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1 **Nitrogen controls plant canopy Light-Use-Efficiency in temperate and**
2 **boreal ecosystems.**

3
4 *Laurent Kergoat¹, Sébastien Lafont², Almut Arneth³, Valérie Le Dantec¹, and Bernard*
5 *Saugier⁴*

6
7 ¹ *CESBIO (CNRS/UPS/CNES/IRD), 18 av. E. Belin, 31401, Toulouse cedex 9, France*

8 laurent.kergoat@cesbio.cnes.fr

9
10 ² *Forest Research Agency, Alice Holt Lodge, Farnham, GU10 4LH, UK*

11 ³ *Dep. of Physical Geography and Ecosystems Analysis, Lund University Sölvegatan 12, 223 62, Lund, Sweden*

12 ⁴ *ESE Université Paris XI 91405 Orsay, France*

13
14
15 **Running title: Light-Use Efficiency and leaf Nitrogen**

1 **Abstract**

2

3 Optimum daily Light-Use Efficiency (LUE) and normalized canopy photosynthesis (GEE*)
4 rate, a proxy for LUE, have been derived from eddy covariance CO₂ flux measurements
5 obtained at a range of sites located in the mid to high latitudes. These two variables were
6 analyzed with respect to environmental conditions, plant functional types (PFT) and leaf
7 nitrogen concentration, in an attempt to characterize their variability and their potential
8 drivers. LUE averaged 0.0182 mol/mol with a coefficient of variation of 37% (42% for
9 GEE*). Foliar nitrogen N of the dominant plant species was found to explain 71% of LUE
10 (n=26) and 62% of GEE* (n=44) variance, across all PFTs and sites. Mean Annual
11 Temperature, MAT, explained 27 % of LUE variance, and the two factors (MAT and N)
12 combined in a simple linear model explain 80 % of LUE and 76% GEE* variance. These
13 results showed that plant canopies in the temperate, boreal and arctic zones fit into a general
14 scheme closely related to the one, which had been established for plant leaves worldwide. The
15 N-MAT-LUE relationships offer perspectives for LUE-based models of terrestrial
16 photosynthesis based on remote sensing. On a continental scale, the decrease of LUE from the
17 temperate to the arctic zone found in the data derived from flux measurements is not in line
18 with LUE resulting from inversion of atmospheric CO₂.

19

20

1 **1 Introduction**

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

16
17 Because it is the ratio of two key physiological properties (light capture and photosynthesis),
18 LUE subsumes a broad range of processes and has also been applied as an integrative
19 diagnostic tool. As such it has been used, for instance, to analyze and intercompare output
20 from ecosystem models that differ in their complexity, their parameterizations and/or their
21 representation of processes. An example was provided by the intercomparison of global
22 models of NPP [*Ruimy et al., 1999*], which demonstrated that grid-cell light-absorption and
23 NPP were highly correlated for ten out of twelve global models, the two ‘exceptions’ being
24 models that predicted NPP on the basis of the nitrogen cycle. *Ruimy et al. [1999]* also drew
25 attention to the large differences among average LUE values from the ten LUE-like global
26 models, highlighting the need for accurate estimates of large-scale LUE. In addition, their

1 results indicated that the relationship between LUE and the nitrogen cycle still has to be
2 clarified at the global scale. The importance of accurate LUE values is also exemplified by
3 atmospheric inversion studies. Such studies infer the surface sinks and sources of CO₂ from
4 atmospheric measurements and transport models. LUE-based estimates of productivity are
5 often used as a constraint in or as an end-product of the inversion process [*Randerson et al.*,
6 2002; *Kaminski et al.*, 2002; *Still et al.*, 2004; *Chevallier et al.*, 2005, among others].

7
8 Originally, field studies suggested LUE being rather invariable among different, well-watered
9 crops [*Monteith*, 1977] but later reviews by *Prince* [1991], *Ruimy et al.* [1994] and *Medlyn*
10 [1998] have demonstrated significant variation among vegetation types at least for LUE
11 derived from NPP (LUE_{NPP}). Part of this variation may be related to measurement aspects as
12 neither NPP nor APAR are easy to capture precisely, especially across sites and across Plant
13 Functional Types (PFT) [*Gower et al.*, 1999], but there is little doubt overall that the
14 assumption of a constant LUE_{NPP} does not provide an accurate description of terrestrial
15 ecosystems [*Binkley et al.*, 2004, *Bradford et al.*, 2005].

16 From a physiological perspective some authors have argued that LUE derived from GPP
17 (LUE_{GPP}) should be less variable than LUE_{NPP}, mainly because differences in carbon
18 allocation and respiration estimates are responsible for some of the variability in LUE_{NPP} and
19 should not affect LUE_{GPP} [*Ruimy et al.*, 1996a, *Goetz and Prince*, 1999]. The first analyses of
20 LUE_{GPP} led however to a somewhat contradictory picture with the ratio either being more or
21 less constant across ecosystems (ca. 0.02 mol CO₂/mol APAR, *Ruimy et al.*, [1995]) or
22 varying widely [*Turner et al.*, 2003, *Turner et al.*, 2005]. Intuitively a certain fluctuation of
23 LUE_{GPP} would be expected as GPP varies not only with APAR but also with other factors,
24 e.g., soil water and nutrient availability, the ratio of direct to diffuse radiation, canopy age or
25 site history [*Alton et al.*, 2007, *DeLucia et al.*, 2007]. Yet, when investigating LUE over the
26 course of one to several years, water and nutrient supply will be reflected to some extent in

1 the canopy leaf area index, and therefore in the absorbed PAR. How LUE and the fraction of
2 absorbed PAR (fPAR) are related to environmental constraints is largely unknown. Whether
3 light capture and light-use efficiency show coordinated responses to environmental
4 constraints has received theoretical interest [*Field et al.*, 1995, *Goetz and Prince*, 1999], but
5 little observational support so far, and the opposite view of light-use efficiency increasing
6 with decreasing light availability has also been considered [*Binkley et al.*, 2004].

7
8 In addition to the question on the range and variability of LUE there is also a debate on its
9 global patterns. When plotted against latitude LUE increased towards the north for some
10 global models, but decreased for others [*Ruimy et al.*, 1999], illustrating the lack of consensus
11 on the underlying processes. *Kaminski et al.* [2002] and *Still et al.* [2004] showed that large-
12 scale CO₂ inversion studies tend to impose a large increase of LUE from temperate to arctic
13 ecosystems. In terms of modeling, *Haxeltine and Prentice* [1996] suggested that a pole-ward
14 increasing trend in plant nitrogen content could support higher LUE at higher latitudes.
15 Conversely, based on CO₂ flux data over boreal sites, *Lafont et al.* [2002] found a correlation
16 between mean annual temperature and LUE, which leads to a decrease in LUE towards high
17 northern latitudes. This result was supported by the analysis of *Schwalm et al.* [2006] who, in
18 addition, did not detect any significant correlation with foliar nitrogen based on 11 flux
19 measurement sites.

