

Temporal and among-site variability of inherent water use efficiency at the ecosystem level

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[1] Half-hourly measurements of the net exchanges of carbon dioxide and water vapor between terrestrial ecosystems and the atmosphere provide estimates of gross primary production (GPP) and evapotranspiration (ET) at the ecosystem level and on daily to annual timescales. The ratio of these quantities represents ecosystem water use efficiency. Its multiplication with mean daylight vapor pressure deficit (VPD) leads to a quantity which we call “inherent water use efficiency” (IWUE*). The dependence of IWUE* on environmental conditions indicates possible adaptive adjustment of ecosystem physiology in response to a changing environment. IWUE* is analyzed for 43 sites across a range of plant functional types and climatic conditions. IWUE* increases during short-term moderate drought conditions. Mean annual IWUE* varied by a factor of 3 among all sites. This is partly explained by soil moisture at field capacity, particularly in deciduous broad-leaved forests. Canopy light interception sets the upper limits to canopy photosynthesis, and explains half the variance in annual IWUE* among herbaceous ecosystems and evergreen needle-leaved forests. Knowledge of IWUE* offers valuable improvement to the representation of carbon and water coupling in ecosystem process models.

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1. Introduction

[2] Both photosynthesis and transpiration at the leaf level are dependent on local microclimate and coupled aerodynamic and stomatal conductances. Leaf-level demand for water has to be matched by soil water extraction by the plant, and this depends on root distribution, soil water content, and hydraulic conductivity in the soil matrix. If plant water use exceeds soil water recharge, it can lead to restrictions on plant water uptake, reduce stomatal conduc-

tance, and cause a feedback on leaf-level processes and evaporative losses. It has been proposed [Cowan and Farquhar, 1977] that plants control stomata to optimally satisfy the trade-off between the amount of carbon assimilated and the amount of water transpired. The amount of carbon gained per unit of water loss, called water use efficiency (WUE), is used to quantify this trade-off. Leaf-level measurements, however, have demonstrated the strong dependence of stomatal conductance on the difference between ambient and inner-leaf vapor pressure [Lange et al., 1971; Schulze and Hall, 1982]. Stomatal conductance determines both diffusion of CO₂ into the leaf and diffusion

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Table 1. Definitions of Water Use Efficiency, Intrinsic Water Use Efficiency, and Inherent Water Use Efficiency at Different Levels of Organization^a

	Water Use Efficiency	Intrinsic Water Use Efficiency	Inherent Water Use Efficiency
Leaf level	$WUE = A/E$	$WUE_i = A/g$	-
Ecosystem level	$WUE^* = GPP/ET$	$WUE^*_i = GPP/G_s$	$IWUE^* = GPP \cdot VPD/ET$

^aThe star marker indicates definitions of water use efficiency at the ecosystem level. The quantities carbon assimilation (A), transpiration (E), stomatal conductance (g), surface conductance (G_s), gross primary production (GPP), evapotranspiration (ET), and vapor pressure deficit (VPD) represent time integrals over any length. See section 2 for assumptions to be made for moving from the leaf level to the ecosystem level.

of water out of it with the diffusion coefficient being higher for the lighter H_2O molecules. This physical process acts on WUE in addition to the performance of carboxylation in relation to inner-leaf CO_2 concentration. Hence, the ratio between assimilation rate and stomatal conductance called intrinsic WUE (WUE_i) is more appropriate than WUE for describing the biochemical functions of vascular plants (cf. Table 1).

[3] Direct measurements of carbon and water exchange between terrestrial ecosystems and the atmosphere provide the opportunity to examine water use efficiency at the ecosystem level [Law *et al.*, 2002; Lloyd *et al.*, 2002; Arneth *et al.*, 2006]. However, net carbon assimilation and transpiration are not directly quantified from such measurements. Instead, gross primary production (GPP) and evapotranspiration (ET) are derived from measurements of net ecosystem exchange (NEE) and latent heat flux. Section 2 explains how water use efficiency at the ecosystem level (WUE^*) can be computed from GPP and ET, and under which assumptions. The star marker is used in this paper to indicate that water use efficiency is derived from ecosystem-scale observations (cf. Table 1).

[4] Reichstein *et al.* [2007] inferred a slight decrease of WUE^* during the severe drought in European forests in summer 2003. Further conclusions at process level of such findings, however, cannot be clearly drawn because the effect of vapor pressure deficit (VPD) on canopy conductance [Bierhuizen and Slatyer, 1965; Sinclair *et al.*, 1984; Baldocchi *et al.*, 1985; Monteith, 1986; Irvine *et al.*, 2004] confounds the individual responses of GPP and ET to changing environmental conditions. Using *intrinsic* water use efficiency at the ecosystem level (WUE^*_i) is more appropriate than using WUE^* for such purpose.

[5] At the ecosystem level, WUE^*_i can be calculated as the ratio between GPP and surface conductance [Lloyd *et al.*, 2002; Arneth *et al.*, 2006] (cf. Table 1). In doing so, the Penman-Monteith equation needs to be inverted by using meteorological data to infer surface conductance.

[6] In this paper we propose a different method, that is the usage of tower flux data and VPD to investigate a proxy of intrinsic water use efficiency at the ecosystem level, which we call “inherent water use efficiency” ($IWUE^*$). Section 2 explains in detail differences between the definitions of water use efficiency (Table 1) at the leaf level and at the ecosystem level.

[7] The aims of this study are to examine if the intrinsic link between carbon and water fluxes through stomatal conductance exists at the ecosystem level for a global cross section of plant functional types and climate regimes, and to analyze and predict among-site variability of mean annual $IWUE^*$ for different ecosystems. The recent increase in

availability of flux data around the globe has allowed us to expand the analysis to more locations and environmental conditions. Our objectives are (1) to generate new hypotheses about long-term adaptation of plant physiology to environmental conditions and (2) to develop empirical models that can be applied globally to derive spatial patterns of mean $IWUE^*$ of ecosystems [cf. Beer *et al.*, 2007]. Such spatial details of $IWUE^*$ will enable a novel and important evaluation of process-based terrestrial ecosystem models. They will also allow for a data-driven scaling of GPP from the ecosystem level to the globe.

