Contributions of climate, leaf area index and leaf physiology to variation in gross primary production of six coniferous forests across Europe: a model-based analysis

R.A. DUURSMA,[1,2,*] P. KOLARI,[1] M. PERÄMÄKI,[1] M. PULKKINEN,[1] A. MÄKELÄ,[1] E. NIKINMAA,[1] P. HARI,[1] M. AURELA,[3] P. BERBIGIER,[4] CH. BERNHOFER,[5] T. GRÜNWALD,[5] D. LOUSTAU,[4] M. MÖLDER,[6] H. VERBEECK[7,8] and T. VESALA[9]

[1] *Department of Forest Ecology, University of Helsinki, P.O. Box 27, FI-00014 Helsinki, Finland*

[2] *Corresponding author (remkoduursma@gmail.com)*

[3] *Finnish Meteorological Institute, Climate and Global Change Research, P.O. Box 503, FI-00101 Helsinki, Finland*

[4] *INRA, UR1263 EPHYSE, 71 Av Edouard Bourlaux, F-33883 Villenave d'Ornon, France*

[5] *Department of Meteorology, Institute of Hydrology and Meteorology, Technical University Dresden, Pienner Strasse 23, D-01737 Tharandt, Germany*

[6] *Department of Physical Geography and Ecosystems Analysis, Lund University, SE-223 62 Lund, Sweden*

[7] *Research Group of Plant and Vegetation Ecology, Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerp, Belgium*

[8] *Laboratory of Plant Ecology, Department of Applied Ecology and Environmental Biology, Ghent University, Coupure Links 653, B-9000 Ghent, Belgium*

[9] *Division of Atmospheric Sciences, Department of Physics, University of Helsinki, P.O. Box 64, FI-00014 Helsinki, Finland*

Summary Gross primary production (GPP) is the primary source of all carbon fluxes in the ecosystem. Understanding variation in this flux is vital to understanding variation in the carbon sink of forest ecosystems, and this would serve as input to forest production models. Using GPP derived from eddy-covariance (EC) measurements, it is now possible to determine the most important factor to scale GPP across sites. We use long-term EC measurements for six coniferous forest stands in Europe, for a total of 25 site-years, located on a gradient between southern France and northern Finland. Eddy-derived GPP varied threefold across the six sites, peak ecosystem leaf area index (LAI) (all-sided) varied from 4 to 22 $m^2\ m^{-2}$ and mean annual temperature varied from -1 to 13 °C. A process-based model operating at a half-hourly time-step was parameterized with available information for each site, and explained 71–96% in variation between daily totals of GPP within site-years and 62% of annual total GPP across site-years. Using the parameterized model, we performed two simulation experiments: weather datasets were interchanged between sites, so that the model was used to predict GPP at some site using data from either a different year or a different site. The resulting bias in GPP prediction was related to several aggregated weather variables and was found to be closely related to the change in the effective temperature sum or mean annual temperature. High R^2s resulted even when using weather datasets from unrelated sites, providing a cautionary note on the interpretation of R^2 in model comparisons. A second experiment interchanged stand-structure information between sites, and the resulting bias was strongly related to the difference in LAI, or the difference in integrated absorbed light. Across the six sites, variation in mean annual temperature had more effect on simulated GPP than the variation in LAI, but both were important determinants of GPP. A sensitivity analysis of leaf physiology parameters showed that the quantum yield was the most influential parameter on annual GPP, followed by a parameter controlling the seasonality of photosynthesis and photosynthetic capacity. Overall, the results are promising for the development of a parsimonious model of GPP.

Keywords: forest carbon uptake, forest productivity, process-based model.

* Present address: Centre for Plant and Food Science, University of Western Sydney, Bourke Street, Richmond, NSW 2753 Australia

Introduction

Gross primary production (GPP) is the primary source of all carbon fluxes in the ecosystem. Understanding variation

in GPP is vital for understanding and quantifying the car-bon sink of terrestrial ecosystems, and all subsequent car-bon flows such as growth, litter fall and respiration. There is a strong need for methods to scale GPP across sites both for quantification of the global carbon sink (Running et al. 1999) and as input to forest production models (Mäkelä et al. 2000). The eddy-covariance (EC) methodology is now a widely available tool for the measurement of net ecosystem CO_2 exchange (NEE), from which estimates of GPP can be derived by subtracting total ecosystem respiration (TER) (Falge et al. 2001, Reichstein et al. 2005). The large number of EC towers in forested sites (flux sites) now allows advancement in understanding site-to-site variation in GPP. A number of studies have analyzed EC data across a large number of sites, often focusing on NEE (e.g., Falge et al. 2002, van Dijk et al. 2005), but others have performed detailed analyses of GPP across sites and years as well (Law et al. 2002, Reichstein et al. 2007).

Factors that determine GPP can be roughly divided into climate, canopy structure and leaf-level physiology. Where leaf area index (LAI) – an important canopy-structure parameter – indicates the total amount of foliage that intercepts light and assimilates carbon, both leaf-level physiology and climatic factors determine the relative activity of this foliage. It is not easy to decide which of these factors is more important in scaling GPP across sites, because all of them have a large influence. It is often stressed that LAI is a primary determinant of carbon uptake of forest canopies (e.g., Running and Coughlan 1988). For example, O'Neill and DeAngelis (1980) found that woody increment is strongly related to leaf biomass across a large number of diverse sites, particularly for gymnosperms. On the other hand, Law et al. (2002) found that 50% of variation in GPP was explained by mean annual temperature across all FLUXNET sites, even though LAI varied 10-fold across sites. Another strong scalar across sites has emerged from relating productivity to integrate absorbed light by the canopy (Linder 1985, Landsberg et al. 1996, Mäkelä et al. 2008), which would combine the effects of light availability (climate factor) and interception of light (canopy structure). Instantaneous GPP is strongly related to incident light availability (Ruimy et al. 1995, Medlyn et al. 2003) for a given site – but how well does it explain variation across sites? Finally, variation in leaf physiological parameters has received much attention (e.g., Wright et al. 2004), in particular photosynthetic capacity which may help scale GPP across sites (Baldocchi and Meyers 1998). All these main factors impact annual GPP, but it is not clear which of them is more important to scale GPP within a single biome. In this study, we are primarily interested in site-to-site variation in GPP of coniferous forests, and limit the study to instantaneous effects on GPP, so that we ignore long-term effects of the nitrogen cycle (e.g., Magnani et al. 2007), and assume that site fertility is indirectly represented in LAI and leaf physiology.

To more clearly focus on stand structure versus climate effects, we exclude the effects of soil water availability on GPP in our model analysis. The difficulty with including a soil water feedback is the general paucity of required data such as soil water holding capacity, soil texture and water retention characteristics and rooting depth. Other studies have successfully modeled GPP in temperate coniferous forests without including soil water feedbacks (Turner et al. 2003b, Medlyn et al. 2005a, Mäkelä et al. 2008), and a widely-used method for scaling GPP across large spatial scales (MODIS; Turner et al. 2003a) does not include the effect of soil water feedbacks – but is still able to capture much site-to-site variation in observed GPP. We assume that, across sites, LAI has adapted to the average soil water balance of the site (Grier and Running 1977, Gholz 1982, Kergoat 1998), so that soil water balance is implicitly represented in stand structure. It is thus useful to study how much within-year, between-years within-sites and across-site variation in GPP can be explained with a model that does not include the effect of soil water content on stomatal conductance.

Process-based models (PBMs) that scale leaf physiology to the canopy and across time may help define how different factors interact to yield annual GPP, and which of these factors are most influential. It is common to perform a sensitivity analysis of a PBM to identify the influential parameters and components (e.g., Falge et al. 1997). However, usual sensitivity analyses are univariate, meaning that they evaluate the change in model predictions when one parameter is varied at a time. Such analyses are useful for quantifying the influence of parameters that vary independently of other parameters, but if strong correlations between inputs exist, then this method is much less informative (Guan 1999, Radtke et al. 2001). To test the influence of weather variables on GPP, for example, it makes little sense to change air temperature while keeping light and vapor pressure deficit (VPD) constant because these three variables are strongly correlated both within years and across sites. Medlyn et al. (2005a) suggested a simple method to determine relative influences of climate, physiology and canopy structure on annual GPP as estimated by a PBM, and applied it to three coniferous sites in Europe. The weather dataset, canopy-structure information or leaf physiology is switched between the sites, and the effect on simulated annual GPP is determined. This process can be repeated between all site-to-site combinations, to determine the 'aggregate' sensitivity of the PBM to variation in weather, canopy structure or leaf physiology.

In this study, we test the relative importance of climate, canopy structure and leaf physiology across a gradient of six conifer-dominated sites in Europe, from northern Finland to southern France. Across these six sites, LAI varies from 4 to 22 $m^2\ m^{-2}$ and mean annual temperature varies from -1 to $13\ °C$. We perform an experiment where climate and canopy-structure information is exchanged between sites, and the resulting bias in model predictions is compared to summary variables describing

the difference in climate and canopy structure between the sites. Finally, we perform a sensitivity analysis on important leaf physiological parameters. We use a model that scales leaf-level physiology to the canopy that has been tested successfully against EC-derived estimates of GPP (Mäkelä et al. 2006).

Methods

GPP from EC data

We used data from six flux sites in conifer-dominated forests across Europe: Sodankylä (Finland), Hyytiälä (Finland), Norunda (Sweden), Tharandt (Germany), Le Bray (France) and Brasschaat (Belgium) (see Table 1 for details; and Figure 1 for a map). All stands were coniferous with either Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L.) or maritime pine (*Pinus pinaster* Ait.), with the exception of Brasschaat, where the patchy overstory consists of Scots pine with a significant proportion of patches with the deciduous pedunculate oak (*Quercus robur* L.). Site-specific information on EC measurements can be found in the references given in Table 1.

The GPP was estimated as the difference between measured net ecosystem exchange (NEE) and estimated TER (Falge et al. 2001). Half-hourly TER was modeled from nighttime NEE measurements as an Arrhenius-type function of either air temperature (Norunda and Tharandt), the average of air and soil temperature (Le Bray) or soil surface (organic layer) temperature (Brasschaat, Hyytiälä and Sodankylä). The NEE was filtered by turbulence and atmospheric stability, the criteria varying from site to site. For Le Bray, Tharandt and Sodankylä, we applied site-specific friction velocity ($u*$) thresholds of 0.2–0.35 m s^{-1}. Fluxes in Hyytiälä were filtered with combined $u*$ and Obukhov length thresholds (Markkanen et al. 2001). For Brasschaat, the data were binned into wind direction sectors and different criteria for atmospheric stability were applied for each sector according to the fetch in that direction (Nagy et al. 2006).

The temperature dependence of nighttime TER was applied to daytime, and the half-hourly daytime GPP was computed by subtracting the estimated TER from the measured NEE. For Sodankylä, Hyytiälä and Le Bray, the GPP estimation procedure followed the methods described in detail by Mäkelä et al. (2006). In short, the temperature sensitivity of TER and the curvature of photosynthetic light response were estimated over a 2-month period in a summer when there was no apparent effect of drought on fluxes. This was done only in 1 year per site to eliminate the inter-annual variation that would be largely random due to the noisy EC data. The basal level of TER (respiration in standard temperature) and GPP (light-saturated photosynthesis) were then estimated daily in a moving time window. Some details of the estimation varied between sites such as the length of the moving time window.

For each site, half-hourly measurements of photosynthetic photon flux density (PPFD) above the canopy (μmol m^{-2} s^{-1}), air temperature (°C), CO_2 concentration (ppm) and absolute H_2O concentrations (ppm) were available. The VPD was estimated from H_2O concentration using standard equations.

