Nitrogen controls plant canopy light-use efficiency in temperate and boreal ecosystems

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Running title: Light-Use Efficiency and leaf Nitrogen

Abstract

Optimum daily Light-Use Efficiency (LUE) and normalized canopy photosynthesis (GEE*) rate, a proxy for LUE, have been derived from eddy covariance CO_2 flux measurements obtained at a range of sites located in the mid to high latitudes. These two variables were analyzed with respect to environmental conditions, plant functional types (PFT) and leaf nitrogen concentration, in an attempt to characterize their variability and their potential drivers. LUE averaged 0.0182 mol/mol with a coefficient of variation of 37% (42% for GEE*). Foliar nitrogen N of the dominant plant species was found to explain 71% of LUE (n=26) and 62% of GEE* (n=44) variance, across all PFTs and sites. Mean Annual Temperature, MAT, explained 27 % of LUE variance, and the two factors (MAT and N) combined in a simple linear model explain 80 % of LUE and 76% GEE* variance. These results showed that plant canopies in the temperate, boreal and arctic zones fit into a general scheme closely related to the one, which had been established for plant leaves worldwide. The N-MAT-LUE relationships offer perspectives for LUE-based models of terrestrial photosynthesis based on remote sensing. On a continental scale, the decrease of LUE from the temperate to the arctic zone found in the data derived from flux measurements is not in line with LUE resulting from inversion of atmospheric CO_2.

1 Introduction

Canopy light-use efficiency (LUE), defined as either the ratio of gross (GPP) or net primary productivity (NPP) to absorbed light has received increasing attention over the last decades, primarily because the combination of remotely-sensed absorbed photosynthetically active radiation (APAR) and estimates of LUE allows investigations of GPP and NPP over large areas. Since the launch of the NOAA-TIROS satellites in 1981 and the consequent development of algorithms to derive APAR from space, LUE-based approaches have become a widely applied tool [*Prince*, 1991; *Potter et al.*, 1993; *Ruimy et al.*, 1994; *Field et al.*, 1995; *Running et al.*, 2004] and LUE-based productivity models have greatly contributed to the characterization of the temporal variability of global-scale terrestrial productivity [e.g., *Nemani et al.*, 2003]. At a smaller scale, productivity models based on LUE, often called Production Efficiency Models (PEM), have been developed for a range of different ecosystems. Such models take advantage of field datasets of productivity and biomass when details of physiology or ecology are not known [e.g., *Prince*, 1991; *Medlyn*, 1998; *Mäkelä et al.*, 2008]. Both, global and ecosystem models depend on accurate estimates of LUE.

Because it is the ratio of two key physiological properties (light capture and photosynthesis), LUE subsumes a broad range of processes and has also been applied as an integrative diagnostic tool. As such it has been used, for instance, to analyze and intercompare output from ecosystem models that differ in their complexity, their parameterizations and/or their representation of processes. An example was provided by the intercomparison of global models of NPP [*Ruimy et al.*, 1999], which demonstrated that grid-cell light-absorption and NPP were highly correlated for ten out of twelve global models, the two 'exceptions' being models that predicted NPP on the basis of the nitrogen cycle. *Ruimy et al.* [1999] also drew attention to the large differences among average LUE values from the ten LUE-like global models, highlighting the need for accurate estimates of large-scale LUE. In addition, their results indicated that the relationship between LUE and the nitrogen cycle still has to be clarified at the global scale. The importance of accurate LUE values is also exemplified by atmospheric inversion studies. Such studies infer the surface sinks and sources of CO_2 from atmospheric measurements and transport models. LUE-based estimates of productivity are often used as a constraint in or as an end-product of the inversion process [*Randerson et al.*, 2002; *Kaminski et al.*, 2002; *Still et al.*, 2004; *Chevallier et al.*, 2005, among others].

Originally, field studies suggested LUE being rather invariable among different, well-watered crops [*Monteith*, 1977] but later reviews by *Prince* [1991], *Ruimy et al.* [1994] and *Medlyn* [1998] have demonstrated significant variation among vegetation types at least for LUE derived from NPP (LUE_{NPP}). Part of this variation may be related to measurement aspects as neither NPP nor APAR are easy to capture precisely, especially across sites and across Plant Functional Types (PFT) [*Gower et al.*, 1999], but there is little doubt overall that the assumption of a constant LUE_{NPP} does not provide an accurate description of terrestrial ecosystems [*Binkley et al.*, 2004, *Bradford et al.*, 2005].

From a physiological perspective some authors have argued that LUE derived from GPP (LUE_{GPP}) should be less variable than LUE_{NPP}, mainly because differences in carbon allocation and respiration estimates are responsible for some of the variability in LUE_{NPP} and should not affect LUE_{GPP} [*Ruimy et al.*, 1996a, *Goetz and Prince*, 1999]. The first analyses of LUE_{GPP} led however to a somewhat contradictory picture with the ratio either being more or less constant across ecosystems (ca. 0.02 mol CO_2/mol APAR, *Ruimy et al.*, [1995]) or varying widely [*Turner et al.*, 2003, *Turner et al.*, 2005]. Intuitively a certain fluctuation of LUE_{GPP} would be expected as GPP varies not only with APAR but also with other factors, e.g., soil water and nutrient availability, the ratio of direct to diffuse radiation, canopy age or site history [*Alton et al.*, 2007, *DeLucia et al.*, 2007]. Yet, when investigating LUE over the course of one to several years, water and nutrient supply will be reflected to some extent in the canopy leaf area index, and therefore in the absorbed PAR. How LUE and the fraction of absorbed PAR (fPAR) are related to environmental constraints is largely unknown. Whether light capture and light-use efficiency show coordinated responses to environmental constraints has received theoretical interest [*Field et al.*, 1995, Goetz and Prince, 1999], but little observational support so far, and the opposite view of light-use efficiency increasing with decreasing light availability has also been considered [*Binkley et al.*, 2004].

In addition to the question on the range and variability of LUE there is also a debate on its global patterns. When plotted against latitude LUE increased towards the north for some global models, but decreased for others [*Ruimy et al.*, 1999], illustrating the lack of consensus on the underlying processes. *Kaminski et al.* [2002] and *Still et al.* [2004] showed that large-scale CO_2 inversion studies tend to impose a large increase of LUE from temperate to arctic ecosystems. In terms of modeling, *Haxeltine and Prentice* [1996] suggested that a pole-ward increasing trend in plant nitrogen content could support higher LUE at higher latitudes. Conversely, based on CO_2 flux data over boreal sites, *Lafont et al.* [2002] found a correlation between mean annual temperature and LUE, which leads to a decrease in LUE towards high northern latitudes. This result was supported by the analysis of *Schwalm et al.* [2006] who, in addition, did not detect any significant correlation with foliar nitrogen based on 11 flux measurement sites.