20 Clearly, for increased confidence in satellite-derived productivity estimates as well as to offer
21 better diagnostics to large-scale ecology, it is important to reduce the uncertainties affecting
22 large-scale LUE patterns and to identify the relevant drivers for its variation. The large
23 number of net CO₂ flux data that are by now becoming available give an unprecedented
24 access to estimates of ecosystem GPP, owing to effort in collecting and processing data in
25 networks like FLUXNET [*Baldocchi et al.*, 2001; *Friend et al.*, 2007; *Owen et al.*, 2007]. For
26 this study, we derive LUE from CO₂ flux time-series to estimate LUE_{GPP} over a variety of

1 sites spanning the temperate, boreal and arctic ecosystems. The questions we address are: i) Is
2 optimum LUE_{GPP} (when GPP achieves seasonal maxima) variable among these ecosystems?
3 ii) If yes, what are the large-scale and local-scale patterns behind LUE variability? iii) What
4 are the major controls of spatial LUE variation, and how can it be parameterized?

5

6 **2 Data and methods**

7 **2.1 Sites characteristics**

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

17 For each site, canopy leaf area index (LAI; projected leaf area basis and usually including
18 understorey vegetation) or fPAR (the fraction of PAR absorbed), and mean annual
19 temperature (MAT) data were compiled (Table 1). MAT was either provided by the database
20 and reference articles or derived from climatology, using the gridpoint closest to the site
21 [Leemans and Cramer, 1991, updated 1995]. The vegetation at the sites was classified into
22 the following Plant Functional Types: Evergreen needleleaf, evergreen broadleaf, deciduous
23 needleleaf, deciduous broadleaf, mixed forest, tundra and boreal wetlands, C4 grasses and
24 crops, and C3 grasses and crops. Databases and literature were screened for site leaf or needle
25 nitrogen content expressed on a mass basis (gN/g dry matter, hereafter N). For most sites,
26 only the dominant species have been sampled for N, with a few exceptions in herbaceous
27 canopies, which provide canopy-average nitrogen. For evergreen plants, most studies

1 provided an average over the different needle or leaf age-classes. When seasonal course of
2 nitrogen content was available, we retained the values closest to the date of maximum CO₂
3 flux. Leaf nitrogen was not corrected for sugar content.

4 **2.2 Derivation of Light-Use-Efficiency and normalized photosynthetic rate.**

5 From the CO₂ flux time series two variables were derived: Optimum daily photosynthetic
6 light-use-efficiency (hereafter simply noted LUE), and a proxy for LUE which is the
7 normalized maximum photosynthesis rate (or Gross Ecosystem Exchange) noted GEE*. The
8 CO₂ flux data compiled in this study are of two types (noted I and II), for which different
9 methods had to be used.

10 **Type I dataset**

11 For 42 datasets, typically one year or longer, for which flux data were available, time-series of
12 half-hourly GEE were derived from NEE and an estimate of ecosystem respiration R_{eco} . As
13 used here, GEE is considered positive, whereas NEE and R_{eco} follow the classical
14 micrometeorological conventions, being positive when the CO₂ flux is upward.

$$\text{GEE} = -\text{NEE} + \text{Reco} \quad \text{Eq. 1}$$

15
16 For the long-term comprehensive data it was possible to estimate R_{eco} using two different
17 methods, including a simple one, which can also be applied for the less comprehensive type II
18 data (see below). The first method estimates R_{eco} from soil temperature using an Arrhenius-
19 type relationship with parameters that may vary seasonally. Nighttime flux data were selected
20 above wind speed and/or friction velocity thresholds before fitting eq. (2) to soil temperature
21 (5 to 10 cm) for consecutive two-month periods of time [e.g. *Falge et al.*, 2001]. This allows
22 to account for seasonal variations in plant phenology, water budget and microbial processes.

23

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

1 where T_0 is the reference soil temperature (283.16 K), F_0 is the fitted respiration rate at
2 reference temperature, E_a is the fitted activation energy and R is the gas constant.

3

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

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

$$Reco = \langle NEE \rangle_{R_g < 10} \quad \text{Eq. 3}$$

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

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

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

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

1

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

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

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

with $k=0.5$ and Θ_s being the sun elevation at solstice

4

5 **Type II data**

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

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

$$GEE^* = GEE_{\max} \frac{fPAR_c \cos(\Theta = 0)}{fPAR \cos(\Theta_s)} \quad \text{Eq. 7}$$

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

20 **Sensitivity tests**

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

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

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

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

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

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

11 **3 Results and Discussion**

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

18 GEE_{max} computed with eq. 3 were well correlated ($r^2=0.81$) with the maximum GEE derived
 19 from 25 FLUXNET sites by Falge *et al.* [2002]. Our values were slightly higher since Falge
 20 *et al.* [2002] used a smoothing over 15 days to compute the seasonal course of 'all weather'
 21 GEE whereas we are interested here in optimum half-hourly values. The general agreement

1 between our GEE_{max} and the one given in *Falge et al.* [2002], based on a detailed examination
2 of the data and methods supports our simplified data processing.

3 **Analysis of LUE and GEE* variability**

4 As expected LUE and GEE* from type I data were highly correlated (Figure 1) with a r^2 of
5 0.88 (n=42). Or in other words, GEE* can be used as a proxy for LUE for type II dataset.
6 Since the full dataset for GEE* spans a larger range of ecosystems, latitudes, soil and
7 environmental conditions, especially in the harsh arctic environment, it provides more robust
8 statistics than an analysis restricted to long term comprehensive flux data. Therefore in the
9 following, results are shown for both LUE and GEE*. For the purpose of clarity, plots
10 showing GEE* have a second y-axis (on the right) that maps GEE* into LUE units based on
11 the linear relationship of Figure 1b ($LUE = 0.0006 GEE^* + 0.0023$).

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

18 The canopy LUE values derived here are naturally lower than commonly measured leaf-level
19 quantum yields which may be of the order of 0.06 under normal environmental conditions
20 [e.g. *Ehleringer and Pearcy*, 1983]. Several reasons underlie the leaf vs. canopy difference:
21 Photosynthesis of leaves saturates in high irradiance, thereby decreasing canopy daily LUE,
22 which is integrated over the course of a day and includes periods of high and low irradiance.
23 Moreover, although we select the optimum seasonal LUE value, environmental conditions
24 still impose some stress on the plants. Highest canopy LUE were obtained for two crops in the
25 data set, rice and corn (Table 1), which show almost no saturation of leaf level GEE / PAR