Missing data

From the available data, several site-years were discarded because of a large proportion of missing data, these were: 2003 in Sodankylä; 1998 in Norunda; 1998, 1999, 2001 and 2003 in Brasschaat; and 2004 in Hyytiälä, leaving a total of 25 site-years.

When measured NEE was not available for a half-hour period, either gap-filled NEE was used (Tharandt) or GPP was directly estimated as a saturating function of PPFD (Sodankylä, Hyytiälä, Le Bray and Brasschaat) or global radiation (Norunda). In Tharandt, NEE was gap-filled with the 'look-up table method' (Falge et al. 2001) using the averages of the observations with similar air temperature, global radiation and VPD and taken within a 14-day time window (Wang et al. 2003).

When more than nine half-hourly measurements of PPFD or T_{air} were missing per day, the day was treated as a missing value. The number of missing days in modeled GPP due to missing input variables was 28 days on average for all site-years. Most missing days were for the Norunda site (60 days on average) and least for Tharandt (5 days on average) and Sodankylä (11 days on average) sites. The other sites had ca. 25 days missing per year on average. These missing days were gap-filled for the purpose of comparing the annual total measured GPP to the annual total predicted by the model. For gap-filling, a rectangular hyperbola was fitted to modeled GPP as a function of daily PPFD for 1 month at a time using nonlinear regression, and a linear regression if no fit could be obtained. The fit was generally good ($R^2 > 0.8$), except at very low temperature (in which case GPP was also very low and errors on annual GPP were therefore small).

PBM predictions of GPP

The detailed model used here is stand photosynthesis program (SPP) (Mäkelä et al. 2006), and it consists of a light-attenuation model from Oker-blom et al. (1989) coupled with a leaf-level photosynthesis model (Hari and Mäkelä 2003, Mäkelä et al. 2004). Using this model, excellent fits to GPP were achieved at the Hyytiälä site (Mäkelä et al. 2006), where it was parameterized with automated cuvette data (Mäkelä et al. 2004, Kolari et al. 2007). Detailed descriptions of the sub-models are given in the study of Mäkelä et al. (2006), but it has been briefly outlined in the following sections.

The forest stand consists of tree crowns (cones or ellipsoids) with shoots or leaves randomly distributed within

Table 1. Basic description of the six flux sites.

Site	Sodankylä	Hyytiälä	Norunda	Brasschaat	Tharandt	Le Bray
Country	Finland	Finland	Sweden	Belgium	Germany	France
Dominant species	*Pinus sylvestris*	*Pinus sylvestris*	*Pinus sylvestris, Picea abies*	*Pinus sylvestris, Quercus robur*	*Picea abies*	*Pinus pinaster*
Latitude	67°22′ N	61°51′ N	60°05′ N	51°18′ N	50°58′ N	44°42′ N
Longitude	26°38′ E	24°18′ E	17°29′ E	4°31′ E	13°34′ E	0°46′ W
Altitude (m a.s.l.)	180	170	45	16	375	61
Peak LAI[1] ($m^2 m^{-2}$)	3.8	6.3	13.1	9.8	22	5.4
Age (years)	50–160	45	ca. 100	78, 71	105	37
Stand density (ha^{-1})	2100	1300	870	375, 320	450	408
Precipitation (mm $year^{-1}$)	ca. 500	697	527	750	819	930
Mean T (°C)	−1.0	2.9	5.5	10	7.7	12.8
References	Aurela (2005)	Vesala et al. (2005)	Lundin et al. (1999), Lagergren et al. (2005)	Carrara et al. (2003)	Grünwald and Bernhofer (2007)	Delzon (2000), Berbigier et al. (2001)

[1]LAI is on an all-sided area basis including understory.

Figure 1. Location of the six flux sites. 1, Sodankylä; 2, Hyytiälä; 3, Norunda; 4, Brasschaat; 5, Tharandt and 6, Le Bray. See Table 1 for more details.

the crown volume, and multiple 'size classes' are possible, for example, to separate species or over- and understory. Required inputs to describe the stand are length, width and shape of crowns for each size class and tree leaf area. For each size class, it is assumed that trees are randomly distributed in space, vastly simplifying the calculations of between-tree shading. This also obviates the need for spatial coordinates of trees in a stand. Phenology is not simulated by the model, but it is possible to provide daily values of

LAI to account for seasonality, particularly for deciduous species. Leaf temperature is assumed to equal air temperature, a defensible assumption for coniferous forests (e.g., Martin et al. 1999).

The attenuation of irradiance inside tree crowns is a function of the distance the solar beam travels within the crown, and the extinction coefficient within tree crowns in the direction of the solar beam, which depends on shoot clumping or shoot to total area ratio (Oker-blom et al. 1989, Stenberg 1996). This component of the model is similar to the model MAESTRO (Wang and Jarvis 1990), except that SPP only estimates attenuation of photosynthetically active radiation. The shading caused by surrounding trees is estimated based on the assumption that trees are randomly distributed in space (Oker-blom et al. 1989). The average irradiance on leaves is determined numerically by dividing the crowns into a large number of small boxels (20 each in the horizontal and 50 each in the vertical direction). In each boxel, leaves are separated into sunlit and shaded (Norman 1993, Campbell and Norman 2000) and used to estimate photosynthesis of the boxel (see below). The total for a crown is calculated by summing all the boxels. For all simulations, we used a time-step of 30 min.

Leaf photosynthesis model

The leaf photosynthesis model is based on the idea of optimal stomatal control (Cowan and Farquhar 1977, Hari et al. 1986), extended with a seasonal acclimation model of photosynthetic capacity (Mäkelä et al. 2004, Kolari et al. 2007). In this model, the relationship between CO_2 assimilation rate and leaf intercellular CO_2 concentration (c_i) is linear, and the slope of this relationship, the carboxylation efficiency, is a saturating function of leaf irradiance (see Appendix A). A single parameter controls the sensitivity of stomatal conductance to VPD (λ), that can be interpreted

as the marginal cost of water (Appendix A). This optimal stomatal control model has been tested extensively on automated cuvette data at the Hyytiälä site (Hari and Mäkelä 2003, Mäkelä et al. 2004, Kolari et al. 2007), and compares well to the often used Ball–Berry model in conjunction with the Farquhar photosynthesis model (Aalto et al. 2002).

Photosynthetic capacity is a delayed function of T_{air} (Mäkelä et al. 2004), and as such controls the recovery of photosynthesis in the spring (Kolari et al. 2007), and to a lesser extent the decline of photosynthesis in the fall (which is mostly light driven, at least in boreal conditions). In this model, we do not use an instantaneous temperature response of photosynthetic capacity (Medlyn et al. 2002), because for Scots pine, this response is uncertain (Linder and Troeng 1980). Mäkelä et al. (2004) showed that the seasonal acclimation model explained 92% of variation in daily values of the carboxylation efficiency and similar results were obtained by Kolari et al. (2007).

In the model simulations, we have used the simplification that photosynthetic capacity is constant within the canopy, because insufficient data were available to parameterize this variation. Within Scots pine a canopy variation in photosynthetic capacity is typically low (P. Kolari, unpublished data collected at the Hyytiälä site). However, in Norway spruce large variation in photosynthetic capacity is common in response to variation in light availability (Grassi and Bagnaresi 2001). This introduces some error in the current simulations.

Inclusion of a model that links stomatal conductance to soil water potential is under development, based on a model by Duursma et al. (2008), but is not included in the present simulations due to lack of data for parameterization and testing at most sites. Instead, we test if we introduce a systematic bias by ignoring soil water content by plotting weekly average residuals of predicted GPP against average soil water content over the rooting profile for three sites where soil water content measurements were available for the studied years (Hyytiälä, Le Bray and Brasschaat).

Parameterization

For each site, GPP was modeled using the PBM, with parameter values from measurements or literature, avoiding any further calibration or fine-tuning. The first set of parameters described the stand structure, including stand density, crown size (length and width), LAI and the seasonal pattern in LAI (particularly for the deciduous species) for each of the important species at the site. The second set of parameters described the leaf gas exchange such as photosynthetic capacity and stomatal control. For Hyytiälä and Sodankylä, we used leaf gas exchange parameters derived from long-term monitoring at those sites (Mäkelä et al. 2004, Kolari et al. 2007), but with the exception of some understory species (see sections Brasschaat and Le Bray) we did not have information on photosynthetic capacity and stomatal control at any of the other sites.

Thus, for all sites except Sodankylä, we used leaf gas exchange parameters from Hyytiälä. Rather than fine-tuning parameter values for each site, we chose to use the best information available – even if this information is scant – to predict GPP for a site. Details of the parameterization for each site are given in the following sections, and the general characteristics of the six sites are given in Table 1.

Hyytiälä Many detailed measurements are available for the Hyytiälä site (Vesala et al. 1998), and this is the main site where SPP has been developed, parameterized and tested (Mäkelä et al. 2006). The leaf photosynthesis and stomatal conductance model was calibrated to long-term automatic monitoring of shoot gas exchange at this site (Kolari et al. 2007). Details about the parameterization of SPP at Hyytiälä can be found in the study of Mäkelä et al. (2006), but the following changes were made. Intra-annual variation in LAI was estimated from the measurements of the timing of needle expansion and litterfall (E. Nikinmaa and J. Pumpanen, unpublished data), and by assuming four needle cohorts. The precise timing of this intra-annual fluctuation in LAI affected the annual total GPP only a little (a few percent change if the timing was changed several weeks). The understory was included by assuming it to be a homogenous layer, with photosynthesis parameters derived from gas exchange measurements at the site from the study of Kolari et al. (2006).

Sodankylä Site characteristics were taken from the study of Aurela (2005). The leaf photosynthesis model was calibrated to long-term automated measurements of gas exchange at Värriö, a site also in North-East Lapland about 120 km east of Sodankylä (Kolari et al. 2007). Details of derivation of gas exchange parameters from automated cuvette data follow the descriptions given by Mäkelä et al. (2004).

Brasschaat The Brasschaat site is far from homogenous, consisting of a mosaic of small-scale stands of trees. As a result, species composition in the footprint of the eddy tower varies with wind direction, but we did not take this into account, and assumed this variation would average out on an annual scale. Instead, we constructed a stand with separate size classes for four species, and determined LAI for each of the species by their relative proportions of the forest. De Pury and Ceulemans (1997) reported species composition of the site and Gond et al. (1999) reported LAI of the species when they would be the dominant species. The two most important species in the canopy are Scots pine (*P. sylvestris*) (69%) and oak (*Q. robur*) (31%), while the understory is dominated by an exotic cherry species (*Prunus serotina* Ehrh.) (46%) and purple moor grass (*Molinia coerulea* (L.) Moench.) (54%). The seasonal pattern of LAI was also taken from the study of Gond et al. (1999) for all species except Scots pine, for which we assumed a constant LAI. The peak

all-sided LAI of the stand was 8.8 m^2 m^{-2}, with a minimum of 3.4 m^2 m^{-2} in the winter. Leaf photosynthesis parameters for Scots pine were assumed to be the same for the Hyytiälä site, because estimates of maximum carboxylation rate (V_{cmax}) at the Brasschaat site (De Pury and Ceulemans 1997) compared well to the estimates of photosynthetic capacity for Hyytiälä. For oak, De Pury and Ceulemans reported V_{cmax} which was converted to photosynthetic capacity for use in our leaf physiology model as explained in Appendix A. For *Molinia*, the parameters developed for the Le Bray site were used.