Clearly, for increased confidence in satellite-derived productivity estimates as well as to offer better diagnostics to large-scale ecology, it is important to reduce the uncertainties affecting large-scale LUE patterns and to identify the relevant drivers for its variation. The large number of net CO_2 flux data that are by now becoming available give an unprecedented access to estimates of ecosystem GPP, owing to effort in collecting and processing data in networks like FLUXNET [*Baldocchi et al.*, 2001; *Friend et al.*, 2007; *Owen et al.*, 2007]. For this study, we derive LUE from CO_2 flux time-series to estimate LUE_{GPP} over a variety of sites spanning the temperate, boreal and arctic ecosystems. The questions we address are: i) Is optimum LUE_{GPP} (when GPP achieves seasonal maxima) variable among these ecosystems? ii) If yes, what are the large-scale and local-scale patterns behind LUE variability? iii) What are the major controls of spatial LUE variation, and how can it be parameterized?

2 Data and methods

2.1 Sites characteristics

CO_2 fluxes based on the eddy covariance technique have been compiled from the FLUXNET, EUROFLUX, AMERIFLUX, BOREAS and EUROSIBERIAN CARBONFLUX databases [*Baldocchi et al.*, 2001; *Heimann*, 2002; *Sellers et al.*, 1995; *Valentini et al.*, 2003] as well as from studies that had been conducted independently of these data sets. The emphasis has been put on mid to high latitude sites. Site descriptions and references are summarized in table 1. As a result of the considerable efforts of the participants to these projects, there is a relatively high degree of homogeneity in the methods and algorithms used at different sites. To take advantage of this effort, we considered only fluxes measured with eddy covariance methods, and did not retain for example, fluxes measured and up-scaled from chamber techniques.

For each site, canopy leaf area index (LAI; projected leaf area basis and usually including understorey vegetation) or fPAR (the fraction of PAR absorbed), and mean annual temperature (MAT) data were compiled (Table 1). MAT was either provided by the database and reference articles or derived from climatology, using the gridpoint closest to the site [*Leemans and Cramer*, 1991, updated 1995]. The vegetation at the sites was classified into the following Plant Functional Types: Evergreen needleleaf, evergreen broadleaf, deciduous needleleaf, deciduous broadleaf, mixed forest, tundra and boreal wetlands, C4 grasses and crops, and C3 grasses and crops. Databases and literature were screened for site leaf or needle nitrogen content expressed on a mass basis (gN/g dry matter, hereafter N). For most sites, only the dominant species have been sampled for N, with a few exceptions in herbaceous canopies, which provide canopy-average nitrogen. For evergreen plants, most studies provided an average over the different needle or leaf age-classes. When seasonal course of nitrogen content was available, we retained the values closest to the date of maximum CO_2 flux. Leaf nitrogen was not corrected for sugar content.

2.2 Derivation of Light-Use-Efficiency and normalized photosynthetic rate.

From the CO_2 flux time series two variables were derived: Optimum daily photosynthetic light-use-efficiency (hereafter simply noted LUE), and a proxy for LUE which is the normalized maximum photosynthesis rate (or Gross Ecosystem Exchange) noted GEE*. The CO_2 flux data compiled in this study are of two types (noted I and II), for which different methods had to be used.

Type I dataset

For 42 datasets, typically one year or longer, for which flux data were available, time-series of half-hourly GEE were derived from NEE and an estimate of ecosystem respiration R_{eco}. As used here, GEE is considered positive, whereas NEE and R_{eco} follow the classical micrometeorological conventions, being positive when the CO_2 flux is upward.

$$GEE = - NEE + R\text{eco} \qquad \text{Eq. 1}$$

For the long-term comprehensive data it was possible to estimate R_{eco} using two different methods, including a simple one, which can also be applied for the less comprehensive type II data (see below). The first method estimates R_{eco} from soil temperature using an Arrhenius-type relationship with parameters that may vary seasonally. Nighttime flux data were selected above wind speed and/or friction velocity thresholds before fitting eq. (2) to soil temperature (5 to 10 cm) for consecutive two-month periods of time [e.g. *Falge et al.*, 2001]. This allows to account for seasonal variations in plant phenology, water budget and microbial processes.

$$Reco = F_0 \, e^{\frac{Ea}{R}\left(\frac{1}{T_0}-\frac{1}{T}\right)} \qquad \text{Eq. 2}$$

where T0 is the reference soil temperature (283.16 K), F0 is the fitted respiration rate at reference temperature, Ea is the fitted activation energy and R is the gas constant.

To obtain daily totals, R_{eco} was extrapolated during daytime periods based on soil temperature and GEE computed accordingly.

A second, simpler method estimates ecosystem respiration rate as the average of nighttime fluxes (i.e., period when global radiation Rg < 10 W/m^2 over a 24 h period of time, eq. 3)

$$Reco = \langle NEE \rangle_{Rg<10} \qquad \text{Eq. 3}$$

where brackets indicate averaging. Half-hourly GEE were computed using a constant value for half-hourly R_{eco} over a given day. This simple method assumes that the differences between nighttime-average and mid-day ecosystem respiration are small compared to seasonal and inter-sites differences, which is applicable in ecosystems where respiration does not respond strongly to rainfall events.

Once time-series of GEE had been derived, the maximum canopy photosynthesis, GEE_{max}, was computed as the average of the upper 98.5-99.5 % bin of the half-hourly GEE histogram. These 98.5 and 99.5 thresholds were defined to retain photosynthesis rates typical of optimal environmental conditions, while discarding outliers. All days with at least one half-hourly GEE value falling in the 98.5-99.5 % interval were considered 'optimal' in terms of environmental conditions. For these days, 24h totals (GEE_{24h}, PAR_{24h}) were derived from half-hourly GEE and PAR. An optimum daily light-use-factor (LUF), based on incident PAR was derived from the slope of the linear relationship between GEE_{24h} and PAR_{24h}. To avoid circular analysis no gap filled data sets were used since light is used to fill gaps in NEE and GEE time series.

$$GEE_{24h} = LUF.\ PAR_{24h} \qquad \text{Eq. 4}$$

To account for differences in PAR absorption due to canopy openness, daily LUE was computed as:

$$\mathrm{LUE} = \mathrm{LUF} / \mathrm{fPAR} \qquad \text{Eq. 5}$$

Depending on the site, fPAR was either obtained from literature and database sources or derived from projected LAI using:

$$fPAR = 0.95 \times \left(1 - e^{-k\frac{LAI}{\cos\Theta s}}\right) \qquad \text{Eq. 6}$$

with k=0.5 and Θs being the sun elevation at solstice

Type II data

For the additional 35 type II datasets, which either were short-term studies or not included in the above databases, maximum rates of canopy photosynthesis GEE_{max} were derived by averaging 3 consecutive half-hourly CO_2 flux values during optimal environmental conditions. Averaging consecutive data prevents overestimation of GEE_{max} created by statistical variation sometimes present in the half-hourly eddy flux data. A few studies directly provide GEE time series either from temperature driven R_{eco}, or from the intercept of light/NEE curves, otherwise, R_{eco} was estimated with equation 3.

