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Article

Simulation of CO_2 Fluxes in European Forest Ecosystems with the Coupled Soil-Vegetation Process Model "LandscapeDNDC"

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Abstract: CO_2 exchange processes in forest ecosystems are of profound ecological and economic importance, meaning there is a need for generally applicable simulation tools. However, process-based ecosystem models, which are in principal suitable for the task, are commonly evaluated at only a few sites and for a limited number of plant species. It is thus often unclear if the processes and parameters involved are suitable for model application at a regional scale. We tested the LandscapeDNDC forest growth module PnET (derived from the Photosynthetic / EvapoTranspiration model) with site-specific as well as multi-site calibrated parameters using independent data sets of eddy covariance measurements across a European transect. Although site-specific parametrization is superior (r^2 for pooled Gross Primary Production (GPP) during calibration period: site-specific = 0.93, multi-site = 0.88; r^2 for pooled Net Ecosystem Exchange (NEE) during calibration period: site-specific = 0.81, multi-site = 0.73), we show that general parameters are able to represent carbon uptake over periods of several years. The procedure has been applied for the three most dominant European tree species *i.e.*, Scots pine, Norway spruce and European beech. In addition, we discuss potential model improvements with regard to the sensitivity of parameters to site conditions differentiated into climate, nutrient and drought influences.

Keywords: LandscapeDNDC; process-based ecosystem model; parametrization; carbon exchange processes; model evaluation; site conditions; Scots pine; Norway spruce; European beech

1. Introduction

Forests play a major role in the global carbon (C), nitrogen (N) and water cycle and have great potential to reduce atmospheric greenhouse gases [1]. Especially with regard to atmospheric CO_2, the development and responses of forests to climate change are of major importance due to their C sink capacity [2]. Therefore, understanding forest CO_2 exchange processes (e.g., Gross Primary Production "GPP", Terrestrial Ecosystem Respiration "TER", Net Ecosystem Exchange "NEE") is of major ecological and economic interest, in particular under changing environmental conditions [3]. For process understanding, a number of observational networks have been established (e.g., Ameriflux, Fluxnet, Euroflux, MedeFlux, AsiaFlux, *etc.*) using the eddy covariance (EC) methodology with standardized measuring and data processing techniques [4]. This data can be used for regional and global analysis of flux balances as well as for calibrating process-based ecosystem models [5,6]. Proper calibration of process-based ecosystem models is crucial for assessing the impacts of climate change scenarios on the terrestrial C cycle.

A number of forest ecosystem models have recently been developed which do allow estimating ecosystem C cycling under current and future climatic conditions at site and global scales [7–12]. In Europe, deterministic models such as CASTANEA [13], ORCHIDEE [14], CoupModel [15], MAESTRA [16] and others [12,17] have been calibrated and evaluated against EC flux records (e.g., GPP, TER, NEE). The degree of compliance between model results and field observations depends both on the level of process implemented (e.g., photosynthesis, phenology, allocation, senescence, mineralization of soil organic C pools) and on respective parameter calibration [18]. Chen *et al.* [19] showed that predicted CO_2 fluxes at the regional scale may vary significantly between general and specific parameter calibrations. The reason for such deviations can be twofold. Firstly, the level of process description does not allow for sufficient model sensitivity to changing environmental conditions, and secondly, genetic acclimation of species to surrounding ecosystem properties may substantially vary with the geographical range [19–21]. Genetic differentiation and adaptation to local environmental conditions is a common phenomenon and has been reported for pine [22], spruce [23] beech [24] and other species [21,25,26]. Assuming a sufficient degree of complexity in process description, model parameter calibration to individual ecosystems (site-specific) might be able to address the response of stand acclimation to local biotic and abiotic conditions. Nevertheless, the procurement of site-specific parameters for every individual ecosystem inside a region is currently almost impossible. This is because process-based ecosystem models require detailed input information (climate-vegetation-soil-hydrology). For regional or continental inventories, a multi-site calibration can be adopted if the model is (a) sensitive to a multitude of environmental and anthropogenic impacts and (b) based on general principles of eco-physiology and biogeochemistry. In this study, we present a general set of parameters that cover CO_2 exchange independently of the geographical location. To the best of our knowledge, there is no existing study that applies multi-site calibration to represent seasonal patterns of CO_2 fluxes over a crosscut of forest ecosystems in Europe.

In this work, the LandscapeDNDC model [27] is used to simulate C exchange processes for 10 forest ecosystems including the species *Pinus sylvestris* (Scots pine), *Picea abies* (Norway spruce) and *Fagus sylvatica* (European beech), which are dominant in Central Europe [28–31]. We apply site-specific and multi-site calibration for the 27 most important physiological parameters of the plant growth module PnET (derived from the Photosynthetic / EvapoTranspiration model [32]). Overall, the objectives of this study are: (1) testing the ability of the PnET module in LandscapeDNDC to represent forest CO_2 exchanges under a wide range of environmental conditions; and (2) determining the benefit of site-specific *vs.* general parameter sets.

2. Experimental Section

2.1. Model Framework

LandscapeDNDC is a process-based ecosystem model that simulates C, N and water cycling within forest, arable, and grassland ecosystems for site and regional scale applications [27]. It unifies the biogeochemical process description from the agricultural model of DeNitrification and DeComposition (DNDC) [33] and the Forest-DNDC [34] models and uses the PnET model as one option to represent carbon and nitrogen in homogeneous deciduous and evergreen forests [35,32]. LandscapeDNDC links modules describing microclimate, water cycle, soil-biogeochemistry, plant physiological processes and dimensional changes by daily time step integration. All processes and state variables are considered in a vertically structured one-dimensional column including tree canopy, humus horizons and mineral soil [36]. Detailed process descriptions and evaluations have been reported in earlier studies including water balance [37,38], soil respiration and N trace gas emission [39] and nitrate leaching [40]. In addition, a general physiological process model and the dimensional growth routine have been evaluated within the framework of LandscapeDNDC [41] but less emphasis has been placed on the evaluation of the original forest growth module PnET, which is described in the annex section.

Initialization of LandscapeDNDC is based on general site and soil information including latitude, vertical profile information of soil physicochemical characteristics (*i.e.*, humus type, clay content, organic C- and N-content, bulk density, saturated conductivity, stone content, pH, water field capacity and wilting point) as well as initial vegetation information (*i.e.*, tree species, height, tree diameter at breast height, number of trees or stem volume per hectare). LandscapeDNDC uses weather data on temperature (average, minimum, maximum), precipitation, and radiation at a daily resolution as well as additional information on atmospheric CO_2 concentration and N deposition for model simulations. For further details, please see Haas *et al.* [27].

2.2. Site Description

LandscapeDNDC is applied to simulate C cycling in10 different forest stands, each dominated by one of the following tree species: *P. sylvestris* (n = 4), *P. abies* (n = 3), and *F. sylvatica* (n = 3). The stands comprise a large latitudinal range representing boreal, temperate and Mediterranean climatic conditions across Europe (Table 1). The mean annual temperature varied from 0.8 to 10.8 °C while annual precipitation ranged from 500 to 965 mm. Stand age varied between 46 years (French beech forest at Hesse) and 154 years (Finnish pine stand at Sodankylä). Atmospheric CO_2 concentration was set to a constant value of 370 ppm. Atmospheric N deposition varied across sites, from 2 to 50 kg N $ha^{-1}\cdot a^{-1}$. Data for model initialization regarding vegetation and soil properties (summarized in Table 1) as well as management data (thinning events) were obtained from literature (see references in Table 1) and from the European flux database cluster (http://gaia.agraria.unitus.it/) [42]. Daily weather data for running the simulation as well as daily GPP, TER and NEE for evaluating the model were also downloaded from the European flux database cluster.

2.3. Model Parameter Calibration

In this study, we calibrated the 27 parameters that define the responses of the PnET forest growth model as implemented within the LandscapeDNDC model framework. Parameters were separated into four characteristic groups: (a) allocation and respiration; (b) nitrogen; (c) temperature; (d) water and light (see Tables 2–4). We have used the Metropolis algorithm to make a random walk through the whole parameter space (defined by literature and expert knowledge as given in Table 2) and have derived a database with thousands of parameter sets (between 7500 and 19,000 depending on site). All parameter sets in this database were ranked using the normal distribution function in order to determine the probabilities of discrepancies between simulation and observations [43]. The ranking was done separately for GPP and NEE and the highest score for the average value was taken to select the "best" parameter set.

