Research paper

Does canopy mean nitrogen concentration explain variation in canopy light use efficiency across 14 contrasting forest sites?

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The maximum light use efficiency (LUE = gross primary production (GPP)/absorbed photosynthetic photon flux density (aPPFD)) of plant canopies has been reported to vary spatially and some of this variation has previously been attributed to plant species differences. The canopy nitrogen concentration [N] can potentially explain some of this spatial variation. However, the current paradigm of the N-effect on photosynthesis is largely based on the relationship between photosynthetic capacity (A_{max}) and [N], i.e., the effects of [N] on photosynthesis rates appear under high PPFD. A maximum LUE–[N] relationship, if it existed, would influence photosynthesis in the whole range of PPFD. We estimated maximum LUE for 14 eddy-covariance forest sites, examined its [N] dependency and investigated how the [N]–maximum LUE dependency could be incorporated into a GPP model. In the model, maximum LUE corresponds to LUE under optimal environmental conditions before light saturation takes place (the slope of GPP vs. PPFD under low PPFD). Maximum LUE was higher in deciduous/mixed than in coniferous sites, and correlated significantly with canopy mean [N]. Correlations between maximum LUE and canopy [N] existed regardless of daily PPFD, although we expected the correlation to disappear under low PPFD when LUE was also highest. Despite these correlations, including [N] in the model of GPP only marginally decreased the root mean squared error. Our results suggest that maximum LUE correlates linearly with canopy [N], but that a larger body of data is required before we can include this relationship into a GPP model. Gross primary production will therefore positively correlate with [N] already at low PPFD, and not only at high PPFD as is suggested by the prevailing paradigm of leaf-level A_{max}–[N] relationships. This finding has consequences for modelling GPP driven by temporal changes or spatial variation in canopy [N].

Keywords: canopy nitrogen concentration, eddy covariance, gross primary production, light use efficiency, quantum yield, vegetation productivity

Introduction

Forest productivity varies greatly within the temperate and boreal vegetation zones. Gross primary productivity (GPP) models based on the concept of light use efficiency (LUE) try to explain this variability, typically by assuming that vegetation has a certain maximum LUE and that the variability in GPP is

primarily caused by differences in intercepted photosynthetic photon flux density (PPFD) and environmental constraints that regulate actual LUE (Monteith and Moss 1977, Kumar and Monteith 1981, Landsberg and Waring 1997). Recently, the maximum LUE—the LUE reached in optimal conditions—has also been reported to vary by plant functional type (PFT) (Turner et al. 2003, Kergoat et al. 2008). Models of GPP, on the other hand, differ in their assumptions about the variation of maximum LUE, which is an important parameter. Some models assume that it is constant, while others assume that it varies by biome or PFT (cf. Running et al. 2000, Yuan et al. 2007). Replacing maximum LUE variation by biome, PFT or species with a general approach could potentially improve the accuracy of global GPP estimates.

Recent studies have reported that canopy mean leaf nitrogen concentration [N] (on a mass basis) correlates with shortwave surface albedo and near-infrared reflectance (800–1200 nm; Ollinger et al. 2008, Fisher 2009, Ollinger et al. 2009) and that maximum LUE correlates with canopy [N] (Kergoat et al. 2008). Because [N] can be remotely sensed (Ollinger et al. 2008), this would facilitate continuous detection of spatial variation (within and across PFTs or species) in GPP. One could thus derive better GPP estimates by measuring canopy [N] remotely over large spatial scales and incorporating canopy [N] effects on maximum LUE into GPP models, which already account for the other environmental factors that influence GPP.

It has long been known that leaf photosynthetic capacity, i.e., the light-saturated rate of photosynthesis (A_{max}), is correlated with leaf nitrogen concentration on an area and mass basis (Field and Mooney 1986, Evans 1989, Reich et al. 1995, 1997, Wright et al. 2004). A_{max} is related to the capability of Rubisco to catalyse RuP_2 (ribulose-1,5-bisphosphate) carboxylation, because RuP_2 accumulates quickly under high irradiation (Farquhar et al. 1980). A large share of total leaf N is bound in Rubisco (Field and Mooney 1986, Evans 1989). However, apparent quantum yield of photosynthesis (q), i.e., the slope of photosynthesis with PPFD under low PPFD, has not been reported to change with [N]. Canopy response may, however, differ from that of single leaves.

Dense canopies have a high proportion of shaded foliage, which facilitates high LUE under high incident PPFD (assuming growing conditions are close to optimal), although the top of the canopy is light saturated. Canopy structure also varies vertically, which is likely to promote high LUE under high irradiance: leaf [N] per area, morphology, structure and orientation change with depth in the canopy (Ellsworth and Reich 1993, Stenberg et al. 1995, Kull and Niinemets 1998).

Despite these canopy-level mechanisms, measurements have confirmed the reduction of actual LUE of canopies under high PPFD (Schwalm et al. 2006, Ibrom et al. 2008), which can be at least partly explained by the leaf-level A_{max}–irradiance relationship and the distribution of irradiance within the canopy (Medlyn 1998). Due to the acclimation of canopies to canopy gradients in PPFD, the actual LUE of the canopy is, however, likely less sensitive to canopy mean [N] than leaf A_{max} is to leaf [N]. We hypothesize that maximum canopy LUE, on the other hand, is not related to [N] as it occurs under low PPFD, given that there is no reported q–[N] relationship on leaf level.

Recent studies based on eddy-covariance measurements have still reported correlations between maximum canopy LUE and mean [N] (Green et al. 2003, Kergoat et al. 2008, Ollinger et al. 2008). However, use of various definitions for maximum LUE complicates the comparison between theory and observations. Xiao (2006) has pointed out that estimates of maximum LUE depend on the type of model they are estimated with. Non-linear models accounting for light saturation tend to have a higher maximum LUE than models that estimate LUE based on a linear regression of GPP on aPPFD. It is also possible that the estimation method for maximum LUE influences its [N] relationship. According to Kergoat et al. (2008), maximum daily LUE is significantly correlated with [N], but their LUE definition was based on days having high values of half-hourly GPP. Light use efficiency of high GPP days could be more sensitive to [N], as these days are likely to have high PPFD as well. Ollinger et al. (2008) reported a LUE–[N] relationship whereby maximum LUE apparently accounted for light saturation but was estimated under 'reasonable "full-sun"' day conditions when other environmental factors were the least limiting. Schwalm et al. (2006), on the other hand, did not find a [N] relationship in peak growing season LUE estimates across nine sites. There has also been a long tradition of defining LUE on the basis of net primary production (NPP) (Monteith and Moss 1977), whereby a LUE–[N] relationship has been reported (Green et al. 2003). However, GPP should provide a better basis for assessing the direct environmental effects on photosynthesis (Goetz and Prince 1999).

Mäkelä et al. (2008) built a GPP model that was fitted empirically to data from five eddy-covariance forest sites. The maximum LUE of that model, which was called 'potential LUE' of a canopy, is, by definition, unaffected by weather and irradiance, whereas the actual daily LUE is influenced by these environmental factors. According to Mäkelä et al. (2008), daily temperature, vapour pressure deficit (VPD) and absorbed PPFD accounted for most of the daily variation of GPP in the model but unexplained variation remained in the site-specific maximum LUE, which correlated linearly with canopy [N] (Mäkelä et al. 2008). Based on the hypothesis represented above, this correlation could have emerged from the effects of [N] on GPP under high PPFD. Introducing such a linear response to the model could therefore overestimate GPP under low PPFD.

The objectives of this study were to investigate the relationship of mass-based canopy mean [N] and maximum LUE. Two methods to estimate daily maximum LUE were used: (i) the

potential LUE is estimated as a site-specific parameter of the GPP model, and (ii) the maximum actual LUE is estimated as the highest actual LUE detected at the site. This estimate is obtained directly from eddy-covariance sites' GPP and aPPFD data, as the upper percentiles of the observed distributions of the ratio of daily GPP to daily aPPFD, and it is estimated for all days, and days with low, medium and high PPFD. In this study, both maximum LUEs were determined for 14 eddy-covariance forest sites, and their relationships with canopy mean [N] were studied across the sites. We hypothesized that the maximum actual LUE will not correlate with [N] because maximum LUE should occur on low PPFD days when the GPP is not light saturated. The LUE of high PPFD days, on the other hand, will have a strong [N] relationship, and some of this relationship is also reflected in potential LUE estimated with the model. We further investigated how [N] could be incorporated into the model, and whether its inclusion will improve the performance of the model.

Materials and methods

Gross primary productivity model

The GPP model, Prelued, used in this study is adopted from previous work of Mäkelä et al. (2008). Prelued predicts photo-synthetic production P_k (GPP, g C m^{-2} day^{-1}) during day k:

$$P_k = \beta f_{APAR,k} \phi_k \prod_i f_{i,k} \qquad (1)$$

where β is the potential LUE (g C mol PPFD^{-1}), ϕ_k is photosynthetic photon flux density (PPFD, mol m^{-2}) during day k, $f_{APAR,k}$ is the fraction of PPFD absorbed by the canopy during day k and $f_{i,k}$ are other modifiers that account for the suboptimal conditions i of day k. All modifiers range from 0 to 1. The Appendix lists the symbols and units used in this study.

Actual LUE β_k (g C mol PPFD^{-1}) of the site on day k is the product of potential LUE and the current values of the modifiers:

$$\beta_k = \frac{P_k}{\phi_k f_{APAR,k}} = \beta \prod_i f_{i,k} \qquad (2)$$

Here we briefly introduce the methodology of the f_i-modifiers that scale down the potential photosynthetic production with suboptimal conditions during the day. More details and a figure about f_i-modifier responses to the environment are provided in Mäkelä et al. (2008).