For comparison among sites with different leaf area index, GEE_{max} was normalized by fPAR, using a reference fPARc of 0.95 corresponding to a closed canopy. Additionally, GEE_{max} was normalized by the cosine of Θs, to compensate for difference in incident PAR caused by latitude, assuming optimum conditions for CO_2 flux occurring near the solstice.

$$GEE^* = GEE_{max} \frac{fPARc}{fPAR} \frac{\cos(\Theta = 0)}{\cos(\Theta s)} \qquad \text{Eq. 7}$$

GEE* is expected to be a good proxy for LUE in type II data sets since both variables share the same normalization by absorbed PAR, although simplified in the case of GEE*, providing that daily integrated GPP and daily maximum GPP values are related.

Sensitivity tests

To evaluate the robustness of eq. 5 and 7 to fPAR (eq. 6), we tested the sensitivity of LUE and GEE* to three fPAR estimates. Firstly, we assumed that the period of maximum GEE departs from solstice depending on latitude, ranging from day of year 180 at 45° to 220 at 80° [*Falge et al.*, 2002]. Θs is then replaced by the sun elevation at 12h (local solar time) for the corresponding day of year. Secondly, fPAR was assumed to be a linear mixture of fPAR for direct (eq. 6) and diffuse irradiance:

$$fPAR_2 = \lambda \times fPAR + (1-\lambda) \times 0.95 \times \left(1 - e^{-kLAI}\right) \qquad \text{Eq. 8}$$

assuming a fraction of direct PAR, λ, of 0.65.

Lastly, we tested the hypothesis that the extinction coefficient k is PFT dependent [e.g. *Yuan et al.*, 2007].

$$fPAR_3 = 0.95 \times \left(1 - e^{-k_{pft} \frac{LAI}{\cos \Theta s}}\right) \qquad \text{Eq. 9}$$

assuming k_{pft} =0.45 for needleleaf, 0.55 for broadleaf, and 0.5 for other canopies instead of using k=0.5 for all sites.

3 Results and Discussion

The consistency of the GEE* estimation methods was first evaluated using the 42 type I dataset (Table 1). GEE* derived from either eq. 2 or 3 were similar (r^2=0.93, slope 1.02, intercept -0.3 μmol $s^{-1}m^{-2}$). A similar picture was found for LUE data based on eq. 2 and 3 (r^2=0.87, slope 0.93, intercept -0.0007 mol/mol). Therefore, in the following, we choose to use eq. 3, which allowed us to merge type I and type II into a homogeneous GEE* dataset. For consistency, we consequently used eq. 3 also for derivation of LUE.

GEE_{max} computed with eq. 3 were well correlated (r^2=0.81) with the maximum GEE derived from 25 FLUXNET sites by *Falge et al.* [2002]. Our values were slightly higher since *Falge et al.* [2002] used a smoothing over 15 days to compute the seasonal course of 'all weather' GEE whereas we are interested here in optimum half-hourly values. The general agreement between our GEE_{max} and the one given in *Falge et al.* |2002], based on a detailed examination of the data and methods supports our simplified data processing.

Analysis of LUE and GEE* variability

As expected LUE and GEE* from type I data were highly correlated (Figure 1) with a r^2 of 0.88 (n=42). Or in other words, GEE* can be used as a proxy for LUE for type II dataset. Since the full dataset for GEE* spans a larger range of ecosystems, latitudes, soil and environmental conditions, especially in the harsh arctic environment, it provides more robust statistics than an analysis restricted to long term comprehensive flux data. Therefore in the following, results are shown for both LUE and GEE*. For the purpose of clarity, plots showing GEE* have a second y-axis (on the right) that maps GEE* into LUE units based on the linear relationship of Figure 1b (LUE = 0.0006 GEE* + 0.0023).

The histogram of LUE (Fig. 1a) reveals a significant variability in among-site LUE, with a mean of 0.0182 mol/mol, and a standard deviation of 0.0067 resulting in a coefficient of variation of 37 % (n=42, Table 2). Considering the range of ecosystems included, it is not surprising that GEE*, derived for the entire dataset in Table 1 was also highly variable, averaged at 26.2 $\mu mol m^{-2} s^{-1}$, with a standard deviation of 11 $\mu mol m^{-2} s^{-1}$ and a coefficient of variation of 42 % (n=77).

The canopy LUE values derived here are naturally lower than commonly measured leaf-level quantum yields which may be of the order of 0.06 under normal environmental conditions [e.g. *Ehleringer and Pearcy*, 1983]. Several reasons underlie the leaf *vs*. canopy difference: Photosynthesis of leaves saturates in high irradiance, thereby decreasing canopy daily LUE, which is integrated over the course of a day and includes periods of high and low irradiance. Moreover, although we select the optimum seasonal LUE value, environmental conditions still impose some stress on the plants. Highest canopy LUE were obtained for two crops in the data set, rice and corn (Table 1), which show almost no saturation of leaf level GEE / PAR curves at the half hourly time step, despite rice being a C3 plant. The average value of 0.018 is close to but lower than the value of 0.02 proposed by *Ruimy et al.* [1995, 1996b].

For further illustration Figure 2 shows LUE and GEE* as functions of MAT at the site separated per PFT. MAT correlated weakly but significantly with LUE (Fig 2a, r^2 = 0.27, n=42, P=0.0004) and GEE* (Fig 2b, r^2 = 0.34, n=77, P<10e-7). The sensitivity tests performed with the different formulations of fPAR and APAR (eq. 8, 9) did not affect these results (not shown). Since PAR irradiance tends to decrease from temperate to arctic latitudes, the trend of maximum GPP versus MAT is obviously stronger than GEE* (not shown).