Le Bray   The Le Bray site is a stand of maritime pine (*P. pinaster*), with a significant understory consisting of purple moor grass (*M. coerulea*). Estimates of LAI of maritime pine were available from destructive site measurements (A. Porté, personal communication, INRA, Bordeaux) and for purple moor grass from Denis Loustau (personal communication, 2006). For both maritime pine and purple moor grass, the estimates of the seasonal variation in LAI were available. At peak leaf area, maritime pine and *Molinia* had a similar LAI. For maritime pine, estimates of photosynthetic capacity were derived from data obtained by Porté and Loustau (1998). Unfortunately, no data were available to estimate the degree of stomatal control (λ), so we used the estimate for Scots pine from Hyytiälä. For *Molinia*, the leaf photosynthesis and stomatal control model (see Appendix A) was calibrated to data on assimilation rate (A) and internal CO_2 concentration (c_i), and a parameterized stomatal conductance reported by Delzon (2000). The three parameters of the stomatal control model were varied to optimize the fit to predictions of Delzon's stomatal conductance model across a range of VPD as well as PPFD and to the A–c_i data at the same time.

Tharandt   Only scant model input data were available for the Tharandt site, nevertheless we decided to include the site in the analysis because of the high LAI, expanding the range of LAI for the simulation study. An allometry-based estimate of LAI was reported by Wang et al. (2003) and converted to all-sided area using a conversion coefficient of 3.08 (Sellin 2001), yielding nearly 22 m^2 m^{-2} (all-sided). An estimate of stand density was also taken from the study of Wang et al. (2003). No information was available for leaf physiology, and photosynthetic capacity could also not be estimated from leaf nitrogen content because no nitrogen data were available. As a first estimate, we used the leaf photosynthesis model for Scots pine as parameterized in Hyytiälä. We test the assumption that photosynthetic capacity is similar in the two species given in Appendix B, where a review of literature values shows more variation within the species than between. In the sensitivity analysis for leaf physiological parameters, we attempt to quantify the possible errors that we make with this assumption.

Norunda   Similar to the Tharandt site, we had little information on the Norunda site for detailed parameterization, so that the parameters of the leaf physiology model were assumed to be the same for the Hyytiälä site. Total LAI was taken from the study of Lagergren et al. (2005) and was converted to all-sided LAI using a conversion of 3.08 (Sellin 2001). Although the stand consists of Norway spruce as well as Scots pine, we did not split the stand into two size classes, because no information on leaf physiology was available for either species. Also, there is marked variation in tree size within the stand, but this could not be taken into account in the simulations as insufficient data were available. The simulations for Norunda need to be interpreted as a 'first guess' prediction of GPP, using only climate and LAI as reliable input data.

Model simulations

First, we used the best data available to predict daily GPP for each site-year, to assess if the model could explain variation in annual GPP across sites, and across years within sites. Possible problems with the annual cycle in GPP could then be highlighted. Next, we performed two virtual transplanting experiments to test the influence of climate and stand structure on GPP.

In the first experiment, GPP was estimated for each site-year with SPP, using observed weather data for that year, and using weather data from all other available site-years from the same site and all other sites. This exercise results in a total of 25×25 simulations. For each site-year, the 25 measures of goodness-of-fit (R^2 and absolute bias) are grouped into 'own site, own year', 'own site, other year' and 'other site and year', and averaged. The bias of GPP prediction was compared to difference in aggregated weather variables of the different weather datasets. These aggregated variables were mean annual temperature, number of days with average temperature above 5 °C, total incident PPFD and latitude. These variables are correlated with each other (Figure 4).

In the second experiment, we tested the effect of stand structure on the estimation of GPP for the six coniferous sites. We chose 1 year that was available for most sites (2001; for Brasschaat we chose 2000), and simulated GPP using the six available stand-structure descriptions for each site. Stand structure included LAI, stand density and crown size, and most sites have more than one 'size class' (different species or the inclusion of an understory, see Table 1). Bias in GPP prediction was compared to the difference in LAI used in prediction of GPP and actual LAI of the site, as well as the difference in absorbed PPFD.

Leaf physiology sensitivity analysis

Because limited information was available on leaf-level photosynthesis and stomatal conductance parameters, except for the Hyytiälä site, the effect of photosynthetic capacity, the degree of stomatal control and two

parameters that control the seasonal acclimation of photosynthetic capacity were tested in a sensitivity analysis. We performed the sensitivity analysis at two sites with contrasting climate, at Hyytiälä and Le Bray, both for the year 2001, using the predictions of GPP of the overstory only. For each parameter, we varied the value several orders of magnitude around the default value for the site, and also reported the relative sensitivity of the model to small perturbations of the parameters around their default value. Relative sensitivity was calculated as $(GPP(Y + \delta) - GPP(Y))/\delta$, where GPP is the model prediction of GPP with the default value of the parameter Y, that is incremented by a small amount δ.

Statistics

We used two metrics to summarize the goodness-of-fit of the model predictions to GPP derived from EC measurements

$$\text{BIAS} = \frac{1}{n} \sum_{i=1}^{n} (y_i - \hat{y}_i), \tag{1}$$

$$R^2 = 1 - \frac{\sum_{i=1}^{n} \varepsilon_i^2}{\sum_{i=1}^{n} (y_i - \bar{y})^2}, \tag{2}$$

where y_i is measured GPP on day i, $\hat{y}_i$ is simulated GPP, ε is the residual of the linear regression of measured GPP versus modeled GPP and $\bar{y}$ is the mean measured GPP. The bias measures how far on average the model predictions are from measurements, whereas the R^2 is a measure of how well the model reproduces the pattern of observations that is dominated by the seasonal variability. In addition to the bias, which may be negative, we also use the absolute value of the bias to ease comparisons across sites. A high R^2 does not indicate an unbiased prediction, whereas a low bias may not indicate a good fit, rather, it means on an annual basis a small bias was achieved (this may be achieved by compensating errors in different times of the year). Some statistics combine both bias and goodness-of-fit, such as the model efficiency (e.g., Medlyn et al. 2005b), but these are not used in this study because we wish to interpret these two different aspects of model fit separately.

Results

We tested the sensitivity of a process-based simulation model (PBM) to three groups of inputs: weather, stand structure and leaf physiology. This 'aggregated' model sensitivity was compared across six coniferous sites located along a climatic gradient in Europe. Simulation experiments were carried out for a total of 25 site-years where weather datasets or stand-structure information were switched between sites, and compared the bias in model predictions to the difference in climate and stand structure between the sites.

Site characteristics and EC-derived GPP

Annual total GPP varied nearly threefold between the 25 site-years, from 600 gC m^{-2} year^{-1} in Sodankylä (2001) to 1805 gC m^{-2} year^{-1} in Tharandt (2002; Table 2). Despite this large variation, average maximum daily GPP in summer months apparently varied little between the sites, as did total daily light availability (Figure 2; Table 2). Average incident light varied from ca. 25 mol m^{-2} day^{-1} in Le Bray to ca. 15.5 mol m^{-2} day^{-1} in Sodankylä, a 40% decrease while GPP varied more than twofold between Le Bray and Sodankylä (Table 2). On the other hand, mean annual temperature varied strongly along the transect, with 13 °C at Le Bray to −1 °C at Sodankylä, which affected the length of the productive period (Figure 2).

The choice of the six sites suited the objectives of the study well, because peak leaf area index (LAI$_{max}$) was not related to mean annual temperature, so that LAI did not confound the climatic gradient (Figure 3). The LAI$_{max}$ also showed large variation between the sites, varying from 3.8 m^2 m^{-2} in Sodankylä to 22 m^2 m^{-2} in Tharandt. Measured total GPP was related both to LAI$_{max}$ and T_{mean}, but slightly stronger to T_{mean} (Figure 3). A linear regression model using LAI$_{max}$ and T_{mean} explained 63% of the variation in annual GPP across all 25 site-years (using the data in Table 2), while PPFD did not explain any additional variation (when added to the linear model, or as an interaction with either PPFD or T_{mean}). Total GPP was not significantly related to any other site factor such as age, height or stand density.

The PBM was used to predict daily GPP for all site-years using the best information available, without additional calibration or fine-tuning. A large proportion of within-year variation in daily totals of GPP was explained with the model (Table 2). The best fits were obtained for Hyytiälä, Sodankylä and Brasschaat, and poorest fits in Le Bray, especially in 2002. As expected, best fits were obtained at Hyytiälä site, where detailed information on both stand structure and leaf physiology were available. Across site-years, about 62% in variation of annual total GPP could be explained with the model, similar to a linear regression with T_{mean} and LAI (see the previous paragraph). The GPP in Tharandt was underestimated for 2 of the 3 years, and the model gave overestimates at Brasschaat for most years. Between years at a given site, the model explained little variation (Figure 5). Overall, the model results give confidence that the model captures the most important factors for prediction of GPP across sites with a wide variation in climate and LAI. Because soil water content was not used in predictions of GPP at any of the sites, we performed a residual analysis for three sites where soil water data were available (Figure 6). There was no clear evidence that the

Table 2. Mean annual temperature (T_{mean}), mean incident light (PPFD), GPP derived from EC, GPP estimated with the PBM, R^2 of the linear regression between daily totals of EC and modeled GPP and the bias in annual total of the model estimate for each of the 25 site-years.

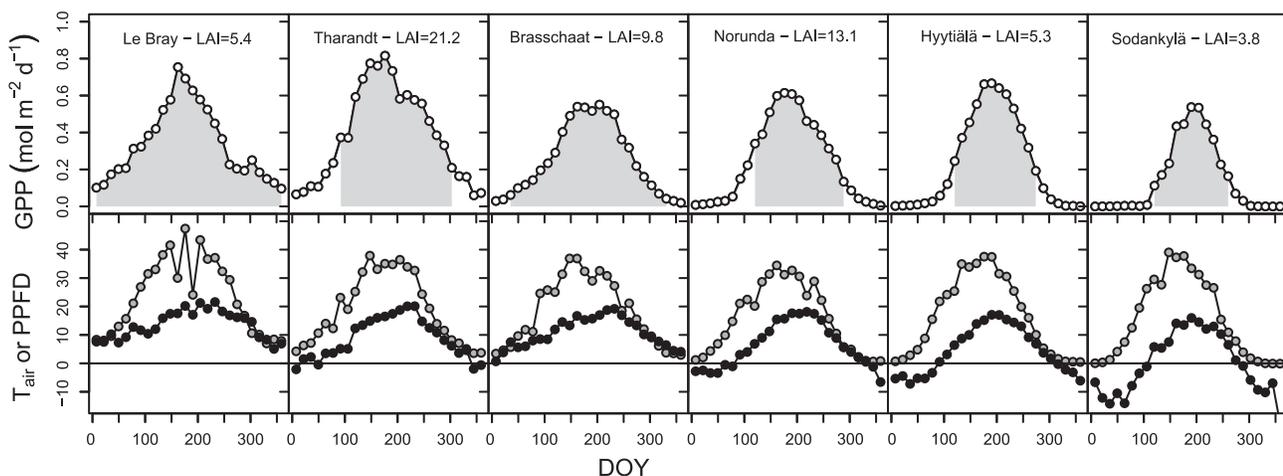| Site	Year	T_{mean} (°C)	PPFD (mol m^{-2} day^{-1})	Eddy GPP (gC m^{-2} year^{-1})	Model GPP (gC m^{-2} year^{-1})	R^2	Bias (gC m^{-2} year^{-1})
Brasschaat	1997	10.75	20.89	1000	1270	0.88	−270
	2000	10.72	18.62	1296	1254	0.95	42
	2002	10.33	18.52	1176	1216	0.93	−39
	2004	11.48	19.89	938	1236	0.75	−298
Hyytiälä	1997	4.33	18.36	999	981	0.96	17
	1998	3.51	15.98	1004	844	0.96	159
	1999	4.36	17.82	952	1032	0.94	−81
	2000	5.71	16.78	1094	986	0.96	107
	2001	5.52	16.66	991	831	0.96	160
	2002	4.4	18.77	1084	1092	0.96	−8
	2003	3.84	16.34	974	952	0.96	22
	2005	4.53	17.11	1072	974	0.96	98
Le Bray	2001	13.32	26.17	1722	1605	0.89	117
	2002	13.77	24.57	1236	1620	0.82	−384
Norunda	1996	4.68	17.29	1141	1082	0.87	60
	1997	6.99	20.78	1059	1181	0.76	−121
	1999	6.63	20.03	1049	1271	0.89	−222
	2000	5.94	14.5	1028	1049	0.91	−21
	2001	5.32	17.58	1018	1142	0.87	−124
	2002	7.22	18.42	1094	1325	0.85	−231
Sodankylä	2001	−0.11	15.14	599	573	0.93	26
	2002	0.4	16.6	686	679	0.93	7
Tharandt	2001	8.25	17.31	1696	1345	0.81	351
	2002	8.98	19.00	1806	1459	0.86	347
	2003	9.02	21.65	1588	1586	0.71	−2