The dataset (GPP and NEE measurements) was further split in two parts: (a) calibration period "CP" (≥4 years between 1998 and 2005, except at DE-Hoeg where only 2 years of measurements were available: 2008–2009) and (b) evaluation period "EP" (≥3 years between 2005 and 2010). The calibration data set covered thinning events (only at DE-Tha, FR-Hes, FI-Hyy) as well as extreme climate conditions such as the drought event in the year 2003 for all cases except DE-Hoeg. The calibration was done for all sites independently (site-specific calibration, Table 3), grouping them species-specifically (multi-site calibration, Table 4).

2.4. Statistics

The coefficient of variation (CV) is used to show variations of model parameters. All temperature-related parameters *i.e.*, PSNTMAX, PSNTOPT and PSNTMIN (see Table 2 for description), were converted to Kelvin. Model performance was evaluated using the coefficient of determination (r^2), model efficiency (ME) and normalized root mean square prediction error (RMSPEn) [40,44,45]. Model performance criteria were calculated for daily as well as for monthly aggregated values.

Table 1. Site characteristics of investigated forest ecosystems (soil type is arranged according FAO classification).

Site	Shortcut	Tree Species	Latitude	Average Annual Climate Conditions		Stand Age	N Dep. (kg N $ha^{-1}\cdot a^{-1}$)	Organic Layer			Soil (First 5 cm)				
				T (°C)	P (mm)			Humus Type	C (%)	C:N	Soil Type	Clay (%)	C (%)	C:N	pH
Hyytiälä—Finland *	FI-Hyy	*Pinus sylvestris*	*N* 61°50′	4.0	614	56	4	MODER	32	39	sandy loam	8–13	3.4	31	4.6
Brasschaat—Belgium	Be-Bra	*Pinus sylvestris*	*N* 51°18′	10.8	825	87	40	MODER	44	28	loamy sand	1–4	5.0	23	3.8
Loobos—Netherlands	NL-Loo	*Pinus sylvestris*	*N* 52°10′	10.1	788	106	50	MODER	44 *	27	sand	2	8.5	17	3.4
Sodankylä—Finland	FI-Sod	*Pinus sylvestris*	*N* 67°21′	0.8	500	60–154	2	MODER	32	29 ***	sand	2–9	2.2	29 ***	3.3
Höglwald—Germany	DE-Hoeg	*Picea abies*	*N* 50°30′	8.7	856	109	30	MODER	35	30	loam	5–25	4.2	19	3.6
Tharandt—Germany *	DE-Tha	*Picea abies*	*N* 50°57′	8.9	860	125	30	MODER	41	24	silty loam	13–16	6.3	20	3.9
Wetzstein—Germany	DE-Wet	*Picea abies*	*N* 50°27′	6.5	865	61	21	MODER	36	26	loamy sand	7–11	7.0	10	3.7
Collelongo—Italy	IT-Col	*Fagus sylvatica*	*N* 46°35′	4.7	830	47	12	MODER	38	33	silty clay	25–27	9.0	13	4.1
Soroe—Denmark	DK-Sor	*Fagus sylvatica*	*N* 55°29′	8.6	752	95	27	MODER	45 ***	22 ***	sandy loam	23–26	2.5	15	4.6
Hesse—France **	FR-Hes	*Fagus sylvatica*	*N* 48°40′	10.2	965	46	16	MULL	41	41	silty clay	22–29	3.9	15	4.6

FI-Hyy: [36,46,47], European fluxes database cluster; **BE-Bra**: [48,49], European fluxes database cluster; **NL-Loo**: [50–52], European fluxes database cluster; **FI-Sod**: European fluxes database cluster; **DE-Hoeg**: [53–56]; **DE-Tha**: [41,52,57–59], European fluxes database cluster; **DE-Wet**: [59,60], European fluxes database cluster; **IT-Ren**: [61], European fluxes database cluster; **DK-Sor**: [13,62–65], European fluxes database cluster; **FR-Hes**: [41,62,63], European fluxes database cluster; * Thinning event 2002; ** Thinning event 2005; *** Model default value.

Table 2. Summary of physiological parameters subject to calibration, description and value ranges. In case no publications were found, we refer to our own parameter adjustments to specific sites. Parameters are grouped by carbon allocation and respiration (A), nitrogen (N), temperature (T) and water availability and light extinction (W_L).

Group	Parameter	Description	Units	Fagus Sylvatica			Picea Abies			Pinus Sylvestris		
				Min	Max	References	Min	Max	References	Min	Max	References
A	BASEFOLRESPFRAC	respiration as fraction of max. photosynthesis	(0–1)	0.05	0.15	[66] +/−0.05	0.05	0.15	[66] +/−0.05	0.05	0.15	[66] +/−0.05
A	FRTALLOC_BASE	intercept of relationship between foliar and root allocation	-	0.0	130	[32,66]	0.0	130.0	[32,66]	0.0	130.0	[32,66]
A	FRTLOSS_SCALE	slope of relationship between foliar and root allocation	-	1.0	7.0	+	1.0	7.0	+	1.0	7.0	+
A	GRESPFRAC	growth respiration as fraction of allocation	(0–1)	0.20	0.25	[32,67]	0.2	0.3	[32,66]	0.2	0.3	[32,66]
A	MFOLOPT	foliage biomass under optimal closed canopy condition	kg $DW \cdot m^{-2}$	0.23	0.39	[68,69]	1.10	1.66	++, [70]	0.39	0.96	[71,72]
A	QWODFOLMIN	min. ratio of carbon allocation to wood and foliage	-	0.3	5.0	+	0.3	5.0	+	0.3	5.0	+
A	RESPQ10	temperature dependency of leaf respiration	°C	1.8	2.3	[73,74]	2.0	5.0	[32,75]	2.0	2.3	[76–78]
A	ROOTMRESPFRAC	fine root maintenance respiration, fraction of allocation	-	0.5	1.0	[32,66]	0.5	1.0	[32,66]	0.5	1.0	[32,66]
A	WOODMRESPA	wood maintenance respiration, fraction of allocation	(0–1)	0.07	0.35	[32,66]	0.07	0.35	[32,66]	0.07	0.35	[32,66]
N	AMAXB	nitrogen dependency of photosynthesis	nmol CO_2 $g^{-1} \cdot s^{-1}$/ % N	36.0	71.9	[35,79]	0.0	75.6	[79–81]	0.0	75.6	same as PIAB
N	EXPL_NH4	exploitation rate of NH4	%	0.00	0.50	+++	0.00	0.50	++	0.0	0.5	[40]
N	EXPL_NO3	exploitation rate of NO3	%	0.00	0.35	+++, [82]	0.00	0.15	++	0.0	0.3	[40]

Table 2. *Cont.*

Group	Parameter	Description	Units	Fagus Sylvatica			Picea Abies			Pinus Sylvestris		
				Min	Max	References	Min	Max	References	Min	Max	References
N	FRET_N	max. fraction of nitrogen retranslocated before tissue loss	(0–1)	0.2	0.7	[67,83]	0.15	0.50	[84,85]	0.56	0.62	[86,87]
N	NCFOLOPT	opt. nitrogen concentration of foliage	$g N \cdot g DW^{-1}$	0.015	0.035	[88–90]	0.011	0.020	[91,92]	0.013	0.022	[93,94]
N	NCFRTOPT	opt. nitrogen concentration of fine roots	$g N \cdot g DW^{-1}$	0.007	0.01	[13,95]	0.005	0.02	[96,97]	0.0027	0.01	[91,98]
N	NCSAPOPT	opt. nitrogen concentration of living wood	$g N \cdot g DW^{-1}$	0.001	0.002	[83,99]	0.001	0.002	[100], +	0.001	0.002	[91,100]
N	SENESCSTART	day of year after which leaf death can occur	day number	195	325	++++/−65	205	335	[75] +/−0.65	205	325	[35] +/−0.65
T	GDDFOLEND	max. temperature sum for foliage activity offset	°C	200	1300	[35] +/−400	1100	1400	[75,101]	1100	1400	[102,103]
T	GDDFOLSTART	min. temperature sum for foliage activity onset	°C	100	580	[13,35]	250	350	[75,101]	190	280	[86,104]
T	GDDWODEND	max. temperature sum for wood activity offset	°C	900	1700	++++/−400, [35]	1000	1800	[75] +/−400, [35]	1400	2200	[103] +/−400
T	GDDWODSTART	min. temperature sum for wood activity onset	°C	100	400	++++/−150, [35]	100	400	[75] +/−150	200	500	[103] +/−150
T	PSNTMAX	max. temperature for photosynthesis	°C	25	45	[76] +/−10	32	52	[105] +/−10	27	47	[76] +/−10
T	PSNTMIN	min. temperature for photosynthesis	°C	0	10	[76] +/−5	−8	2	[105] +/−5	−7	3	[76] +/−5
T	PSNTOPT	opt. temperature for photosynthesis	°C	14	34	[76] +/−10	14	34	[75] +/−10	8	28	[76] +/−10
W_L	EXT	light extinction (attenuation) coefficient	(0–1)	0.25	0.65	[106,107]	0.40	0.67	[80,108]	0.40	0.65	[108,109]

