day.

Amongst the three aspects of model evaluation, i.e. accuracy, generality and realism, a quantitative comparison in this study was carried out for model *accuracy* through the goodness-of-fit by comparing the model results to the measured flux data. All models showed high correlation with the measured carbon flux data, and also low systematic and unsystematic prediction errors at one or more sites of flux measurements. The results were similar in the case of several models when the water fluxes were considered. According to this result, most models fulfilled the criteria of sufficient accuracy for the ability to predict the carbon and water exchange between forests and the atmosphere.

The second aspect, model *generality*, could be evaluated through the application range of the models. Three models of six could be applied for both deciduous and coniferous forests. Furthermore, four models were applied both for boreal and temperate conditions. However, it should be noted that the range of data available in this study for evaluation model generality is rather limited. For example, there was only one site of flux measurements at the whole boreal zone. Therefore, the generality of the models at different conditions within the boreal zone could not be tested profoundly. Furthermore, as stated above, the applicability of the models at the conditions with strong water stress could not be tested. In addition, another aspect of model generality, namely generality over time, was a subject of only limited testing. The data of flux measurements covered the period of one year. The models could predict reasonably well the seasonal trends of carbon and water fluxes (Fig. 3), which indicate that the processes related to phenology are well described in the models. However, the year-to-year variation caused by varying weather conditions could not be considered in this study. This is a serious limitation, especially due to the fact that these models are aimed to be used for predicting the impacts of climate change, and therefore model-testing, covering several years, is still required. The comparison of the model results with the EUROFLUX data shows systematic variation in the goodness-of-fit between different sites. At the temperate region, the models provided generally more accurate results for the deciduous sites compared to the coniferous ones. This is partly explained by the ability of the models to predict the seasonal changes of carbon sequestration in deciduous trees, especially the timing of spring bud burst and subsequent rapid increase of carbon uptake. Therefore, since the variation of the daily values of the carbon exchange is mainly due to seasonality, high r^2 values are expected. On the contrary, in temperate coniferous trees the seasonal changes are less abrupt, and therefore the comparison between measured and modelled fluxes is more limited to the day-to-day variation. However, at the boreal conditions, strong seasonality of carbon exchange occurs also in conifers in which the photosynthetic capacity is strongly limited during winter and recovers relatively abruptly in spring (Leinonen 1996; Jarvis & Linder 2000). The timing of this recovery was predicted in a similar way in the applied models by using a temperature dependent function (Pelkonen & Hari 1980). Thus, due to the accurate predictions of seasonal trends of photosynthesis, good r^2 values for the Hytiälä site were found in the results of all models.

The third aspect of model evaluation, the *realism* of the models, is the most important in a case like this, where process-based forest growth models are aimed to be used to assess the possible impacts of future climatic conditions, i.e. partly outside the range for which test data is available. Model realism is also by far the most difficult criterion to evaluate because complex process-based models differ in a large number of aspects.

There appear to be two main causes for the systematic model errors when comparing the modelled environmental responses of fluxes with those estimated on the basis of the EUROFLUX results. These are the temperature response of ecosystem respiration and the radiation response of GPP. In the case of ecosystem respiration, there is a lack of empirical data on the environmental response of the respiration of different components in trees and that of the different carbon pools in the soil. All models use a Q_{10}-approach to describe the response of respiration to temperature (Table 2). They may differ in parameter value for this although it was stipulated for this exercise that similar parameter values should be used, if possible obtained from the ECOCRAFT database (Medlyn & Jarvis 1997). The Q_{10} value, however, is

temperature dependent itself; thus the value may not be representative of certain temperature ranges (Tjoelker *et al*. 2001). For example, the fact that GOTILWA overestimates the ecosystem respiration in Hytiälä (Boreal forest) could be due to the fact that the Q_{10} is derived from Mediterranean data (Fig. 5A). Another important factor in respiration is the supply of material that is respired, especially roots because these have the highest turnover of the plant components. The rate and temperature sensitivity of respiration is thereby indirectly driven by photosynthesis and allocation of assimilates to roots. The most likely explanation of the low response of ecosystem respiration to temperature as found for TREEDYN and FINNFOR is the low GPP (Fig. 4A) resulting in a low amount of readily decomposable material at high temperatures. Whereas the high GPP of GOTILWA (Fig. 4A) results in a large amount of readily decomposable material, also at high temperatures (Fig. 5C). Also, Janssens *et al*. (2001) found in their analysis of flux data of soil and ecosystem respiration across European forests that soil respiration is driven by site productivity. Nevertheless, several models produced realistic results for the temperature response of ecosystem respiration and were accurate in the predictions of the amount of total annual respiration.