2. Methods

2.1. Intrinsic Link Between Carbon and Water Fluxes in Vascular Plants

[8] Under steady state environmental conditions, the rate of carbon assimilation (A) equals the rate of diffusion of CO_2 molecules into the leaf, and the rate of transpiration (E) equals the rate of diffusion of H_2O molecules out of the leaf [Lambers *et al.*, 1998]. A and E thus can be described following Fick [1855]:

$$A = D_{CO_2} \cdot a \cdot \frac{c_a - c_i}{p_a} \quad (1)$$

$$= g \cdot \frac{c_a - c_i}{p_a} \quad (2)$$

$$E = D_{H_2O} \cdot a \cdot \frac{e_i - e_a}{p_a} \quad (3)$$

$$= 1.6 \cdot g \cdot \frac{e_i - e_a}{p_a} \quad (4)$$

[9] Here, D_{CO_2} and D_{H_2O} denote to the diffusion coefficients of carbon dioxide and water vapor, respectively. a is the cross-sectional area of the stomata, p_a the atmospheric pressure, $c_a - c_i$ the difference between ambient and inner-leaf partial pressure of carbon dioxide, and $e_i - e_a$ the related water vapor pressure difference. $g = D_{CO_2} \cdot a$ is stomatal conductance. The factor 1.6 arises because lighter H_2O molecules diffuse more rapidly than does CO_2 . At the leaf level, the intrinsic water use efficiency

$$WUE_i = \frac{A}{g} = \frac{c_a - c_i}{p_a} = \frac{c_a}{p_a} \cdot \left(1 - \frac{c_i}{c_a}\right) \quad (5)$$

is used to express the performance of a particular c_i or a particular c_i/c_a by the plant under given environmental conditions [Wong *et al.*, 1979; Katul *et al.*, 2000].

[10] At the ecosystem level, a measure analogous to WUE_i is $WUE^*_i = GPP/G_s$ (cf. Table 1) with G_s being surface conductance derived from meteorological variables and the latent energy flux by inverting the Penman-Monteith equation. Such an approach, however, made it difficult to extrapolate GPP to whole watersheds as performed by Beer *et al.* [2007], because of the large number of variables required. Hence, in this paper, we use an alternative representation of intrinsic water use efficiency (1) by approximating the vapor pressure difference $e_i - e_a$ by atmospheric vapor pressure deficit (VPD) under the assumption of equal temperatures of leaves and atmosphere, (2) by neglecting aerodynamic resistance through the boundary layer, and (3) by approximating carbon assimilation A and transpiration E by GPP and ET inferred from flux tower observations of NEE and latent energy during dry days (cf. section 2.3).

[11] With these assumptions, equation (4) can be resolved to g^* as

$$g^* = \frac{ET \cdot p_a}{1.6 \cdot VPD}. \quad (6)$$

[12] The introduction of this equation into equation (2) leads to an ecosystem-level representation of WUE_i alternative to WUE^*_i , which we call inherent water use efficiency (IWUE*):

$$IWUE^* = \frac{GPP \cdot VPD}{ET} = \frac{c_a^* - c_i^*}{1.6} [\text{hPa}]. \quad (7)$$

[13] The usage of the star marker indicates that $IWUE^*$ is based on measures at the ecosystem level. Both WUE_i and $IWUE^*$ describe the status of c_i but at different spatial scales, leaf, and ecosystem. High c_i of a specific leaf will be expressed by low WUE_i under constant c_a and p_a (equation (5)). In equation (7) c^*_i represents a weighted average through the canopy and within the tower footprint. If this value increases everywhere under constant c_a , $IWUE^*$ will be low, independent of p_a . However, changing of this weighting of c_i values within the canopy will also influence $IWUE^*$.

2.2. Water Use Efficiency as a Ratio of Time-Integrated Quantities

[14] WUE is defined by the ratio between carbon assimilation and transpiration, both integrated over a certain time period [Farquhar *et al.*, 1982]. This quantity equals the slope of the linear function $A = f(E)$ because this function theoretically passes the (0, 0) point. Both quantities, however, are not directly measurable by means of the eddy covariance technique. Therefore, surrogates like $\frac{dNEE}{dET}$ or $\frac{dGPP}{dET}$ under a constant $e_i - e_a > 0$ have been used at the ecosystem level [Baldochi *et al.*, 2001; Law *et al.*, 2002; Kuglitsch *et al.*, 2008], because changing NEE or GPP as a function of changing ET is mainly determined by WUE. For the few purposes of the discussion in section 3.1, we will therefore present the slope of the regression line in addition

to the ratio of integrals. Otherwise, WUE , WUE^* , WUE_i , WUE^*_i , and $IWUE^*$ are always defined by quantities that are integrated or averaged over time (Table 1). For the analysis of spatial variability, $IWUE^*$ is first calculated annually and then averaged over the years of measurement at each site.

2.3. Flux Data Processing

[15] Common data processing was performed to derive daily carbon dioxide and water vapor fluxes from half-hourly measurements. The storage component of the carbon flux is corrected and spikes are removed according to Papale *et al.* [2006]. Days with low turbulent mixing are filtered out using a threshold for friction velocity following Reichstein *et al.* [2005]. Daily data are only used if 100% of the respective half-hourly data were original or gap-filled with high confidence according to Reichstein *et al.* [2005].

[16] $IWUE^*$ will represent different temporal resolutions in the following depending on the underlying timescale of interest, either on a daily scale using daily sums of GPP and ET, and mean daylight VPD, or on an annual scale integrating GPP and ET, and averaging daylight VPD using the data from available days within the growing season.

[17] To focus the analysis on transpiration rather than bare soil evaporation and interception of the measured total evapotranspiration, data from rainy days as well as the two subsequent, postrainfall days were excluded from the analysis. This is based on the informed assumption that interception storage is largely depleted within 2 days following rain events [Grelle *et al.*, 1997], and that the contribution of soil evaporation declines relatively rapidly following rain events.

[18] GPP represents carboxylation rate minus photorespiration in this study. At night, NEE consists of all respiratory processes except photorespiration. Accounting for the temperature sensitivity of this respiration component results in the equivalent respiration during the day which is further subtracted from daytime NEE to derive GPP [Reichstein *et al.*, 2005].

[19] A description of the 43 sites used in this study can be found in Table 2. The sites are distributed throughout the globe with highest density in Europe and lowest density in the Southern Hemisphere. The sites cover a large climatic range with mean annual air temperatures between 0 and 25°C and annual precipitation from 440 to 3300 mm (Figure 1). The main limitation to the usage of flux sites was the availability of ancillary data describing the state of the ecosystem (see section 2.4).