Table 2. *Cont.*

Group	Parameter	Description	Units	Fagus Sylvatica			Picea Abies			Pinus Sylvestris		
				Min	Max	References	Min	Max	References	Min	Max	References
W_L	H2OREF_A	relative available soil water content at which conductance is affected	(0–1)	0.2	0.6	[106] +/−0.2	0.2	0.6	[110] +/−0.2	0.2	0.6	[111] +/−0.2
W_L	WUECMAX	max. water use efficiency	mg CO_2·g H_2O^{-1}	4.6	14.0	[112], +++	4.8	13.9	[75,113]	4.1	12.0	[114,115]

+ (estimated based on plausibility tests); ++ (adjusted to Höglwald spruce forest); +++ (adjusted to Höglwald beech forest); ++++ (adjusted to Hyytiälä pine forest).s

Table 3. Site-specific parameters per tree species. Parameters are grouped by allocation and respiration (A), nitrogen availability (N), temperature (T) and water availability and light extinction (W_L). The results are ordered from highest to lowest coefficient of variation (CV).

Group	Fagus Sylvatica			Picea Abies			Pinus Sylvestris		
	Parameter	Mean	CV (%)	Parameter	Mean	CV (%)	Parameter	Mean	CV (%)
A	FRTALLOC_BASE	88.715	54.429	FRTALLOC_BASE	52.227	123.389	FRTALLOC_BASE	75.717	74.642
A	WOODMRESPA	0.181	47.023	QWODFOLMIN	3.094	61.075	QWODFOLMIN	1.363	51.107
A	BASEFOLRESPFRAC	0.097	28.491	RESPQ10	2.981	51.829	WOODMRESPA	0.221	46.430
A	QWODFOLMIN	4.028	24.632	BASEFOLRESP FRAC	0.093	46.728	FRTLOSS_SCALE	3.352	44.372
A	FRTLOSS_SCALE	3.303	24.178	WOODMRESPA	0.111	42.231	MFOLOPT	0.699	32.916
A	MFOLOPT	0.338	16.603	FRTLOSS_SCALE	5.369	25.779	BASEFOLRESP FRAC	0.106	25.451
A	RESPQ10	1.981	16.064	GRESPFRAC	0.228	16.925	ROOTMRESPFRA C	0.881	8.171
A	ROOTMRESPFRAC	0.776	6.718	ROOTMRESPFRAC	0.598	12.930	GRESPFRAC	0.262	4.283

Table 3. *Cont.*

Group	Fagus Sylvatica			Picea Abies			Pinus Sylvestris		
	Parameter	Mean	CV (%)	Parameter	Mean	CV (%)	Parameter	Mean	CV (%)
A	GRESPFRAC	0.222	5.815	MFOLOPT	1.420	11.100	RESPQ10	2.064	1.509
N	FRET_N	0.466	47.019	EXPL_NO3	0.149	76.562	AMAXB	44.4	44.553
N	EXPL_NO3	0.202	42.584	EXPL_NH4	0.217	74.349	NCFRTOPT	0.006	42.086
N	EXPL_NH4	0.363	21.501	AMAXB	37.2	37.917	EXPL_NH4	0.333	41.451
N	AMAXB	55.6	14.698	NCSAPOPT	0.002	37.124	EXPL_NO3	0.252	15.294
N	NCSAPOPT	0.001	14.343	NCFRTOPT	0.009	23.406	SENESCSTART	240.4	10.535
N	NCFRTOPT	0.007	13.070	FRET_N	0.243	13.592	NCFOLOPT	0.019	5.071
N	NCFOLOPT	0.030	10.683	NCFOLOPT	0.012	5.573	NCSAPOPT	0.001	3.988
N	SENESCSTART	240.7	8.768	SENESCSTART	208.6	0.915	FRET_N	0.599	2.194
T	GDDFOLSTART	304.1	56.337	GDDWODEND	1591.5	35.090	GDDWODSTART	367.8	45.798
T	GDDWODEND	1643.8	34.031	GDDWODSTART	179.8	9.172	GDDWODEND	1538.2	26.710
T	GDDFOLEND	603.6	25.309	GDDFOLSTART	299.8	8.838	GDDFOLSTART	239.5	16.397
T	GDDWODSTART	232.3	18.472	GDDFOLEND	1235.4	6.737	GDDFOLEND	1287.6	3.857
T	PSNTMAX *	316.4	2.410	PSNTOPT *	301.8	3.754	PSNTOPT *	292.8	1.730
T	PSNTOPT *	301.7	1.073	PSNTMAX *	310.6	0.737	PSNTMAX *	314.6	0.907
T	PSNTMIN *	278.1	0.316	PSNTMIN *	270.3	0.252	PSNTMIN *	272.1	0.801
W_L	EXT	0.354	34.717	H2OREF_A	0.239	21.531	H2OREF_A	0.347	49.831
W_L	H2OREF_A	0.271	17.406	EXT	0.597	10.762	WUECMAX	10.295	17.160
W_L	WUECMAX	13.343	2.472	WUECMAX	13.589	2.489	EXT	0.580	6.529

* Values given in K for CV calculation.

Table 4. Summary of physiological parameters obtained by multi-site calibrations per species type. Parameters are grouped by allocation and respiration (A), nitrogen availability (N), temperature (T) and water availability and light extinction (W_L).

Parameter	Group	Fagus Sylvatica	Picea Abies	Pinus Sylvestris
BASEFOLRESPFRAC	A	0.085	0.133	0.146
FRTALLOC_BASE	A	86.0	17.7	52.4
FRTLOSS_SCALE	A	2.423	5.689	4.240
GRESPFRAC	A	0.240	0.214	0.238
MFOLOPT	A	0.332	1.583	0.423
QWODFOLMIN	A	3.052	4.123	0.602
RESPQ10	A	1.693	2.637	2.094
ROOTMRESPFRAC	A	0.662	0.553	0.759
WOODMRESPA	A	0.166	0.130	0.118
AMAXB	N	62.6	23. 3	52.0
EXPL_NH4	N	0.245	0.306	0.209
EXPL_NO3	N	0.301	0.189	0.062
FRET_N	N	0.520	0.420	0.617
NCFOLOPT	N	0.030	0.016	0.014
NCFRTOPT	N	0.009	0.020	0.004
NCSAPOPT	N	0.001	0.001	0.001
SENESCSTART	N	208.9	207.3	258.4
GDDFOLEND	T	521.3	1257. 7	1054.3
GDDFOLSTART	T	184.4	311.3	234.1
GDDWODEND	T	1738.9	1012.9	1317.1
GDDWODSTART	T	139.7	256.9	202.5
PSNTMAX	T	45.1	38.8	40.6
PSNTMIN	T	4.450	−2.494	0.650
PSNTOPT	T	34.5	35.1	20.5
EXT	W_L	0.532	0.632	0.560
H2OREF_A	W_L	0.349	0.295	0.212
WUECMAX	W_L	12.3	13.7	10.3

3. Results

3.1. Site-Specific Parameter Variability

3.1.1. Allocation and Respiration Parameters

Model parameters describing carbon allocation show the largest variations both between sites and between tree species (Tables 3 and 4). The parameter "relative share of foliage growth to root growth" (FRTALLOC_BASE) exhibits the largest CV for all tree species (>50%). The only other parameter that shows CVs >40% for all tree species is the "wood maintenance respiration as a fraction of gross photosynthesis" (WOODMRESP). In addition, spruce and pine both show high CVs (>50%) for the "minimum ratio of carbon allocation to wood and foliage" (QWODFOLMIN). Specifically for spruce forests, high CVs are further obtained for the respiration-related parameters RESPQ10 (>50%) and BASEFOLRESPFRAC (>40%) (see Table 2 for explanations). In contrast, pine specific high CVs are obtained for FRT_LOSS_SCALE (>40%). All other parameters of this group consistently exhibit CVs <35% for all tree species.