1 curves at the half hourly time step, despite rice being a C3 plant. The average value of 0.018
2 is close to but lower than the value of 0.02 proposed by *Ruimy et al.* [1995, 1996b].
3 For further illustration Figure 2 shows LUE and GEE* as functions of MAT at the site
4 separated per PFT. MAT correlated weakly but significantly with LUE (Fig 2a, $r^2 = 0.27$,
5 $n=42$, $P=0.0004$) and GEE* (Fig 2b, $r^2 = 0.34$, $n=77$, $P<10e-7$). The sensitivity tests
6 performed with the different formulations of fPAR and APAR (eq. 8, 9) did not affect these
7 results (not shown). Since PAR irradiance tends to decrease from temperate to arctic latitudes,
8 the trend of maximum GPP versus MAT is obviously stronger than GEE* (not shown).
9 LUE was not to be expected to be a simple function of MAT due to a range of additional
10 factors. In continental high latitude ecosystems photosynthesis takes place over a short (2-3
11 months) and well defined period with sometimes quite warm temperatures [e.g., *Lloyd et al.*,
12 2002; *Arneeth et al.*, 2002]. However, the correlation almost disappears when MAT is replaced
13 by the temperature corresponding to the period of CO₂ flux data retained to compute LUE and
14 GEE* ($r^2= 0.12$, $P=0.06$ and $r^2=0.19$, $P= 0.01$ respectively). What is more, effects of
15 physiology may override those of temperature with, for instance, LUE of a well-fertilized, C4
16 crop is expected to be higher than that of a 'natural' system at similar MAT. Nevertheless,
17 LUE and GEE* tended to be organized along a MAT gradient (Fig. 2a, b), with a clear
18 tendency to form clusters for some of the plant types like deciduous broadleaved forests,
19 whereas for most of the other types a large variability was found (e.g., needleleaved forests,
20 grasses and crops, and tundra/wetlands). The better correlation with GEE* is caused by a
21 broader sampling of the possible range of MAT, including a number of sites with low annual
22 temperatures ($MAT < 0$). The correlation of LUE and GEE* with MAT we find here is lower
23 than the values reported by *Lafont et al.* [2002] for 18 boreal sites and closer to results
24 reported by *Schwalm et al.* [2006] for yearly mean LUE at 17 Canadian forest and wetland
25 sites. The broader range of PFT included here, especially inclusion of warmer broadleaved
26 evergreen, grasses, crops on the one hand and cold climate fens and deciduous forests on the

1 other hand explains the difference with *Lafont et al.* [2002]. These PFT add to the scattering
2 of the GEE*/MAT relationship (Fig 2b and Table 2). Averaged per PFT, LUE ranges from
3 0.0116 for tundra and wetlands to 0.0270 for C3 grasses and crops (Table 2).

4 **Role of leaf nitrogen content**

5 At the leaf level, numerous studies have demonstrated a strong link between nitrogen content
6 and photosynthesis [*Field and Mooney*, 1986; *Wullschleger*, 1993]. A general framework for
7 leaf structure and function, relating leaf assimilation rate, leaf nitrogen content and leaf mass
8 per area (LMA) has been proposed by *Reich et al.* [1997] and extended worldwide by *Wright*
9 *et al.* [2004]: Leaf photosynthesis (on a mass basis) correlates positively with leaf nitrogen
10 (on a mass basis) and negatively with LMA. At the canopy level, several studies point
11 towards a similarly strong incidence of nitrogen on photosynthesis, productivity and even net
12 CO₂ flux [e.g. *Choudhury*, 2001; *Williams et al.*, 2000; *Smith et al.*, 2002]. However,
13 *Schwalm et al.* [2006] did not find any significant correlation between foliar nitrogen and
14 canopy LUE across 9 forest sites. How leaf-level relations translate to the canopy level
15 therefore remained elusive so far.

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

24 Table 1 and Figures 3a and 3b show the large differences in leaf N that exist among, and also
25 within, plant types. Still, LUE and GEE* tended to group in well-defined PFT-clusters. In that

1 respect, canopy-level data behave like the leaf-level data presented by *Reich et al.* [1997],
2 which also show such PFT clusters.

3

4 **Combination of MAT and N**

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

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

16 This simple model explained 80 % of LUE variance ($LUE = 0.0063 \text{ N} + 0.00036 \text{ MAT} +$
17 0.0064 , $n= 26$) and 76 % of GEE* variance ($GEE^*=10.85 \text{ N} + 0.66 \text{ MAT} + 8.41$, $n=44$).
18 These regression coefficients are quite high, considering that the derivation of LUE and GEE*
19 are affected by several approximations and uncertainties (fPAR estimates at low LAI for
20 instance).

21 Differences in leaf nitrogen reflect site quality combined with plant type. As opposed to foliar
22 N, which is central to plant photosynthesis and physiology, MAT is a surrogate for a number
23 of variables and processes in interaction, like the length of the growing season, the nutrient
24 cycle, the water budget, to mention only three. Therefore, the relationship of LUE with MAT
25 is best viewed as a large-scale pattern that subsumes these effects and that is locally
26 supplanted by the role of PFT, leaf nitrogen, and other factors. A good example comes from

1 the BOREAS data, where stands of aspen, Jack pines and black spruce co-exist at the
 2 landscape scale but show dramatically different LUE and leaf N, sometimes even within the
 3 same stand type [O'Connell *et al.*, 2003]. At the regional scale, averages of the LUE,
 4 weighted by the relative surface of the different PFT in BOREAS Northern and Southern
 5 Sites, tend to fall into the general large scale MAT/LUE gradient (not shown). Large scale
 6 patterns of LUE therefore depend on the relative surfaces occupied by different PFT or plant
 7 differing in N content, in line with the findings of *Still et al.* [2004] of higher LUE in Eurasia
 8 than North America due to higher deciduous trees cover, combined to the overall
 9 environmental conditions correlated to MAT.

10 **Canopy index and function**

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

$$\text{LUE} \propto \frac{N_{\text{canopy}} \cdot \langle \text{LMA} \rangle}{f\text{PAR}} \propto \frac{[N] \cdot \text{LAI}}{f\text{PAR}} \quad \text{Eq. 10}$$

17 When applied to our dataset, the canopy index (hereafter noted I_G) was found to explain a
 18 similar variance of LUE than foliar nitrogen alone (cf., Fig 6a, b compared to 3a, b). This was
 19 the case for both the percentage of variance explained as well as for the complementarities
 20 between I_G and MAT. The comparison of Figures 6 and 3 confirms the analysis by *Green et*
 21 *al.* [2003] such that a canopy index increases the linearity of LUE prediction compared to leaf
 22 nitrogen alone. However, the scatter also increased in our data and the overall predictive
 23 power did not improve. Particularly the C4 sites stand out as outliers in the I_G index / GEE*
 24 relationship. Alternative formulations were developed and tested, that accounted for both, a
 25 non-linear relationship between leaf photosynthesis and leaf N, as well as for the differences

1 in incoming PAR to refine *Green et al.* [2003] formulation. This revised index, ($N^{0.77}$
2 LAI/fPAR.1/Ipar; see Appendix) still did not improve the overall r^2 of the relationship shown
3 in Fig. 6, suggesting that the scattering of canopy index / LUE or GEE* may come from
4 assumptions in scaling leaf level to canopy level, possibly in averaging LMA or leaf
5 properties over the canopy. Given the limited number of sites and the approximations in fPAR
6 derivation, it is at this stage difficult to further evaluate the appropriateness of the different
7 mass-based canopy indices. Indeed, canopy structure, foliage clumping, non-leaf tissues can
8 make the derivation of the factor LAI/fPAR particularly difficult, especially at the scale of a
9 flux tower footprint.

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

1 concentration or mass-basis leaf N may be robust predictors of canopy functioning in terms of
2 light use.