Figure 2. Two-week averages of GPP derived from EC measurements (top row), and averages of air temperature (T_{air}, °C, black circles) and incident light (PPFD, mol m^{-2} day^{-1}, gray circles). In the top panel, the area colored gray shows the time period where average T_{air} for the two-week period was > 5 °C. Data for sites are in order of latitude from low to high. The LAI is all-sided. Averages are for all years at the site, see Table 1 for number of years per site that were included. Note that the maximum GPP in the summer varies only little between the sites, but the duration of the period of near-maximum GPP varies clearly with latitude. Note also that total incident light shows little variation between sites.
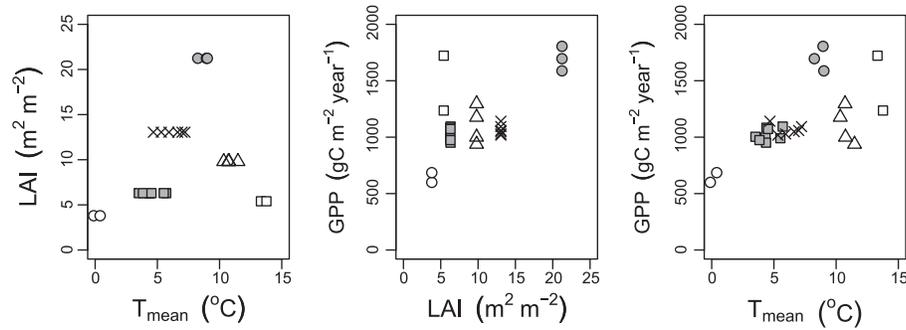
Figure 3. Relationships between peak LAI (all-sided), GPP and T_{mean} for the six sites and 25 site-years in this study. The LAI is not related to T_{mean} ($P > 0.2$) and GPP was weakly correlated with LAI ($P < 0.001$, $R^2 = 0.29$), but not when Tharandt was excluded ($P > 0.8$). Relationships between GPP and T_{mean} were significant ($P < 0.001$, $R^2 = 0.33$). No relationships could be found between GPP and T_{mean} within sites, and the same was true for season length, or total incident PPFD. Symbols as in Figure 5.
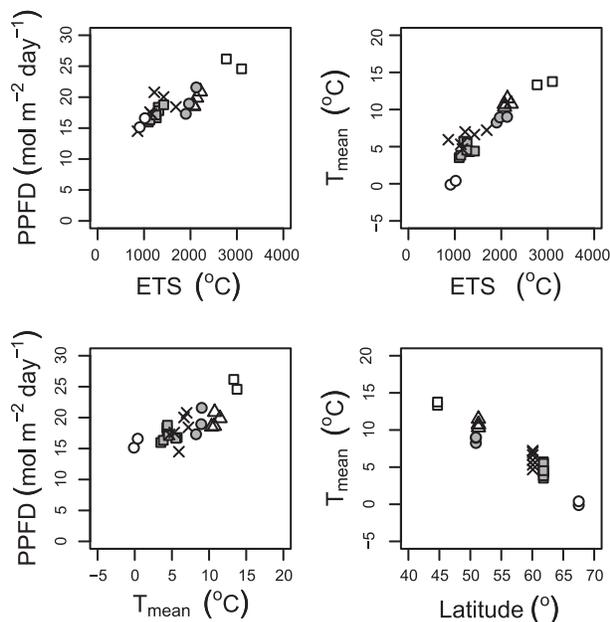
Figure 4. Relationships between aggregated weather variables across the 25 site-years: PPFD is the annual average photosynthetic photon flux density, T_{mean} is the average annual temperature and ETS is the effective temperature sum (sum of daily average temperature above 5 °C). Symbols as in Figure 5.
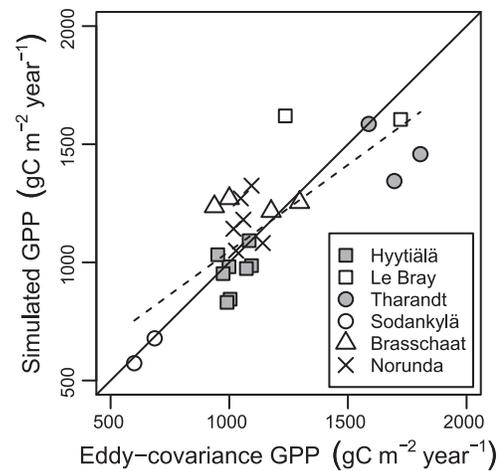

Figure 5. Comparison between GPP derived from EC measurements and GPP estimated with the model. Note that across sites, variation in GPP is explained well, but not between years. The solid line is a 1:1 line and the dashed line is a regression line ($y = 273.5 + 0.78 * x$, $R^2 = 0.62$, $P < 0.0001$).

errors in GPP predictions were related to soil water content, except for the year 2002 in Le Bray.

Effect of weather on simulated GPP

In the first model experiment, we tested the sensitivity of model predictions to weather data. Rather than changing one variable at a time, we switched weather datasets between sites, so that correlations between weather variables within and across datasets (Figure 4) would be maintained. The proportion of explained variation in daily totals of GPP within years (R^2) declined when a weather dataset from a different year, but for the same site, was used

(Figure 7). The R^2 indicates how well the annual pattern of GPP within a year is matched by model predictions, and only decreased by 17% on average, but still reaching 70–80% for more than half of the site-years. Because we did not attempt to optimize the fit for each site, absolute bias did not change on average if weather dataset from a different year, but for the same site, was used (Figure 7), for some of the sites the bias actually decreased. Absolute bias did, however, increase by 105% if weather data from different site-years were used. The high R^2 values can be readily explained by high correlations of weather variables across years within sites; Pearson's correlation coefficients ranged from 0.68 to 0.8 for daily mean temperature, from 0.57 to 0.77 for PPFD and from 0.23 to 0.58 for VPD. When weather datasets from different sites were used to predict GPP for a target site, R^2 decreased a bit more: 20% on average, but was still between 54% and 77%. This means that up to 77% of variation in daily totals of GPP
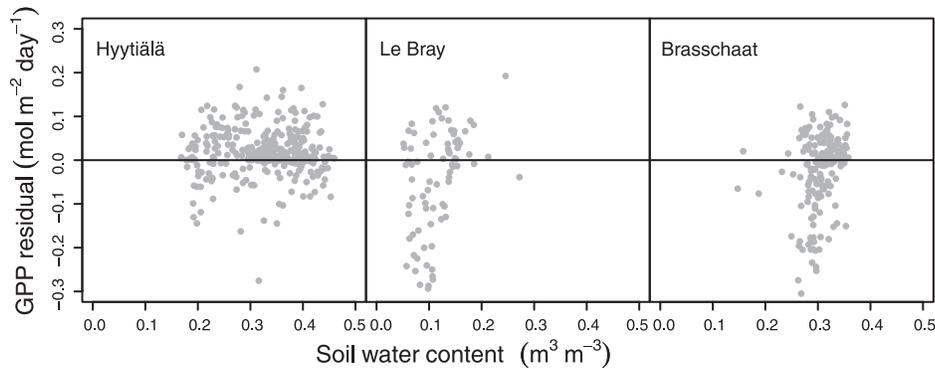
Figure 6. Weekly averages of residuals of GPP predictions (measured minus modeled) plotted against soil water content for three sites.
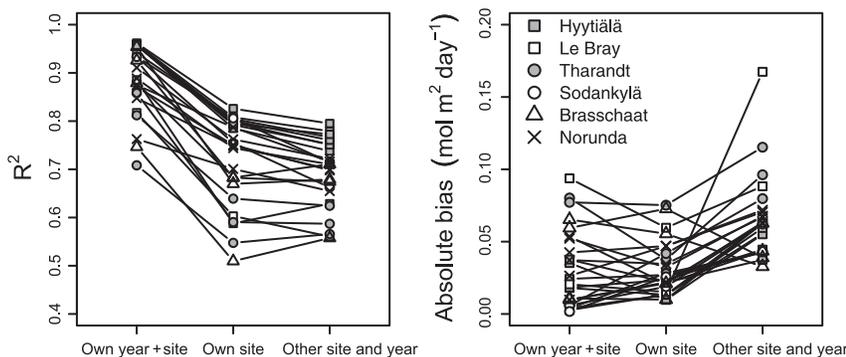

Figure 7. Coefficient of determination (R^2) and absolute bias for the simulation experiment where different weather datasets were used to estimate GPP at a target site. In the default case, the weather dataset for a certain site-year was used to estimate GPP for that site-year (own year + site), secondly a weather dataset from the same site was used for a different year (own site) and finally a different site and year (other site and year). For a given site, different symbols denote a different year.

was explained when using a weather dataset from a completely different site and year, and 54% at the least.

We tested four aggregated variables in their ability to summarize the bias in GPP prediction when a different weather dataset was used: mean annual temperature, effective temperature sum (ETS) (sum of daily temperatures above 5 °C), season length (number of days above 5 °C) and annual total light availability (PPFD). For each site-year, the bias in GPP prediction resulting from using a weather dataset from a different site-year was related to the change in either of the four aggregated weather variables. In Figure 8, the method is illustrated for the comparison of the bias to mean annual temperature. For all sites, bias in GPP prediction was most closely related to the ETS and almost as strongly to the mean annual temperature. Season length and total PPFD explained substantially less of the variation in the change in bias. For all site-years on average, simulated annual GPP increased 63.8 gC m^{-2} year^{-1} per 1 °C increase in T_{mean}, while T_{mean} varied 13.8 °C across all site-years, for a total of 885 gC m^{-2} year^{-1} change in simulated GPP across the observed range of T_{mean} across all site-years.

Effect of stand structure on simulated GPP

In the second simulation experiment, information on stand structure (stand density, tree height, crown size and LAI) was switched between the sites and GPP was simulated for 1 year. This simulation experiment was equivalent to

replacing the stand with a stand from a different site, and testing the effect on simulated GPP with this different stand structure. The bias in GPP was compared to the difference in LAI between the original and the transplanted stand, and the difference in annual intercepted PPFD (Figure 9). Bias in GPP prediction was strongly related to the change in LAI or intercepted PPFD, even though canopy structure (tree size, number of trees per hectare and understory) was changed. No individual effects on model bias of these other canopy-structure variables could be found, indicating that LAI summarized canopy structure well. For the 6 site-years on average, simulated annual GPP increased 24.6 gC m^{-2} year^{-1} per 1 m^2 m^{-2} increase in LAI, while LAI varied 17.4 m^2 m^{-2} across all site-years, for a total of 442 gC m^{-2} year^{-1} simulated change in GPP across the observed range in LAI across the six sites.