2.4. Ancillary Data

[20] In addition to micrometeorological and meteorological data, we used biological and ancillary data, such as maximum leaf area index (LAI) and volumetric soil water content at field capacity (Θ).

[21] LAI is used to estimate maximum canopy light interception (Foliage Projective Cover, FPC),

$$FPC = 1 - \exp(-k \cdot LAI), \quad (8)$$

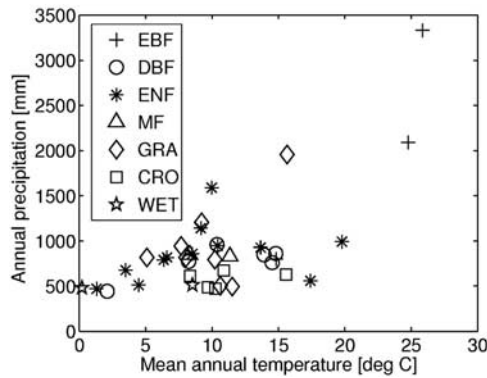


Figure 1. Distribution of considered flux tower sites in the temperature-precipitation space. See Table 2 and references therein for a description of site characteristics and abbreviations of vegetation types.

according to the Lambert-Beer Law [Bouguer, 1729], where k is assumed to be 0.7 for deciduous broad-leaved forests, 0.5 for evergreen needle-leaved forests, and 0.4 for herbs [Monsi and Saeki, 1953; Lambers et al., 1998]. Θ is derived following Cosby et al. [1984] by statistical relationships to the amount of sand, silt and clay as measured at the sites.

3. Results and Discussion

3.1. $GPP \cdot VPD$ Relations to ET at the Ecosystem Scale

[22] Figures 2 to 6 show typical relations between GPP and ET, and between the product $GPP \cdot VPD$ and ET for different ecosystems. In general, the relation between GPP and ET is not as strong as the relation between $GPP \cdot VPD$ and ET because in the latter case the nonlinear effect of VPD on ET is taken into account (section 2.1). The consideration of VPD improves the correlation coefficient not only for selective site years but also for the majority of site years (cf. histograms in Figure S1¹). These results demonstrate that the intrinsic link between carbon and water fluxes through stomatal conductance (section 2.1) also exists at the ecosystem level and on an annual timescale. Random error in the data is responsible for a large part of the remaining scatter in the relationship between $GPP \cdot VPD$ and ET. In addition, VPD has often been used as a surrogate for water availability [e.g., Running et al., 2004], but VPD and soil water content do not necessarily covary, so some of the scatter may be due to VPD's poor representation of water availability. Other possible influences on IWUE* include the effect of temperature on the carboxylation rate [Larcher, 1969; Farquhar et al., 1980].

[23] ET alone is capable of predicting $GPP \cdot VPD$ independent of global radiation (R_g), indicated by the color scale in Figures 2 and 3. This predictive capability of ET is also independent of air temperature (cf. color scale of Figure 4). In general, photosynthesis is limited by availability of radiation, water, nutrients, and temperature and

vapor pressure deficit. When radiation is not limiting and water deficits exist, canopy conductance is adjusted to balance atmospheric demand with rates of water uptake and supply from soils, resulting in a decrease in GPP. On the other hand, deficits in radiation, temperature or nutrient supply that cause a decrease in GPP will lead to lower canopy conductance and ET.

[24] The crossings of the axes by the regression line in Figures 2 and 3 tell us more about plant functioning at extreme environmental conditions. When VPD is very low (humidity high), transpiration is similarly low, regardless of GPP. This explains the positive crossing of the ordinate by the regression line on the left. However, while taking into account the VPD effect (right panel), $GPP \cdot VPD$ will be close to zero in these cases, and only the bare soil evaporation component of ET leads to a positive crossing of the abscissa (negative crossing of the ordinate) by the regression line.

[25] Interestingly, $GPP \cdot VPD$ relates to ET more non-linearly for grasslands (Figures 2 and 4). Figure 4 shows that increasing air temperature (color scale) leads to increasing GPP relative to $\frac{ET}{VPD}$ independent of global radiation (Figure 2, color scale). A likely explanation is that high decoupling of canopies from the atmosphere in herbaceous ecosystems [Jarvis and McNaughton, 1986] makes the approximation $e_i - e_a = VPD$ invalid; it leads to lower transpiration (higher e_a) than would be expected from the VPD values measured in the atmosphere.

[26] An extreme drought was experienced in Europe in the summer of 2003, and two of our sites showed different responses of WUE* and IWUE* to the drought. Annual integral WUE* (ratio) was slightly lower in 2003 at the deciduous broadleaved forest (DE-Hai; Figure 5) compared to average conditions in 2001 (left panel). However, this was not observed in the evergreen needle-leaved forest (DE-Tha; Figure 6, left). GPP values on days with very low soil water content in August (cf. color scale and number of month) are not significantly higher than GPP values on days with the same ET but higher soil water content (cf. isolines in Figures 5 and 6, left). We thus conclude that there is not a clear single effect of drought on WUE* on short to medium timescales.

[27] In contrast to WUE*, IWUE* on an annual timescale increases significantly in 2003 (Figures 5 and 6, right). Also, $GPP \cdot VPD$ on days with low soil water content in August is higher than the average for the respective ET under normal soil moisture conditions. Hence, increasing IWUE* during drought periods is observed consistently on daily to annual timescales. These analyses show that the quite conservative (only slightly decreasing) WUE* at DE-Hai reported by Reichstein et al. [2007] can be explained by the increase in IWUE*, which partly counteracts the detrimental effect of increased VPD.

[28] Annual IWUE* results for each site year show that year-to-year variability of IWUE* is about 1.5 (Tables S1 and S2; ratio of maximum and minimum IWUE*). This finding is in agreement with the analyses of GPP as a function of G_s for a Siberian Scots pine forest by Lloyd et al. [2002] and for a Mopane woodland in southern Africa by Arneeth et al. [2006].

¹Auxiliary materials are available in the HTML. doi:10.1029/2008GB003233.