3 **Idealized Canopy models**

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

18 Our compilation of data allows to test some aspects of these concepts. It becomes apparent
19 (Figure 7), for instance, that LUE and GEE*, although highly variable, are not related to light
20 resource capture (i.e., fPAR) in a simple way. Likewise, leaf nitrogen and fPAR are not
21 related (Fig 8). Arguably, there are few high LUE associated with very low fPAR sites in our
22 dataset, suggesting that high light-use efficiency is generally accompanied by high fPAR at
23 least in the absence of opposing management practices, which is in line with *Binkley et al.*
24 [2004]. The same is true for higher leaf N (e.g., >1.5%) being associated with relatively larger
25 fPAR. However, other factors are required to explain the occurrence of LUE and N variability
26 at similarly high fPAR level. For instance, the possible role of dense evergreen foliage as a

1 nitrogen reservoir in nutrient poor environment (resulting in high mass of foliage with
2 relatively low N) plays against a scaling of maximum LUE with fPAR because it increases
3 fPAR and not LUE. It must be kept in mind though, that we investigate optimum LUE only.
4 Using time-integrated variables may result in a different picture [*Field et al.*, 1995] but based
5 on our analysis there is little evidence for theoretical schemes relating of resource use to
6 resource capture.

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

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

1

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

3 A simple relationship of N with either, fPAR, MAT or latitude would facilitate the
4 development and use of global LUE models greatly but the existence of such large-scale
5 patterns is a matter of debate. Some studies point towards an increase of foliar N with latitude,
6 MAT, and altitude, whereas others point towards an opposite pattern [*Reich and Oleskyn,*
7 2004, and references therein]. *Reich and Oleskyn* [2004] found the highest foliar N values for
8 mid-latitude and a weak decrease towards the coldest climate zones. In the data analyzed in
9 our study the only significant trend in N versus latitude was for the evergreen needleleaf PFT.

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

18 Overall, our estimate of optimum LUE and GEE* along latitude gradients (e.g. Fig. 9a and b)
19 indicates a decreasing trend towards high latitude, supporting the statement of *Kaminski et al.*
20 [2002], who considered obtaining the highest LUE for tundra as unrealistic.

21 A variety of reasons may help to explain the discrepancy between our findings and LUE
22 derived from inversion analyses: atmospheric inversion studies rely on an estimate of the
23 heterotrophic respiration and other surface processes like snow-related processes (insulation
24 effect, impact on water availability), whose errors can impair LUE estimates [*Randerson et*
25 *al., 2002*]. However, inaccuracy of the atmospheric vertical mixing or meridional transport
26 may also cause such a discrepancy. If this were to be the case, the consequences on the

1 estimates and localization of the carbon sinks/sources might be significant, as it has been
2 shown by *Stephens et al.* [2007], and deserve further examination.

3 Overall, our results strongly support the view that LUE varies significantly both across and
4 within biomes, and Plant Functional Types. Our data do not support the view that LUE_{GPP}
5 might be less variable than LUE_{NPP} and might therefore span a small range of values [*Goetz*
6 *and Prince*, 1999; *Ruimy et al.*, 1996a]. Our extensive use of the flux measurement network
7 strengthens and extends the results of *Turner et al.* [2003] and *Yuan et al.* [2007], who
8 compared LUE_{GPP} from 4 and 28 flux measurement sites respectively, as well as *Choudhury*
9 [2001], who used data and canopy modeling and suggested a significant variability of
10 LUE_{GPP} . Convergent conclusions were drawn for aboveground LUE_{NPP} in the past [*Gower et*
11 *al.*, 1999 and references therein]. Given the high diversity of measurement sites, which
12 encompass managed and unmanaged stands, mono- or pluri-specific canopies, leaf nitrogen
13 emerges as a strong organization factor of optimum canopy LUE and canopy photosynthesis
14 rate.

15 As far as remote-sensing models are concerned LUE-based GPP models therefore have to
16 account for variability in optimum LUE within an ecosystem and on biome scale. This has
17 important consequences for the validation of global LUE-models with local data. Such
18 models often combine an optimum LUE with different stress factors. Temporal variability in
19 stress factors, incoming and absorbed PAR usually result in favorable model/data comparison,
20 especially if site quality is accounted for [e.g. *Yuan et al.*, 2007; *Mäkelä et al.*, 2008]. Remote
21 sensing of the xanthophylls cycle (PRI), surface radiative temperature or fluorescence may
22 help capturing some of the short to seasonal variability of LUE [*Grace et al.*, 2007] and may be
23 included in the next generation of LUE based models. Improvements of optimum LUE
24 estimates will be achieved if information on leaf nitrogen can be obtained in addition to
25 fPAR, which may be done using ground based or airborne sensor (e.g. AVIRIS, CASI). For
26 instance, *Smith et al.* [2002] showed that forest productivity could be assessed through

1 estimation of leaf nitrogen content mapped with AVIRIS. *Boegh et al.* [2002] were able to
2 simulate canopy photosynthesis for different crops combining nitrogen-based modeling and
3 hyperspectral data from CASI. The robustness of inversion methods for chlorophyll and
4 nitrogen content, based on satellite-borne sensors like MERIS, CHRIS-PROBA or
5 HYPERION, has to be investigated in the perspective of LUE-modeling.

1 **Appendix**

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

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

5
 6 Note that the use of GEE* as a proxy for LUE is based on the same assumption (GEE* being
 7 close to eq 11 right-hand-side). Assuming the maximum canopy photosynthesis rate is
 8 proportional to the integral of leaf level maximum photosynthesis rate (on a surface
 9 basis, A_s^{max}), we have

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

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

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

12

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

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

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

17

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10

1 Reference

- 2 Alton, P.B., P.R. North, and S.O. Los (2007), The impact of diffuse sunlight on canopy
3 light-use efficiency, gross photosynthetic product and net ecosystem exchange in
4 three forest biomes, *Global Change Biol.*, 13, 776-787.
- 5 Anderson, D.E., R. Striegl, D.D. Baldocchi, and D. Stannard (1995), The Fluxes of CO₂
6 and Water Vapor Measured Above and Within Young and Mature Jack Pine
7 Forests of Central Canada, paper presented at IUFRO Interactive Environmental
8 Effects on Forest Stands Workshop, New Zealand.
- 9 Aradóttir, A.L., H. Thorgeirsson, J.H. McCaughey, I.B. Strachan, and A. Robertson
10 (1997), Establishment of a black cotton wood plantation on an exposed site in
11 Iceland: plant growth and site energy balance, *Agric. For. Meteorol.*, 84, 1-9.
- 12 Arneth, A., F.M. Kelliher, T.M. McSeveny, and J.N. Byers (1998), Assessment of
13 annual carbon exchange in a water-stressed *Pinus radiata* plantation: an analysis
14 based on eddy covariance measurements and an integrated biophysical model,
15 *Global Change Biol.*, 5, 531-545.
- 16 Arneth, A., J. Kurbatova, O. Kolle, O.B. Shibistova, J. Lloyd, N.N. Vygodskaya, and
17 E.D. Schulze (2002), Comparative ecosystem-atmosphere exchange of energy and
18 mass in a European Russian and a central Siberian bog II. Interseasonal and
19 interannual variability of CO₂ fluxes, *Tellus, Ser. B*, 54, 514-530.
- 20 Aubinet, M., B. Chermanne, M. Vandenhaute, B. Longdoz, M. Yernaux, and E. Laitat
21 (2001), Long term carbon dioxide exchange above a mixed forest in the Belgian
22 Ardennes, *Agric. For. Meteorol.*, 108, 293-315.
- 23 Aurela, M, J.P. Tuovinen JP, and T. Laurila (2001), Net CO₂ exchange of a subarctic
24 mountain birch ecosystem, *Theor. Appl. Climatol.*, 70, 135-148.