The light modifer (f_L) scales down the potential photosynthetic production with high PPFD on day k, with

$$f_{L,k} = \frac{1}{\gamma \phi_k + 1} \qquad (3)$$

For low incident PPFD, this modifier approaches unity. On cloudy days, PPFD is generally lower, and a larger fraction of it is diffuse, which promotes high LUE and canopy quantum yield (Gu et al. 2002, Schwalm et al. 2006) because a more even distribution of PPFD within the canopy enhances GPP (Roderick et al. 2001). Our f_L is not, however, restricted to effects of diffuse fraction or cloudiness but rather describes overall effects of light saturation of LUE.

The effects of VPD on GPP are accounted for with the f_D-modifier, which scales down potential photosynthetic production in the canopy with high values of VPD, D (kPa):

$$f_{D,k} = e^{\kappa D_k} \qquad (4)$$

To account for the temperature-related effects, we used a modifier for temperature acclimation (Mäkelä et al. 2004). The following functions describe its behaviour:

$$X_k = X_{k-1} + \frac{1}{t}(T_k - X_{k-1}), \text{ where } X_1 = T_1$$
$$S_k = \max\{X_k - X_0, 0\} \qquad (5)$$
$$f_{S,k} = \min\left\{\frac{S_k}{S_{max}}, 1\right\}$$

where the state of acclimation S_k (°C) is estimated using a first-order dynamic delay model for X_k (°C), which is the a priori estimate for the state of acclimation. It is influenced by the ambient temperature T_k (°C) on day k, and its value for the previous day (X_{k-1}). τ is a constant related to the speed of response of the current acclimation status to changes in T_k. X_0 (°C) is a threshold for X_k defining the low limit above which S_k starts to increase f_S, and S_{max} (°C) is the value where the acclimation modifier reaches its optimum.

The Prelued model with its f_L-modifier (when f_S, f_D and f_{APAR} are unity) is analogous to the frequently used rectangular hyperbola photosynthesis model where GPP saturates to parameter P_{max}, with initial slope q (i.e., apparent quantum yield) at zero PPFD:

$$P = \frac{q P_{max} \phi}{q\phi + P_{max}} \qquad (6)$$

The parameters of this model can be obtained from Prelued parameters as follows: $P_{max} = \beta/\gamma$ and $q = \beta$. The analogy suggests that if [N] influences β, P will be influenced in the whole range of PPFD. Using the analogy, we also studied if [N] influenced only P_{max}, i.e., P would be influenced by [N] only under high PPFD.

Determination of potential LUE

The parameterization procedure for the Prelued model was adopted from Mäkelä et al. (2008), where it is described in more detail. Equation (1) was parameterized to yield estimates

Table 1. Models to study the effects of canopy [N] on LUE.

Model	Potential LUE, β	β–[N] effect	P_{max}–[N] effect	Purpose
1	Site-specific	—	—	For comparison of Models 2–6
2	Shared	—	—	For comparison of Models 3–6
3	Shared	Eq. (8)	—	Is the potential LUE–[N] relationship linear?
4	Shared	Eq. (9)	—	Is the effect of [N] larger at high [N]?
5	Shared	Eq. (10)	—	Does potential LUE saturate at high N?
6	Shared	—	Eq. (11)	Does the incorporation of [N] with P_{max} yield a better model than incorporating it with potential LUE?

for potential LUE (β) and the parameters of the f_L and f_D modifiers γ and κ. Table 1 lists all model versions that were parameterized in this study.

In Model 1, β was allowed to vary by site and the parameters were estimated with non-linear regression:

$$P_{s,k} = \beta_s f_{APAR,k} \phi_k f_{S,k} f_{D,k} f_{L,k} + \varepsilon_{s,k} \qquad (7)$$

where subscript s stands for site. While β_s was site specific, the parameters for modifiers f_i were shared across the sites. $\varepsilon_{s,k}$ is a random error term that was assumed to be normally distributed. We also fitted two additional models in order to confirm whether [N] influenced P_{max} rather than q. In these models, (i) γ of the f_L was site specific and β shared, and (ii) both γ and β were site specific.

In the parameterization of Model 1, the parameters γ, κ and β_s were estimated conditionally to the parameters of the f_S-modifier, τ, X_0 and S_{max}. First a coarse resolution grid of τ, X_0 and S_{max} values was generated. The model parameters γ, κ and β_s, and the root mean square error (RMSE) of the model were estimated for each grid point. The RMSE values of the coarse grid were examined and a fine dense grid was generated for the region with the smallest RMSE in the coarse grid. Model parameters γ, κ and β_s, and RMSE were then estimated for the fine grid, and the parameter set that had the smallest RMSE in the non-linear regression was selected as the final model parameter set.

Model 2 was similar to Model 1, except that β was shared across the sites. This corresponds to the hypothesis that potential LUE is invariable across sites.

The Model 2 fit was made conditional to values of τ, X_0 and S_{max} obtained from the Model 1 fit, as the model was previously found to be rather insensitive to τ, X_0 and S_{max}, whether site specific or not (see Table 2 in Mäkelä et al. 2008).

The parameters were estimated using the nls-function in R (R Development Core Team 2009); all other analyses were also conducted in R.

Determination of maximum actual LUE

Maximum actual LUE (B_s) was simply defined as the highest achieved actual daily LUE at the site. The second LUE definition complemented the first definition in the following aspects: First, contrary to potential LUE, it is not sensitive to model assumptions on vegetation response to environment, and that the response is similar across sites. Second, we did not have soil water data from every site to calibrate a soil water modifier. Some of the sites in this study (Bray and Metolius) experience severe drought that could influence their potential LUE estimate, and bias the investigations of its [N] relationship. Wind River also has a significant drought season during July–October. Third, estimated β_s can emerge from either the P_{max}–[N] or the q–[N] relationship (Eq. (6)), but estimating B_s for different PPFD levels allows distinguishing whether the B_s–[N] relationship exists only under high PPFD as we assumed.

To estimate maximum actual LUE, we first estimated actual daily LUE as the ratio of daily GPP to aPPFD (see the first part of Eq. (2)). To exclude outliers in the data, observations of LUE further away than 3 standard deviations (SD) from the mean (i.e., 0.25% of observations) were discarded. In addition, observations where PPFD was lower than 0.1 times the growing season average of the site were removed because very small values of PPFD increase the uncertainty of actual LUE.

The maximum actual LUE at each site was estimated as the 98th percentile of all daily LUE. The same choice of percentile was made in Kergoat et al. (2008). The downside of estimating LUE in this way is the sensitivity of maximum actual LUE to subjective decisions upon the percentile. High percentiles are generally also sensitive to outliers. Therefore, in addition to using a fixed 98th percentile of all daily observations for each site we also used other percentiles above or equal to the 95th percentile, and tested their relationship with canopy mean [N]. Note also that our approach differs from that of Kergoat et al. (2008) in one essential way. They estimated maximum daily LUE from days with the highest GPP (when PPFD is generally high), whereas we defined it from its own percentile, i.e., using all days. High GPP does not necessarily generate high LUE as the latter is also affected by absorbed PPFD. We also estimated B_s for subsets of low (2–25 mol m^{-2}), medium (25–50 mol m^{-2}) and high (>50 mol m^{-2}) PPFD days in order to examine PPFD dependency of the B_s–[N] relationship.

Regressions to explain LUE variability

In order to explain the across-site variation of estimated potential and maximum actual LUE ($\hat{\beta}_s$, B_s), we performed linear regressions of LUE against canopy mean [N] (dry mass based),

Table 2. Study sites.

Code	Site	Location	MAT (°C)	Vegetation type (dominant tree species)	Age (a)	LAI (m^2 m^{-2})	f_{APAR}	GPP (gC m^{-2} a^{-1})	VPD growing season mean (kPa)	Years of data	References
SD	Sodankylä, Finland	67°22′N 26°38′E	−1.0	Coniferous (*Pinus sylvestris*)	65[1]	1.7	0.60	610	0.43	2001–2002	Aurela (2005)
HY	Hyytiälä, Finland	61°51′N 24°18′E	2.9	Coniferous (*Pinus sylvestris*)	45	3.3	0.75	1006	0.44	1997–2004	Ilvesniemi and Liu (2001), Suni et al. (2003)
NO	Norunda, Sweden	60°05′N 17°29′E	5.5	Coniferous (*Pinus sylvestris, Picea abies*)	108	4.3	0.87	1076	0.56	1995–1997, 1999–2002	Lundin et al. (1999), Lagergren et al. (2005)
TH	Tharandt, Germany	50°58′N 13°34′E	7.5	Coniferous (*Picea abies*)	113	7.6	0.94	1697	0.63	2001–2003	Grünwald (2003), Grünwald and Bernhofer (2007)
BR	Bray, France	44°42′N 0°46′W	13.0	Coniferous (*Pinus pinaster*)	35	1.7	0.66	1460	0.46	2001–2002	Berbigier et al. (2001), Delzon et al. (2004)
ME	Metolius, USA	44°27′N 121°33′W	8.6	Coniferous (*Pinus ponderosa*)	60[1]	2.5	0.70	1393	0.96	2002–2005	Law et al. (2001, 2003, 2006), Schwarz *et al.* (2004)
NOBS	NOBS, Canada	55°53′N 98°29′W	−3.2	Coniferous (*Picea mariana*)	160	4.2	0.85	679	0.83	2000–2002	Gower et al. (1997), Dunn et al. (2007)
AB	Abisko, Sweden	68°21′N 18°47′E	0.6	Deciduous (*Betula pubescens subsp. tortuosa*)	−[2]	1.1[3]	0.45	530	0.33	2005	Johansson (2006)
BA	Brasschaat, Belgium	51°18′N 4°31′E	9.8	Mixed (*Pinus sylvestris, Quercus robur*)	75	3.0[4]	0.62	1126	0.43	1997–1998, 2000–2002, 2004	Carrara et al. (2003), Gond et al. (1999)
RE	Renon, Italy	46°35′N 11°26′E	4.1	Coniferous (*Picea abies*)	0–180	5.5	0.93	1057	0.35	1999, 2001–2005	Marcolla et al. (2005)
SO	Sorø, Denmark	55°29′N 11°38′E	8.3	Mixed (*Fagus sylvatica, Picea abies*)	82	5.0[3]	0.82	1656	0.35	2005–2006	Pilegaard et al. (2003)
TE	Teshio, Japan	45°03′N, 142°06′E	5.7	Mixed (*Quercus crispula, Betula ermanii, Abies sachalinensis*)	165	3.0[3]	0.69	1458	0.34	2002	Takagi et al. (2009)