Leaf physiology sensitivity analysis

Finally, sensitivity of model predictions of annual GPP to changes in leaf physiological parameters was tested both at the Hyytiälä site and at the Le Bray site for the year 2001. Five parameters were varied that control the leaf gas exchange model: photosynthetic capacity (k_{max}), quantum yield per unit intercellular CO_2 concentration (α) (similar to the quantum yield of electron transport, see Appendix A), degree of stomatal control (λ) and two parameters that control the annual cycle of photosynthetic capacity in response to temperature (S_{max}, a parameter that
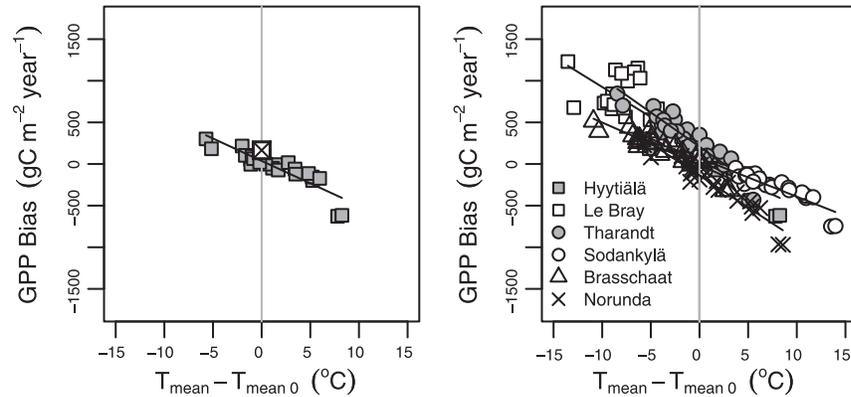
Figure 8. Bias in simulated annual GPP when using a weather dataset from a different site-year, in relation to the difference in mean annual temperature (T_{mean}) between the used weather dataset (T_{mean}) and that of the GPP data ($T_{mean\ 0}$). In the left panel, this method is illustrated for the Hyytiälä site. The white square is the simulation bias for the year 2001 in Hyytiälä, when using the correct weather dataset. When using datasets from lower latitudes, with higher T_{mean}, the bias becomes negative: GPP is overestimated. In the right panel, these relationships are shown for all site-years, using the year 2001 as the base site-year in each case.
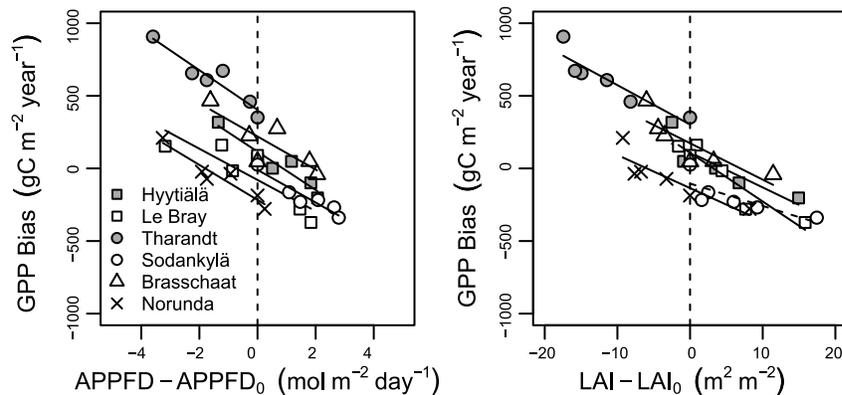

Figure 9. Results from the simulation experiment where stand-structure information was interchanged between sites. Bias in GPP (measured minus modeled) is shown as a function of difference in absorbed PPFD and difference in LAI (all-sided) from those estimated for its own site. For example, Sodankylä has an LAI of 3.8 (Table 1), but stand information of all other sites are used which result in an LAI of up to 22 (Tharandt). Note that for Tharandt, there is substantial bias even when using Tharandt's stand information, but that the bias increases when information from other sites is used (where LAI and thus APPFD are lower).

controls the degree of seasonality and T_0, a temperature threshold, see Appendix A).

The relative sensitivity of GPP to k_{max} was 0.235 (Table 3), meaning an increase of k_{max} by 10% increased GPP by 2.35%, but for the Le Bray site this was 0.325, showing a higher sensitivity to photosynthetic capacity in a warmer climate. In contrast, annual GPP was nearly proportional to changes in α; the relative sensitivity was ca. 0.9 for both sites. Much smaller sensitivity to λ was found, and the sensitivity was not different for the two sites. A higher sensitivity to S_{max} and T_0, the parameters that control the seasonality of photosynthesis (see Appendix A), was found in the boreal Hyytiälä site than in the Mediterranean Le Bray site. Model predictions were insensitive to τ that controls the smoothness of the response of photosynthetic capacity to air temperature (see Appendix A).

Discussion

Using the best information available for each site-year, the model provided satisfactory predictions of daily and annual totals of GPP, but there is room for improvement. Good fits were obtained for the Hyytiälä site, which is perhaps not surprising because detailed input data were available for this intensive long-term research site (Mäkelä et al. 2006). Also, good fits were obtained in Sodankylä, a site in Finnish Lapland that was parameterized with long-term measurements of leaf gas exchange in a site also in Lapland, which allowed us to get a good estimate of the annual cycle in photosynthesis (Kolari et al. 2007). Little information was available for estimating parameters at Norunda and Tharandt, but still reasonable fits were obtained by using leaf physiology parameters from Hyytiälä (Table 2). Still, improvement is warranted, particularly in terms of

Table 3. Relative sensitivity of SPP to changes in five important leaf physiological parameters, using weather data for the year 2001 both in Hyytiälä and Le Bray sites. A value of 1 means that the modeled annual total of GPP is directly proportional to a change in the parameter. The S_{max} and T_0 control the intra-annual dependence of photosynthetic capacity to temperature (Appendix A), α is the quantum yield of carboxylation efficiency, λ is the degree of stomatal control and k_{max} is the photosynthetic capacity (in the absence of temperature stress).

Parameter	Hyytiälä	Le Bray
S_{max}	−0.530	−0.346
T_0	0.072	0.032
α	0.929	0.900
λ	−0.129	−0.134
k_{max}	0.235	0.329
τ	−0.019	0.003

the photosynthetic capacity and phase of the annual cycle of photosynthesis at these sites, and in terms of more detailed tree and stand information. The worst fit to within-year variation in GPP was obtained in Le Bray, perhaps because of the use of leaf physiology parameters from a different species, or the significant grass understory at the site (which was, however, included in the model). Another possibility is the occurrence of drought in both years 2001 and 2002 (discussed in the sixth paragraph). As it was not our goal to optimize model fits for particular site-years, but rather to see how worse the fit is when we use information from other sites, we conclude that the model fits were good enough for the current objective.

The PBM explained only 62% of variation in annual GPP across site-years, similar to a simple linear regression with LAI and T_{mean} as explanatory variables. Reichstein et al. (2007) found a similar R^2 across a number of flux sites, using only T_{mean} as the explanatory variable. However, within sites, the model did not explain any variation in total GPP between years (see Figure 5). Why does the PBM not explain more variation between-years within-sites, when within-year patterns of GPP could be well replicated? One of the reasons apart from potential soil drought effects (discussed further below) is the much smaller variation in GPP within-sites as compared to between-sites, thus reducing the signal-to-noise (model and measurement error) ratio. Another reason may be varying LAI between years, for example, as a response to water availability or ontogeny, but model runs used the same LAI for each year. Finally, quality of GPP data derived from EC may vary between years.

The first part of our simulation experiment was to use a weather dataset from a different site-year as input to the PBM to predict GPP. This experiment allowed us to test the effect of 'weather' as a whole on predicted GPP, rather than univariate responses to VPD, temperature or other environmental drivers. We believe this approach is useful because across weather datasets, different environmental drivers are strongly correlated, particularly PPFD and temperature (Nöjd and Hari 2001), and VPD and temperature (Campbell and Norman 2000) (Figure 4), so that sensitivity analysis of a model to either one of these environmental drivers is not useful to scale GPP across sites with different climate. When weather datasets were switched within a site, large amounts of variation were still explained in daily totals of GPP within a year (Figure 7) because weather variables show high correlations across years within sites. This result shows that the broad pattern in temperature and light availability explains a large portion of the within-year variation in GPP at a site, because smaller-scale variations between years added only little in the explained variation. It is easy to achieve an R^2 above 50%, because many low values occur in the winter, which inflate the R^2 (by increasing the variance of GPP, see Eq. (2)). Medlyn et al. (2005b) also warned that the R^2 easily achieves a high value, because of the strong influence of diurnal and annual cycles to the variation in GPP, which would be captured by even a simple model.

In contrast to within-year patterns of GPP, severe bias in annual GPP was found when switching weather datasets (Figure 8). The bias was compared to simple summary variables of the change in weather from one site-year to another. We found that the ETS (and similarly the mean annual temperature) explained the most variation in model bias when using weather data from a different site, substantially better than light availability or other environmental drivers. Simulated annual GPP increased 63.8 gC m^{-2} year^{-1} per 1 °C increase in T_{mean} on average for all site-years, a rather strong effect of temperature on annual GPP. Because we did not include an instantaneous effect of temperature on leaf photosynthesis (Appendix A), the effect of temperature on GPP is almost solely due to the phase of the annual cycle in photosynthesis and, to a minor extent, due to the temperature-driven respiration. The simulations thus showed that the seasonality in photosynthetic capacity explains much variation in GPP from site to site, more than a change in light availability (Figure 8), partly because light availability varied much less across the gradient than temperature (Figure 2). Several studies agree with the strong influence of the length of the season on either NEE (Goulden et al. 1996, Suni et al. 2003) or GPP (Bergh et al. 1998, White et al. 1999), while other studies have confirmed strong control of surface temperature on GPP (Sims et al. 2008). We conclude that seasonal pattern of temperature, particularly during spring warm-up, is vital for accurate prediction of annual total GPP, and that this process is well captured by the seasonal acclimation model of photosynthetic capacity used in this study (Mäkelä et al. 2006).

As expected, switching the stand-structure information between sites had a large effect on total simulated GPP. Although several aspects of stand structure were switched at the same time, the bias was related strongly to the change in LAI, or similarly to the change in annual intercepted PPFD (Figure 9). For the six site-years on average,

simulated annual GPP increased 25.3 gC m^{-2} year^{-1} per 1 m^2 m^{-2} increase in LAI. Other studies have also found that LAI is an important parameter in predicting GPP with models (e.g., Falge et al. 1997), evidence for which goes back to empirical biomass productivity studies (Kira 1975, O'Neill and DeAngelis 1980, Gower et al. 1997). This result is supportive of the widely-used light-use efficiency (LUE) model (Landsberg and Hingston 1996), where annual GPP is proportional to intercepted light (a function of LAI and incident PPFD), because although canopy structure is fairly complex in the model, effects on annual GPP were well summarized by LAI or intercepted PPFD alone. On the other hand, the weather switch experiment showed that intercepted PPFD could not explain site-to-site variation in GPP when PPFD is varied (because of latitude) and when LAI is held constant. This helps explain why LUE models typically use temperature modifiers (Landsberg and Hingston 1996, Landsberg and Waring 1997), because PPFD alone cannot explain much variation in GPP across sites.