LUE was not to be expected to be a simple function of MAT due to a range of additional factors. In continental high latitude ecosystems photosynthesis takes place over a short (2-3 months) and well defined period with sometimes quite warm temperatures [e.g., *Lloyd et al.*, 2002; *Arneth et al.*, 2002]. However, the correlation almost disappears when MAT is replaced by the temperature corresponding to the period of CO_2 flux data retained to compute LUE and GEE* (r^2= 0.12, P=0.06 and r^2=0.19, P= 0.01 respectively). What is more, effects of physiology may override those of temperature with, for instance, LUE of a well-fertilized, C4 crop is expected to be higher than that of a 'natural' system at similar MAT. Nevertheless, LUE and GEE* tended to be organized along a MAT gradient (Fig. 2a, b), with a clear tendency to form clusters for some of the plant types like deciduous broadleaved forests, whereas for most of the other types a large variability was found (e.g., needleleaved forests, grasses and crops, and tundra/wetlands). The better correlation with GEE* is caused by a broader sampling of the possible range of MAT, including a number of sites with low annual temperatures (MAT < 0). The correlation of LUE and GEE* with MAT we find here is lower than the values reported by *Lafont et al.* [2002] for 18 boreal sites and closer to results reported by *Schwalm et al.* [2006] for yearly mean LUE at 17 Canadian forest and wetland sites. The broader range of PFT included here, especially inclusion of warmer broadleaved evergreen, grasses, crops on the one hand and cold climate fens and deciduous forests on the other hand explains the difference with *Lafont et al.* [2002]. These PFT add to the scattering of the GEE*/MAT relationship (Fig 2b and Table 2). Averaged per PFT, LUE ranges from 0.0116 for tundra and wetlands to 0.0270 for C3 grasses and crops (Table 2).

Role of leaf nitrogen content

At the leaf level, numerous studies have demonstrated a strong link between nitrogen content and photosynthesis [*Field and Mooney*, 1986; *Wullschleger*, 1993]. A general framework for leaf structure and function, relating leaf assimilation rate, leaf nitrogen content and leaf mass per area (LMA) has been proposed by *Reich et al.* [1997] and extended worldwide by *Wright et al.* [2004]: Leaf photosynthesis (on a mass basis) correlates positively with leaf nitrogen (on a mass basis) and negatively with LMA. At the canopy level, several studies point towards a similarly strong incidence of nitrogen on photosynthesis, productivity and even net CO_2 flux [e.g. *Choudhury*, 2001; *Williams et al.*, 2000; *Smith et al.*, 2002]. However, *Schwalm et al.* [2006] did not find any significant correlation between foliar nitrogen and canopy LUE across 9 forest sites. How leaf-level relations translate to the canopy level therefore remained elusive so far.

When plotted against leaf nitrogen content expressed on a mass basis, both LUE and GEE* significantly increased with N, Figure 3a and b. The variance explained by N, in a single variable 1:1 linear relationship, reaches values of r^2= 0.71 (n=26, all type I sites with nitrogen data) and r^2= 0.62 (n=44, all sites with nitrogen data) for LUE and GEE* respectively. It can be seen from Figure 3a that the increase of LUE with N becomes less well defined at leaf N levels > ca. 2% for deciduous broadleaf forest sites, suggesting a curvilinear relationship might exist for some biomes. The C4 crops and grasses achieved high LUE and GEE* at relatively low levels of leaf N.

Table 1 and Figures 3a and 3b show the large differences in leaf N that exist among, and also within, plant types. Still, LUE and GEE* tended to group in well-defined PFT-clusters. In that respect, canopy-level data behave like the leaf-level data presented by *Reich et al.* [1997], which also show such PFT clusters.

Combination of MAT and N

MAT and leaf N were not related in the data set analyzed here (Fig. 4), except for a weak tendency of evergreen tree N to increase with temperature and for deciduous trees and the two crop sites to have higher leaf N across the entire range of MAT when compared with other PFTs.

However, the residuals of the linear regression between LUE and N (Fig. 3a) were weakly correlated with MAT (not shown) which implies that the N:LUE relationships were not completely independent of climate. At same levels of leaf nitrogen, highest LUE were thus observed at warmest temperature. This was true also for the N *vs*. GEE* residuals. Consequently the combination of N and MAT explained a larger part of LUE and GEE* variability and a simple linear model LUE = a MAT + b N + c was therefore fitted to the data (Fig 5a, same for GEE* Fig 5b).

This simple model explained 80 % of LUE variance (LUE = 0.0063 N + 0.00036 MAT + 0.0064, n= 26) and 76 % of GEE* variance (GEE*=10.85 N + 0.66 MAT + 8.41, n=44). These regression coefficients are quite high, considering that the derivation of LUE and GEE* are affected by several approximations and uncertainties (fPAR estimates at low LAI for instance).

Differences in leaf nitrogen reflect site quality combined with plant type. As opposed to foliar N, which is central to plant photosynthesis and physiology, MAT is a surrogate for a number of variables and processes in interaction, like the length of the growing season, the nutrient cycle, the water budget, to mention only three. Therefore, the relationship of LUE with MAT is best viewed as a large-scale pattern that subsumes these effects and that is locally supplanted by the role of PFT, leaf nitrogen, and other factors. A good example comes from the BOREAS data, where stands of aspen, Jack pines and black spruce co-exist at the landscape scale but show dramatically different LUE and leaf N, sometimes even within the same stand type [*O'Connell et al.*, 2003]. At the regional scale, averages of the LUE, weighted by the relative surface of the different PFT in BOREAS Northern and Southern Sites, tend to fall into the general large scale MAT/LUE gradient (not shown). Large scale patterns of LUE therefore depend on the relative surfaces occupied by different PFT or plant differing in N content, in line with the findings of *Still et al.* [2004] of higher LUE in Eurasia than North America due to higher deciduous trees cover, combined to the overall environmental conditions correlated to MAT.

Canopy index and function

To make use of the explanatory power of LMA, in addition to foliar nitrogen, it is tempting to scale the leaf level relationship of *Reich et al.* [1997] up to the canopy level. This was done by *Green et al.* [2003], who proposed a 'Canopy Index', as a combination of canopy nitrogen, LMA and fPAR. Such a canopy index is theoretically related to canopy LUE (eq. 10, see Appendix). *Green et al.* [2003] further expressed LUE in terms of LAI, fPAR and leaf nitrogen (see Appendix for equations and suggestions on alternative index derivation)

$$\mathrm{LUE} \propto \frac{N_{canopy} \cdot \langle LMA \rangle}{fPAR} \propto \frac{[N].LAI}{fPAR} \qquad \text{Eq. 10}$$

When applied to our dataset, the canopy index (hereafter noted I_G) was found to explain a similar variance of LUE than foliar nitrogen alone (cf., Fig 6a, b compared to 3a, b). This was the case for both the percentage of variance explained as well as for the complementarities between I_G and MAT. The comparison of Figures 6 and 3 confirms the analysis by *Green et al.* [2003] such that a canopy index increases the linearity of LUE prediction compared to leaf nitrogen alone. However, the scatter also increased in our data and the overall predictive power did not improve. Particularly the C4 sites stand out as outliers in the I_G index / GEE* relationship. Alternative formulations were developed and tested, that accounted for both, a non-linear relationship between leaf photosynthesis and leaf N, as well as for the differences in incoming PAR to refine *Green et al.* [2003] formulation. This revised index, ($N^{0.77}$ LAI/fPAR.1/Ipar; see Appendix) still did not improve the overall r^2 of the relationship shown in Fig. 6, suggesting that the scattering of canopy index / LUE or GEE* may come from assumptions in scaling leaf level to canopy level, possibly in averaging LMA or leaf properties over the canopy. Given the limited number of sites and the approximations in fPAR derivation, it is at this stage difficult to further evaluate the appropriateness of the different mass-based canopy indices. Indeed, canopy structure, foliage clumping, non-leaf tissues can make the derivation of the factor LAI/fPAR particularly difficult, especially at the scale of a flux tower footprint.