Continued

Table 2. Continued

Code	Site	Location	MAT (°C)	Vegetation type (dominant tree species)	Age (a)	LAI (m² m⁻²)	f_{APAR}	GPP (gC m⁻² a⁻¹)	VPD growing season mean (kPa)	Years of data	References
WR	Wind River, USA	45°49′N 121°57′W	8.7	Coniferous (*Pseudotsuga menziesii, Tsuga heterophylla*)	500[5]	8.8	0.98	1376	0.59	1999–2004	Shaw et al. (2004), Falk et al. (2005)
ZO	Zotino, Russia	60°45′N 89°23′E	−3.7	Coniferous (*Pinus sylvestris*)	200	1.5	0.68	470[6]	0.83	1999–2000[6]	Lloyd et al. (2002)

[1]Mean age of uneven-aged stand; in Sodankylä, ages of trees vary between 50 and 160 years; in Metolius, the mean age of the oldest 10% of the trees is 90 years.
[2]Not known.
[3]Peak value over year.
[4]Mean over year, also understorey included.
[5]Age of the largest, dominant *Pseudotsuga menziesii* trees. Age of the dominant trees is between 350 and 500 a.
[6]Julian days 150–250.

growing season and annual means of climatic variables (VPD, temperature), leaf area index (LAI) and latitude.

Canopy nitrogen f-modifiers

The possibility of including canopy mean [N] in our GPP model was studied by the introduction of f_N-modifiers. We wanted to test whether we could improve the model in comparison to a model where the LUE parameter is shared, and if there would be a change in other parameter estimates (κ and γ) due to the inclusion of [N]. For this purpose, we incorporated an f_N-function into Model 2.

Three alternative f-modifiers that can represent different shapes of the potential LUE–[N] relationship were formulated. These f-modifiers multiply our original model (Eq. (7)):

$$f_N = b[N] + a \tag{8}$$

$$f_N = \frac{1}{\rho_{N,u}[N] + 1} \tag{9}$$

$$f_N = \frac{[N]}{\rho_{N,sat} + [N]} \tag{10}$$

When multiplied with the shared β model (Model 2), Eq. (8) yields 'Model 3', Eq. (9) yields 'Model 4', Eq. (10) yields 'Model 5', and Eq. (11) yields 'Model 6'.

The first modifier (Eq. (8)) was directly derived using linear regression of [N] to fitted β_s, so no additional parameter estimation was required in that case. In contrast, parameters β, γ and κ of Models 3 and 4 were estimated simultaneously with the ρ parameters of Eqs. (7) and (8).

Two other modifiers were incorporated into the model fit in order to see whether possible correlation of modifiers will affect the form of the [N] response, and to estimate the values of their parameters ($\rho_{N,j}$, where subscript $j = u$ and $j = sat$ marks parameters for Models 4 and 5, respectively). Modifiers in Models 4 and 5 differ in one essential aspect from each other. The former can take a non-saturating form with increasing [N] when its parameter $\rho_{N,u}$ is negative, whereas the latter has a saturating response to increasing [N], which was weakly evident in the data of Kergoat et al. (2008). Note also that the formulations of modifiers for Models 3 and 4 can change the meaning of the LUE parameter, as they are not necessarily bounded between [0, 1]. However, since we were testing the shape of the response to canopy mean [N], this effect was not regarded as essential.

The fourth N-response model was incorporated into the f_L-modifier, so that the N-effect is dependent on PPFD and influences the saturation level of GPP but not the potential LUE:

$$f_{L,N} = \frac{1}{(\gamma \phi_k / [N]) + 1} \tag{11}$$

In the context of Eq. (6), [N] linearly increases P_{max} but does not influence q. Replacing f_L with $f_{L,N}$, 'Model 2' yields 'Model 6'.

Lastly, the models were compared with respect to the RMSE and R^2_{adj} values of the non-linear regressions.

Data

We used data from 14 forest sites located across the northern hemisphere with eddy-covariance measurement towers (Table 2). Ten of the sites were coniferous, one deciduous and

three mixed. The sites were contrasting in terms of LAI, stand structure, age and GPP (Table 2). There were 1–8 years of daily data at each site, for a total of 53 site-years. For five of the sites in Europe (Sodankylä, Hyytiälä, Norunda, Tharandt and Bray) and two in North America (Metolius and Northern Old Black Spruce (NOBS)), the data have been described and their estimation processes documented in our previous work (Mäkelä et al. 2008). The slight changes made here in the processing of the Metolius and NOBS data are explained below. For the seven new sites (Abisko, Brasschaat, Renon, Sorø, Teshio, Wind River and Zotino), the data were obtained via the site Principal Investigators, except for Brasschaat and Renon whose data were taken from the CarboEurope-IP database (http://gaia.agraria.unitus.it/database/carboeuropeip/, Level 2 data for Brasschaat, Level 3 and 4 data for Renon).

Daily totals of above-canopy PPFD (mol m^{-2}) and daily means of air temperature (°C) and VPD (kPa) were computed from gap-filled half-hourly measurements. If >30% (14/48) of the half-hourly observations per day were gap filled, the daily value was treated as missing. This rule was also applied to the NOBS data that were not filtered for missing observations in the previous work.

Daily totals of ecosystem GPP (g C m^{-2}) were summed from half-hourly estimates. Half-hourly GPP was estimated as the difference between measured net ecosystem exchange (NEE) and estimated total ecosystem respiration (TER). Half-hourly TER was modelled from half-hourly night-time NEE as a site-specific function of air temperature, soil organic layer temperature, top soil temperature or/and soil moisture. This dependence of night-time TER on temperature or/and soil moisture was then extrapolated to daytime, and the half-hourly daytime GPP was computed by subtracting the estimated TER from the measured NEE. Before these computations, half-hourly NEE was filtered with site-specific criteria for turbulence and atmospheric stability. When the NEE measurement was discarded or missing, either NEE was gap filled, or GPP was directly estimated as a saturating function of PPFD or global radiation. If >30% of the half-hourly NEE observations were inadequate or missing, the daily value of GPP was coded as missing, except at Hyytiälä (years 1997–2000 and 2004), Metolius, NOBS, Abisko, Brasschaat and Teshio, where the proportion was relaxed to 50% (24/48) to keep the number of missing daily GPP values reasonable. The GPP estimation procedure is documented in more detail in Duursma et al. (2009) for Brasschaat, in Takagi et al. (2009) for Teshio, in Falk et al. (2008) for Wind River, and in Lloyd et al. (2002) for Zotino; for Renon and Sorø, the estimation followed the CarboEurope-IP practice (Reichstein et al. 2005); for NEE gap filling, see also Falge et al. (2001) and Wang et al. (2003). In Table 2, the average annual total GPP over the observation years in the data is given for each site.

Daily totals of aPPFD were estimated as site-specific fractions (f_{APAR}) of daily totals of above-canopy PPFD. At the coniferous sites, f_{APAR} could be estimated reasonably precisely as constant over time. At Renon and Wind River, f_{APAR} was estimated from daily PPFD measurements taken above and below the canopy. At Zotino, f_{APAR} was obtained with the Lambert–Beer law, using projected LAI and an extinction coefficient of 0.75 based on the model simulations by Alton et al. (2005). At Metolius, the unrealistically low f_{APAR} value used in Mäkelä et al. (2008) was corrected by substituting projected LAI and an extinction coefficient of 0.48 in the Lambert–Beer equation. At the deciduous and mixed sites, seasonal variation was incorporated in f_{APAR} (Figure 1). At Abisko, Sorø and Teshio, f_{APAR} was estimated from daily PPFD measurements, taken above and below the canopy as a piecewise linear function of day of year. At Brasschaat, f_{APAR} was estimated from light interception output of model simulations (Duursma et al. 2009) based on half-hourly PPFD, air temperature and VPD in the data, and seasonally changing LAI taken from Gond et al. (1999), and resulting in a combination of a constant and a quadratic function of day of year. Due to inadequate data, ground vegetation was not accounted for, except at Brasschaat where the LAI used in the model simulations comprised also the understorey. In Table 2, the average f_{APAR} over the observation days is given for each site.

The number of missing daily values was notable only for GPP: at Sodankylä, NOBS, Abisko, Brasschaat and Teshio, more than half of the daily GPP values per year were missing on average. For above-canopy PPDF, air temperature and VPD, not >20% daily values were missing at any site in any year. At Zotino, only data for Julian days 150–250 were available.

Contrary to area-based leaf nitrogen content, dry-mass-based leaf [N] varies fairly little within the tree canopy (Niinemets 2007) and could therefore provide a better basis for correlating tree canopy [N] and maximum LUE. Determination of representative mean leaf [N] for a tree canopy is still laborious, especially in a forest with a heterogeneous canopy structure, as [N] varies along with species. For this reason, data availability and quality varied between sites. The site-specific values of dry-mass-based mean leaf [N] used in this study, and information on their estimation, are given in Table 3.