The sensitivity analysis to leaf physiological parameters for the Hyytiälä site revealed that annual GPP is not sensitive to the light-saturated photosynthetic capacity or to the degree of stomatal control, but approximately proportional to the quantum yield (Table 3). Presumably because the majority of leaves in the canopy are subject to low-light levels, responses at low-light levels are more important than the light-saturated capacity to assimilate CO_2. There is much interest in the variation in photosynthetic capacity across species and sites (Wright et al. 2004), but our results indicate that it may not be a useful scalar for annual GPP across sites with similar species. However, slightly higher sensitivity was achieved for the Le Bray site, where photosynthetic capacity is more important because the length of the season is longer. Baldocchi and Meyers (1998) proposed that the product of LAI and V_{cmax} (CO_2 and light-saturated photosynthetic capacity) is a good summary of canopy CO_2 uptake capacity, but their study integrated across different biome types with large variation in photosynthetic capacity. In contrast, Scots pine and Norway spruce have similar photosynthetic capacity (Niinemets 2002) and geographical variation in photosynthetic capacity in Scots pine is apparently not large (Luoma 1997). The quantum yield of electron transport (α), on the other hand, is typically assumed to vary little between plant species (Singsaas et al. 2001), based on the stoichiometry of electron transport. However, measured apparent quantum yield in the field is often much lower than the theoretical maximum (see Ibrom et al. 2006) and varies substantially within years with temperature (Mäkelä et al. 2004). A high sensitivity to the quantum yield found in this study, which is in agreement with other simulation studies (Falge et al. 1997, Ibrom et al. 2006) implies that more data on site-to-site and interspecies variation in α is necessary.

The sensitivity analysis showed that the degree of stomatal control was not an influential parameter on annual GPP

(Table 3), even though the model was a bit more sensitive at a warmer site where summer VPDs are higher. However, the degree of stomatal control is an important parameter for the prediction of transpiration rate because where CO_2 assimilation rate shows a saturating response to stomatal conductance, transpiration is directly proportional to stomatal conductance in the absence of a significant boundary layer (Jones 1992). If the model is coupled to a water balance model, the degree of stomatal control would in turn affect the soil water balance, and the likely occurrence of drought. The interaction with soil drought was not included in the present study, but may be important in some of the site-years included in this study (see Figure 6). We argue that some of the effects of drought may be partially captured in higher VPDs during rain-free periods. In support of this, for three of the six sites (shown in Figure 6), regressions between weekly average VPD and soil water content were significant ($P < 0.001$), although weak ($R^2 < 0.1$). Still, the model gave a rather poor fit at the Le Bray site, where a rather severe drought occurred in 2002, and to a lesser extent in 2001 (Duursma et al. 2008). In 2003, some effect of drought could be seen at the Norunda and Tharandt sites (Granier et al. 2007), but not at the Hyytiälä site as previously claimed (Granier et al. 2007). In Hyytiälä, a brief dry period occurred in the fall of 2002 (having no noticeable effect on eddy-derived GPP), and a more severe drought in August 2006 (Duursma et al. 2008), but the year 2006 was not included in this study. Further analyses are needed with a model that includes the effect of soil water content on stomatal conductance to confirm that the model bias in some of the sites and years is due to drought effects.

The uncertainty in the EC-based GPP estimates is another source of systematic error across the sites. Measured NEE contains systematic error that depends on the topography and the micrometeorology of the site, the instrumentation and the derivation of time-averaged fluxes from the raw data (Aubinet et al. 2000). Underestimation of nighttime CO_2 fluxes is an important origin of by bias in EC fluxes. In conditions of calm wind and stable atmospheric stratification, a large part of the CO_2 released from the forest is transported advectively instead of by turbulent mixing and thus remains undetected by EC. In a patchy landscape, the extension of the source area (footprint) of EC fluxes outside the studied stand introduces bias. This was an important issue for Brasschaat where the forest stand was bordered by an urban area in the north and the west. Therefore, the fluxes were carefully filtered to minimize the contribution of the surrounding areas (Nagy et al. 2006).

Derivation of GPP by subtracting extrapolated ecosystem respiration from the measured NEE introduces additional bias. Estimating TER versus temperature (T) relationships for Hyytiälä with different explanatory factors (air temperature, ground surface temperature and mineral soil temperature) and different time windows for determining the sensitivity of TER to each type of temperature

resulted in range variation of about ±9% in the annual GPP (Mäkelä et al. 2006). There is currently no consensus on the 'correct' method to estimate TER (Richardson et al. 2006), but the worst-case uncertainty can be reduced considerably in two ways. First, we determine the temperature sensitivity of TER in a time window that is long enough to capture the temperature response from the noisy EC fluxes, but so short that the instantaneous temperature response is not confounded by seasonal co-variation in temperature and in the basal level of respiration (cf. Reichstein et al. 2005), which may itself be related to the seasonal course of GPP (Sampson et al. 2007). The explanatory variables of the TER model should also be mechanistically appropriate drivers of the actual component CO_2 fluxes that constitute TER. We have found that temperature at the ground surface (organic layer) well describes the actual partitioning of TER in Hyytiälä; CO_2 efflux from the ground slightly dominates over the aboveground respiration (e.g., Mammarella et al. 2007, Zha et al. 2007). Using air temperature as the explanatory variable for TER tends to yield slightly higher within- and between-day variation in TER and GPP, whereas soil temperature with small diurnal amplitude will underestimate the variation and result in lower annual GPP and TER than air temperature. Desai et al. (2008) compared different TER and GPP partitioning methods with a dataset consisting of 10 site-years. They obtained an average difference of about 5% between the annual GPP derived from air temperature and GPP derived from soil temperature when using least-squares regression methods similar to those used in our study. They concluded that the ability to detect between-site variation in GPP and TER can be improved by using the same method across all sites. The explanatory variables in our study were slightly inconsistent from site to site because ground surface temperature was not measured at every site and for some sites (Tharandt and Norunda) it was feasible to trade the mechanistic basis of the driver for robustness of temperature sensitivity estimation. There is no method to determine the actual site-specific bias but we can estimate that the uncertainty in annual GPP arising from different TER models is in the order of 5% or 0.01–0.02 molC m^{-2} day^{-1}; clearly smaller than the bias in the model predictions (Figure 7).

There is much interest in the development of simplified models to predict GPP over large spatial and temporal scales because more detailed models require large amounts of data (Yuan et al. 2007, Mäkelä et al. 2008). The current study gives a vital insight into the question of which variables and interactions should be included in such a 'summary model'. Switching weather datasets between sites meant switching temperature, light (and day length, solar angle), relative humidity, as well as the seasonal pattern and their temporal correlation in these variables. But after the switch, the generated bias in simulated GPP was strongly related to the change in the ETS (Figure 8), although ETS is a simple aggregate variable that does not capture detailed temporal trends. This means that although each of these weather variables affects GPP, they all correlate with ETS across sites, so that ETS – or a similar variable – explains a large amount of the variation in GPP across sites. Similar reasoning can be applied to the stand structure switch experiment; although number of trees, crown size, species composition and canopy layering were all switched between sites, the generated bias was strongly related to either LAI or intercepted PPFD. We can further conclude that for this set of six flux sites, T_{mean} had a larger effect on annual GPP than LAI, based on the relationship between simulated bias in GPP across the range in T_{mean} across the sites (Figure 7) and the bias related to change in LAI across the sites (Figure 9).

Summary and conclusion

We studied variation in GPP in a set of six flux sites in predominantly coniferous vegetation, and attempted to unravel the importance of three different sources of variation: climate, stand structure and physiology. A PBM gave generally good predictions of GPP, as compared to GPP derived from EC measurements. As a sensitivity analysis, we switched weather datasets between the sites, and found that the resulting bias in GPP predictions was strongly related to the difference in annual mean temperature or ETS between the sites while keeping stand structure constant. On the other hand, switching detailed stand-structure information between the sites while keeping weather constant resulted in bias that was well explained by LAI or intercepted light alone. Variation in physiology across the sites could not be assessed, but a sensitivity analysis showed that the quantum yield of electron transport and parameters that define the sensitivity of photosynthetic capacity to the annual cycle in temperature are important – but little is known about their variation across sites. Results are promising for the construction of a parsimonious model for the prediction of GPP from climate and canopy structure, and they reveal that annual mean temperature and LAI alone are able to explain much of the variation in GPP across the set of six coniferous forest stands across a climatic gradient in Europe.

and the Flemish Research Institute for Nature and Forest (INBO) for the meteodata of the Brasschaat site.

References

Aalto, T., P. Hari and T. Vesala. 2002. Comparison of an optimal stomatal regulation model and a biochemical model in explaining CO_2 exchange in field conditions. Silva Fenn. 36:615–623.

Aubinet, M., A. Grelle, A. Ibrom et al. 2000. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. Adv. Ecol. Res. 30:113–175.

Aurela, M. 2005. Carbon dioxide exchange in subarctic ecosystems measured by a micrometeorological technique. Ph.D. Thesis. Finnish Meteorological Institute Contributions 39 p.

Baldocchi, D. and T. Meyers. 1998. On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and trace gas fluxes over vegetation: a perspective. Agric. For. Meteorol. 90:1–25.

Berbigier, P., J.M. Bonnefond and P. Mellman. 2001. CO_2 and water vapour fluxes for 2 years above Euroflux forest site. Agric. For. Meteorol. 108:183–197.

Bergh, J., R.E. McMurtrie and S. Linder. 1998. Climatic factors controlling the productivity of Norway spruce: a model-based analysis. For. Ecol. Manag. 110:127–139.

Berninger, F., E. Sonninen, T. Aalto and J. Lloyd. 2000. Modeling ^{13}C discrimination in tree rings. Global Biogeochem. Cycles 14:213–223.

Campbell, C. and J.M. Norman. 2000. An introduction to environmental biophysics. Springer Verlag, New York.

Carrara, A., A.S. Kowalski, J. Neirynck, I.A. Janssens, J.C. Yuste and R. Ceulemans. 2003. Net ecosystem CO_2 exchange of mixed forest in Belgium over 5 years. Agric. For. Meteorol. 119:209–227.

Cowan, I. and G.D. Farquhar. 1977. Stomatal function in relation to leaf metabolism and environment. *In* Integration of Activity in the Higher Plant. Ed. D.H. Jennings. Cambridge University Press, Cambridge, pp 471–505.

Delzon, S. 2000. Photosynthèse de la Molinie en sous bois d'un peuplement de pin maritime adulte au site du BRAY. Rapport de stage de DEA. Université de Paris XI, Orsay.

De Pury, D.G.G. and R. Ceulemans. 1997. Scaling-up carbon fluxes from leaves to stands in a patchy coniferous/deciduous forest. *In* Impacts of Global Change on Tree Physiology and Forest Ecosystems. Eds. G.M.J. Mohren, K. Kramer and S. Sabate. Kluwer Academic Publishers, Dordrecht, pp 263–272.

Desai, A.R., A.D. Richardson, A.M. Moffat et al. 2008. Cross-site evaluation of eddy covariance GPP and RE decomposition techniques. Agric. For. Meteorol. 148:821–838.

Duursma, R.A., P. Kolari, M. Peramaki, E. Nikinmaa, P. Hari, S. Delzon, D. Loustau, H. Ilvesniemi, J. Pumpanen and A. Mäkelä. 2008. Predicting the decline in daily maximum transpiration rate of two pine stands during drought based on constant minimum leaf water potential and plant hydraulic conductance. Tree Physiol. 28:265–276.

Falge, E., R.J. Ryel, M. Alsheimer and J. Tenhunen. 1997. Effects of stand structure and physiology on forest gas exchange: a simulation study for Norway spruce. Trees 11:436–448.