3.1.2. Nitrogen Dependency

Parameters representing N dependencies varied across all tree species (Table 3). For beech forests, the highest CV is obtained for the parameter "maximum fraction of nitrogen retranslocated before tissue loss" (FRET_N). There is small variability in the parameters "optimum nitrogen concentration of foliage" (NCFOLOPT) and "day of year after which leaf death can occur" (SENESCSTART). For spruce stands, CV values are high for parameters describing the exploitation of nitrate and ammonium (EXPL_NH4 and EXPL_NO3) and low for the parameter SENESCSTART. For pine, the largest variations are obtained for the parameters "nitrogen dependency of photosynthesis" (AMAXB), "optimum nitrogen concentrations of fine roots" (NCFRTOPT) and EXPL_NH4 while the lowest CV value is found for FRET_N.

3.1.3. Temperature Dependency

Model parameters used to describe the temperature dependency vary substantially across sites (Table 3). The highest CV values for all tree species are found for the parameters "minimum temperature sum for foliage activity onset" (GDDFOLSTART), "wood activity offset" (GDDWODEND) and "wood activity onset" (GDDWODSTART). All tree species consistently show lowest CV values (<4%) for the parameters "maximum temperature for photosynthesis" (PSNTMAX), "optimum temperature for photosynthesis" (PSNTOPT) and "minimum temperature for photosynthesis" (PSNTMIN).

3.1.4. Water Dependency

The parameters describing tree water acquisition and water use efficiency of photosynthesis differed considerably between tree species (Table 3). For spruce and pine stands, the variation is highest for the "relative available soil water content at which stomata conductance is affected" (H2OREF_A), whereas for beech the highest CV is found for the "light extinction attenuation coefficient" (EXT) parameter. The smallest variation for beech and spruce had been obtained for the "maximum water use efficiency constant" (WUECMAX) while for pine, EXT shows the lowest CV.

3.2. Species-Specific Parameter Variability

Species-specific parameter values differ from each other for all tree species (Table 4). Only the parameter "optimum nitrogen concentration of living wood" (NCSAPOPT) shows similar values for all tree species. Parameters describing allocation and nitrogen dependencies varied most. AMAXB, which is a sensitive parameter for CO_2 assimilation (see Table 2 for description), was highest for beech and lowest for spruce. In contrast, the main parameter describing respiration as fraction of maximum photosynthesis" (BASEFOLRESPFRAC) was high for spruce and low for beech forests.

3.3. Measured vs. Simulated Daily and Monthly CO_2 Exchange Fluxes

3.3.1. Comparison of Model Performances for the Calibration and Evaluation Periods

The application of site-specific and multi-site parameters improved simulation results for GPP and NEE on average by 27% and 38%, respectively, as compared to *a priori* parameter sets (data not shown). For the calibration period r^2 values for the comparison of measured and simulated daily CO_2 exchange fluxes are in between 0.51 to 0.90, model efficiency (ME) ranges from 0.48 to 0.85 and RMSPEn from 0.39 to 0.72. As can be expected, model performance criteria were slightly less good for the evaluation period in most cases (see Table 5; a comparison of simulated and measured C fluxes separated by forest sites for both periods are also illustrated in Figure 1). Looking at the slope of the relationship between simulations and measurements, simulations generally underestimate GPP and NEE, which is more expressed with multi-site parametrization than with the site-specific parameters (except GPP for the evaluation period; see Figure 1). The following result and discussion sections only refer to the sequences of data corresponding to the evaluation period.

Table 5. Comparison of model evaluation criteria for daily CO_2 exchange fluxes with site-specific parameters during the calibration period (CP) and evaluation period (EP).

Tree Species	Site	CO_2 Flux	r^2		ME		$RPMSE_n$	
			CP	EP	CP	EP	CP	EP
Pinus sylvestris	FI-Hyy	GPP	0.85	0.86	0.85	0.81	0.39	0.44
		NEE	0.65	0.71	0.61	0.63	0.62	0.61
	BE-Bra	GPP	0.85	0.80	0.83	0.73	0.41	0.52
		NEE	0.70	0.70	0.64	0.63	0.60	0.61
	NL-Loo	GPP	0.90	0.71	0.84	0.65	0.39	0.59
		NEE	0.74	0.51	0.70	0.47	0.55	0.72
	FI-Sod	GPP	0.78	0.68	0.78	0.34	0.47	0.81
		NEE	0.64	0.35	0.63	0.22	0.61	0.88
Picea abies	DE-Hoeg	GPP	0.67	-	0.62	-	0.61	-
		NEE	0.51	-	0.48	-	0.72	-
	DE-Tha	GPP	0.85	0.80	0.85	0.79	0.39	0.45
		NEE	0.65	0.65	0.61	0.60	0.62	0.63
	DE-Wet	GPP	0.85	0.79	0.83	0.77	0.41	0.48
		NEE	0.70	0.56	0.64	0.54	0.60	0.68
Fagus sylvatica	IT-Col	GPP	0.79	0.66	0.77	0.63	0.48	0.60
		NEE	0.70	0.57	0.70	0.55	0.55	0.67
	DK-Sor	GPP	0.84	0.85	0.81	0.83	0.43	0.42
		NEE	0.67	0.69	0.64	0.67	0.60	0.57
	FR-Hes	GPP	0.83	0.87	0.71	0.84	0.54	0.40
		NEE	0.72	0.73	0.69	0.70	0.56	0.55

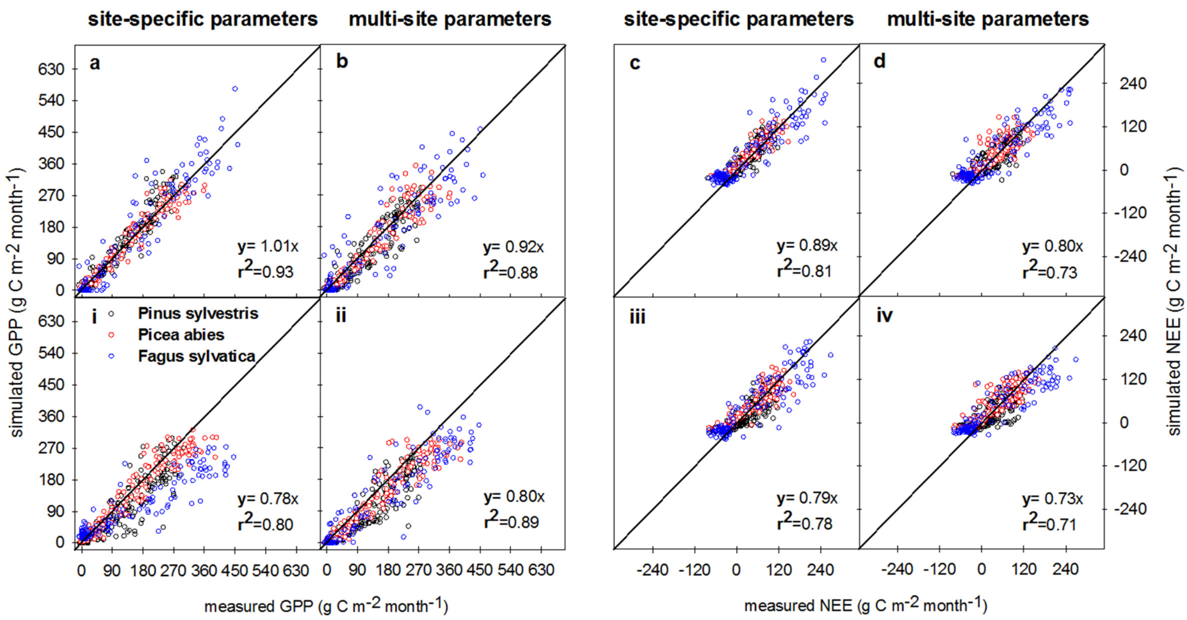

Figure 1. Comparison of monthly aggregated Gross Primary Production "GPP" (left) and Net Ecosystem Exchange "NEE" (right) for all 10 forest ecosystems for the calibration period (upper panel: (**a**–**d**)) and the evaluation period (lower panel: (**i**–**iv**)). Different species are pooled but indicated with different colors (see description in panel (i)).

3.3.2. Gross Primary Productivity (GPP)

The model evaluation for daily CO_2 fluxes based on simulations using site-specific parametrizations produced r^2 measures of 0.66–0.87, ME values of 0.34–0.84 and RMSPEn values of 0.40–0.81, while multi-site calibration produced an r^2 of 0.66–0.87, ME values of 0.53–0.77 and RMSPEn values of 0.48–0.69 (Table 6). For the evaluation of monthly aggregated GPP, indicators always show better agreement compared to daily values with both site-specific and multi-site calibrations (Table 7).