Results

Potential LUE

The mean potential LUE of mixed/deciduous species was 0.63 g C mol^{-1} higher than the mean of coniferous sites, 0.53 g C mol^{-1} ($P = 0.06$) (Table 4). Across all sites, potential LUE estimates ($\hat{\beta}_s$) significantly correlated with canopy mean [N] ($P = 0.043$) (Figure 2), but no correlation was found between $\hat{\beta}_s$ and growing season mean T, VPD or ϕ, indicating that f_S, f_D and f_L functions represented these sources of variation. In additional regressions where the effect of [N] on P_{max} was studied,

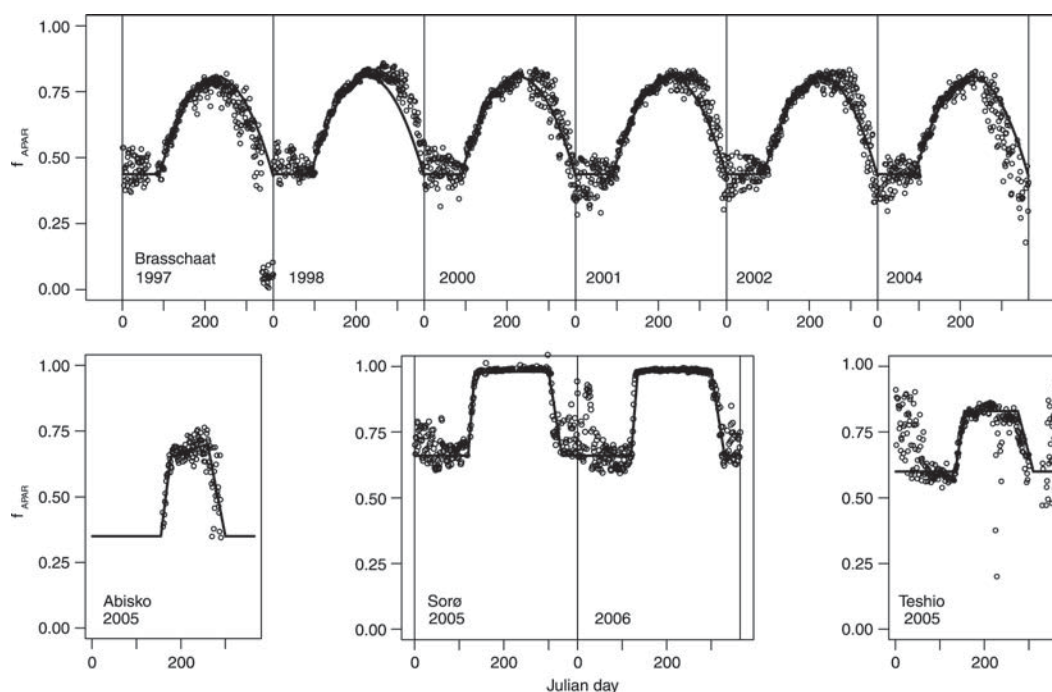Figure 1. Daily fraction of PPFD absorbed by the canopy (f_{APAR}) at deciduous and mixed sites in the data: measured (or simulated) values, and the models estimated from them and used in the Prelued model (Eq. (1)). At each site, the f_{APAR} model was estimated with all the observation years pooled together. At Brasschaat, absorption by the ground vegetation is also contained in f_{APAR}.

canopy mean [N] had a weakly significant effect on $\hat{\gamma}_s$ ($P = 0.07$) when β was shared. Neither $\hat{\gamma}_s$ nor $\hat{\beta}_s$ correlated significantly with [N] when they both were set site specific (Figure 3).

The site-to-site variability in $\hat{\beta}_s$ due to variation in [N] was best explained by a nearly linear shape taken by the unsaturating f_N-model (Model 4) in the non-linear regressions of Models 3–6 (Table 5). However, inclusion of the linear (Model 3), unsaturating (Model 4) or saturating (Model 5) [N]–LUE relationship (f_N-modifier) in the model only improved the R^2_{adj} of the production efficiency model fit by 1–2% in comparison to Model 2 where β was constant. Coefficients of [N] ($\rho_{N,u}$ and $\rho_{N,s}$) had small error ranges (Table 4) and also had significant P values. Furthermore, the values of the other f-modifier parameters (γ and κ) were relatively insensitive to the inclusion of [N]. Model 6 which included [N] in the light modifier yielded similar performance as Models 2–5 but with one less parameter.

All of the models involving a canopy mean [N]–LUE relationship gave worse fits to the data than Model 1, whereby β_s was allowed to vary by site (Table 4). Fitted LUE model with [N] (Model 3) performed reasonably well ($R^2 > 0.8$) on sites SD, HY, NOBS, BA and SO in comparison to Model 1, but had poorer performance at the other sites (Figure 4). Within seasons, Model 1 had a tendency to underpredict GPP when GPP was high, and overpredict GPP when GPP was low (Figure 5). Other models shared the same seasonal trends in residual errors, as shown in Figure 5 for Model 3. The

differences between predictions of Model 1 and other models were systematic throughout the season, implying that fitted f_N-modifiers could not properly explain site differences in GPP levels.

Maximum actual LUE

Similar to $\hat{\beta}_s$, mean B_s at deciduous/mixed sites (0.60 g C mol^{-1}) was larger than that at conifer sites (0.43 g C mol^{-1}) ($P = 0.03$) (Table 4). Across all sites, maximum actual LUE (B_s) was correlated with canopy mean [N] ($P = 0.022$) and also by mean growing season VPD ($P = 0.004$, Figure 6). The correlation coefficient of mean growing season VPD and canopy mean [N] was −0.53 across sites and it was significant ($P = 0.04$). Annual or growing season mean temperature ($r = -0.17$, $P = 0.56$), LAI ($r = 0.07$, $P = 0.8$) and latitude ($r = 0.00$, $P = 0.9$) did not significantly correlate with B_s. Mixed and deciduous sites had higher mean [N] (1.95%, compared with 1.1% for conifers) and lower mean VPD (0.36 kPa; conifers: 0.61 kPa). Mean growing season VPD significantly correlated with B_s in the conifer sites ($P = 0.03$) but [N] did not ($P = 0.11$). Significances of regression coefficients were not sensitive to the selection of percentile used in the estimation of maximum actual LUE in the range 95–100%.

The days from which B_s values were estimated [i.e., between percentiles [98, 100]] had high mean f_D and f_S at every site. Their averages and standard deviations were 0.92 ± 0.04 (corresponds to VPD = 0.27 kPa) and f_S (0.96 ± 0.05, $T_{air} = 12.3\,°C$). The corresponding average estimate for f_L

Table 3. Canopy [N] at study sites.