1 Baldocchi, D.D., C. Vogel, and B. Hall (1997), Seasonal variation of carbon dioxide
2 exchange rates above and below a boreal jack pine forest, *Agric. For. Meteorol.*,
3 83, 147-170.

4 Baldocchi, D.D., et al. (2001), FLUXNET: A new tool to study the temporal and spatial
5 variability of ecosystem-scale carbon dioxide, water vapor, and energy flux
6 densities, *Bull. Am. Met. Soc.*, 82, 2415-2434.

7 Berbigier, P., J.M. Bonnefond, and P. Mellmann (2001), CO₂ and water vapour fluxes
8 for 2 years above Euroflux forest site, *Agric. For. Meteorol.*, 108, 183-197.

9 Binkley, D., J.L. Stape, and M.G. Ryan (2004), Thinking about efficiency of resource
10 use in forests, *For. Ecol. Manage.*, 193, 5-16.

11 Boegh, E., H. Soegaard, N. Broge, C.B. Hasager, N.O. Jensen, K. Schelde, and A.
12 Thomsen (2002), Airborne multispectral data for quantifying leaf area index,
13 nitrogen concentration, and photosynthesis efficiency in agriculture, *Rem. Sens.*
14 *Env.*, 81, 179-193.

15 Bradford, J.B., J.A. Hicke, and W.K. Lauenroth (2005), The relative importance of
16 light-use efficiency modifications from environmental conditions and cultivation
17 for estimation of large-scale net primary productivity, *Rem. Sens. Env.*, 96, 246-
18 255.

19 Campbell, C.S., J.L. Heilman, K.J. McInnes, L.T. Wilson, J.C. Medley, G. Wu, and
20 D.R. Cobos (2001), Seasonal variation in radiation use efficiency of irrigated rice,
21 *Agric. For. Meteorol.*, 110, 45-54.

22 Chen, J., M. Falk, E. Euskirchen, K.T. Paw U, T.H. Suchanek, S.L. Ustin, B.J. Bond,
23 K.D. Brosofske, N. Phillips, and R. Bi (2002), Biophysical controls of carbon
24 flows in three successional Douglas-fir stands based on eddy-covariance
25 measurements, *Tree Physiol.*, 22, 169-177.

1 Chevallier, F., R.J. Engelen, and P. Peylin (2005), The contribution of AIRS data to the
2 estimation of CO₂ sources and sinks, *Geophys. Res. Lett.*, **32**, L23801,
3 doi:10.1029/2005GL024229

4 Choudhury, B.J. (2001), Estimating gross photosynthesis using satellite and ancillary
5 data: approaches and preliminary results, *Rem. Sens. Env.*, *75*, 1-25.

6 Clement, R., J.B. Moncrieff, and P.G. Jarvis (2003), Net carbon productivity of sitka
7 spruce forest in Scotland, *Scottish Forestry*, *57*, 5-10.

8 Davis, K.J., P.S. Bakwin, C. Yi, B.W. Berger, C. Zhao, R.M. Teclaw, and J.G.
9 Isebrands (2003), The annual cycles of CO₂ and H₂O exchange over a northern
10 mixed forest as observed from a very tall tower, *Global Change Biol.*, *9*, 1278–
11 1293.

12 DeLucia, E.H., J.E. Drake, R.B. Thomas, and M. Gonzalez-Melers (2007), Forest
13 carbon use efficiency: is respiration a constant fraction of gross primary
14 production? *Global Change Biol.*, **13**, 1157-1167.

15 Dolman, A.J., E.J. Moors, and J.A. Elbers (2002), The carbon uptake of a mid latitude
16 pine forest growing on sandy soil, *Agric. For. Meteorol.*, *111*, 157-170.

17 Ehleringer, J., and R.W. Pearcy (1983), Variation in quantum yield for CO₂ uptake
18 among C₃ and C₄ plants, *Plant Physiol.*, *73*, 555-559.

19 Falge, E., et al. (2002), Seasonality of ecosystem respiration and gross primary
20 production as derived from FLUXNET measurements, *Agric. For. Meteorol.*, *113*,
21 53-74.

22 Falge, E., et al. (2001), Gap filling strategies for defensible annual sums of net
23 ecosystem exchange, *Agric. For. Meteorol.*, *107*, 43-69.

24 Fan, S.M., M.L. Goulden, J.W. Munger, B.C. Daube, P.S. Bakwin, S.C. Wofsy, J.S.
25 Amthor, D.R. Fitzjarrald, K.E. Moore, and T.R. Moore (1995), Environmental
26 controls on the photosynthesis and respiration of a boreal lichen woodland: A

1 growing season of whole-ecosystem exchange measurements by eddy correlation,
2 *Oecologia*, 102, 443-452.

3 Field, C.B., and H.A. Mooney (1986), The photosynthesis-nitrogen relationship in wild
4 plants, in *On the economy of plant form and function*. Ed T.J. Givnish, Cambridge
5 University Press, pp 25-55, New York.

6 Field, C.B., J.T. Randerson, and C.M. Malmström (1995), Global net primary
7 production – Combining ecology and remote sensing, *Rem. Sens. Env.*, 51, 74-88.

8 Flanagan, L.B., L.A. Wever, and P.J. Carlson (2002), Seasonal and interannual variation
9 in carbon dioxide exchange and carbon balance in a northern temperate grassland,
10 *Global Change Biol.*, 8, 599-615.

11 Friend, A.D., et al. (2007), FLUXNET and modelling the global carbon cycle, *Global*
12 *Change Biol.*, 13, 610-633.

13 Goetz, S.J., and S.D. Prince (1999), Modelling terrestrial carbon exchange and storage:
14 Evidence and implications of functional convergence in light-use efficiency, *Adv.*
15 *Ecol. Res.*, 28, 57-92.

16 Goldstein, A.H., N.E. Hultman, J.M. Fracheboud, M.R. Bauer, J.A. Panck, M. Xu, Y.
17 Qi, A.B. Guenther, and W. Baugh (2000), Effects of climate variability on the
18 carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation
19 in the Sierra Nevada (CA), *Agric. For. Meteorol.*, 101, 113-129.

20 Goulden, M.L., B.C. Daube, S.M. Fan, D.J. Sutton, F.A. Bazzaz, J.W. Munger, and S.C.
21 Wofsy (1997), Physiological responses of a black spruce forest to weather, *J.*
22 *Geophys. Res.*, 102D, 28987-28996.

23 Gower, S.T., C.J. Kucharik, and J.M. Norman (1999), Direct and indirect estimation of
24 leaf area index, Fapar and net primary production of terrestrial ecosystems. *Rem.*
25 *Sens. Env.*, 70, 29-51.

1 Grace, J., C. Nichols, M. Disney, P. Lewis, T. Quaife, and P. Bowler (2007), Can we
2 measure terrestrial photosynthesis from space directly, using spectral reflectance
3 and fluorescence? *Global Change Biol.*, *13*, 1484-1497 doi:10.1111/j.1365-
4 2486.2007.01352.x

5 Granier, A., et al. (2000), The carbon balance of a young beech forest, *Funct. Ecol.*, *14*,
6 312-325.

7 Green, D.S., J.E. Erickson, and E.L. Kruger EL (2003), Foliar morphology and canopy
8 nitrogen as predictors of light-use-efficiency in terrestrial vegetation, *Agric. For.*
9 *Meteorol.*, *115*, 165-173.