Whether a unique nitrogen-based relationship can be applied to estimate LUE for different plant types is central to both application of remote sensing data and understanding and interpreting the observed LUE patterns. Leaf N concentration may be a better predictor of productivity than total N integrated over the canopy as soon as different plant types are considered. For instance, *Smith et al.* [2002] were able to relate aboveground NPP to canopy averaged N concentration for deciduous and evergreen tree species using the same relationship. Conversely, different relationships for deciduous and evergreen trees emerged when canopy total N was used. Considering trees, grasses and crops, *Green et al.* [2003] drew a similar conclusion, favoring N concentration rather than canopy total N. Similarly, expressing leaf nitrogen on a mass basis rather than on a surface basis may also seem counter-intuitive [see also discussion by *Smith et al.*, 2002 and Hikosaka, 2004]. From a practical point of view, foliar nitrogen content expressed on a mass basis is far less variable within the canopy than area basis nitrogen, and therefore easier to measure. As a consequence, mass basis N or indices based on mass basis N prove more convenient to evaluate in the field and can provide general framework for canopy LUE variability when addressing global or regional issues. So far our own, and other published evidence indicate that both canopy N concentration or mass-basis leaf N may be robust predictors of canopy functioning in terms of light use.

Idealized Canopy models

Considerations about the optimum functioning of canopies have suggested that the capture of different resources, like PAR, water, and nutrients could be regarded in an integrated fashion. Such an integrated perspective would ensure coordinated resource acquisition resulting in a Balanced Canopy Functioning [*Field et al.*, 1995], an appealing theoretical concept. As a result, plant canopies should not invest in PAR acquisition if PAR can not be transformed into NPP due to other resource limitations or environmental conditions. Leaf N content may reflect nutrient limitation, and therefore may co-vary with APAR. Other studies have suggested that resource-use could be either constant over a wide range of conditions [*Goetz and Prince*, 1999] or related to resource-capture. Opposing views postulate either that resource use efficiency increases when resources availability decreases, or that resource use efficiency increases with the availability of a resource, as a result of improved overall functioning [*Binkley et al.*, 2004]. Development of such theoretical frameworks and their evaluation with observations are necessary to develop and test plant productivity models [see *Field et al.*, 1995].

Our compilation of data allows to test some aspects of these concepts. It becomes apparent (Figure 7), for instance, that LUE and GEE*, although highly variable, are not related to light resource capture (i.e., fPAR) in a simple way. Likewise, leaf nitrogen and fPAR are not related (Fig 8). Arguably, there are few high LUE associated with very low fPAR sites in our dataset, suggesting that high light-use efficiency is generally accompanied by high fPAR at least in the absence of opposing management practices, which is in line with *Binkley et al.* [2004]. The same is true for higher leaf N (e.g., >1.5%) being associated with relatively larger fPAR. However, other factors are required to explain the occurrence of LUE and N variability at similarly high fPAR level. For instance, the possible role of dense evergreen foliage as a nitrogen reservoir in nutrient poor environment (resulting in high mass of foliage with relatively low N) plays against a scaling of maximum LUE with fPAR because it increases fPAR and not LUE. It must be kept in mind though, that we investigate optimum LUE only. Using time-integrated variables may result in a different picture [*Field et al.*, 1995] but based on our analysis there is little evidence for theoretical schemes relating of resource use to resource capture.

At the leaf level, both empirical evidence and mechanistic analyses have established the strong relationship between N and photosynthesis. Leaf nitrogen is recognized as critical for the photosynthesis apparatus, but extensive discussions have addressed the observed departures from a single inter-specific relationship. Allocation of N to Rubisco, activity of Rubisco, C3 or C4 metabolisms, diffusion of CO2, respiration are some factors, which change the N-photosynthesis relationship [*Hikosaka* 2004 and references therein}. Differences between evergreen and deciduous trees have been reviewed by *Warren and Adams* [2004], who pointed CO2 diffusion and overinvestment in Rubisco as important factors. At the canopy level however, mechanisms are still lacking and it is not possible to associate the relationship between LUE and nitrogen of the dominant plant to patterns of allocation of N to Rubisco, chlorophyll or other forms. The factors explaining inter-specific differences in leaf-level data potentially drive canopy-level differences. The question is complicated by the existence of gradients of N allocation within canopies. Different studies have found a trade-off between N allocation to Rubisco and chlorophyll according to light availability, but such allocation pattern has often been shown to be sub-optimal.

The empirical evidence in our dataset either implies that there is a scaling between leaf N of the dominant plants and the whole canopy functioning, or implies that the variability within canopies is of second order compared to the explanatory power of leaf N of the dominant plants. The lack of relation between LUE or N and fPAR, as well as the relatively poor results of idealized canopy models, show that more pluri-specific studies are needed.

Concluding remarks: Latitudinal patterns of LUE and remote sensing based models.

A simple relationship of N with either, fPAR, MAT or latitude would facilitate the development and use of global LUE models greatly but the existence of such large-scale patterns is a matter of debate. Some studies point towards an increase of foliar N with latitude, MAT, and altitude, whereas others point towards an opposite pattern [*Reich and Oleskyn*, 2004, and references therein]. *Reich and Oleskyn* [2004] found the highest foliar N values for mid-latitude and a weak decrease towards the coldest climate zones. In the data analyzed in our study the only significant trend in N versus latitude was for the evergreen needleleaf PFT.

It has been argued that LUE may increase with latitude because of a parallel increase in leaf nitrogen [*Haxeltine and Prentice*, 1996]. LUE derived from atmospheric inversions [e.g. Knorr and Heimann, 1995; *Kaminski et al.*, 2002; *Randerson et al.*, 2002; *Still et al.*, 2004] tend to indicate increasing LUE values from temperate to arctic latitudes, together with an increase for highly continental zones [*Kaminski et al.*, 2002]. Interestingly, Still et al., [2004] found higher LUE for continental Eurasia than for North America and suggested that the distribution of deciduous trees with higher needle N could explain this pattern, which is inline with our study.