| Code	Site	Mean [N] (%)	Std. dev. of [N] (%)	Range of [N] (%)	Data and estimation	Time of measurement	References
SD	Sodankylä, Finland	1.05	0.11	0.90–1.33	Mean of samples from 2 youngest needle cohorts in 10 *Pinus sylvestris* trees in each year, altogether 20 samples	Feb. 2001, Feb. 2003	Unpublished
HY	Hyytiälä, Finland	1.20			Average of 3 values: (i) mean (1.20%) of needle samples taken with a shotgun from 3 layers of outer crown of 3 *Pinus sylvestris* trees, (ii) mean (1.17%) of 20-needle samples taken from 5 branches at systematic heights in 6 *Pinus sylvestris* trees, altogether 30 samples, and (iii) literature value (1.2%)	(i) Spring 2003 (ii) summer 1997	(i) Unpublished (ii) Palmroth and Hari (2001) (iii) Berg and McClaugherty (2008)
NO	Norunda, Sweden	0.87		0.69–1.00	Mean of samples from 3 heights in crowns of 1 *Pinus sylvestris* tree (mean 0.98%, range 0.94–1.00%) and 1 *Picea abies* tree (mean 0.76%, range 0.69–0.84%)	Jan. 2003	Unpublished
TH	Tharandt, Germany	1.53	0.19		Mean of samples taken from 1st-year and 3rd-year needles of *Picea abies* trees, 10 samples per cohort, altogether 20 samples	Oct. 1996	Ngo et al. (2001)
BR	Bray, France	1.19	0.11		Mean of samples taken from 1-year-old and 3-year-old shoots at 3 heights in 1 *Pinus pinaster* tree, 3 replications, altogether 18 samples	May 1995	Porté and Loustau (1998)
ME	Metolius, USA	1.19			Average of 2 reported values: (i) mean (1.02%) of samples consisting of all needles of 1 branch in mid-canopy position in 5 co-dominant *Pinus ponderosa* trees, altogether 5 samples, and (ii) mean (1.35%) of needle samples collected from the top, mid and lower canopy of *Pinus ponderosa* trees	(i) Mar., May, Aug., Oct. 1990, Jun. 1991, (ii) unknown	(i) Pierce et al. (1994), (ii) Law et al. (2000)
NOBS	NOBS, Canada	0.83	0.04		Mean of samples from all needle age classes from upper and lower canopy layers in *Picea mariana* trees, at least 10 replications per layer and age class in each sampling time, altogether 181 samples	Jun. 1, Jul. 28, Sep. 13 1994	Middleton et al. (1997)
AB	Abisko, Sweden	1.79			Mean of large amount of leaves collected from *Betula pubescens* subsp. *tortuosa* trees not exactly at the specific site	Jul., Aug. 2003	Unpublished
BA	Brasschaat, Belgium	2.04	0.19		Mean of samples from different heights in crowns of 5 *Pinus sylvestris* trees	1995	Unpublished
RE	Renon, Italy	1.25	0.12	1.09–1.50	Mean of 11 samples from *Picea abies* trees	2005	Unpublished
SO	Sorø, Denmark	2.30	0.20			Summer 2007	Unpublished
TE	Teshio, Japan	1.63	0.40		Mean of 8 samples from 3 *Quercus crispula* trees, 12 samples from 4 *Betula ermanii* trees and 27 samples from 3 *Abies sachalinensis* trees, altogether 47 samples	Aug. 2001, Aug. 2002, Aug. 2003	Takagi et al. (2010)
WR	Wind River, USA	1.11	0.12	0.95–1.35	Mean of samples of 2nd-year needles from 4 heights in crowns of 4 *Pseudotsuga menziesii* trees, 4 *Thuja plicata* trees and 4 *Tsuga heterophylla* trees, altogether 48 samples	Sep. 2003	Klopatek et al. (2006)
ZO	Zotino, Russia	0.93	0.16		Mean of 231 samples of 1–3-year-old needles from 107 *Pinus sylvestris* trees at 22 stands of age 2–383 in Siberia, this eddy-covariance site included	Summers 1995–1999	Wirth et al. (2002)
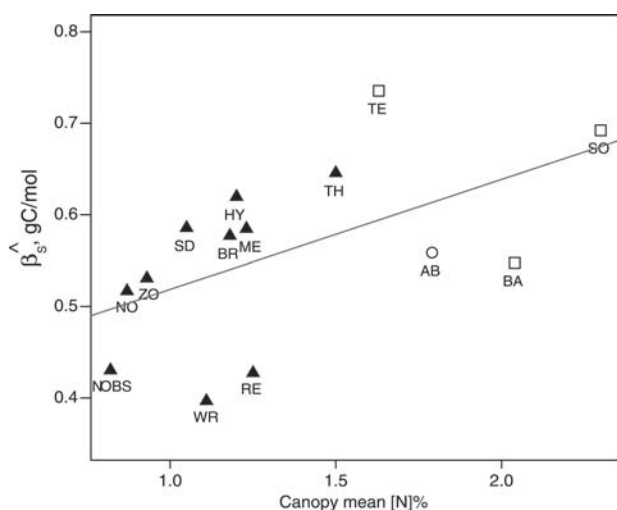
Figure 2. Potential light use efficiencies ($\hat{\beta}_s$) vs. canopy mean [N]. The black solid line represents linear fit $\hat{\beta}_s = 0.12(\pm 0.05)$ [N] $+ 0.40(\pm 0.08)$, $P = 0.043$, $R^2_{adj} = 0.24$, RMSE = 0.085. Conifer sites are marked with black site codes (filled triangle), whereas mixed (open square) and deciduous (open circle) sites are marked with open symbols. Fit to conifers only was insignificant.
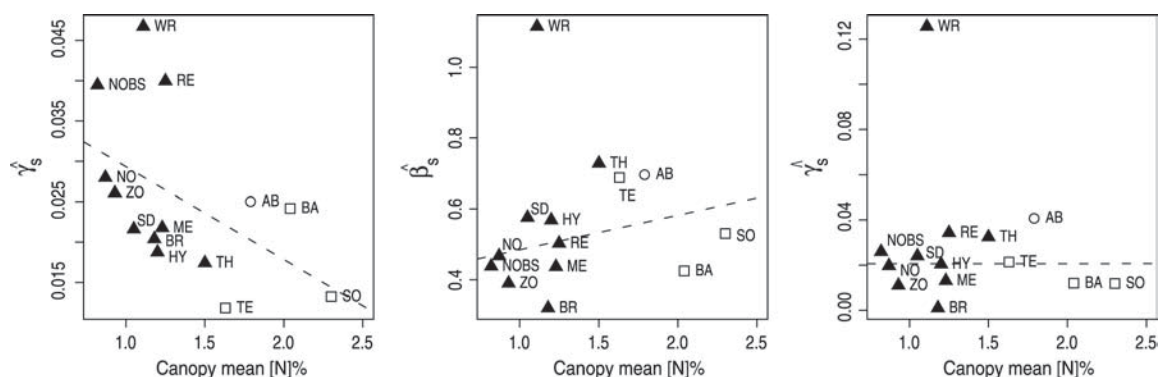
(Figure 8). When regressions of B_s with [N] for low, medium and high PPFD days were compared, the slopes of [N] for the high and medium PPFD subset did not differ significantly from the slope of [N] for the low subset ($P > 0.42$, nested ANOVA).

Discussion

We hypothesized that maximum LUE is not influenced by canopy mean [N] because incident PPFD is low when high LUE occurs. This hypothesis was not confirmed by the data from 14 different eddy-covariance sites. Instead, maximum LUE depended similarly and linearly on [N] at all levels of incident PPFD.

Across all sites, our estimates of the LUE–[N] effect indicated that canopy LUE increased by 23% when canopy mean [N] changed from 1 to 2% (for $\hat{\beta}_s$; 40% for B_s), which is somewhat less than could be expected from previously published estimates for deciduous and conifer forests (48%; Kergoat et al. 2008). All of these changes are considerably

Figure 3. Site-specific estimates of the γ parameter in the light-response modifier when β was shared (left panel), and estimates of β_s and γ_s (middle and right panel, respectively) when both β and γ were site-specific parameters. Regression (dash line) of estimates with [N]% yielded P values 0.07, 0.2 and 0.9 from left to right. WR was excluded from linear regressions.

across sites was 0.74 ± 0.08 (PPFD = 15.1 mol m^{-2}, i.e., 17–20% maximum daily PPFD at sites), indicating that days with high maximum actual LUE were close to optimal, except in terms of saturating photosynthesis. Suboptimal efficiency to use irradiance (according to our f_L) in data from which B_s was calculated may explain larger values of $\hat{\beta}_s$ than those of B_s (Figure 7).

When B_s was estimated from subsets of low ([2, 25) mol m^{-2}), medium ([25, 50) mol m^{-2}) and high (> 50 mol m^{-2}) PPFD days, the mean B_s in the low PPFD subset (0.53 ± 0.03(SE)) was closer to the mean of $\hat{\beta}_s$ (0.56 mol m^{-2}); means of B_s for medium and high PPFD subsets were 0.38 ± 0.03 and 0.24 ± 0.03, respectively. All estimates in these classes differed significantly from each other ($P < 0.0003$, pairwise t-tests).

The slopes of canopy mean [N] for the B_s estimated for low and medium PPFD subsets significantly differed from zero

smaller than previously estimated for mass-based canopy mean A_{max} when canopy [N] changes from 1 to 2% (210% under 'full-sun'; Ollinger et al. 2008). Using data published by Wright et al. (2004), for trees worldwide, a change of mass-based leaf [N] from 1 to 2% would suggest an approximately twofold increase in mass-based leaf A_{max}. Our study also implied a weak relationship between [N] and canopy P_{max} (as defined in Eq. (6)), expressed as a correlation between γ_s and [N] ($P = 0.07$), but the estimates of γ_s proved to be fully independent of [N] in the regression where both γ_s and β_s were allowed to vary simultaneously. It is noteworthy that while maximum LUE was dependent on [N], such dependence was less clear for the canopy P_{max}. The relationship between B_s and [N] was also present under all PPFD levels, which justified the attempts to incorporate the multiplicative β–[N] relationship into the GPP model. In terms of nitrogen use

Table 4. Potential LUE (β) estimated with non-linear regression, and maximum actual LUE (B) estimated as 98% percentiles.

Site, s	$\hat{\beta}_s$ (SE)	$\hat{B}_s$
SD	0.59 (0.02)	0.50
HY	0.62 (0.01)	0.51
TH	0.65 (0.01)	0.58
BR	0.58 (0.01)	0.48
ME	0.58 (0.01)	0.30
NOBS	0.43 (0.01)	0.31
AB	0.56 (0.02)	0.55
BA	0.55 (0.01)	0.45
RE	0.43 (0.01)	0.40
SO	0.69 (0.01)	0.65
TE	0.74 (0.02)	0.78
WR	0.40 (0.01)	0.44
ZO	0.53 (0.01)	0.3
Coniferous[1]	0.53 (0.09)	0.43 (0.09)
Deciduous/mixed[1]	0.63 (0.09)	0.60 (0.14)
P value	0.06[2,3]	0.04[2]
Mean of all sites	0.56 (0.10)	0.48 (0.13)

[1]Means and standard deviation across sites.
[2]One-sided t-test for testing mean LUE of coniferous is less than that of mixed/deciduous. Note that the t-test was done with small sample number ($n1 = 9$, $n2 = 4$).
[3]Correlations of $\hat{\beta}_s$ across sites, which ranged from 0.20 to 0.76 in the conifer group and from 0.16 to 0.47 in the deciduous/mixed group, led to underestimates of group variances in the t-test, and thus the resulting P value is optimistic.
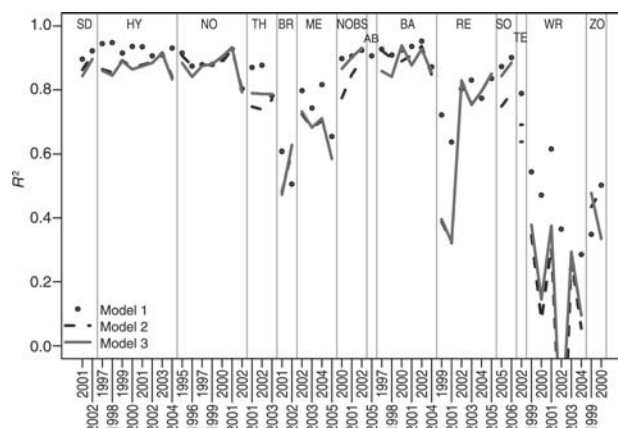

Figure 4. Performance of Models 1, 2 and 3 at different sites in different years in terms of R^2 ($=1 - \sum(y_i - \hat{y}_i)^2 / \sum(y_i - \bar{y}_i)^2$). R^2 for each site as estimated from all observations is on the dotted line.

efficiency ($= \beta/N$ invested in photosynthetic tissues), it is interesting to note that the modest slopes detected here and by Kergoat et al. (2008) suggest that canopies with high N are less efficient in using N than canopies with low N (under optimal conditions).