Table 2. Characteristics of Flux Tower Sites Used in This Study^a

	Lat	Long	ID	Veg	LAI	Soil	WUE*	IWUE*	Reference
1	47.12	11.32	AT-Neu	GRA	6.5	0	3.79	25.94	Wohlfahrt et al. [2008a]
2	51.31	4.52	BE-Bra	MF	3	3	3.99	26.71	Carrara et al. [2004]
3	50.55	4.74	BE-Lon	CRO	5.3	0	2.83	17.35	Moureaux et al. [2006]
4	50.31	6	BE-Vie	MF	5.1	5	5.08	33.91	Aubinet et al. [2002]
5	-2.61	-60.21	BR-Ma2	EBF	4.7	6	2.82	29.6	n.a.
6	49.87	-125.29	CA-Ca2	ENF	2.2	3	3.06	24.26	Humphreys et al. [2005]
7	49.53	-124.90	CA-Ca3	ENF	3	1	3.53	19.65	Jassal et al. [2008]
8	53.63	-106.2	CA-Oas	DBF	2.1	10	3.41	28.18	Krishnan et al. [2006]
9	54	-105.12	CA-Obs	ENF	3.8	1	3.05	21.77	Krishnan et al. [2008]
10	47.29	7.7	CH-Oe1	GRA	4.85	0	2.86	17.88	Ammann et al. [2007]
11	31.52	122	CN-Do1	GRA	5.13	0	2.62	19.15	Wu et al. [2005]
12	51.10	10.91	DE-Geb	CRO	4	0	4.02	27.39	Anthoni et al. [2004b]
13	50.95	13.51	DE-Gri	GRA	4.8	0	4.35	31.17	Gilmanov et al. [2007]
14	51.08	10.45	DE-Hai	DBF	6	10	5.31	29.37	Knohl et al. [2003; Kutsch et al., 2008]
15	50.89	13.52	DE-Kli	CRO	9.7	0	3.58	25.01	n.a.
16	50.96	13.57	DE-Tha	ENF	7.6	5	4.55	32.4	Grünwald and Bernhofer [2007]
17	50.45	11.46	DE-Wet	ENF	4.75	1	5.42	26.17	Anthoni et al. [2004a]
18	39.35	-0.32	ES-ES1	ENF	2.63	3	2.77	20.27	Sanz et al. [2004]
19	61.85	24.3	FI-Hyy	ENF	2.1	3	3.61	22.68	Suni et al. [2003]
20	69.14	27.3	FI-Kaa	WET	0.7	0	1.23	4.58	Aurela et al. [2004]
21	67.36	26.64	FI-Sod	ENF	1.2	2	2.82	15.6	Thum et al. [2007]
22	48.67	7.07	FR-Hes	DBF	7.6	8	4.51	42.71	Granier et al. [2000]
23	44.71	-0.77	FR-LBr	ENF	4.8	2	2.63	29.47	Berbigier et al. [2001]
24	45.64	2.74	FR-Lq1	GRA	3	0	2.75	18.79	Allard et al. [2007]
25	45.64	2.74	FR-Lq2	GRA	3	0	2.42	16.36	Allard et al. [2007]
26	43.74	3.63	FR-Pue	EBF	2.9	7	3.14	30.61	Rambal et al. [2003]
27	46.69	19.60	HU-Bug	GRA	2.5	0	2.1	19.53	Nagy et al. [2007]
28	47.84	19.73	HU-Mat	CRO	4	0	2.32	17.05	Nagy et al. [2007]
29	41.90	13.61	IT-Amp	GRA	2	0	3.16	21.45	Wohlfahrt et al. [2008b]
30	41.85	13.59	IT-Col	DBF	5	8	6.07	43.39	Valentini et al. [1996]
31	41.70	12.38	IT-Cpz	EBF	3.5	2	3.51	30.61	Tirone et al. [2003]
32	46.01	11.05	IT-MBo	GRA	2.88	0	3	13.99	n.a.
33	44.69	11.09	IT-Non	DBF	1.7	11	3.15	36.56	n.a.
34	45.20	9.06	IT-PT1	DBF	3.5	1	2.98	27.91	n.a.
35	42.39	11.92	IT-Ro2	DBF	3.9	7	3.54	41.54	Tedeschi et al. [2006]
36	51.97	4.93	NL-Ca1	GRA	11	0	2.29	20.58	Jacobs et al. [2007]
37	52.17	5.74	NL-Loo	ENF	2.2	2	3.77	19.77	Dolman et al. [2002]
38	52.76	16.31	PL-Wet	WET	2.5	0	1.73	12.24	n.a.
39	64.11	19.46	SE-Fla	ENF	3.4	1	2.66	17.88	Lindroth et al. [2007]
40	36.61	-97.49	US-ARM	CRO	2.05	0	1.57	18.76	Fischer et al. [2007]
41	45.20	-68.74	US-Ho1	ENF	5.7	1	3.98	34.5	Hollinger et al. [2004]
42	29.75	-82.16	US-SP3	ENF	1.94	2	2.35	22.08	Clark et al. [2004]
43	-15.44	167.19	VU-Coc	EBF	5.65	10	3.17	30.33	Roupsard et al. [2006]

^aThe number in the first column is used in Figures 7 and 8 to indicate the sites. The station ID consists of two characters describing the country and 3 characters as abbreviation for the site name (cf. <http://www.fluxnet.ornl.gov/fluxnet/index.cfm>). Also shown are coordinates, vegetation class (EBF = evergreen broad-leaved forest, DBF = deciduous broad-leaved forest, ENF = evergreen needle-leaved forest, MF = mixed forest, GRA = grassland, CRO = cropland, WET = wetland), maximum leaf area index, soil texture type for forests according to [Cosby et al., 1984] (otherwise 0), mean WUE* [g C/kg H₂O], mean IWUE* [g C · hPa/kg H₂O], and a reference to site characteristics.

3.2. Among-Site Variability of Water Use Efficiency

[29] Annual IWUE* varies by a factor of about three among forests and herbaceous ecosystems (ordinates in Figures 7 and 8). Although IWUE* is higher for deciduous broad-leaved forests than evergreen needle-leaved forests (Figure 7; see also regression coefficients in equations (10) and (11)), dominant plant functional types are not sufficient to explain all of this high variation. For example, there are large differences in IWUE* among the sites SE-Fla, DE-Wet, and DE-Tha which all are dominated by Norway spruce.