3.3.3. Net Ecosystem Exchange (NEE)

The PnET module predicts daily and monthly NEE dynamics at DE-Hoeg and DE-Tha, FI-Hyy, NL-Loo, FR-Hes, IT-Col, FI-Sod, but is imprecise for BE-Bra, DK-Sor and DE-Wet sites with both, site-specific and multi-site parameters. At the latter sites, total ecosystem respiration (TER) is underestimated, particularly during winter. At a daily time resolution, site-specific calibration revealed r^2 values ranging from 0.35 to 0.73, ME from 0.22 to 0.70 and RMSPEn from 0.55 to 0.88 while the multi-site calibration showed an r^2 of 0.35 to 0.73, ME of 0.22 to 0.70 and RMSPEn of 0.55 to 0.88 (Table 6 and Figure 2). Again, aggregating to monthly values increases the values for r^2, ME and RMSPEn with both applied calibrations (Table 7).

Table 6. Annual means of daily measured and simulated GPP and NEE fluxes obtained with either site-specific or multi-site derived parameters (annual daily means represent >320 measurement points per years at most sites). Abbreviations: ME: model efficiency, RMSPEn: normalized root mean square prediction error.

Tree Species	Site	Period		Calibration Type	Annual Mean CO_2 Fluxes ($g\ C\ m^{-2}\ day^{-1}$) Measured Mean	Measured STD.	SIMULATED Mean	SIMULATED STD.	Model r^2	ME	RMSPEn
Pinus sylvestris	FI-Hyy	2004–2009	GPP	multi-site	3.04	3.28	2.19	2.74	0.84	0.76	0.49
				site-specific	3.04	3.28	2.32	2.76	0.86	0.81	0.44
			NEE	multi-site	0.74	1.87	0.29	1.20	0.59	0.51	0.70
				site-specific	0.74	1.87	0.34	1.21	0.71	0.63	0.61
	BE-Bra	2006–2010	GPP	multi-site	3.72	3.31	3.32	2.80	0.79	0.77	0.48
				site-specific	3.72	3.31	2.97	2.58	0.80	0.73	0.52
			NEE	multi-site	0.32	2.35	1.10	1.53	0.69	0.55	0.67
				site-specific	0.32	2.35	0.54	1.39	0.70	0.63	0.61
	NL-Loo	2006–2010	GPP	multi-site	4.39	3.16	3.42	3.17	0.73	0.61	0.62
				site-specific	4.39	3.16	4.26	3.40	0.71	0.65	0.59
			NEE	multi-site	1.30	1.88	1.11	1.69	0.50	0.46	0.74
				site-specific	1.30	1.88	1.34	1.72	0.51	0.47	0.72
	FI-Sod	2005–2008	GPP	multi-site	1.55	2.11	0.72	1.04	0.87	0.53	0.69
				site-specific	1.55	2.11	0.60	0.96	0.68	0.34	0.81
			NEE	multi-site	−0.10	0.99	0.05	0.45	0.35	0.31	0.83
				site-specific	−0.10	0.99	−0.11	0.23	0.35	0.22	0.88
Picea abies	DE-Tha	2006–2010	GPP	multi-site	5.52	4.55	4.34	3.54	0.84	0.76	0.49
				site-specific	5.52	4.55	5.12	4.03	0.80	0.79	0.45
			NEE	multi-site	1.71	2.41	1.66	2.16	0.68	0.68	0.57
				site-specific	1.71	2.41	1.94	2.39	0.65	0.60	0.63
	DE-Wet	2006–2008	GPP	multi-site	4.68	3.99	4.05	3.74	0.78	0.75	0.50
				site-specific	4.68	3.99	4.13	3.63	0.79	0.77	0.48
			NEE	multi-site	0.38	2.61	1.26	2.04	0.48	0.36	0.80
				site-specific	0.38	2.61	0.74	1.87	0.56	0.54	0.68
Fagus sylvatica	IT-Col	2004–2007	GPP	multi-site	3.95	4.62	3.61	4.53	0.66	0.63	0.61
				site-specific	3.95	4.62	3.28	4.15	0.66	0.63	0.60
			NEE	multi-site	1.57	3.40	1.02	2.59	0.54	0.51	0.70
				site-specific	1.57	3.40	1.12	2.74	0.57	0.55	0.67
	DK-Sor	2005–2009	GPP	multi-site	5.01	5.23	3.47	4.17	0.84	0.74	0.51
				site-specific	5.01	5.23	4.36	5.31	0.85	0.83	0.42
			NEE	multi-site	0.68	3.18	1.07	2.38	0.72	0.69	0.56
				site-specific	0.68	3.18	0.95	2.33	0.69	0.67	0.57
	FR-Hes	2006–2009	GPP	multi-site	4.97	5.48	3.91	4.19	0.82	0.77	0.48
				site-specific	4.97	5.48	5.17	6.03	0.87	0.84	0.40
			NEE	multi-site	1.40	3.49	1.30	2.40	0.69	0.67	0.57
				site-specific	1.40	3.49	1.72	3.47	0.73	0.70	0.55

Table 7. Averaged annual means of monthly aggregated measured and simulated GPP and NEE fluxes obtained with either site-specific or multi-site parameters. Abbreviations: ME: model efficiency, RMSPEn: normalized root mean square prediction error.

Tree Species	Site	Period		Calibration Type	Annual Mean CO_2 Fluxes (kg C m^{-2} $month^{-1}$) Measured Mean	Measured STD.	Simulated Mean	Simulated STD.	Model r^2	Model ME	Model RMSPEn
Pinus sylvestris	FI-Hyy	2004–2009	GPP	multi-site	0.09	0.09	0.07	0.08	0.90	0.81	0.43
				site-specific	0.09	0.09	0.07	0.08	0.94	0.87	0.36
			NEE	multi-site	0.02	0.05	0.01	0.03	0.65	0.53	0.68
				site-specific	0.02	0.05	0.01	0.03	0.87	0.71	0.53
	BE-Bra	2006–2010	GPP	multi-site	0.11	0.09	0.10	0.08	0.93	0.91	0.30
				site-specific	0.11	0.09	0.09	0.07	0.95	0.86	0.37
			NEE	multi-site	0.01	0.06	0.03	0.04	0.89	0.66	0.58
				site-specific	0.01	0.06	0.02	0.04	0.88	0.78	0.47
	NL-Loo	2006–2010	GPP	multi-site	0.13	0.09	0.10	0.09	0.84	0.72	0.52
				site-specific	0.13	0.09	0.13	0.10	0.80	0.76	0.49
			NEE	multi-site	0.04	0.04	0.03	0.04	0.69	0.62	0.61
				site-specific	0.04	0.04	0.04	0.04	0.65	0.58	0.65
	FI-Sod	2005–2008	GPP	multi-site	0.05	0.06	0.02	0.03	0.96	0.54	0.67
				site-specific	0.05	0.06	0.02	0.03	0.73	0.35	0.80
			NEE	multi-site	0.00	0.02	0.00	0.01	0.44	0.38	0.78
				site-specific	0.00	0.02	0.00	0.00	0.46	0.24	0.86
Picea abies	DE-Tha	2006–2010	GPP	multi-site	0.17	0.13	0.13	0.10	0.96	0.82	0.42
				site-specific	0.17	0.13	0.16	0.11	0.93	0.90	0.31
			NEE	multi-site	0.05	0.06	0.05	0.05	0.87	0.87	0.36
				site-specific	0.05	0.06	0.06	0.05	0.82	0.80	0.45
	DE-Wet	2006–2008	GPP	multi-site	0.14	0.11	0.12	0.10	0.92	0.89	0.33
				site-specific	0.14	0.11	0.13	0.10	0.94	0.91	0.30
			NEE	multi-site	0.01	0.06	0.04	0.05	0.58	0.35	0.80
				site-specific	0.01	0.06	0.02	0.03	0.83	0.70	0.55
Fagus sylvatica	IT-Col	2004–2007	GPP	multi-site	0.12	0.13	0.11	0.13	0.82	0.81	0.43
				site-specific	0.12	0.13	0.10	0.12	0.83	0.80	0.44
			NEE	multi-site	0.05	0.10	0.03	0.07	0.71	0.67	0.57
				site-specific	0.05	0.10	0.03	0.08	0.75	0.72	0.52
	DK-Sor	2005–2009	GPP	multi-site	0.15	0.15	0.11	0.12	0.94	0.80	0.44
				site-specific	0.15	0.15	0.13	0.15	0.93	0.91	0.29
			NEE	multi-site	0.02	0.09	0.03	0.06	0.85	0.79	0.45
				site-specific	0.02	0.09	0.03	0.06	0.86	0.80	0.45
	FR-Hes	2006–2009	GPP	multi-site	0.15	0.16	0.12	0.12	0.92	0.84	0.40
				site-specific	0.15	0.16	0.16	0.17	0.95	0.94	0.23
			NEE	multi-site	0.04	0.10	0.04	0.07	0.85	0.79	0.45
				site-specific	0.04	0.10	0.05	0.09	0.86	0.84	0.39