What could cause such an increase of maximum LUE with canopy N, and explain the increases in B_s with [N] under all levels of PPFD (Figure 8)? The quantum yield has not been

reported to vary with leaf N, but there is plenty of evidence of an A_{max}–N relationship (Reich et al. 1997, Wright et al. 2004). It seems that canopies transfer the leaf-level A–N response that saturates at high PPFD to the canopy level, such that the maximum LUE of the canopy increases linearly with mean canopy [N]. One could expect that if leaf-level A_{max}–N generated the linear N response of LUE at the canopy level, the maximum LUE–[N] relationships would get stronger at high irradiance. However, it is possible that this relationship becomes weak due to compensating mechanisms related to absorption of PPFD that presumably aim at maximizing GPP at the canopy scale.

The fraction of PPFD absorbed by the canopy is partially dependent on leaf morphological properties, such as leaf N and LMA (leaf mass per area) and how they, leaf area, and leaf and shoot orientations are distributed within the canopy. Leaf-level traits such as LMA and [N] tend to be correlated (Reich et al. 1997, Wright et al. 2004), and there is also evidence that at least some leaf traits change in concert with canopy depth. Photosynthetic photon flux density absorption to chlorophyll should also change with canopy depth, thus contributing to the overall compensation mechanism. Increasing absorptance with [N] has also been attributed as a primary cause for a reported apparent increase in quantum yield (Pons et al. 1989). The absorption–[N] relationship has led some authors to define LUE relative to the chlorophyll content of the canopy instead of LAI, because the fraction of absorbed PPFD increases with increasing [N] due to higher chlorophyll concentration of leaves (Xiao et al. 2005, Xiao 2006). Detailed simulation studies of canopy photosynthesis with measured material would be useful in resolving how the effects of mean canopy [N] are reflected to canopy maximum LUE. Optimization models that can predict the coordinated change in leaf traits through the canopy (McMurtrie and Dewar 2011) offer a tempting opportunity to study how and under what circumstances maximum LUE emerges if canopy performance (GPP, NPP or related variable) is maximized in the long term.

There are several sources of uncertainty in these kinds of cross-site studies, which may influence the slope of the maximum LUE against [N]. Part of the between-site variation in estimated potential LUE and maximum actual LUE can be attributed to differences in ground vegetation and the uncertainty it causes in f_{APAR} estimation. Eddy-covariance measurements provide estimates of ecosystem GPP, including the contribution of ground vegetation, whereas f_{APAR} was here estimated for tree canopy only, due to lack of data on understorey (except at Brasschaat, the effect of ground vegetation, consisting mostly of rhododendrons, black cherries and purple moorgrass and contributing to the total LAI approximately as much as the dominating Scots pine and pendunculate oak trees, was included in the model simulations from which f_{APAR} was estimated). Ignoring ground vegetation naturally results in
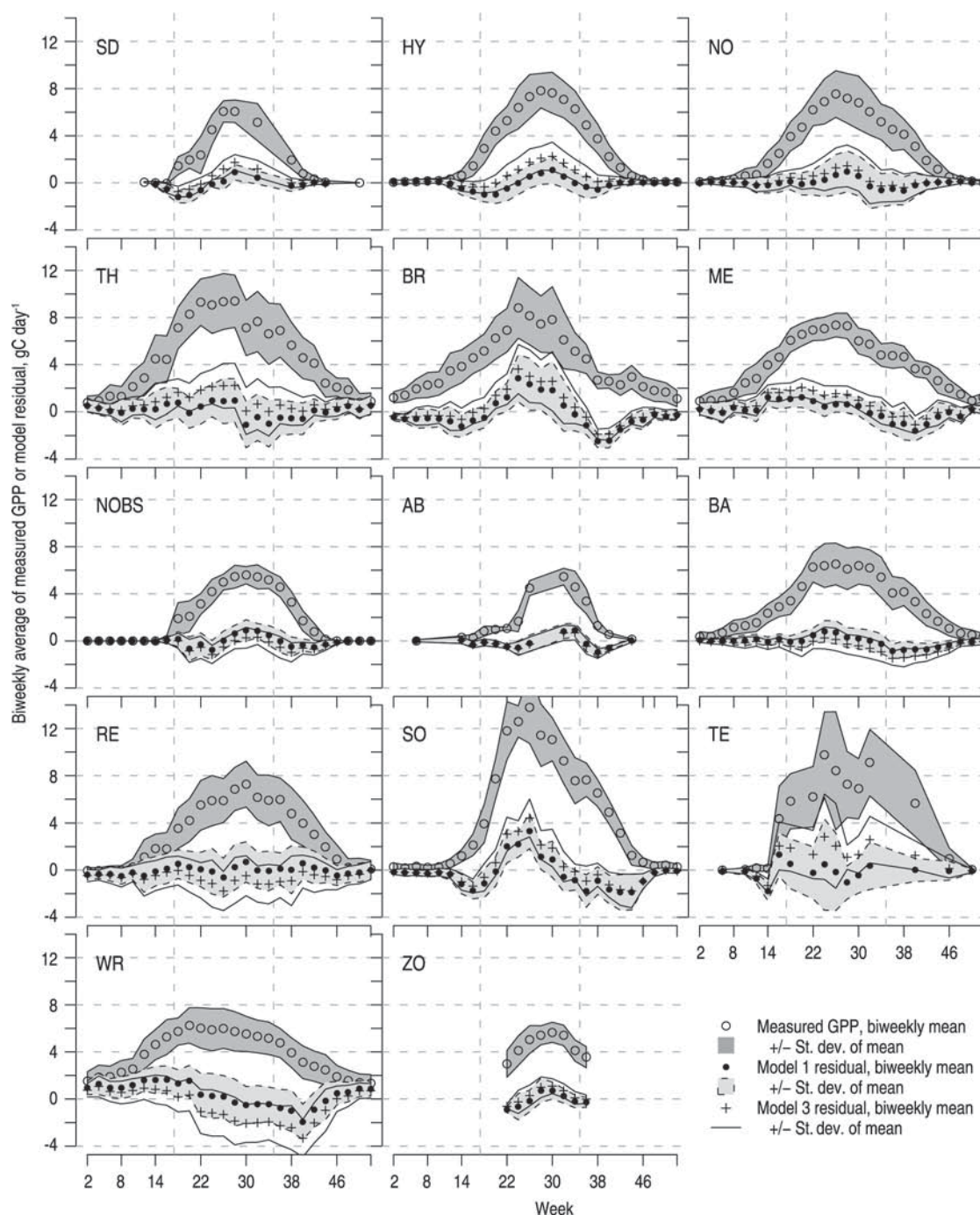
Figure 5. Biweekly averages and standard deviations of measured GPP and model residuals at study sites across all observation years. Fortnights having less than 50% missing daily GPP measurements are included in the graph. The first day of each year starts the week numbering. Vertical dash lines indicate 1 May and 1 September. Averaging for weekly bins showed similar trends (not shown).

underestimation of ecosystem f_{APAR}: the error either is a simple level difference, if seasonality of ground vegetation LAI (and other properties influencing radiation absorption) is similar to that of tree canopy, or has a more intricate effect, if seasonalities differ. In this case, radiation absorbed by the ecosystem, and thereby maximum actual LUE, becomes overestimated. Also the estimate of potential LUE is likely to become too high: if f_{APAR} does not vary seasonally, this is evident, as these two

parameters are then multiplicative in the Prelued model; if there is seasonality in f_{APAR}, errors in its estimates may also affect parameters other than the potential LUE parameter in the Prelued model. Similarly, overestimation of f_{APAR}, which is conceivable in the case of scarce ground vegetation, leads to underestimation of potential and maximum actual LUE.

Ground vegetation contributed notably to ecosystem GPP at the deciduous/mixed sites of Abisko, Sorø and Teshio and at
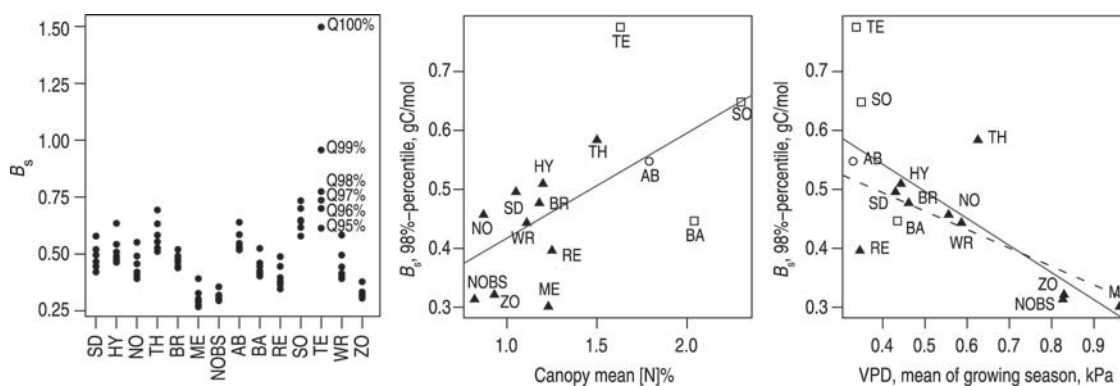
Figure 6. Maximum actual light use efficiencies as defined by different percentiles Q (left panel). Middle and right panels show B_s (percentile, $Q = 98\%$) fitted against canopy mean $[N]\%$ and growing season mean VPD, $D_{gs, mean}$ (continuous line: all sites; dash line: conifers only). Middle panel: $B_s = 0.18(\pm 0.07)[N]\% + 0.24(\pm 0.10)$, $P = 0.022$, RMSE $= 0.11$, $R^2_{adj} = 0.31$; conifers-only fit was not significant ($P = 0.11$). Right panel: $B_s = -0.46(\pm 0.13)D_{gs, mean} + 0.72(\pm 0.07)$, $P = 0.004$, RMSE $= 0.09$, $R^2_{adj} = 0.47$; conifers only: $B_s - 0.31(\pm 0.12)D_{gs, mean} + 0.62(\pm 0.08)$, $P = 0.03$, RMSE $= 0.07$, $R^2_{adj} = 0.38$.