[30] IWUE* is correlated with volumetric soil water content at field capacity (Θ) and FPC (Figure 7). The relation between IWUE* and maximum LAI is a half-saturation type function and after linearization to FPC (section 2.4), a bivariate regression to both Θ and FPC

results in a coefficient of determination of 0.6. The respective linear equation is estimated to

$$IWUE^* = 25.4 \cdot \Theta + 25 \cdot FPC$$

$$(R^2 = 0.56, p < 0.001, N = 26). \quad (9)$$

[31] This linear equation is assumed to pass the (0, 0) point because GPP has to be zero without any light absorption or water-holding capacity. The respective linear equations for deciduous broad-leaved forests (equation (10)) and for evergreen needle-leaved forests alone (equation (11)) are, however, estimated to

$$IWUE^* = 55.2 \cdot \Theta + 15 \cdot FPC$$

$$(R^2 = 0.37, p = 0.24, N = 7) \quad (10)$$

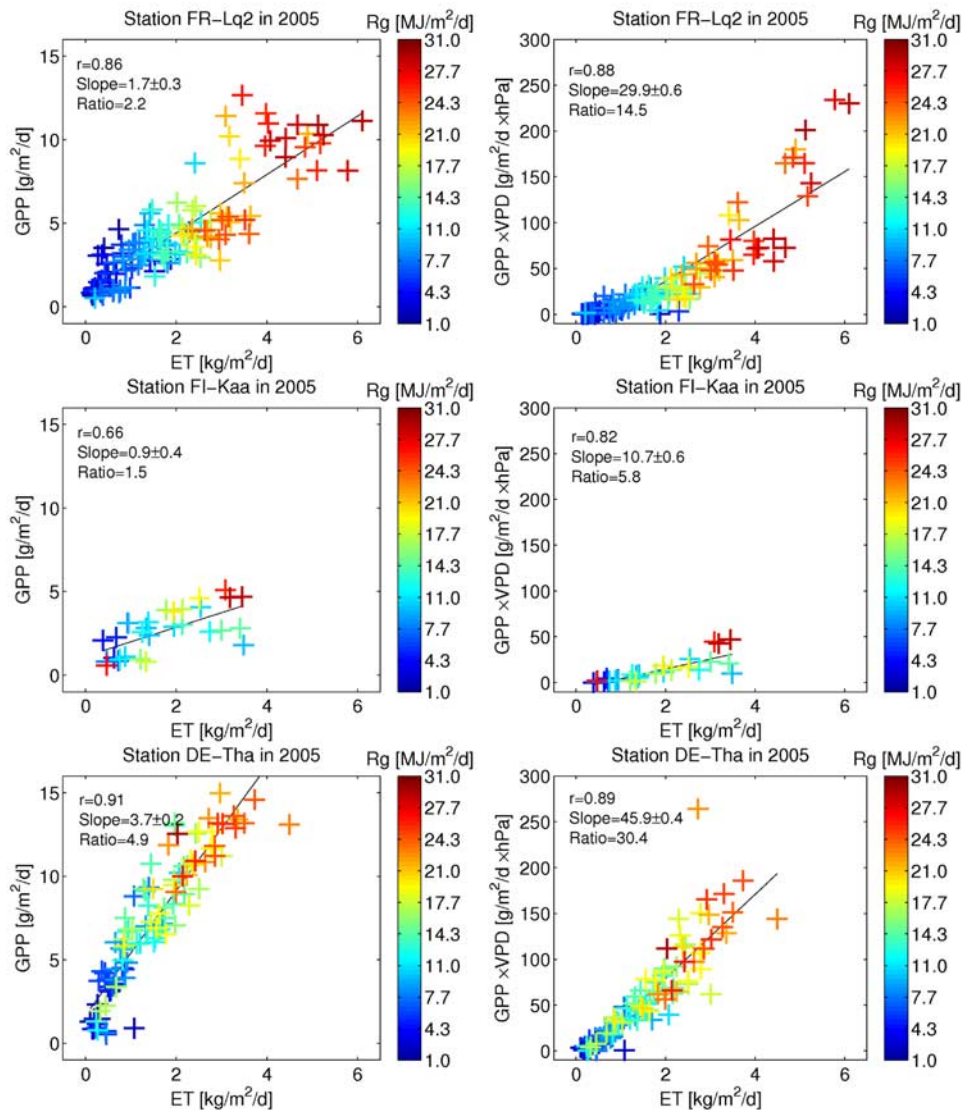


Figure 2. Relationship between (left) GPP and ET and between (right) GPP · VPD and ET for a grassland site (FR-Lq2), a wetland site (FI-Kaa), and an evergreen needle-leaved forest site (DE-Tha) on a daily basis. Also shown is the correlation coefficient, the slope of the linear fit between these variables, the ratio of annual sums (GPP, ET) or means (daylight VPD) according to equation (7), and the global radiation on the color scale. The p values of all regressions are below the 0.1% significance level. More sites are shown in Figure 3.

$$IWUE^* = -10.2 \cdot \Theta + 33.7 \cdot FPC$$

$$(R^2 = 0.57, p < 0.002, N = 13). \quad (11)$$

The differences in the regression coefficients indicate a strong correlation of $IWUE^*$ to FPC for evergreen needle-leaved forests and a strong effect of Θ on $IWUE^*$ for deciduous broad-leaved forests. Herbaceous ecosystems (C_3) also show the half-saturation relationship to LAI (Figure 8), i.e., the linear relationship to FPC, and interestingly, the coefficient (25.6) is similar to that of all forests (25, equation (9)).

[32] The right panels of Figures 7 and 8 show the validation of the regression models applying for all data points the

highest subset of the data set without the point under consideration (leave-one-out method). The RMSE for both models are only about 5 g C/kg H₂O · hPa.

3.3. Overall Discussion

[33] The concept of intrinsic water use efficiency, meaning carbon assimilation per unit stomatal conductance, is useful for characterizing different physiological responses of plant functional types to environmental changes. Because carbon assimilation is proportional to GPP (dark respiration being the difference), measurements of carbon and water fluxes by means of the eddy covariance technique can be used to approximate intrinsic water use efficiency at the ecosystem level (inherent water use efficiency, $IWUE^*$).