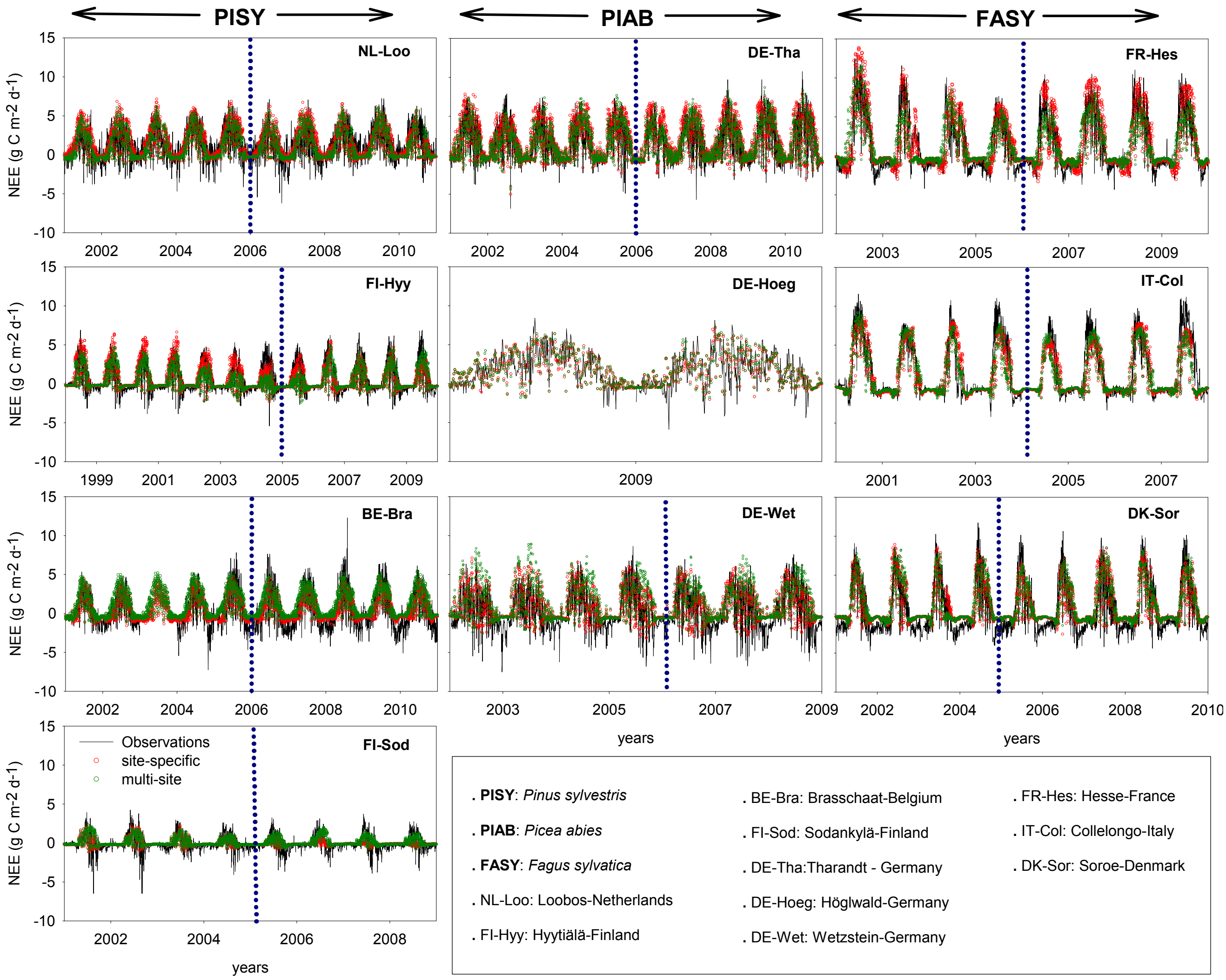

Figure 2. Comparison of daily simulated and measured Net Ecosystem Exchange (NEE) for all investigated sites. The dotted line separates simulations with calibrated (left side) and non-calibrated (right side) parameters. For DE-Hoeg, no evaluation run with a non-calibrated parameter set has been carried out.

4. Discussion

This study shows that species-specific or multi-site parameters can be derived and evaluated even for a complex forest growth module such as PnET. In order to address the optimization of plant physiological processes that describe C exchange processes, it is necessary to keep parameters from other model parts such as those describing soil organic matter decomposition. Therefore, the possibility of adjusting respiration fluxes at the ecosystem scale, which originate from plant (autotrophic) as well as soil (heterotrophic) respiratory processes, was limited. With respect to those processes, we thus relied on a previous parameter calibration study of the soil biogeochemistry sub-module [43]. In the current investigation, the parameter derivation of the plant physiology module reveals that: (a) parameters are specific to particular ecosystem properties (see Section 4.1); and (b) generally defined (species-specific) model parameters can still describe forest gas exchange across a multitude of sites (see Sections 4.2 and 4.3).

4.1. Site-Specific versus Multi-Site (Species-Specific) Parametrization

CO_2 gas exchange rates as well as parameter values are correlated with site properties (see Figure 3). This reflects the fact that parameters restrict model applications to a certain range of environmental conditions. The fact that site-specific parameters perform better indicates that (a) the underlying process representation in the model misses some sensitivity to environmental drivers and (b) the model is limited in its ability to reflect plant adaptations to changes in site conditions. However, parameters derived at specific sites are often inferior to multi-site parametrizations at sites other than those where they have been obtained (Figure 4). Hence, site-specific calibration is particularly suitable to address responses to current climate conditions but should be used with caution if acclimation processes to local biotic and abiotic conditions are expected [20,21,26,116,117]. For example, the inter-site differences for model parameters involved for photosynthetic activity *i.e.*, AMAXB, PSNTOPT, between boreal and temperate pine forests are large. Site-specific calibration for "nitrogen dependency of photosynthesis" (AMAXB) results in a higher value (in average 50%) in boreal compared to temperate pine stands which is in accordance with experimental findings [118]. Acclimation to local environmental conditions has been reported for pine [22], spruce [23] beech [24] and other tree species [21,25]. Gornall and Guy [116] as well as Soolanayakanahally *et al.* [21] point out that the variability of photosynthetic activity (in our model AMAXB) can be very large across geographical regions. Therefore, sometimes latitude information is used to describe a shifting response to environmental gradients of radiation, temperature, nutrient and water availability [119]. However, this is only an empirical work-around for missing process sensitivity that fails to describe an increase in C uptake efficiency originating from growing season length, radiation or nitrogen and water availability along latitudinal gradients [116]. Similarly, the "optimum temperature for photosynthesis" (PSNTOPT) is found to be much lower for boreal (FI-Hyy, FI-Sod, in average 8.74 °C) than for temperate forest (NL-Loo, BE-Bra). This is in agreement with field experiments where the link between photosynthetic response potentials and prevailing growing season temperatures had been demonstrated [120]. The differentiation of site-calibrated parameters in this study indicates the degree of acclimation of trees to specific environmental conditions. That the adaptation of only a few parameters such as AMAXB can improve the representation of NEE, GPP *etc.* across different climates has been demonstrated before [121,122]. However, according to our knowledge, a comparison of site-specific paramemters and multi-site parameters has not been done in this context before.

On the other hand multi-site parametrizations can reasonably perform over a wider range of environmental conditions: GPP and NEE (and thus total ecosystem respiration) during spring and summer, where 90% of the CO_2 exchange fluxes occurs, are well-represented (Figure 5). Also, an overall representation of r^2 values between 0.66 and 0.87 indicates a good representation of GPP and NEE throughout the year (Table 5 and Figure 1). This ability of the model suggests that ecosystem responses to seasonal and inter-annual variations in environmental conditions are covered due to the representation of general principles of eco-physiology and biogeochemistry. It also indicates that the general parametrization can be used with some caution at a wider regional scale, such as for Central Europe.