the coniferous site of Bray: At Abisko, the heath-type field layer together with grasses, mosses and lichens had a larger peak value of LAI than the open mountain birch canopy (1.5 vs. 1.1 m^2 m^{-2}); see Johansson (2006) and Lindroth et al. (2008). At Sorø, there was flourishing ground vegetation in April before beech bud-break, mainly composed of wood anemone and dog's mercury (Pilegaard et al. 2003), which probably contributed to the early peaking of ecosystem GPP and its relatively high maximum value (see Figure 6; compare, e.g., with Tharandt). At Teshio, the LAI of the dense bamboo undergrowth clearly exceeded that of trees in the full-growing period (4.0–4.5 vs. 3.0 m^2 m^{-2}), but both the storeys followed a similar strong seasonal pattern (Takagi et al. 2009); on the basis of measurements made after the clear cutting of the site in 2003, the bamboo undergrowth could be estimated to yield

~1/3 of the total ecosystem GPP (Takagi et al. 2009). At these sites, f_{APAR} was probably underestimated, as it was computed from PPFD measurements taken above and below the canopy. Judging from the results, however, only Teshio and Sorø appeared to suffer from an overestimation bias in potential and maximum actual LUE (Figure 9). At the Bray maritime pine site, there was dense purple moorgrass vegetation with pronounced annual pattern and peak LAI comparable to half of the tree canopy (Loustau and Cochard 1991). Here the estimate of tree canopy f_{APAR} was taken from the literature (Hassika and Berbigier 1998) and involved not only radiation
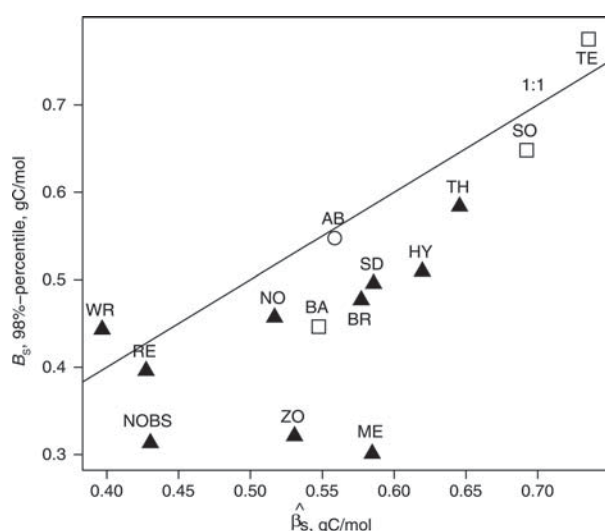

Figure 7. Comparison of potential and maximum LUE defined as upper 98th percentile; correlation coefficient was $r = 0.75$. Coniferous (filled triangle), deciduous (open circle), mixed (open square).
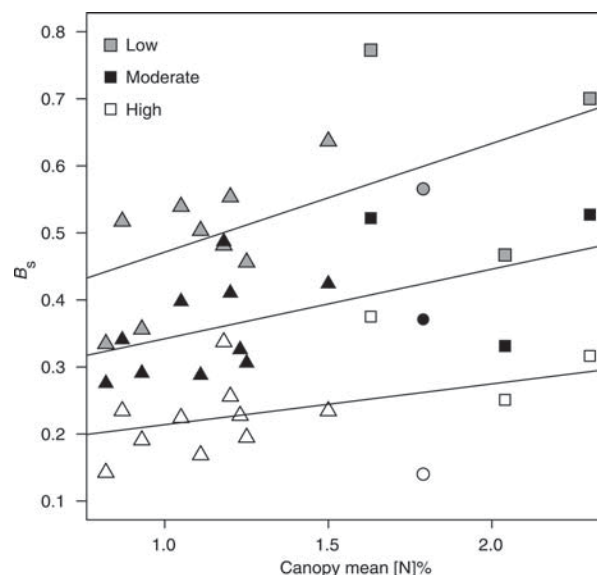

Figure 8. B_s fitted to subsets of low, medium and high PPFD days (triangular is coniferous, square is mixed, circular is deciduous site). Low: $B_s = 0.16(\pm 0.06)[N]\% + 0.31(\pm 0.09)$, $P = 0.027$, RMSE $= 0.10$, $R^2_{adj} = 0.31$. Medium: $B_s = 0.10(\pm 0.05)[N]\% + 0.24(\pm 0.07)$, $P = 0.049$, RMSE $= 0.08$, $R^2_{adj} = 0.23$. High: $B_s = 0.06(\pm 0.04)[N]\% + 0.15(\pm 0.06)$, $P = 0.18$, RMSE $= 0.07$, $R^2_{adj} = 0.08$.

absorption by needles but also that by stems and branches. This can be thought to compensate for some of the ground vegetation effect. Consequently, potential and maximum actual LUE were not necessarily overestimated at Bray.

Besides ground vegetation, there are other potential sources of uncertainty in f_{APAR} estimation, such as spatial heterogeneity (clumping, patchiness) of the forest in the eddy-covariance footprint and change in solar elevation within a year. At sites where the f_{APAR} estimation was based on PPFD measurements above and below the canopy (Norunda, Tharandt, Abisko, Renon, Sorø, Teshio and Wind River), several sensors were placed within the footprint if the forest was considered spatially heterogeneous. At Brasschaat, where the f_{APAR} estimation was based on model simulations (Duursma

et al. 2009), solar elevation was explicitly included in the model and the assumption of random spatial distribution of trees, also included in the model, was considered realistic. At sites where the f_{APAR} estimates were taken from the literature (Sodankylä, Hyytiälä, Bray, Metolius, NOBS and Zotino), the forests in the footprint are relatively homogeneous, and there seems to be no obvious reason to suspect a bias in the f_{APAR} estimates.

The low estimates of potential LUE in Renon and Wind River (Figure 9) are related to the poor fit of the Prelued model at these sites (Figure 4), rather than to overestimation of f_{APAR} (at both sites, f_{APAR} estimation was based on PPFD measurements above and below the canopy). Both are somewhat exceptional sites, Renon due to its high altitude (1730 m) and Wind River
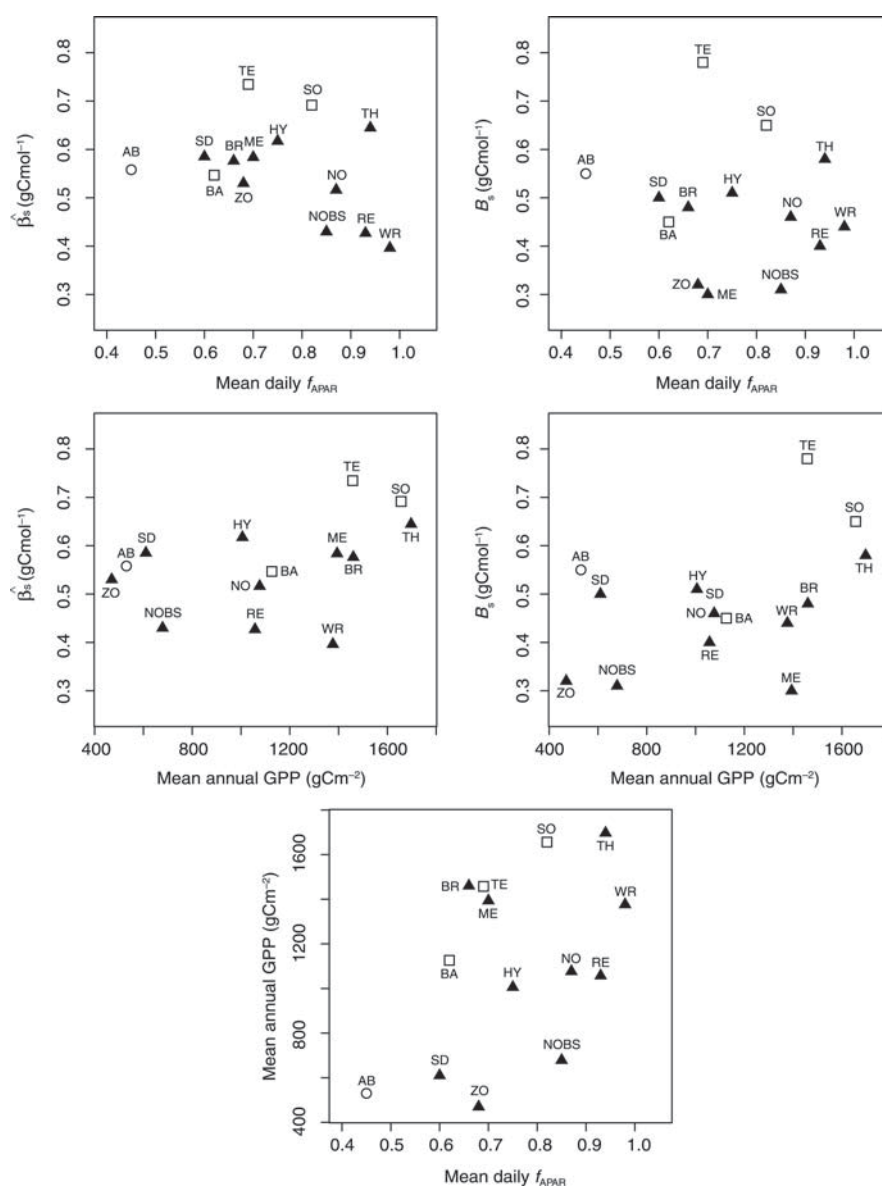

Figure 9. Estimated potential LUE ($\hat{\beta}_s$) and maximum actual LUE B_s with respect to mean daily fraction of PPFD absorbed by the canopy (f_{APAR}) (top panels) and mean annual GPP (middle panels), and mean annual GPP with respect to (f_{APAR}) (low panel).

due to its high age (up to 500 years) and complex canopy structure. At Renon, the low estimate of potential LUE may be partly explained by CO_2 advection that was not taken into account (Marcolla et al. 2005, Montagnani et al. 2009, Feigenwinter et al. 2010), which leads to underestimation of GPP. Although NOBS, too, is non-standard with poor soil and paludified areas in the vicinity, the low estimate of potential LUE there may be partly due to f_{APAR} overestimation, as the Prelued model gave a reasonable fit (the f_{APAR} value was taken from the literature; see Mäkelä et al. 2008). The low estimates of maximum actual LUE at Metolius, NOBS and Zotino (Figure 9), in turn, suggest continuously suboptimal conditions for photosynthesis: the limiting factor seems to be water, as these sites have the highest values of VPD during the growing season (Figure 6).