10 Griffis, T.J., W. and Rouse (2001), Modelling the interannual variability of net
11 ecosystem CO₂ exchange at a subarctic sedge fen, *Global Change Biol.*, *7*, 511-
12 530.

13 Grünwald, T., and C. Bernhofer (2007), A decade of carbon, water and energy flux
14 measurements of an old spruce forest at the Anchor Station Tharandt, *Tellus, Ser.*
15 *B*, *59*, 387-396.

16 Hanan, N.P., G. Burba, S.B. Verma, J.A. Berry, A. Suyker, and E.A. Walter-Shea
17 (2002), Inversion of net ecosystem CO₂ flux measurements for estimation of
18 canopy PAR absorption, *Global Change Biol.*, *8*, 563-574.

19 Harazono, Y, M. Mano, A. Miyata, R.C. Zulueta, and W.C. Oechel (2003), Inter-annual
20 carbon dioxide uptake of a wet sedge tundra ecosystem in the arctic, *Tellus, Ser.*
21 *B*, *55*, 215-231.

22 Haxeltine, A., and I.C. Prentice (1996), A general model for the light-use efficiency of
23 primary production, *Funct. Ecol.*, *10*, 551-561.

24 Heimann, M. (2002), Foreword: The Eurosiberian Carbonflux project, *Tellus, Ser. B*,
25 *54*, 417-419.

1 Hikosaka, H. (2004), Interspecific difference in the photosynthesis-nitrogen
2 relationship: patterns, physiological causes, and ecological importance, *J. Plant*
3 *Res.*, 117, 481-494

4 Hirano, T, R. Hirata, Y. Fujinuma, N. Saigusa, S. Yamamoto, Y. Harazono, M. Takada,
5 K. Inukai, and G. Inoue (2003), CO₂ and water vapor exchange of a larch forest
6 in northern Japan, *Tellus, Ser. B*, 55, 244-257.

7 Hollinger, D.Y., et al. (1998), Forest-atmosphere carbon dioxide exchange in eastern
8 Siberia, *Agric. For. Meteorol.*, 90, 291-306.

9 Hollinger, D.Y., F.M. Kelliher, J.N. Byers, J.E. Hunt, T.M. McSeveny, and P.L. Weir
10 (1994), Carbon dioxide exchange between an undisturbed old-growth temperate
11 forest and the atmosphere, *Ecology*, 75, 134-150.

12 Hollinger, D.Y., S.M. Goltz, E.A. Davidson, J.T. Lee, K. Tu, and H.T. Valentine
13 (1999), Seasonal patterns and environmental control of carbon dioxide and water
14 vapour exchange in an ecotonal boreal forest, *Global Change Biol.*, 5, 891-902.

15 Hunt, J.E., F.M. Kelliher, T.M. McSeveny, J.N. Byers (2002), Evaporation and carbon
16 dioxide exchange between the atmosphere and a tussock grassland during a
17 summer drought, *Agric. For. Meteorol.*, 111, 65-82.

18 Jarvis, P.G., J.M. Massheder, S.E. Hale, J.B. Moncrieff, M. Rayment, and S.L. Scott
19 (1997), Seasonal variation of carbon dioxide, water vapor, and energy exchanges
20 of a boreal black spruce forest, *J. Geophys. Res.*, 102D, 28953-28966.

21 Kaminski, T., W. Knorr, P.J. Rayner, and M. Heimann (2002), Assimilating
22 atmospheric data into a terrestrial biosphere model: A case study of the seasonal
23 cycle, *Global Biogeochem. Cycles*, 16, 1066, doi:10.1029/2001GB001463

24 Katul, G., C.T. Lai, K. Schafer, B. Vidakovic, J. Albertson, D. Ellsworth, and R. Oren
25 (2001), Multiscale analysis of vegetation surface fluxes: from seconds to years,
26 *Adv. Water Resour.*, 24, 1119-1132.

- 1 Klemm, O., and A. Mangold (2001), Ozone deposition at a forest site in NE Bavaria,
2 *Water Air Soil Poll. Focus, 1*, 223-232.
- 3 Kowalski, A.S., S. Overloop, and R. Ceulemans (2000), Eddy fluxes above a Belgian
4 Campine forest and their relationship with predicting variables, in *Forest*
5 *ecosystem modelling, upscaling and remote sensing*, R. Ceulemans, F.
6 Veroustraete, V. Gond, and J. van Rensbergen eds., SPB Academy publishing, pp
7 3-17, The Hague
- 8 Lafleur, P.M., N.T. Roulet, and S.W. Admiral (2001), Annual cycle of CO₂ exchange at
9 a bog peatland, *J. Geophys. Res.*, *106D*, 3071-3081.
- 10 Lafont, S., L. Kergoat, G. Dedieu, A. Chevillard, U. Karstens, and O. Kolle (2002),
11 Spatial and temporal variability of land CO₂ fluxes estimated with remote sensing
12 and analysis data over Western Eurasia, *Tellus, Ser. B*, *54*, 820-833.
- 13 Laurila, T., H. Soegaard, C.R. Lloyd, M. Aurela, J.P. Tuovinen, and C. Nordstroem
14 (2001), Seasonal variations on net CO₂ exchange in European Arctic ecosystems,
15 *Theor. Appl. Climatol.*, *70*, 183-201.
- 16 Law, B.E., P.E. Thornton, J. Irvine, P.M. Anthoni, and S. van Tuyl (2001), Carbon
17 storage and fluxes in ponderosa pine forests at different developmental stages,
18 *Global Change Biol.*, *7*, 755-777.
- 19 Lee, X., J.D. Fuentes, R.M. Staebler, and H.H. Neumann (1999), Long-term observation
20 of the atmospheric exchange of CO₂ with a temperate deciduous forest in
21 southern Ontario, Canada, *J. Geophys. Res.*, *104D*, 15975-15984.
- 22 Leemans, R., and W. Cramer (1991), The IIASA climate database for mean monthly
23 values of temperature, precipitation and cloudiness on a terrestrial grid.
24 Laxenburg, Austria

- 1 Lindroth, A., A. Grelle, and A.S. Morén (1998), Long-term measurements of boreal
2 forest carbon balance reveal large temperature sensitivity, *Global Change Biol.*, 4,
3 443-450.
- 4 Lloyd, C.R. (2001), The measurements and modelling of the carbon dioxide exchange
5 at a high Arctic site in Svalbard, *Global Change Biol.*, 7, 405-426.
- 6 Lloyd, J., O. Shibistova, D. Zolotoukhine, O. Kolle, A. Arneth, C. Wirth, J. Styles,
7 N.M. Tchebakova, and S.D. Schulze (2002), Seasonal and annual variations in the
8 photosynthetic productivity and carbon balance of a central Siberian pine forest,
9 *Tellus, Ser. B*, 54, 590-610.
- 10 Lohila, A., M. Aurela, J.P. Tuovinen, and T. Laurila (2004), Annual CO₂ exchange on
11 peat field growing spring barley or perennial forage grass, *J. Geophys. Res.*,
12 109D, D18116.
- 13 Mäkelä, A., M. Pulkkinen, P. Kolari, F. Lagergren, P. Berbigier, A. Lindroth, D.
14 Loustau, E. Nikinmaa, T. Vesala, and P. Hari (2008), Developing an empirical
15 model of stand GPP with LUE approach: analysis of eddy covariance data at five
16 contrasting conifer sites in Europe, *Global Change Biol.*, 14, 92-108,
17 doi:10.1111/j.1365-2486.2007.01463.x
- 18 Markkanen, T., U. Rannik, P. Keronen, T. Suni, and T. Vesala (2001), Eddy covariance
19 fluxes over a boreal Scots pine forest, *Boreal Environ. Res.*, 6, 65-78
- 20 McCaughey, J.H., P.M. Lafleur, D.W. Joiner, P.A. Bartlett, A.M. Costello, D.E.
21 Jelinski, and M.G. Ryan (1997), Magnitudes and seasonal patterns of energy,
22 water, and carbon exchanges at a boreal young jack pine forest in the BOREAS
23 northern study area, *J. Geophys. Res.*, 102D, 28997-29007.
- 24 Medlyn, B.E. (1998), Physiological basis of the light use efficiency model, *Tree*
25 *Physiol.*, 18, 167-176.