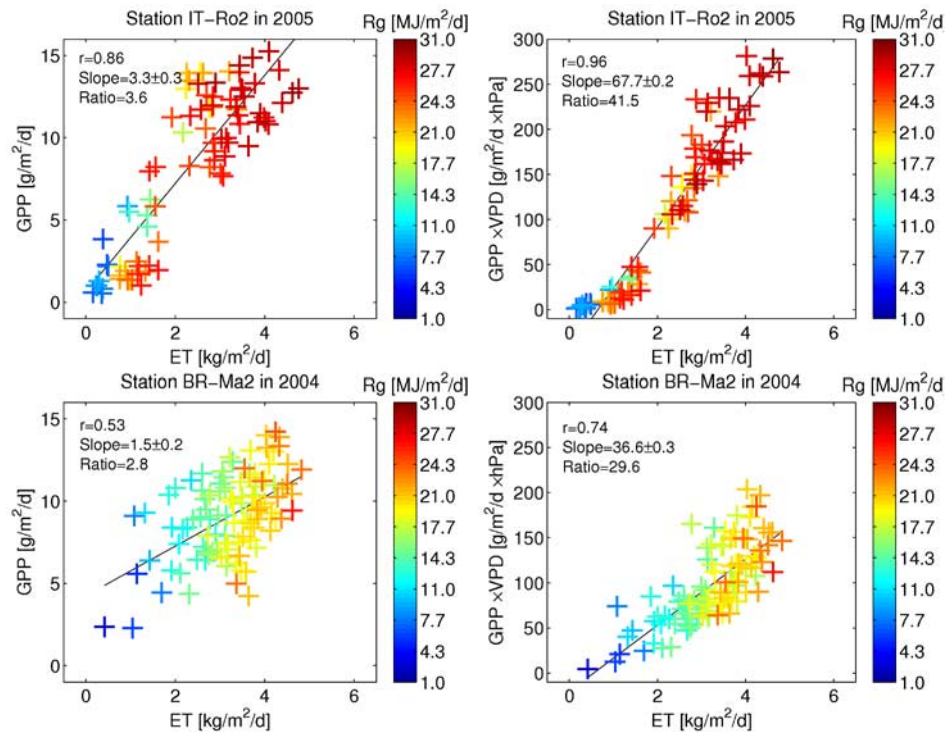


Figure 3. Same as Figure 2 but for a deciduous broad-leaved forest site (IT-Ro2) and an evergreen broad-leaved forest site (BR-Ma2) on a daily basis.

[34] In this study, $IWUE^*$ was computed as the product of GPP (derived from NEE partitioning) and VPD divided by ET (derived from latent heat measurements). In doing so, $\frac{ET}{VPD}$ is a proxy for canopy conductance if the canopy is well coupled to the atmosphere, boundary layer resistance is small, and leaf temperature is similar to air temperature. Herbaceous canopies, however, are more decoupled from the atmosphere than forests [Jarvis and McNaughton, 1986], thus possibly $VPD > e_i - e_a$. Hence, $IWUE^*$ could be overestimated for grasslands and croplands. On the other hand, higher leaf than air temperatures would lead to higher e_i within the canopy, thus possibly $VPD < e_i - e_a$ while e_a remains constant, leading to potential underestimation of

$IWUE^*$ for herbaceous ecosystems. The bias introduced by the approximation of $VPD \approx e_i - e_a$ is unlikely to be responsible for the correlations between mean annual $IWUE^*$ and LAI or Θ .

[35] In section 2.1, we suggested that latent heat flux from the eddy covariance technique could be used in conjunction with meteorological measurements to derive surface conductance (G_s) by the Penman-Monteith equation [e.g., Irvine *et al.*, 2004] for calculation of WUE^*_i as GPP/G_s . This approach was not applied in this study because our aim was to derive as simple as possible a representation of intrinsic water use efficiency for future extrapolation of GPP according to Beer *et al.* [2007]. By using the ratio of annual

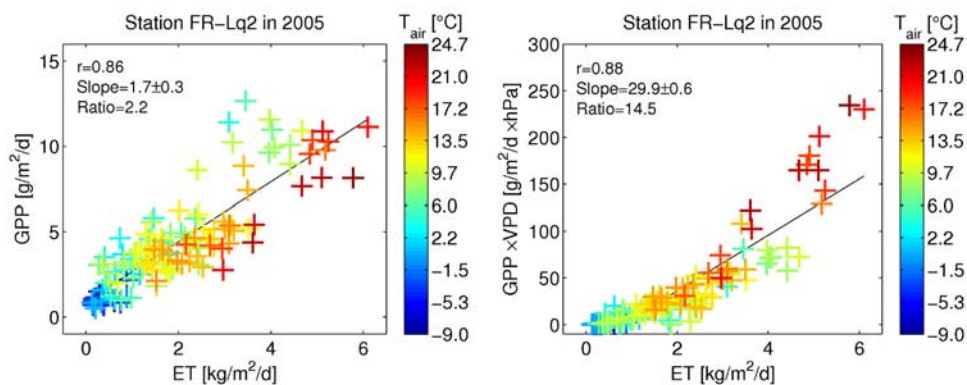


Figure 4. Same relationships as in Figure 2 for a grassland site (FR-Lq2) but with air temperature on the color scale. The p values of both regressions are below the 0.1% significance level.