Overall, our estimate of optimum LUE and GEE* along latitude gradients (e.g. Fig. 9a and b) indicates a decreasing trend towards high latitude, supporting the statement of *Kaminski et al.* [2002], who considered obtaining the highest LUE for tundra as unrealistic.

A variety of reasons may help to explain the discrepancy between our findings and LUE derived from inversion analyses: atmospheric inversion studies rely on an estimate of the heterotrophic respiration and other surface processes like snow-related processes (insulation effect, impact on water availability), whose errors can impair LUE estimates [*Randerson et al.*, 2002]. However, inaccuracy of the atmospheric vertical mixing or meridional transport may also cause such a discrepancy. If this were to be the case, the consequences on the estimates and localization of the carbon sinks/sources might be significant, as it has been shown by *Stephens et al.* [2007], and deserve further examination.

Overall, our results strongly support the view that LUE varies significantly both across and within biomes, and Plant Functional Types. Our data do not support the view that LUE_{GPP} might be less variable that LUE_{NPP} and might therefore span a small range of values [*Goetz and Prince*, 1999; *Ruimy et al.*, 1996a]. Our extensive use of the flux measurement network strengthens and extends the results of *Turner et al.* [2003] and *Yuan et al.* [2007], who compared LUE_{GPP} from 4 and 28 flux measurements sites respectively, as well as *Choudhury* [2001], who used data and canopy modeling and suggested a significant variability of LUE_{GPP}. Convergent conclusions were drawn for aboveground LUE_{NPP} in the past [*Gower et al.*, 1999 and references therein]. Given the high diversity of measurement sites, which encompass managed and unmanaged stands, mono- or pluri-specific canopies, leaf nitrogen emerges as a strong organization factor of optimum canopy LUE and canopy photosynthesis rate.

As far as remote-sensing models are concerned LUE-based GPP models therefore have to account for variability in optimum LUE within an ecosystem and on biome scale. This has important consequences for the validation of global LUE-models with local data. Such models often combine an optimum LUE with different stress factors. Temporal variability in stress factors, incoming and absorbed PAR usually result in favorable model/data comparison, especially if site quality is accounted for [e.g. *Yuan et al.*, 2007; *Mäkelä et al.*, 2008]. Remote sensing of the xanthophylls cycle (PRI), surface radiative temperature or fluorescence may help capturing some the short to seasonal variability of LUE [*Grace et al.*, 2007] and may be included in the next generation of LUE based models. Improvements of optimum LUE estimates will be achieved if information on leaf nitrogen can be obtained in addition to fPAR, which may be done using ground based or airborne sensor (e.g. AVIRIS, CASI). For instance, *Smith et al.* [2002] showed that forest productivity could be assessed through estimation of leaf nitrogen content mapped with AVIRIS. *Boegh et al.* [2002] were able to simulate canopy photosynthesis for different crops combining nitrogen-based modeling and hyperspectral data from CASI. The robustness of inversion methods for chlorophyll and nitrogen content, based on satellite-borne sensors like MERIS, CHRIS-PROBA or HYPERION, has to be investigated in the perspective of LUE-modeling.

Appendix

One way to derive the canopy index proposed by *Green et al.* [2003] is to state that, for different canopies, daily GEE is proportional to GEEmax, the maximum rate of canopy photosynthesis. Thus LUE defined as the ratio of daily GEE to daily absorbed PAR writes:

$$LUE = \frac{GEE}{fPAR.I_{PAR}} \propto \frac{GEE_{\max}}{fPAR.I_{PAR}} \qquad \text{Eq. 11}$$

Note that the use of GEE* as a proxy for LUE is based on the same assumption (GEE* being close to eq 11 right-hand-side). Assuming the maximum canopy photosynthesis rate is proportional to the integral of leaf level maximum photosynthesis rate (on a surface basis, $A_s^{\max}$), we have

$$GEE_{\max} \propto \int_{LAI} A_s^{\max}.dl \qquad \text{Eq. 12}$$

Using the leaf-level equation of *Reich et al.* [1997], (eq 13), and expressing leaf photosynthesis on a mass basis ($A_m^{\max}$), we have:

$$A_m^{\max} \propto [N]^{.77}.LMA^{-.71} \approx [N]/LMA \qquad \text{Eq. 13}$$

$$LUE \propto \frac{\int_{LAI} A_m^{\max}.LMA.dl}{fPAR.I_{PAR}} \propto \frac{\int_{LAI} [N].dl}{fPAR.I_{PAR}} \propto \frac{[N].LAI}{fPAR}.\frac{1}{I_{PAR}} \qquad \text{Eq. 14}$$

Assuming LUE values are measured at similar incident PAR level, LUE is proportional to the index of *Green et al.* [2003]. To avoid assumptions of eq 13 and 14, we also use the following index

$$\frac{[N]^{0.77}.LAI}{fPAR}.\frac{1}{I_{PAR}} \qquad \text{Eq. 15}$$

Acknowledgements

This work would not have been possible without the considerable efforts of a large group of people and many funding agencies (see acknowledgements for each site in the corresponding reference). Each flux measurements site usually requires several scientists and students to be run on the long term. Sites in remote places, in the arctic for instance, are among the most challenging places to run flux systems. The authors would like to thank all these people for sharing their data under “fair-use policy”, as well as providing unpublished information Special thanks to Dennis Baldocchi, who provided energy, ideas and enthusiasm to the FLUXNET community.

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Figure captions

Figure 1: a) Histogram of optimum daily Light-Use Efficiencies (LUE) for the 42 sites with type I data, b) LUE versus canopy normalized photosynthesis GEE* for type I data (n=42)

Figure 2: a) Optimum daily light-use-efficiency (LUE, mol/mol) versus annual mean temperature (MAT) for type I data. Symbols are for ecosystem type (Table 1) as: Evergreen needleleaf (▲), evergreen broadleaf (●), deciduous needleleaf (△), deciduous broadleaf (○), mixed forest (◆), tundra and boreal wetlands (■), C4 grasses and crops (*), and C3 grasses and crops (+).

Figure 2: b) Same as 2 a), but for canopy normalized photosynthesis (GEE*,μmol $s^{-1}m^{-2}$) for type I and II data. Right y-axis is a linear mapping to LUE units (mol/mol), see fig 1.

Figure 3: a) Optimum daily LUE versus leaf nitrogen content N, mass basis.

Figure 3: b) Same as a, but for canopy normalized photosynthesis (GEE*).

Figure 4: Leaf nitrogen N versus annual mean temperature.

Figure 5: a) Optimum daily LUE versus linear combination of annual mean temperature and leaf nitrogen N.

Figure 5: b) GEE* versus linear combination of annual mean temperature and leaf nitrogen N.