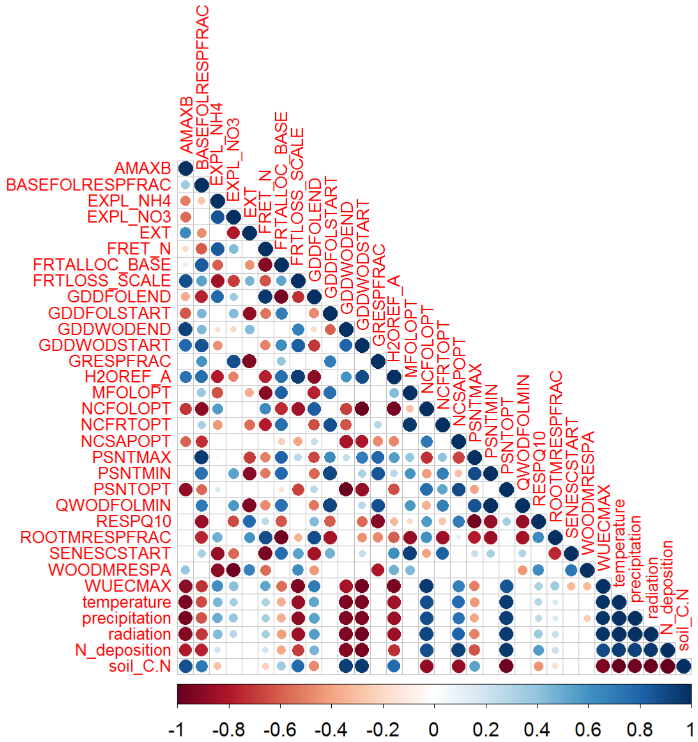

Figure 3. Combined correlation matrix of calibrated parameter values and site properties for Scot pine forests. The correlation is given by r^2 values. The size of the circles relates to the level of significance: small circles indicate significance between 0.01 and 0.05 while big circles correspond to high significance (<0.01). Blank cells indicate that no significant values are obtained ($p > 0.05$). For parameter descriptions, see Table 2. Environmental properties are given in lowercase characters (temperature in annual means, precipitation and N deposition as annual sums and soil C:N ratio for the first 5 cm soil depth) while model parameters are in uppercase characters.

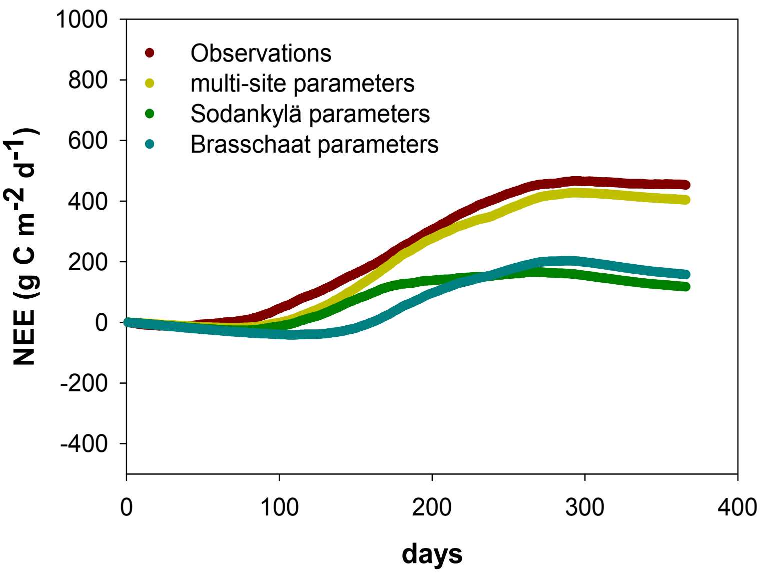

Figure 4. Cumulative daily mean values of the period 2001–2010 of Net Ecosystem Exchange (NEE) obtained with multi-site, boreal and temperate parameters calculated with the specifications of the pine forest of Loobos-Netherlands.

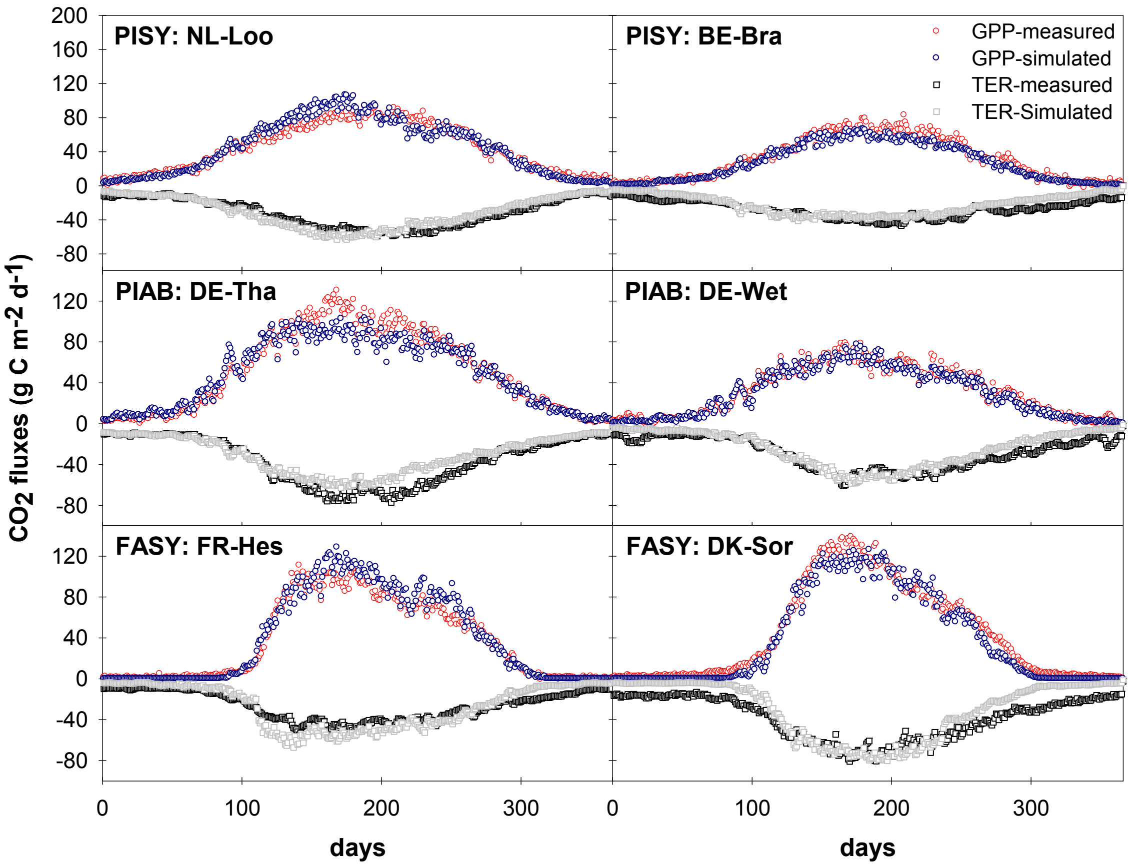

Figure 5. Inter-daily mean for Gross Primary Production (GPP) and Net Ecosystem Exchange (NEE) obtained with site-specific parameters at stands with different model performances (best left site, worst right site). Daily mean values are calculated throughout the evaluation period (see Table 6 for details). PISY: *Pinus sylvestris*, PIAB = *Picea abies*, FASY = *Fagus sylvatica*.

4.2. Gross Primary Production and Respiration

The predictive capability for GPP ($r^2 \geq 0.66$) compares well with other studies using the DNDC forest model [75,121] though LandscapeDNDC results tend to be better-correlated with measurements if site-specific parameters are used (Table 6). In this regard, simulation results are more similar to results obtained with physiologically based models such as the model for Carbon Assimilation and respiration, Transpiration, evaporation and drainage, Allocation and growth in Even Aged forests CASTANEA [13] or the Physiological Simulation Model (PSIM) [41], which are more demanding in terms of parametrization. The use of multi-site parameters resulted in an underestimation of GPP during spring and autumn for evergreen forests, as temperature dependence parameters hamper model processes (*i.e.*, GDDFOLSTART, GDDFOLEND). The latter parameters correspond to the minimum and maximum temperature sum for foliage activity onset, and they are applied across a transect. A more comprehensive uncertainty analysis associated with C flux measurements at the former site can be found in Wu *et al.* [123].