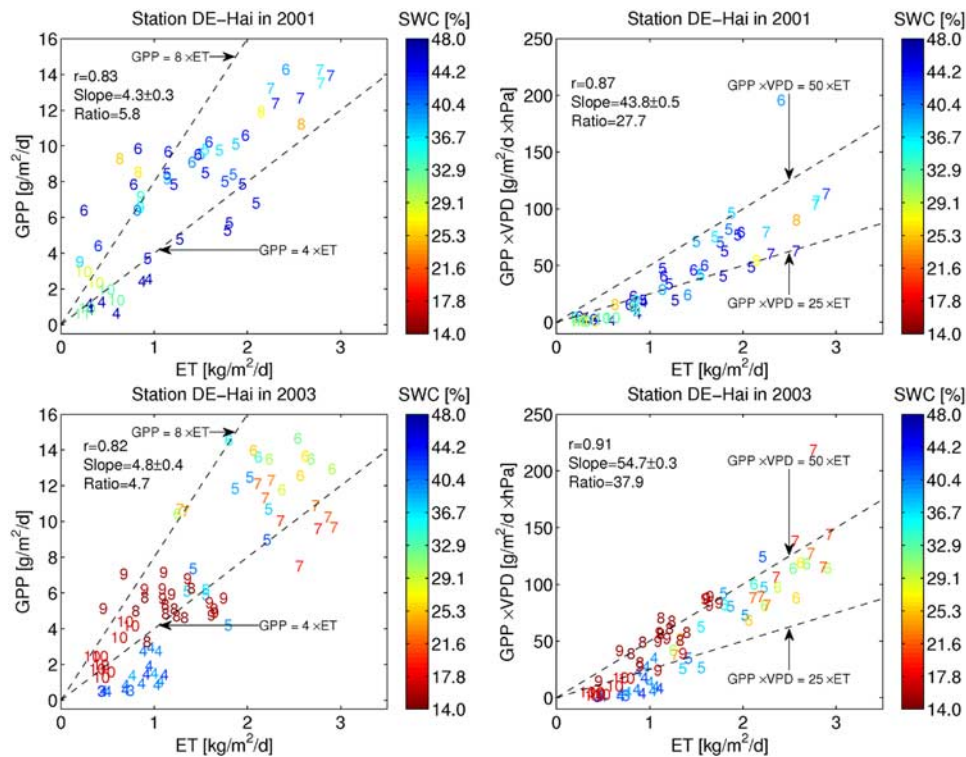


Figure 5. Relationship between (left) GPP and ET and between (right) GPP · VPD and ET for a temperate deciduous broad-leaved forest located in eastern Germany on a daily basis in 2001 (average conditions) and 2003 (extreme drought in August). Also shown is the correlation coefficient, the slope of the linear fit between these variables, the ratio of annual sums (GPP, ET) or means (daylight VPD) according to equation (7), volumetric soil water content of the upper 20 cm on the color scale, and the month of the observations. The p values of all regressions are below the 0.1% significance level.

GPP and $g_{s,i}$, however, the main findings of this study do not change, and, more importantly correlation coefficients do not improve (data not shown).

[36] Latent energy measured at flux towers comprises three sources of water flux, interception, bare soil evaporation, and transpiration. In this study, our sole interest is transpiration. Therefore, we only use data during days without rainfall if the two previous days were also rain-free. In doing so, we greatly reduce the nontranspiration flux with the exception of wetlands where soil evaporation will still be significant. Hence, IWUE* of wetlands presented in Figure 8 are expected to be systematically too low. On the other hand, ET is dominated by transpiration in dense forests.

[37] WUE_i is a conservative variable in the sense that it varies only slightly under constant environmental conditions and for a specific plant [Schulze and Hall, 1982].

[38] At the ecosystem level, however, LAI influences IWUE*. Canopy closure at high LAIs reduces the amount of radiation reaching the ground and thus reduces soil evaporation. In addition, it leads to higher radiation use efficiency at the ecosystem level because it sets the upper limit to photosynthesis and allows a more efficient optimization of nutrients and enzymes within the canopy.

[39] Photosynthetic capacity and stomatal conductance respond differently to leaf water potential which causes a hysteresis in the sense that after surviving a drought period,

photosynthesis increases more than stomatal conductance [Schulze and Hall, 1982; Gallé and Feller, 2007]. This leads to increased WUE_i on monthly to annual timescales. The insight from leaf-level experiments is reproduced at the ecosystem level through an analysis of daily IWUE* (Figures 5 and 6) which is also in agreement with inferences from carbon isotope discrimination [Fessenden and Ehleringer, 2003; Lai et al., 2005; Ponton et al., 2006].

[40] Replacing time with space, the correlation of mean annual IWUE* to volumetric soil water content at field capacity (Θ) found in this study leads to the hypothesis that other processes at the ecosystem level override the short-term response of IWUE*. For instance, maximum CO₂ assimilation as a function of canopy conductance was found to saturate earlier after plants experienced a drought [Schulze and Hall, 1982]. This memory effect could be responsible for an impact of the frequency of drought events on average IWUE*. It would be interesting to study species-dependent differences of such saturation points. Does maximum CO₂ assimilation as a function of canopy conductance saturate earlier for *Pinus* than for *Picea* trees? To test this hypothesis, we would require much longer time series of observations in which several severe drought events are recorded.

[41] The observation of a higher correlation between IWUE* and Θ for deciduous forests leads to the hypothesis

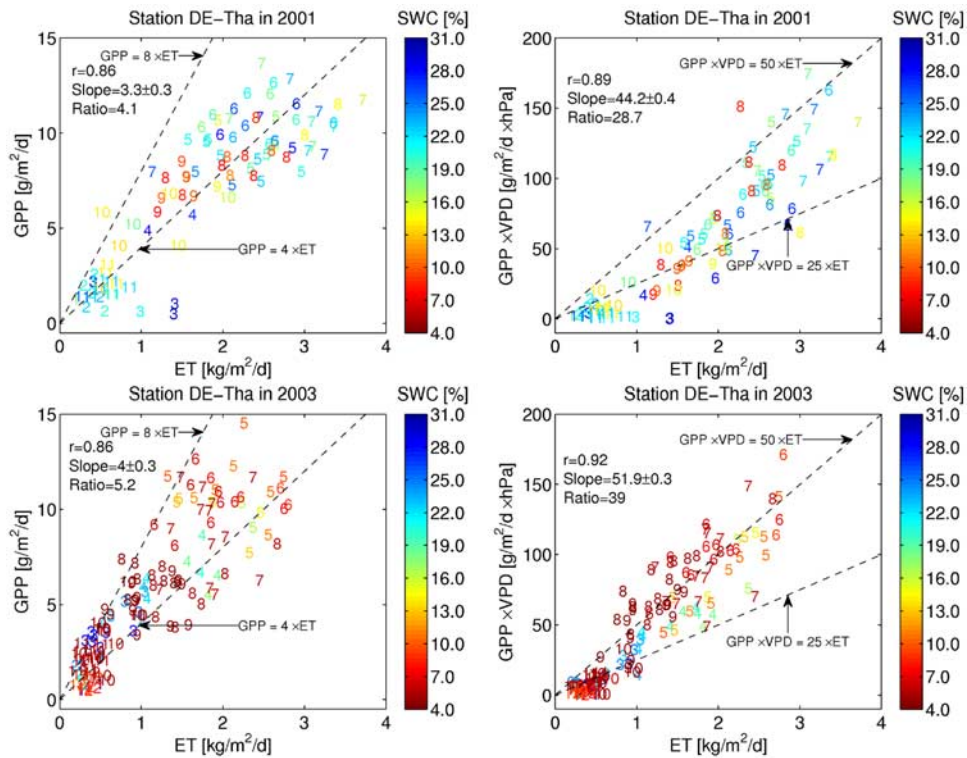


Figure 6. Same as Figure 5 but for a temperate evergreen needle-leaved forest located in eastern Germany. The p values of both regressions are below the 0.1% significance level.

that soil water availability affects phenology and LAI, which strongly influences transpiration and GPP.