Falge, E., D. Baldocchi, R. Olson et al. 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. Agric. For. Meteorol. 107:43–69.

Falge, E., D. Baldocchi, J. Tenhunen et al. 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. Agric. For. Meteorol. 113:53–74.

Farquhar, G.D., S. von Caemmerer and J.A. Berry. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. Planta 149:78–90.

Gholz, H.L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology 63:469–481.

Gond, V., D.G.G. De Pury, F. Veroustraete and R. Ceulemans. 1999. Seasonal variations in leaf area index, leaf chlorophyll, and water content; scaling-up to estimate fAPAR and carbon balance in a multilayer, multispecies temperate forest. Tree Physiol. 19:673–679.

Goulden, M.L., J.W. Munger, S.M. Fan, B.C. Daube and S. Wofsy. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science 271:1576–1578.

Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik, S.J. Steele and T.K. Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102:29029–29041.

Granier, A., M. Reichstein, N. Breda et al. 2007. Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. Agric. For. Meteorol. 143:123–145.

Grassi, G. and U. Bagnaresi. 2001. Foliar morphological and physiological plasticity in *Picea abies* and *Abies alba* saplings along a natural light gradient. Tree Physiol. 21:959–967.

Grier, C.C. and S.W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. Ecology 58:893–899.

Grünwald, T. and C. Bernhofer. 2007. A decade of carbon, water and energy flux measurements of an old spruce forest at the Anchor Station Tharandt. Tellus 59B:387–396.

Guan, B.T. 1999. Effects of correlation among parameters on prediction quality of a process-based forest growth model. For. Sci. 46:269–276.

Hari, P. and A. Mäkelä. 2003. Annual pattern of photosynthesis in Scots pine in the boreal zone. Tree Physiol. 23:145–155.

Hari, P., A. Mäkelä, E. Korpilahti and M. Holmberg. 1986. Optimal control of gas exchange. Tree Physiol. 2:169–175.

Hari, P., A. Mäkelä, F. Berninger and T. Pohja. 1999. Field evidence for the optimality hypothesis of gas exchange in plants. Aust. J. Plant Physiol. 26:239–244.

Ibrom, A., P.G. Jarvis, R. Clement, K. Morgenstern, A. Oltchev, B.E. Medlyn, Y.P. Wang, L. Wingate, J.B. Moncrieff and G. Gravenhorst. 2006. A comparative analysis of simulated and observed photosynthetic CO_2 uptake in two coniferous forest canopies. Tree Physiol. 26:845–864.

Jones, H.G. 1992. Plants and microclimate: a quantitative approach to environmental plant physiology. 2nd Edn. Cambridge University Press, Cambridge, 428 p.

Kergoat, L. 1998. A model for hydrological equilibrium of leaf area index on a global scale. J. Hydrol. 212–213:268–286.

Kira, T. 1975. Primary production of forests. *In* Photosynthesis and Productivity in Different Environments. Ed. J.P. Cooper. Cambridge University Press, New York, pp 5–40.

Kolari, P., J. Pumpanen, M. Kulmala, H. Ilvesniemi, E. Nikinmaa, T. Grönholm and P. Hari. 2006. Forest floor

vegetation plays an important role in photosynthetic production of boreal forests. For. Ecol. Manag. 221:241–248.

Kolari, P., H.K. Lappalainen, H. Hänninen and P. Hari. 2007. Relationship between temperature and the seasonal course of photosynthesis in Scots pine at northern timberline and in southern boreal zone. Tellus 59B:542–552.

Lagergren, F., L. Eklundh, M. Lundblad, M. Mölder, H. Landkreijer and A. Lindroth. 2005. Primary production and light use efficiency in a mixed coniferous forest in Sweden. Plant Cell Environ. 28:412–423.

Landsberg, J.J. and F.J. Hingston. 1996. Evaluating a simple radiation/dry matter conversion model using data from *Eucalyptus globulus* plantations in Western Australia. Tree Physiol. 16:801–808.

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

Landsberg, J.J., S.D. Prince, P.G. Jarvis, R.E. McMurtrie, R. Luxmoore and B.E. Medlyn. 1996. Energy conversion and use in forests: an analysis of forest production in terms of radiation utilisation efficiency. *In* The Use of Remote Sensing in the Modelling of Forest Productivity. Eds. H.L. Gholz, K. Nakane and H. Shimoda. Kluwer Academic Publishers, Dordrecht, pp 273–298.

Law, B.E., E. Falge, L. Gu et al. 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. Agric. For. Meteorol. 113:97–120.

Linder, S. 1985. Potential and actual production in Australian forest stands. *In* Research for Forest Management. Eds. J.J. Landsberg and W. Parsons. CSIRO, Canberra, Australia, pp 11–35.

Linder, S and E. Troeng. 1980. Photosynthesis and transpiration of 20-year old Scots pine. *In* Structure and Function of Northern Coniferous Forests – An Ecosystem Study. Ed. T. Persson. 32:165–181, Ecol. Bull. (Stockh.).

Lundin, L.C., S. Halldin, A. Lindroth et al. 1999. Continuous long-term measurements of soil–plant–atmosphere variables at a forest site. Agric. For. Meteorol. 98–99:53–73.

Luoma, S. 1997. Geographical pattern in photosynthetic light response of *Pinus sylvestris* in Europe. Funct. Ecol. 11: 273–281.

Magnani, F., M. Mencuccini, M. Borghetti et al. 2007. The human footprint in the carbon cycle of temperate and boreal forests. Nature 447:848–850.

Mäkelä, A., J. Landsberg, A.R. Ek, T.E. Burk, M. Ter-Mikaelian, G.I. Agren, C.D. Oliver and P. Puttonen. 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiol. 20:289–298.

Mäkelä, A., P. Hari, F. Berninger, H. Hanninen and E. Nikinmaa. 2004. Acclimation of photosynthetic capacity in Scots pine to the annual cycle of temperature. Tree Physiol. 24:369–376.

Mäkelä, A., P. Kolari, E. Nikinmaa, M. Perämäki and P. Hari. 2006. Modelling five years of weather-driven variation of GPP in a boreal forest. Agric. For. Meteorol. 139:382–398.

Mäkelä, A., M. Pulkkinen, P. Kolari, F. Lagergren, P. Berbigier, A. Lindroth, D. Loustau, E. Nikinmaa, T. Vesala and P. Hari. 2008. An empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. Global Change Biol. 14:92–108.

Mammarella, I., P. Kolari, J. Rinne, P. Keronen, J. Pumpanen and T. Vesala. 2007. Determining the contribution of vertical advection to the net ecosystem exchange at Hyytiälä forest, Finland. Tellus 59B:900–909.

Markkanen, T., U. Rannik, P. Keronen, T. Suni and T. Vesala. 2001. Eddy covariance fluxes over a boreal Scots pine forest. Boreal Environ. Res. 6:65–78.

Martin, T.A., T.M. Hinckley, F.C. Meinzer and D.G. Sprugel. 1999. Boundary layer conductance, leaf temperature and transpiration of *Abies amabilis* branches. Tree Physiol. 19:435–443.

Medlyn, B.E., F.W. Badeck, D.G.G. De Pury et al. 1999. Effects of elevated $[CO_2]$ on photosynthesis in European forest species: a meta-analysis of model parameters. Plant Cell Environ. 22:1475–1495.

Medlyn, B.E., E. Dreyer, D. Ellsworth et al. 2002. Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. Plant Cell Environ. 25:1167–1179.

Medlyn, B.E., D. Barrett, J.J. Landsberg, P.J. Sands and R. Clement. 2003. Conversion of canopy intercepted radiation to photosynthate: review of modelling approaches to regional scales. Funct. Plant Biol. 30:153–169.

Medlyn, B.E., P. Berbigier, R. Clement, A. Grelle, D. Loustau, S. Linder, L. Wingate, P.G. Jarvis, B.D. Sigurdsson and R.E. McMurtrie. 2005*a*. Carbon balance of coniferous forests growing in contrasting climates: model-based analysis. Agric. For. Meteorol. 131:97–124.

Medlyn, B.E., A.P. Robinson, R. Clement and R.E. McMurtrie. 2005*b*. On the validation of models of forest CO_2 exchange using eddy covariance data: some perils and pitfalls. Tree Physiol. 25:839–857.

Nagy, M.T., I.A. Janssens, J. Curiel Yuste, A. Carrara and R. Ceulemans. 2006. Footprint-adjusted net ecosystem CO_2 exchange and carbon balance components of a temperate forest. Agric. For. Meteorol. 139:344–360.

Niinemets, Ü. 2002. Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. Tree Physiol. 22:515–535.

Nöjd, P. and P. Hari. 2001. Instantaneous PAR estimated using long records of daily temperature and rainfall. Agric. For. Meteorol. 109:47–59.

Norman, J.M. 1993. Scaling processes between leaf and canopy levels. *In* Scaling Physiological Processes: Leaf to Globe. Eds. J.R. Ehleringer and C.B. Field. Academic Press, San Diego, pp 41–76.

Oker-blom, P., T. Pukkala and T. Kuuluvainen. 1989. Relationship between radiation interception and photosynthesis in forest canopies – effect of stand structure and latitude. Ecol. Model. 49:73–87.

O'Neill, R.V. and D.L. DeAngelis. 1980. Comparative productivity and biomass relations of forest ecosystems. *In* Dynamic Properties of Forest Ecosystems. Ed. D.E. Reichle. Cambridge University Press, Cambridge, pp 411–449.

Porté, A. and D. Loustau. 1998. Variability of the photosynthetic characteristics of mature needles within the crown of a 25-year-old *Pinus pinaster*. Tree Physiol. 18:223–232.

Radtke, P.J., T.E. Burk and P.V. Bolstad. 2001. Bayesian melding of a forest ecosystem model with correlated inputs. For. Sci. 48:701–711.

Reichstein, M., E. Falge, D. Baldocchi et al. 2005. On the separation of net ecosystem exchange into assimilation and

ecosystem respiration: review and improved algorithm. Global Change Biol. 11:1424–1439.

Reichstein, M., D. Papale, R. Valentini et al. 2007. Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites. Geophys. Res. Lett. 34, doi:10.1029/2006GL027880.

Richardson, A.D., B.H. Braswell, D.Y. Hollinger et al. 2006. Comparing simple respiration models for eddy flux and dynamic chamber data. Agric. For. Meteorol. 141:219–234.

Ruimy, A., P.G. Jarvis, D. Baldocchi and B. Saugier. 1995. CO_2 fluxes over plant canopies and solar radiation: a review. Adv. Ecol. Res. 26:1–68.

Running, S.W. and J.C. Coughlan. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol. Model. 42:125–154.

Running, S.W., D. Baldocchi, D.P. Turner, S.T. Gower, P.S. Bakwin and K.A. Hibbard. 1999. A global terrestrial monitoring network integrating tower fluxes, flask sampling, ecosystem modeling and EOS satellite data. Remote Sens. Environ. 70:108–127.

Sampson, D.A., I.A. Janssens, J.C. Yuste and R. Ceulemans. 2007. Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest. Global Change Biol. 13:2008–2017.

Sellin, A. 2001. Morphological and stomatal responses of Norway spruce foliage to irradiance within a canopy depending on shoot age. Environ. Exp. Bot. 45:115–131.

Sims, D.A., A.F. Rahman, V.D. Cordova et al. 2008. A new model of gross primary productivity for North American ecosystems based solely on the enhanced vegetation index and land surface temperature from MODIS. Remote Sens. Environ. 112:1633–1646.

Singsaas, E.L., D.R. Ort and E.H. DeLucia. 2001. Variation in measured values of photosynthetic quantum yield in ecophysiological studies. Oecologia 128:15–23.