Figure 6: a) LUE versus *Green et al.* [2003] canopy index $I_{G.}$

Figure 6: b) Normalized canopy photosynthesis (GEE*) versus *Green et al.* [2003] canopy index I_G.

Figure 7 a: Optimum daily LUE versus fraction of absorbed PAR (fPAR).

Figure 7 b: Same as 7 a, but for GEE*.

Figure 8: Canopy fPAR versus leaf nitrogen N.

Figure 9: a) Optimum daily LUE as a function of latitude for |lat| >45° .

Figure 9 b) GEE* as a function of latitude for |lat| >45°.

Tables

Table 1

References	Name	Species or canopy type	PFT	Lat	MAT °C	LAI -	FPAR -	N (%)	LUE mol/mol	GEE* $\mu mol m^{-2} s^{-1}$
Harazono et al. 2003	Barrow [a]	wet sedge tundra	■	70.3	-12.4	1.5	0.64	-	0.0157	21.1
Oechel et al 2000	Upad [a]	wet sedge tundra	■	70.3	-8.2	1.5	0.64	-	0.0065	11.7
Vourlitis and Oechel 1999	Happy valley [a]	moist tussock tundra	■	69.0	-11.7	1.5	0.63	-	0.0126	15.2
Wallin et al. 2001	Flakaliden [c]	Norway Spruce	▲	64.1	1.0	2.2	0.73	1.15	0.0184	25.7
Markkanen et al 2001	Hyytiala [c]	Scots Pines	▲	61.8	3.2	4.0	0.86	1.20	0.0190	25.5
Lloyd et al. 2002	Zotino [d]	Scots pine	▲	61.0	-1.5	-	0.70	0.99	0.0129	17.7
Lohila et al. 2004	Joikonnen Barley	Barley	+	60.9	3.9	5	0.91	3.62	0.026	35.2
Lindroth et al 1998	Norunda [c*]	Spruce Pine	▲	60.0	5.5	4.0	0.86	-	0.0099	14.0
Milyukova et al. 2002	Fyodorovskoye [d]	Norway Spruce	▲	56.0	3.8	4.3	0.88	-	0.0190	24.4
Goulden et al. 1997	BN-OBS [b]	old black Spruce	▲	56.0	-2.9	-	0.86	0.66	0.0128	15.6
McCaughey et al 1997	BN-YJP [b]	Young jack Pine	▲	56.0	-2.9	-	0.65	0.93	0.0114	18.4
Moore et al., 2000	BN-OJP [b]	old jack Pine	▲	56.0	-2.9	-	0.76	0.90	0.0068	15.0
Pilegaard et al. 2001	Soroe [c]	Beech forest	○	55.5	8.1	4.8	0.90	-	0.0234	35.3
Yang et al 1999	BS-OA [b]	old Aspen	○	54.0	1.0	-	0.90	2.50	0.0189	30.3
Jarvis et al. 1997	BS-OBS [b]	old black Spruce	▲	54.0	1.0	-	0.85	0.70	0.0131	19.5
Baldocchi et al 1997	BS-OJP [b]	old jack Pine	▲	54.0	1.0	-	0.78	1.00	0.0106	21.8
Dolman et al. 2002	Loobos [c]	Scots pine	▲	52.2	10.3	3.0	0.78	1.81	0.0232	32.1
Kowalski et al. 2000	Braschaat [c]	Scots Pine	◆	51.3	10.2	3.1	0.80	-	0.0170	26.7
Grünwald and Bernhofer 2007	Tharandt [c]	Norway spruce	▲	50.3	8.0	6.0	0.92	-	0.0276	35.1
Aubinet et al. 2001	Vielsalm [c]	fir spruce pine beech	◆	50.3	7.4	4.5	0.89	-	0.0224	28.2
Klemm and Mangold 2001	Weidenbrunnen [c]	Norway spruce	▲	50.0	5.8	5.3	0.91	-	0.0157	23.1
Granier et al 2000	Hesse [c]	Beech	○	48.0	9.2	5.0	0.90	2.50	0.0258	34.8
Davis et al. 2003	Park Fall [a]	maple aspen pine	◆	45.9	6.6	5.0	0.89	-	0.0168	23.6
Hollinger et al. 1999	Howland [a]	Spruce dominated	▲	45.2	6.7	5.3	0.90	1.1	0.0194	25.7
Berbigier et al 2001	Landes [c]	maritime pine	▲	44.7	12.5	3.1	0.85	1.10	0.0176	27.2
Law et al 2001	Metolius-old [a]	ponderosa pine	▲	44.7	7.6	2.1	0.63	1.35	0.0171	25.2
Nakai et al 2003	Japan Forest [a]	Birch Oak	○	43.0	6.5	4.5	0.86	2.25	0.0217	37.4
Valentini et al 1996	Collelongo [c]	Beech	○	42.0	7.0	4.5	0.86	2.40	0.0238	37.9
Wofsy et al. 1993	Harvard forest [a]	Oak Maple Hemlock	○	42.0	8.5	3.4	0.83	1.87	0.0234	32.2
Reichstein et al. 2002	Castelporziano [c]	*Quercus ilex*	●	42.0	15.3	3.5	0.80	1.50	0.0212	28.5
Turner et al 2003	Bondville [a]	Corn	*	40.0	11.2	5.5	0.90	2.30	0.0326	57.8
Turner et al 2003	Bondville [a]	Soybean	+	40.0	11.2	6.7	0.92	-	0.0162	26.6
Monson et al 2002	Niwot [a]	Fir Spruce Pine	▲	40.0	4.0	4.2	0.87	0.99	0.0126	18.5
Goldstein et al. 2000	Blodgett [a]	ponderosa Pine	▲	39.0	10.4	3.1	0.76	1.25	0.0127	25.0
Suyker & Verma 2001	Shidler [a]	Tallgrass prairie	*	37.0	14.7	2.8	0.73	-	0.0266	45.5
Hanan et al. 2002	Ponca City [a]	wheat	+	37.0	15.3	5.0	0.88	-	0.0227	35.7
Wilson and Baldocchi 2000	Walker Branch [a]	Oak maple	○	36.0	14.5	6.0	0.92	1.75	0.0207	33.6
Katul et al 2001	Duke [a]	Pine	▲	36.0	15.5	5.2	0.88	1.08	0.0146	27.4
Meyers 2001	Little Washita [a]	grassland	*	35.0	16.0	2.5	0.69	-	0.0163	28.4
Stylinski et al. 2002	Sky Oaks-young [a]	chaparral	●	33.0	12.2	1.1	0.41	0.80	0.0128	23.5
Stylinski et al. 2002	Sky Oaks-old [a]	chaparral	●	33.0	12.2	3.0	0.74	-	0.0092	15.5
Campbell et al. 2001	Rice	Rice	+	29.2	20.0	5.5	0.89	3.50	0.0386	67.6
Lloyd 2001	Ny Alesund,	Tundra, semi-desert	■	80.0	-6.0	0.3	0.23	-	-	12.7
Nordstoem et al 2001	Zackenberg fen	fen	■	74.5	-9.5	1.1	0.56	-	-	27.8
Soegaard et al 2000	Zackenberg heath	Heath tundra	■	74.5	-9.5	0.2	0.14	-	-	26.8
Laurila et al 2001	Zackenberg willow	Willow tundra	■	74.5	-9.5	0.5	0.31	-	-	26.0
Williams et al. 2000	AFS 1	coastal wet tundra	■	70.5	-8.2	-	0.57	1.14	-	6.7
Williams et al. 2000	AFS 13	Alder tussock tundra	■	70.5	-8.2	-	0.55	1.0	-	12.7
Williams et al. 2000	AFS 14	acidic tussock tundra	■	70.5	-8.2	-	0.50	1.0	-	12.5
Williams et al. 2000	AFS 3	non-acidic tundra	■	70.5	-8.2	-	0.75	0.87	-	6.2
Williams et al. 2000	AFS 4	acidic tussock tundra	■	70.5	-8.2	-	0.83	0.78	-	8.0
Williams et al. 2000	AFS 6	acidic tussock tundra	■	70.5	-8.2	-	0.59	1.0	-	16.5
Williams et al. 2000	AFS 9	Shrub tundra	■	70.5	-8.2	-	0.52	2.05	-	30.8
Williams et al. 2000	AFS heath	Heath tundra	■	70.5	-8.2	-	0.65	0.94	-	6.6
Laurila et al 2001	Kevo	fen	■	69.8	-2.0	0.7	0.38	-	-	24.8
Aurela et al. 2001	Petsikko	mountain Birch	○	69.5	-2.0	2.8	0.83	-	-	22.5
Laurila et al 2001	Kaamanen	fen	■	69.1	-2.0	0.7	0.38	-	-	24.5
Aradóttir et al. 1997	Gunnarsholt [c]	black Cottonwood	○	63.8	5.0	1.4	0.57	-	-	37.3
Röser et al 2002	Zotino-birch [d]	birch	○	61.0	-1.5	2.6	0.75	2.14	-	37.5