1 Meyers, T.P. (2001), A comparison of summertime water and CO₂ fluxes over
2 rangeland for well watered and drought conditions, *Agric. For. Meteorol.*, 106,
3 203-214.

4 Milyukova, I., O. Kolle, A.V. Varlagin, N.N. Vygodskaya, E.D. Schulze, and J. Lloyd
5 (2002), Carbon balance of a southern taiga spruce stand in European Russia,
6 *Tellus, Ser. B*, 54, 429-442.

7 Monson, R.K., A.A Turnipseed, J.P. Sparks, P.C. Harley, L.E. Scott-Denton, K. Sparks,
8 and T.E. Huxman (2002), Carbon sequestration in a high-elevation, subalpine
9 forest, *Global Change Biol.*, 8, 459-478.

10 Monteith, J.L. (1977), Climate and the efficiency of crop production in Britain, *Philos.*
11 *Trans. R. Soc. London, Ser. B*, 281, 277-294.

12 Moore, K.E., D.R. Fitzjarrald, R.K. Sakai, and J.M. Freedman (2000), Growing season
13 water balance at a boreal jack pine forest, *Water Resour. Res.*, 36, 483-493.

14 Nakai, Y., K. Kitamura, S. Suzuki, and S. Abe (2003), Year-long carbon dioxide
15 exchange above a broadleaf deciduous forest in Sapporo, Northern Japan, *Tellus*,
16 *Ser. B*, 55, 305-312.

17 Nemani, R.R., C.D. Keeling, H. Hashimoto, W.M. Jolly, S.C. Piper, C.J. Tucker, R.B.
18 Myneni, and S.W. Running (2003), *Science*, 300, 1560-1563.

19 Nordstroem, C., H. Soegaard, T.R. Christensen, T. Friborg, and B.U. Hansen (2001),
20 Seasonal carbon dioxide balance and respiration of a high-arctic fen ecosystem in
21 NE-Greenland, *Theor. Appl. Climatol.*, 70, 149-166.

22 O'Connell, K.E.B., S.T. Gower, and J.M. Norman (2003), Comparison of Net Primary
23 Production and light-use dynamics of two boreal black spruce forest communities,
24 *Ecosystems*, 6, 236-247, doi:10.1007/s10021-002-0201-x

25 Oechel, W.C., et al. (2000), A scaling approach for quantifying the net CO₂ flux of the
26 Kuparuk river basin, Alaska, *Global Change Biol.*, 6 (Suppl 1), 180-173.

1 Owen, K. E., et al., (2007), Linking flux network measurements to continental scale
2 simulations: ecosystem carbon dioxide exchange capacity under non-water
3 stressed conditions, *Global Change Biol.*, *13*, 734-760.

4 Pilegaard. K., P. Hummelshøj, N.O. Jensen, and Z. Chen (2001), Two years of
5 continuous CO₂ eddy-flux measurements over a Danish beech forest, *Agric. For.*
6 *Meteorol.*, *107*, 29-41.

7 Potter, C.S., J.T. Randerson, C.B. Field, P.A. Matson, P.M. Vitousek, H.A. Mooney,
8 and S.A. Klooster (1993), Terrestrial ecosystem production: A process model
9 based on global satellite and surface data, *Global Biogeochem. Cycles*, *7*, 811-
10 841.

11 Prince, S.D. (1991), A model of regional primary production for use with coarse
12 resolution satellite data, *Int. J. Remote Sens.*, *12*, 1313-1330.

13 Randerson, J.T., et al. (2002), Carbon isotope discrimination of arctic and boreal biomes
14 inferred from remote atmospheric measurements and a biosphere-atmosphere
15 model, *Global Biogeochem. Cycles*, *16*, doi:10.1029/2001GB001435

16 Reich, P.B., and J. Oleskyn (2004), Global patterns of plant leaf N and P in relation to
17 temperature and latitude, *Proc. Natl. Acad. Sci. U.S.A.*, *101*, 11001-11006.

18 Reich, P.B., M.B. Walters, and D.S. Ellsworth (1997), From tropics to tundra: Global
19 convergence in plant functioning, *Proc. Natl. Acad. Sci. U.S.A.*, *94*, 13730-13734.

20 Reichstein, M., J.D. Tenhunen, O. Rouspard, J.M. Orcival, S. Rambal, F. Miglietta, A.
21 Peressotti, M. Pecchiari, G. Tirone, and R. Valentini (2002), Severe drought
22 effects on ecosystem CO₂ and H₂O fluxes at three Mediterranean evergreen sites:
23 revision of current hypothesis? *Global Change Biol.*, *8*, 999-1017.

24 Röser, C., L. Montagnani, E.D. Schulze, D. Mollicone, O. Kolle, M. Meroni, D. Papale,
25 B. Marchesini, S. Federici, R. and Valentini (2002), Net CO₂ exchange rates in

1 three different successional stages of the "Dark Taiga" of central Siberia, *Tellus*,
2 *Ser. B*, 54, 642-654.

3 Ruimy, A., B. Saugier, and G. Dedieu (1994), Methodology for the estimation of
4 terrestrial net primary productivity from remotely sensed data, *J. Geophys. Res.*,
5 99 (D3), 5263-5283.

6 Ruimy, A., G. Dedieu, and B. Saugier (1996a), TURC: A diagnostic model of
7 continental gross primary productivity and net primary productivity, *Global*
8 *Biogeochem. Cycles*, 10, 269-285.

9 Ruimy, A., L. Kergoat, and A. Bondeau (1999), Comparing global models of terrestrial
10 net primary productivity (NPP): Analysis of differences in light absorption and
11 light-use efficiency, *Global Change Biol.*, 5 (s1), 56-64.

12 Ruimy, A., L. Kergoat, C.B. Field, and B. Saugier (1996b), The use of CO₂ flux
13 measurements in models of the global terrestrial carbon budget, *Global Change*
14 *Biol.*, 2, 287-296.

15 Ruimy, A., P.G. Jarvis, D.D. Baldocchi, and B. Saugier (1995), CO₂ fluxes over plant
16 canopies and solar radiation: a review, *Adv. Ecol. Res.*, 26, 1-68.

17 Running, S.W., R.R. Nemani, F.A. Heinsch, M.S. Zhao, M. Reeves, and H. Hashimoto
18 (2004), A continuous satellite-derived measure of global terrestrial production,
19 *Bioscience*, 54, 547-560.