Stenberg, P. 1996. Simulations of the effects of shoot structure and orientation on vertical gradients in intercepted light by conifer canopies. Tree Physiol. 16:99–108.

Suni, T., F. Berninger, T. Markkanen, P. Keronen, Ü. Rannik and T. Vesala. 2003. Interannual variability and timing of growing-season CO_2 exchange in a boreal forest. J. Geophys. Res. 108(D9):4265.

Turner, D.P., W.D. Ritts, W.B. Cohen, S.T. Gower, M. Zhao, S.W. Running, S.C. Wofsy, S. Urbanski, A.L. Dunn and J.W. Munger. 2003a. Scaling gross primary production (GPP) over boreal and deciduous forest landscapes in support of MODIS GPP product validation. Remote Sens. Environ. 88:256–270.

Turner, D.P., S. Urbanski, D. Bremer, S.C. Wofsy, T. Meyers, S.T. Gower and M. Gregory. 2003b. A cross-biome comparison of daily light use efficiency for gross primary production. Global Change Biol. 9:383–395.

van Dijk, A.I.J.M., A.J. Dolman and E.D. Schulze. 2005. Radiation, temperature, and leaf area explain ecosystem carbon fluxes in boreal and temperate European forests. Global Change Biol. 19:GB2029.

Vesala, T., J. Haataja, P. Aalto et al. 1998. Long-term field measurements of atmosphere–surface interactions in boreal forest combining forest ecology, micrometeorology, aerosol physics and atmospheric chemistry. Trends Heat Mass Moment. Transfer 4:17–35.

Vesala, T., T. Suni, Ü. Rannik et al. 2005. Effect of thinning on surface fluxes in a boreal forest. Global Biogeochem. Cycles 19:GB2001, doi:10.1029/2004GB002316.

Wang, Y.P. and P.G. Jarvis. 1990. Description and validation of an array model – MAESTRO. Agric. For. Meteorol. 51: 257–280.

Wang, Q., J. Tenhunen, E. Falge, C. Bernhofer, A. Granier and T. Vesala. 2003. Simulation and scaling of temporal variation in gross primary production for coniferous and deciduous temperate forests. Global Change Biol. 10:37–51.

Warren, C.R., E. Dreyer and M.A. Adams. 2003. Photosynthesis–Rubisco relationships in foliage of *Pinus sylvestris* in response to nitrogen supply and the proposed role of Rubisco and amino acids as nitrogen stores. Trees – Struct. Funct. 17:359–366.

White, M.A., S.W. Running and P.E. Thornton. 1999. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. Int. J. Biometeorol. 42:139–145.

Wright, I.J., P.B. Reich, M. Westoby et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Yuan, W., S. Liu, G. Zhou et al. 2007. Deriving a light use efficiency model from eddy covariance flux data for predicting daily gross primary production across biomes. Agric. For. Meteorol. 143:189–207.

Zha, T., S. Niinisto, Z. Xing, K.Y. Wang, S. Kellomaki and A.G. Barr. 2007. Total and component carbon fluxes of a Scots pine ecosystem from chamber measurements and eddy covariance. Ann. Bot. 99:1239.

Appendix A. Leaf gas exchange model

We use the optimal stomatal control model as introduced by Cowan and Farquhar (1977) and further developed by Hari et al. (1986) and applied to Scots pine data obtained by Hari et al. (1999) and Mäkelä et al. (2004). The central assumption is that stomatal conductance varies in such a way to maximize CO_2 assimilation (A) per unit water used (transpiration rate, E), which yields

$$\frac{\mathrm{d}E}{\mathrm{d}A} = \lambda, \tag{A.1}$$

where λ is the marginal cost of water (mol H_2O mol^{-1} CO_2) and can be interpreted as the degree of stomatal control. Hari et al. (1986) coupled the optimal stomatal control concept to a photosynthesis model, to arrive at a closed-form solution for the stomatal conductance (g_C) in response to VPD, light (Q) and CO_2 concentration (c_a). The solution for g_C is given by

$$g_C = \rho \cdot \left(\sqrt{\frac{c_a}{\lambda \cdot D \cdot 1.6}} - 1 \right) \cdot k_C(Q), \tag{A.2}$$

where g_C is the stomatal conductance to CO_2 (mol m^{-2} s^{-1}), c_a is the ambient CO_2 concentration (mol m^{-3}), λ is the marginal cost of water (mol mol^{-1}), D is the VPD (mol m^{-3}), ρ converts to molar units (mol m^{-3}) and Q is the PPFD (mol m^{-2} s^{-1}). For this solution, it is assumed that photosynthesis is a linear function of
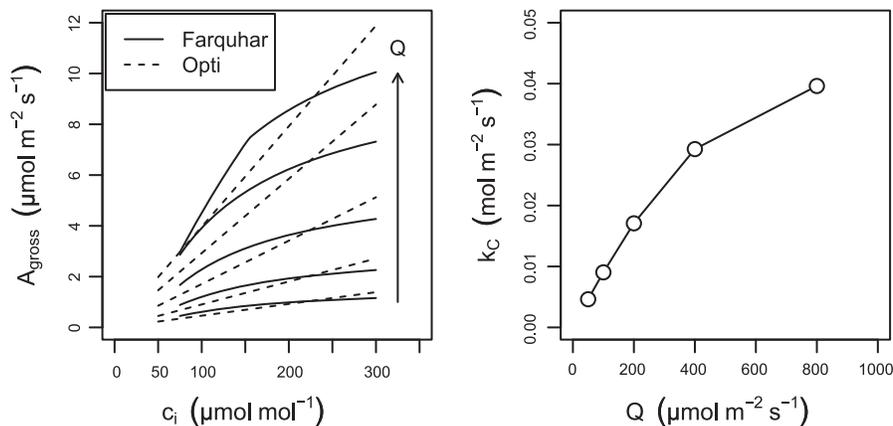
Figure A1. Illustration of the derivation of k_{max} from the Farquhar model parameters V_{cmax} and J_{max}. Curves of gross CO_2 assimilation versus c_i are plotted from the Farquhar model at various light intensities and estimates of k_C at each light intensity are found by linear regression (the dashed lines). These estimates can subsequently be used to fit a rectangular hyperbola (Eq. A.2).
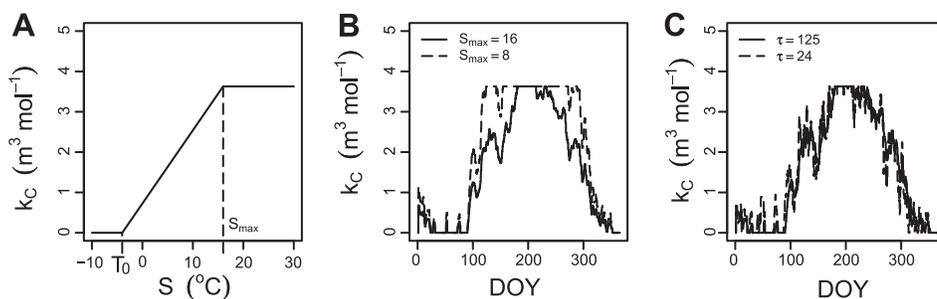

Figure A2. Illustration of the seasonal dependence of photosynthetic capacity on temperature in the leaf photosynthesis model. Values of the state of acclimation (S) are calculated as in Eq. (A.4), and the parameter k_C depends linearly on S up to a maximum. The time when the maximum 'unstressed' k_C is reached depends on the parameter S_{max}. Panels B and C show how the estimated seasonal pattern of k_C changes when S_{max} and τ are varied. The parameter α (Eq. A.3) follows the same seasonal pattern, so that k_C and α are always proportional (Mäkelä et al. 2004).

intercellular CO_2 concentration, but that the slope of this relationship (k_C) varies with Q as a rectangular hyperbola

$$k_C(Q) = \frac{k_{max} \cdot \alpha \cdot Q}{k_{max} + \alpha \cdot Q}, \qquad (A.3)$$

where k_{max} is the photosynthetic capacity (slope of the A–c_i curve at saturating light, m^3 m^{-2} s^{-1}) and α is the quantum yield of $k_C(Q)$ (m^3 mol^{-1}) (the slope of $k_C(Q)$ at $Q = 0$).

In contrast, the widely used photosynthesis model of Farquhar et al. (1980) predicts a concave dependence of assimilation rate (A) on intercellular CO_2 concentration (c_i). Figure A1 shows a set of A–c_i curves as predicted by the Farquhar model (for equations, see example, Medlyn et al. (2002)), and straight lines as assumed in the optimal stomatal control model used in this study. Differences between the two models are rarely > 10%, and differences are small at low light. Aalto et al. (2002) found only small differences in fit of the Farquhar model and the optimal stomatal control model, indicating also that a linear A–c_i dependence gives only small errors in predictions at near ambient CO_2 concentrations. It is possible to use the Farquhar A–c_i curves in an optimal stomatal control framework instead of the linear A–c_i assumption, but there is then no closed-form solution for g_C, and it must be found by numerical methods (e.g., Berninger et al. 2000), which makes the model much too slow for our purposes because we perform many model runs in the simulation experiments.

Temperature dependence of both photosynthetic capacity (k_{max}) and the quantum yield of $k_C(Q)$ (α) follows a seasonal temperature acclimation model as developed by Mäkelä et al. (2004, 2008). A variable representing the 'state of acclimation' (S) is calculated for each day of the year from ambient temperature with a smoothing function,

$$\frac{dS}{dt} = \tau \cdot (T_{air}(t) - S(t)) \quad \text{with } S(1) = T_{air}(1). \quad (A.4)$$

Both k_{max} and α depend on S with a ramp function (Figure A1), with T_0 representing the value of S below which no photosynthesis takes place and S_{max} the value
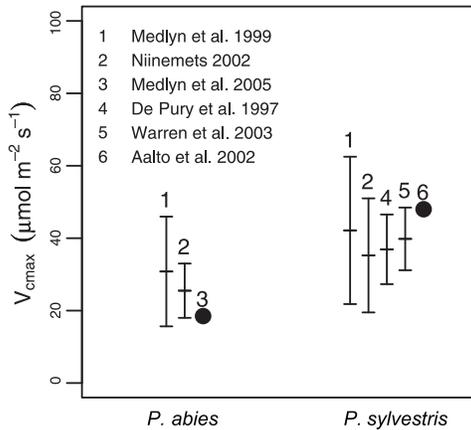
Figure B1. Literature review of maximum carboxylation rate (V_{cmax}) of Norway spruce (*P. abies*) and Scots pine (*P. sylvestris*). The vertical bars denote the range of values reported by each of the studies, which consist of a number of values across trees or sites. The horizontal line at the middle of each bar denotes the midpoint of the range of all values reported in each study, not the sample mean. Two studies reported just one value for V_{cmax}.

above which increases in S do not affect k_{max} or α. The parameter τ represents the smoothness of the dependence of S on air temperature and S_{max} determines the degree of seasonality. See Figure A2 for the effect of S_{max} and τ on the temperature dependency of k_{max} and α.

Appendix B. Review of photosynthetic capacity

We reviewed the literature for values of the maximum carboxylation rate (V_{cmax}) for Scots pine (*P. sylvestris*) and Norway spruce (*P. abies*), in particular summarizing studies that already gathered a number of V_{cmax} estimates for these two species. The results show a wide range in V_{cmax} for both species, with substantial overlap (Figure B1). For Tharandt, we used gas exchange parameters from Scots pine in Hyytiälä, because we did not have estimates of photosynthetic capacity for Norway spruce. This review shows that there is no clear difference between the two species.