Röser et al 2002	Zotino-mixed [d]	fir spruce birch	◆	61.0	-1.5	4.1	0.87	1.43	-	30.3
Röser et al 2002	Zotino-pole [d]	fir	▲	61.0	-1.5	3.5	0.83	1.30	-	29.9
Lohila et al. 2004	Joikonnen Grass	Grass	+	60.9	3.9	4.5	0.90	-	-	26.7
Hollinger et al. 1998	Yakutsk	Larch	△	60.0	-9.6	2.0	0.66	0.81	-	10.8
Griffis and Rouse 2001	Churchill	subarctic fen	■	58.8	-6.9	0.6		-	-	29.1
Clement et al 2003	Aberfeldy [c]	Sitka spruce	▲	56.5	8.0	8	0.94	-	-	30.9
Suyker et al 1997	BS-FEN [b]	boreal fen	■	54.0	1.0	1.3	0.50	-	-	33.6
Anderson et al 1995	BS-YJP [b]	Young jack Pine	▲	54.0	1.0	-	0.69	1.10	-	20.8
Fan et al. 1995	Labrador	Black Spruce	▲	53.8	-4.9	-	0.65	0.59	-	21.5
Flanagan et al. 2002	Lethbridge [a]	grassland	*	49.7	5.3	0.9	0.38	2.10	-	50.7
Chen et al 2002	Wind crane [a]	fir hemlock	▲	46.0	8.7	10.0	0.95	-	-	20.0
Lafleur et al 2001	Mer bleue	ombrotrophic bog	■	45.5	5.8	1.5	0.53	1.50	-	18.6
Lee et al 1999	Camp Borden	Maple Aspen Ash	○	44.3	6.4	4.1	0.84	-	-	38.5
Hirano et al. 2003	Japan Larch	Larch	△	42.7	7.4	5.1	0.89	-	-	32.6
Schmid et al. 2000	Morgan	Maple Tulip poplar Oak	○	39.3	11.1	3.4	0.79	-	-	40.7
Hollinger et al. 1994	Maruia	*Nothofagus*	●	-42.	9.4	7.0	0.94	0.77	-	22.4
Arneth et al. 1998	NewZealand	*Pinus radiata*	▲	-42.8	10.8	7.0	0.95	1.30	-	31.0
Hunt et al 2002	NZ tussock	Tussock grassland	+	-44.2	10.0	0.6	0.26	-	-	22.9

Table 1: List of sites and references and derived information. The first 42 rows contain Type I data (see text) sorted by latitude, the 35 rows below are for type II data. PFT is for Plant Functional Type, Lat is latitude, MAT is mean annual temperature, LAI is Leaf Area Index, fPAR is the fraction of absorbed PAR, N is for leaf nitrogen on a mass basis, LUE is optimum daily light-use efficiency and GEE* is normalized canopy photosynthesis.

[a] data from FLUXNET web site, [b] data from BOREAS CD (revised 2004), [c] data from CARBODATA CD, [d] data from EUROSIB project database.

* values from Lindroth et al. 1998.

PFT are indicated by the following symbols: ▲ evergreen needleleaf, △ deciduous needleleaf, ● evergreen broadleaf, ○ deciduous broadleaf, ◆ mixed forest, ■ tundra or boreal wetland, * C4 grass or crop, + C3 grass or crop.

Table 2

Plant types	LUE	CV	GEE*	CV
Deciduous Broadleaved	.0225	10 (n=7)	34.5	14 (n=13)
Evergreen Broadleaved	.0144	43 (n=3)	22.5	24 (n=4)
Mixed forests	.0187	17 (n=3)	27.2	10 (n=4)
Evergreen Needleleaved	.0155	32 (n=19)	23.6	24 (n=25)
Deciduous Needleleaved	-	-	21.7	71 (n=2)
Tundra, Wetlands	.0116	41 (n=3)	18.0	48 (n=19)
C3 Grasses and Crops	.0270	42 (n=3)	35.8	51 (n=5)
C4 Grasses and Crops	.0245	28 (n=4)	43.6	27 (n=5)
All Grasses and Crops	.0256	32 (n=7)	39.7	38 (n=10)
All plant types	.0182	37(n=42)	26.2	42 (n=77)

Table 2: Optimum daily Light-Use Efficiency (LUE, mol/mol) and canopy normalized photosynthesis (GEE*, $\mu mol\ m^{-2}s^{-1}$): average, coefficient of variation (CV) and number of data, grouped by Plant Functional Types.