Estimation of GPP from eddy-covariance NEE also creates a potential source of uncertainty in determining potential LUE and maximum actual LUE. Gross primary production was not measured directly but derived by subtracting estimated TER from measured NEE; TER, in turn, was estimated by extrapolating the observed regressions of night-time NEE on temperature to daytime. Based on Desai *et al.* (2008), Duursma *et al.* (2009) estimated the uncertainties of GPP arising from different TER models to be 5% of daily GPP. Using this estimate directly for maximum daily LUE may be optimistic, but it leads to an uncertainty between 0.015 and 0.04 g C m^{-2} mol^{-1}. The variation in the maximum LUE between the sites in this study was more than one magnitude larger. Besides the extrapolation uncertainty, site-specific underestimation of night-time NEE can also be a source of error in eddy-covariance GPP.

The estimates of canopy mean foliar [N] available to this study contained some uncertainty: the number of trees and leaf samples per tree, the choice of location and the age of leaves to be sampled within a tree, and the timing of sampling varied between the sites (Table 3). Nonetheless, the values accorded with our general understanding in that deciduous/mixed sites had higher canopy mean [N] than coniferous sites; at the mixed site of Brasschaat, however, foliar [N] was measured in Scots pine trees, the dominating species in the tower footprint, and the high value could be due to a long-term exposure to high N deposition rates in the area (Neirynck et al. 2008). The usage of mass-based [N], instead of area-based [N] that has been reported to vary more within a canopy (Niinemets 2007), gained further support from Hyytiälä observations, where no significant variation was found in needle [N] with respect to canopy depth (Palmroth and Hari 2001 and unpublished measurements; see Table 3).

At some sites of this study, measurement years of canopy [N] and eddy covariance did not coincide (Tables 2 and 3). In principle, stand development and between-year variation in environmental factors could cause variation in canopy [N]. At our sites with fairly mature stands and stable GPP, variation related to stand development was probably negligible. Delzon

et al. (2005) did not find significant variation in needle [N] with stand age in a maritime pine chronosequence. Moilanen et al. (2010) studied the effect of time elapsed from drainage of a Scots pine mire ecosystem and did not find a change in needle [N]. In conifer species, the effects of nearly random weather-driven interannual variation may be suppressed by internal translocation, as canopy [N] is a composite of two or more needle cohorts. Consistently with this hypothesis, Helmisaari (1990) found no significant between-year variation in needle [N] in a mature Scots pine stand. Diehl et al. (2008) did not find significant differences in foliar [N] between dry and wet years in broadleaved species, broad-leaved evergreen species or conifer species in Andean Patagonia either. Within-season variation in photosynthesis and growth could also give rise to within-season variation in foliar [N], especially in broadleaved species. In a mature Scots pine stand, however, Helmisaari (1990) reported insignificant seasonal variation of [N] in 1-year-old needles, and ~10% difference between the seasonal minimum and maximum [N] in older needles.

Ground vegetation was discarded not only when estimating f_{APAR} but also when determining canopy mean [N]. This is likely to confound further the relationship between canopy mean [N] and ecosystem potential or maximum actual LUE. At Teshio, which had a dense bamboo understorey canopy, the mean foliar [N] of the understorey was higher than that of the tree canopy (~1.9 vs. 1.6%; see Fukuzawa 2007). If this, and the probable overestimation of the LUE parameters at Teshio, had been accounted for, the dependence between nitrogen concentration and LUE parameters among all the sites would likely have strengthened (Figures 2 and 6).

It is very difficult to account for all variation in foliar [N] within tree canopies to produce an unbiased estimate for the canopy mean [N] over time and space. Harmonized guidelines for leaf sampling would be needed for producing comparable [N] estimates for cross-site comparisons and studies. However, as such measurements are lacking, we evaluated the sensitivity of our maximum LUE–[N] regressions with simulations by adding normally distributed uncertainty to our [N] estimates (CV = 5%); for $\hat{\beta}_s$ and B_s, standard deviations of the mean of β_s from Table 5 were used. In 54.6 and 91.8% of the simulated cases, $\hat{\beta}_s$–[N] and B_s–[N] regressions were significant ($P < 0.05$), respectively, and in 95.1 and 99.9% they were weakly significant ($P < 0.1$). The uncertainties involved in our estimates of maximum LUE and canopy mean [N] therefore do not explain the significant correlation that we found between them.

Gross primary productivity varies remarkably over large regions. Part of this variability could be explained by the spatial changes in the maximum LUE parameter, and specifically by nitrogen, as shown by our study. Earlier, site differences in maximum LUE have also been related to climatic means (Kergoat et al. 2008). We did not find such relationships for potential LUE,

Table 5. Models that were compared for assessing the N-effect in data with Prelued. Parameters for f_S were the same for all models ($\hat{\tau} = 7.25$, $\hat{X}_0 = -3.7$, $\hat{S}_{max} = 15.1$).

Model	β's type[1]	$\hat{\beta}$	$\hat{\gamma}$	$\hat{\kappa}$	f_N or $f_{L,N}$	f_N-parameters	RMSE	R^2_{adj}	df
1	Variable	Table 3	0.025 (0.000782)	−0.336 (0.00863)			1.24	0.82	1,3340
2	Shared	0.598 (0.00958)	0.0362 (0.00121)	−0.273 (0.0092)			1.47	0.75	1,3353
3	Shared	1.05 (0.0160)[2]	0.035 (0.00113)	−0.255 (0.00886)	Eq. (8)	$a = 0.40$ (0.08), $b = 0.12$ (0.05)	1.43	0.77	1,3351
4	Shared	0.443 (0.00756)[2]	0.0339 (0.00110)	−0.253 (0.00891)	Eq. (9)	$\rho_{N,u} = -0.175 (0.00380)$	1.42	0.76	1,3352
5	Shared	0.943 (0.022)	0.0354 (0.00115)	−0.244 (0.00889)	Eq. (10)	$\rho_{N,sat} = 0.750 (0.038)$	1.43	0.77	1,3352
6	Shared	0.548 (0.00668)	0.0379 (0.00105)	−0.260 (0.00867)	Eq. (11)		1.43	0.77	1,3353

[1]Shared refers to a common estimate of β for all sites.
[2]Estimates of β do not represent LUE and are not fully comparable to estimates of Models 1, 2 and 5 because f_N can take values above one.

although we found a relationship between growing season mean VPD and maximum LUE. The likely reason for this is that, besides explaining the effects of daily weather variation, environmental modifiers also explained differences in climatic means.

Our results suggest that the maximum LUE is linearly correlated with canopy [N], such that a linear increase of GPP with [N] is present irrespective of the irradiance level. Contrary to a widely held view, therefore, the effect of [N] does not appear to be limited to high PPFD days only, where it is thought to take place through a leaf-level A_{max}–[N] relationship. This has considerable implications on modelled productivity estimates, e.g., when evaluating the long-term effects of N-deposition, or when incorporating spatial variation of [N] in regional or global productivity models operating on remotely sensed input.

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Appendix. Symbols and units

Symbol	Units	Name
P	g C m^{-2}	GPP
β	g C mol PPFD^{-1}	Potential LUE
f_{APAR}	Unitless	Fraction of absorbed PPFD
ϕ	mol PPFD^{-1} m^{-2}	Photosynthetic photon flux density, PPFD, daily sum
β_k	g C mol PPFD^{-1} m^{-2}	Actual LUE of a day
f_L	Unitless	Light modifier
γ	mol PPFD^{-1} m^{-2}	Light modifier parameter
f_D	Unitless	VPD modifier
D	kPA	VPD, daily average
f_S	Unitless	Modifier for temperature acclimation
X	°C	A priori estimate for the state of acclimation
X_O	°C	Threshold for state of acclimation change
T	°C	Temperature, daily average
S	°C	Acclimation state
S_{max}	°C	Acclimation state maximum
τ	Unitless	Delay parameter for ambient temperature response
P_{max}	g C m^{-2}	Maximum GPP, corresponds to β/γ
q	g C mol PPFD^{-1}	Apparent daily quantum yield of the canopy, corresponds to LUE
B	g C mol PPFD^{-1}	Maximum actual LUE
f_N	Unitless	Modifier for canopy [N]
[N]	kg kg^{-1}	Mass-based concentration of nitrogen in the canopy
b	Unitless	Slope parameter of linear f_N
a	Unitless	Ordinate parameter of linear f_N
$\rho_{N,u}$	Unitless	Parameter of unsaturating f_N
$\rho_{N,sat}$		Parameter of saturating f_N
$f_{L,N}$	Unitless	Combined modifier of light and nitrogen
k	Unitless	Subscript, day
s	Unitless	Subscript, site