20 Schmid, H.P., C. Susan, B. Grimmond, F. Copley, B. Offerle, and H.B. Su (2000),
21 Measurements of CO₂ and energy fluxes over a mixed hardwood forest in the
22 mid-western United States, *Agric. For. Meteorol.*, 103, 357-374.

23 Schwalm, C.R., et al. (2006), Photosynthetic light use efficiency of three biomes across
24 an east-west continental-scale transect in Canada, *Agric. For. Meteorol.*, 140, 269-
25 286.

1 Sellers, P.J., et al. (1995), The Boreal Ecosystem-Atmosphere Study (BOREAS): an
2 overview and early results from the 1994 field year. *Bull. Am. Met. Soc.*, 76,
3 1549-1577.

4 Smith M.L., S.V. Ollinger, M.E. Martin, J.D. Aber, R.A. Hallett, and C.L. Goodale
5 (2002), Direct estimation of aboveground forest productivity through
6 hyperspectral remote sensing of canopy nitrogen, *Ecol. Appl.*, 12, 1286-1302.

7 Soegaard, H., C. Nordstroem, T. Friberg, and B.U. Hansen (2000), Trace gas exchange
8 in a high-arctic valley 3. Integrating and scaling CO₂ fluxes from canopy to
9 landscape using flux data, footprint modelling, and remote sensing, *Global*
10 *Biogeochem. Cycles*, 14, 725-744.

11 Stephens, B.B., et al. (2007), Weak Northern and strong tropical land carbon uptake
12 from vertical profiles of atmospheric CO₂, *Science*, 316, 1732,
13 doi:10.1126/science.1137004

14 Still, C.J., J.T. Randerson, and I.Y. Fung (2004), Large-scale plant light-use efficiency
15 inferred from the seasonal cycle of atmospheric CO₂, *Global Change Biol.*, 10,
16 1240-1252.

17 Stylinski, C.D., J.A. Gamon, and W.C. Oechel (2002), Seasonal patterns of reflectance
18 indices, carotenoid pigments and photosynthesis of evergreen chaparral species,
19 *Oecologia*, 131, 366-374.

20 Suyker, A.E., and S.B. Verma (2001), Year-round observations of the net ecosystem
21 exchange of carbon dioxide in a native tallgrass prairie, *Global Change Biol.*, 7,
22 279-289.

23 Suyker, A.E., S.B. Verma, and T.J. Arkebauer (1997), Season-long measurements of
24 carbon dioxide exchange in a boreal fen, *J. Geophys. Res.*, 102D, 29021-29028.

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

4 Turner, D.P., et al. (2005), Site-level evaluation of satellite-based global terrestrial gross
5 primary production and net primary production, *Global Change Biol.*, 11, 666-684

6 Valentini, R., G. Matteucci, A.J. Dolman, E.D. Schulze, and P.G. Jarvis (2003), The
7 carbon sink strength of forests in Europe: Results of the EUROFLUX Network. In
8 *Biospheric Exchanges of Carbon Water and Energy of European Forests* (Ed R
9 Valentini), Ecological Studies, 163, pp 225-232, Springer Verlag.

10 Valentini, R., P. De Angelis, G. Matteucci, R. Monaco, S. Dore, and G.E. Scarascia
11 Mugnozza (1996), Seasonal net carbon dioxide exchange of a Beech forest with
12 the atmosphere, *Global Change Biol.*, 2, 199-207.

13 Vourlitis, G.L., and W.C. Oechel (1999), Eddy covariance measurements of CO₂ and
14 energy fluxes of an Alaskan tussock tundra ecosystem, *Ecology*, 80, 686-701.

15 Wallin, G., S. Linder, A. Lindroth, M. Rantfors, S. Flemberg, and A. Grelle (2001),
16 Carbon dioxide exchange in Norway spruce at the shoot, tree and ecosystem scale,
17 *Tree Physiol*, 21, 969-976.

18 Warren C.R., and M. A. Adams (2004), Evergreen trees do not maximize instantaneous
19 photosynthesis, *TRENDS in Plant Science*, 9(6),
20 doi:10.1016/j.tplants.2004.04.004

21

22 Williams, M., W. Eugster, E.B. Rastetter, J.P. McFadden, and F.S. Chapin III (2000),
23 The controls on net ecosystem productivity along an Arctic transect: a model
24 comparison with flux measurements, *Global Change Biol.*, 6 (supp 1), 116-126.

- 1 Wilson, K.B., and D.D. Baldocchi (2000), Seasonal and interannual variability of
2 energy fluxes over a broadleaved temperate deciduous forest in North America,
3 *Agric. For. Meteorol.*, 100, 1-18.
- 4 Wofsy, S.C., M.L. Goulden, J.W. Munger, S.M. Fan, P.S. Bakwin, B.C. Daube, S.L.
5 Bassow, and F.A. Bazzaz, Net exchange of CO₂ in a midlatitude forest, *Science*,
6 260, 1314-1317.
- 7 Wright, I.J., et al. (2004), The worldwide leaf economics spectrum, *Nature*, 428(6985),
8 821-827.
- 9 Wullschleger, S.D. (1993), Biochemical limitations to carbon assimilation in C₃ plants
10 – a retrospective analysis of the A/C_i curves from 109 species, *J. Exp. Bot.*, 44,
11 907-920.
- 12 Yang, P.C., T.A. Black, H.H. Neumann, M.D. Novak, and P.D. Blanken (1999), Spatial
13 and temporal variability of CO₂ concentration and flux in a boreal aspen forest, *J.*
14 *Geophys. Res.*, 104D, 27653-27661.
- 15 Yuan, W., et al. (2007), Deriving a light use efficiency model from eddy covariance
16 flux data for predicting daily gross primary production across biomes, *Agric. For.*
17 *Meteorol.*, 143, 189-207.

1 **Figure captions**

2

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

6

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

12

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

15

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

17

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

19

20 Figure 4: Leaf nitrogen N versus annual mean temperature.

21

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

24

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

26

1 Figure 6: a) LUE versus *Green et al.* [2003] canopy index I_G .

2

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

5

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

7

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

9

10 Figure 8: Canopy fPAR versus leaf nitrogen N.

11

12 Figure 9: a) Optimum daily LUE as a function of latitude for $|\text{lat}| > 45^\circ$.

13

14 Figure 9 b) GEE^* as a function of latitude for $|\text{lat}| > 45^\circ$.

1 **Tables**2 **Table 1**

3

References	Name	Species or canopy type	PFT	Lat	MAT °C	LAI	FPAR	N (%)	LUE mol/mol	GEE* μmolm ⁻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
McCaughy 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	<i>Quercus ilex</i>	●	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	Zackenberf fen	fen	■	74.5	-9.5	1.1	0.56	-	-	27.8
Soegaard et al 2000	Zackenberf heath	Heath tundra	■	74.5	-9.5	0.2	0.14	-	-	26.8
Laurila et al 2001	Zackenberf 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
Laffleur 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	<i>Nothofagus</i>	●	-42.	9.4	7.0	0.94	0.77	-	22.4
Arneeth et al. 1998	NewZealand	<i>Pinus radiata</i>	▲	-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

1

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

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

9 * values from Lindroth et al. 1998.

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

13

1 **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)

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

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