In the response of GPP to radiation, differences between models may occur in the assumptions for photosynthesis and in the scaling up from the leaf to the canopy level. Two approaches were used in predicting the photosynthesis, one based on an optimization theory for photosynthesis and transpiration (COCA-FEF) whereas the other model used the biochemical representation by Farquhar and co-workers (see Table 2 for references for the different models using these approaches). When the goodness-of-fit and the environmental responses of photosynthesis between the models were compared, it appeared that the predictions based on the optimization approach (COCA-FEF) were as accurate as the predictions of several of the models utilising the biochemical approach. On the other hand, strong variation occurred within the results of those models that used the biochemical approach for modelling the photosynthesis. This is partly caused by differences in the details of the model descriptions of the same general approach. Another source of variation is the description of the canopy structure. Thus, variation in the prediction of canopy photosynthesis may be caused by differences in the approaches of light interception. Furthermore, the assumptions concerning the environmental regulation of stomatal conductance differed between models. The EUROFLUX data allowed indirect methods for evaluating the modelled stomatal conductance through the measurements of evapotranspiration. The comparison showed strong variation in the predictions of different models.

Three approaches of stomatal control produced realistic responses of transpiration to environmental variables when compared with the measured evapotranspiration at days without rain. In two conductance models applied, i.e. the Ball-Berry model and the Leuning model, the stomatal conductance is assumed to be dependent on environmental variables indirectly through the rate of carbon assimilation, and directly through the effect of the water vapour pressure deficit (Leuning) or relative humidity (Ball-Berry). The third approach is based on the optimal stomatal control (HYDRALL, see Table 2 for references). Both at the Hytiälä and Hesse sites, no major differences in the goodness-of-fit could be found between the predictions of the models applying the Ball-Berry and Leuning approaches. This finding is contradictory to some earlier studies comparing these approaches, which suggest that the Ball-Berry model may not be sufficient to describe the stomatal conductance at the stand level simulations (van Wijk *et al*. 2000). At the Hytiälä site, however, the HYDRALL model that applies the approach of the optimal stomatal control produced the most accurate predictions of transpiration. In FINNFOR, an emperical method of stomatal conductance is applied in which stomatal conductance is linearly related to the water and temperature conditions in the soil, the lowest daily air temperature, the vapour pressure deficit and irradiance (Kellomäki & Väisänen 1997). The principal difference between this approach and the three other approaches mentioned above is that in the case of FINNFOR there is no interdependence between the rate of leaf photosynthesis and stomatal conductance. The results (Fig. 6A,B) supporting Leuning (1995) conclude that a combined stomatal photosynthesis model is indeed critical to describe photosynthesis and transpiration in C3 plants. An interesting test would be to link a combined stomatal-photosynthesis model to FINNFOR and analyse if this feeds forward in the model by an increased GPP, and thereby respiration because of higher allocation to roots and its sensitivity to temperature.

As a conclusion, several process-based models are available that are able to produce accurate estimates of seasonal and annual carbon and water fluxes at different forest sites throughout Europe. This considerable accuracy fulfils one requirement of models to be able to predict the impacts of climate change on the carbon balance of European forests. However, the results of this study show that the fact that models produced accurate results of forest carbon exchange (NEE) does not guarantee that they behave correctly at the process level, which reduces the reliability of the models in predicting the climatic change responses. In some cases, the seemingly accurate estimates may be due to the aggregation of errors at the lower level processes (Fig. 4). The generality of the models should be further evaluated by expanding the

range of testing both over time and space, whilst the realism of the model assumptions should be evaluated carefully at the level of processes such as respiration and stomatal conductance.

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