In general, only the simulations at the beech site in Denmark (DK-Sor) indicate a systematic underestimation of GPP. A reason for this finding might be the fact that the stand is not a pure beech stand but contains approximately 20% of spruce and larch. Also, the occurrence of ground vegetation and its seasonally specific contribution to GPP might be partly responsible for this result. The importance of phenology for seasonal representation of GPP has been demonstrated in a modeling study which compared 14 different models [124]. In the current investigation we found that the phenology of 9 out of 10 sites was well-represented (see Tables 6 and 7), suggesting that the growing-degree-day approach as implemented in PnET (see appendix) is sufficiently able to describe the forest phenology in Europe. However, the growing-degree-day approach fails in years where vernalization periods are not met, which had been the case in only one occasion here (BE-Bra: 2005). In this single case, the lack of representation of GPP also affects TER because residual respiration rates are calculated as dependent on biomass and temperature with empirically defined parameters.

It should also be noted that the distinction between GPP and TER in measurements is empirically derived from NEE and thus depends on additional assumptions [125]. For example, Lavigne *et al.* [126] showed that nocturnal EC estimates were poorly correlated with chamber measurements at six coniferous boreal sites, with EC based TER underestimating chamber based soil C losses particularly during the early part of the growing season. Eventually this could be one reason for the deviations between simulated and measured TER which occurred in spring and autumn (e.g., DE-Hoeg).

4.3. Net Ecosystem Exchange

NEE represents the smallest ecosystem CO_2 flux and it is susceptible to errors in both assimilation and respiration process simulations. Nevertheless, NEE comparisons showed r^2 ranging from 0.35 to 0.73 throughout a broad range of environmental conditions using the multi-site parametrization (Table 6). These correlations are comparable to those obtained in previous studies which, however, always used site-specific parametrization [12,121]. In fact, the use of site-specific parameters yielded a similar magnitude of model evaluation criteria (*i.e.*, r^2) than more elaborated models e.g., FinnFor [127] or PSIM [36,41]. The largest deviations for NEE is observed at three temperate sites (DK-Sor, BE-Bra, DE-Wet) during the winter period (Figure 5). Since vegetation respiration can be neglected during this period, it is likely that soil respiration is underestimated. This might be attributed to the fact that the snow cover dynamics and its effect on soil temperature is relatively simple as represented in LandscapeDNDC. A further source of uncertainty originates from the derivation of "measured" TER, which has been discussed in the previous paragraph.

NEE depends on boundary conditions which also develop with the forest structure, *i.e.*, tree height and tree number. In turn, these properties are calculated from NEE using allocation and senescence routines while mass balance is preserved [41]. Therefore, some uncertainty in model simulations originates from the representation of these processes and is difficult to evaluate directly. In order to show that these internal dynamics in boundary conditions are considered by the LandscapeDNDC model, we present some evaluations of forest development for sites where these data are available (Figure 6). It should be noted that the growth simulations (similar to water balance or soil biogeochemistry) have not been the target of specific parametrizations.

4.4. Uncertainties of Model Process Implementation and Measurements

Physiological processes that indirectly affect carbon uptake or release might be insufficiently described (e.g., phenology) or fully neglected [128]. For example the French beech stands (FR-Hes) respond much less negatively to the relative dry and warm spring period in 2007 than simulated, indicating possible drought adaptations at the sites, e.g., by regulation of mesophyll conductance. In other years the model overestimates annual GPP and TER, possibly due to stand damage in previous years that were not fully restored or due to disturbances that are not accounted for in the model, e.g., insect damage or masting occurrences. Nevertheless, the day–to-day comparison of simulation results and measurements shows high correlation coefficients for CO_2 exchange processes.

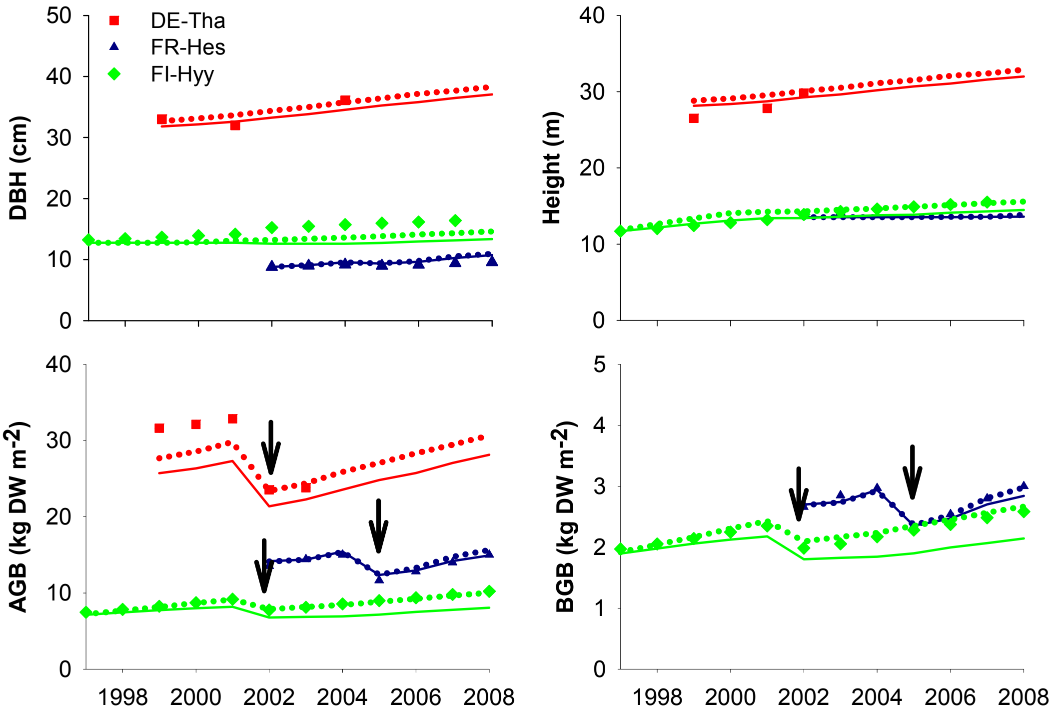

Figure 6. Measured and simulated forest development considering thinning events (indicated by arrows). Different colors indicate tree species: red squared/spruce (DE-Tha = Tharandt Germany), green diamond/pine (FI-Hyy = Hyytiälä Finland), and blue triangle/beech (FR-Hes = Hesse France). Measurements are represented by symbols and simulations by lines using dotted lines for simulations with site-specific parameters and straight lines for those with multi-site parameters. Abbreviations: AGB = aboveground biomass, BGB = belowground biomass, DBH = diameter at the breast height.

On the other hand, measurement uncertainties also need to be considered, particularly since many of the measured daily values of NEE are partly estimated with gap-filling measures during winter time. As mentioned above, TER and GPP are not directly measured but calculated based on statistical relationships, so that bottom-up (based on environmental data and drivers) model results are actually compared with top-down (based on NEE measurements) model results rather than measurements. Finally, eddy covariance-derived fluxes are subject to errors during times of low turbulence such as night time and winter periods [129] and at sites (or footprints) that are not homogenous or where advective fluxes can occur [130,131].

5. Conclusions

We conclude that the PnET module, used in conjunction with the soil process model DNDC, is capable of simulating daily C fluxes of pure stands of beech, spruce and pine for periods of several years. Site-specific as well as multi-site calibration allow model parameters to be found which are best suited to represent either local site conditions or general species responses with respect to CO_2 exchange fluxes. This has been tested for a range of different climatic and soil conditions using one species-specific parameter set, indicating its suitability for application to regional, national and continental scales. For site applications, however, a specific parametrization yields better results because parameters are allowed to reflect the adaptation of ecosystem properties to local conditions. In addition, the present study demonstrates that automated parametrization can serve as a valuable tool to detect the origin of model deficiencies. This can serve to identify which physiological processes need a higher sensitivity to environmental conditions to be applicable for larger regions or greater environmental changes (e.g., climate change).

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Author Contributions

Saúl Molina-Herrera collected measurements, set up the model and performed the LandscapeDNDC simulations. He analyzed simulation results, prepared figures, compiled data into tables and prepared the manuscript. Rüdiger Grote, David Kraus and Steffen Klatt developed the model and elaborated it throughout the calibration and evaluation process. Edwin Haas designed the model calibration, which was carried out by Ignacio Santabárbara. Ralf Kiese and Klaus-Butterbach-Bahl designed the research objective and supervised the work.

Conflicts of Interest

The authors declare no conflict of interest.

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