[42] The empirical correlation between IWUE* and Θ does not necessarily prove a relationship with soil moisture, i.e., a potential long-term decrease in IWUE* with increasing drought events. Soil texture, used here to derive Θ , may determine the nitrogen mineralization rate thus nutrient availability of plants. Nutrient limitation of GPP may partly

explain low IWUE* values at sites with low clay content. This hypothesis could be proven by including information on leaf and soil nitrogen content in the multivariate regression in section 3.2.

[43] It is important to note that the relationship between IWUE* and Θ found in this analysis exists independent of any LAI effect (multivariate regression), particularly for deciduous broad-leaved forests (cf. equations (10) and (11)).

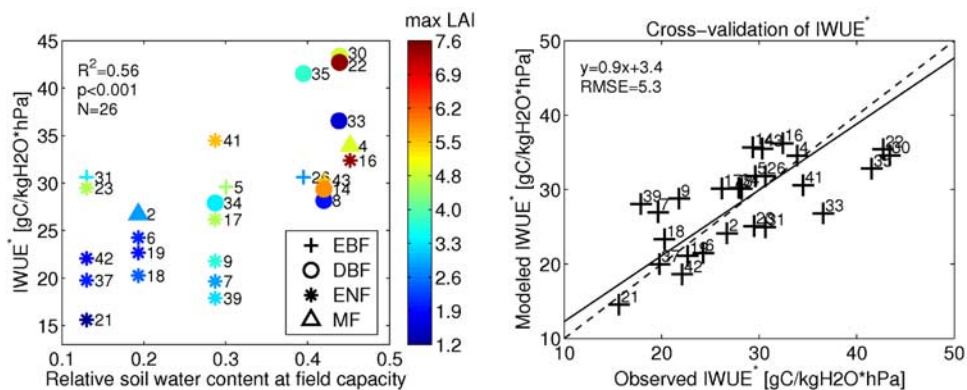


Figure 7. (left) IWUE* following equation (7) as a function of soil moisture at field capacity at forest sites (1996–2006 average). Color scheme shows the maximum LAI at the sites. See Table 2 and references therein for a description of site characteristics and vegetation types. (right) Validation of the bivariate linear regression $IWUE^* = f(\Theta, FPC)$ by leaving one out each time. Shown is the root mean square difference and the regression between observed and modeled values. The regression line (solid) is compared to the 1:1 line (dashed).

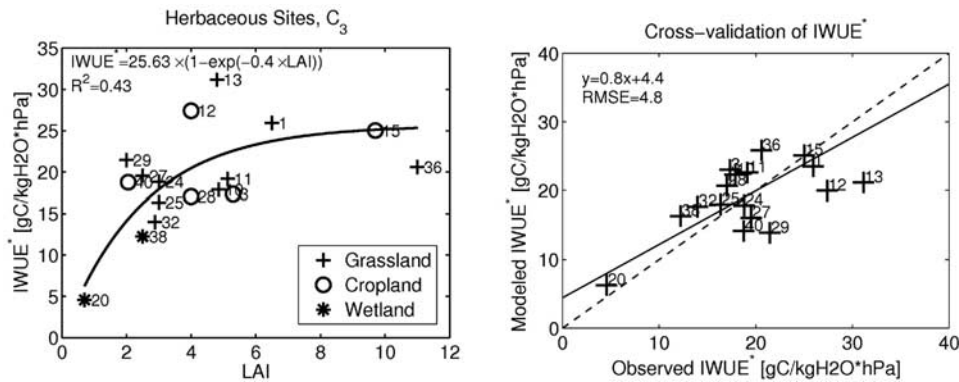


Figure 8. (left) IWUE* as a function of maximum LAI for C3 herbaceous ecosystems. See Table 2 and references therein for a description of site characteristics. (right) Validation of the nonlinear model $IWUE^* = f(LAI)$ by leaving one out each time. Shown is the root mean square difference and the regression between observed and modeled values. The regression line (solid) is compared to the 1:1 line (dashed).

This means that the additional effect of soil water status on allocation patterns and hence LAI [Grier and Running, 1977] is already taken into account. However, the effect of drought on IWUE* via allocation patterns can become important with respect to future climate change. Therefore, mechanistic models of canopy photosynthesis [e.g., Baldocchi and Bowling, 2003; Ogeé et al., 2003] possibly coupled to biogeography models are required to quantify changes in the coupling of terrestrial carbon and water fluxes under changing environmental conditions.

[44] To predict long-term effects of climate change on the terrestrial carbon balance, dynamic global vegetation models of biogeography and biogeochemistry are used to estimate transient plant functional types and their associated carbon and water budgets [Prentice et al., 2007]. Water use efficiency is one way to ensure appropriate coupling of carbon dioxide and water vapor exchange in such models, if water use efficiency can be mapped or estimated via correlation with easily measured environmental variables. Equations (9) to (11) provide a possibility for this purpose. They allow the spatial extrapolation of IWUE* by using gridded LAI and soil texture data. In a next step, spatial details of WUE* can be derived by applying gridded VPD data.

[45] The analysis here dealt with several sources of uncertainties, such as (1) definition of LAI and related measurement practices, (2) classification of soil texture type for later deduction of field capacity, (3) possible missing energy closure due to underestimation of latent energy, (4) possible bias in extrapolating dark respiration during night to dark respiration during the day for GPP inference, and (5) inclusion of bare soil evaporation in measured ET.

[46] Regarding the flux data, we were able to use a standardized data processing scheme and a large number of sites thanks to the FLUXNET project. Therefore, we expect little impact of these uncertainties on the overall findings. However, in forests the additional estimation of transpiration by sapflow measurements [Granier, 1987] would allow investigating the uncertainty related to the water balance [e.g., Reichstein et al., 2002; Irvine et al., 2004]. GPP uncertainty due to the flux partitioning method

was found to be low [Desai et al., 2008]. More critically, we expect high uncertainties in state variables such as LAI and percent clay and silt. First, definitions may be non-standardized, e.g., LAI measurements are sometimes adjusted by a clumping coefficient [e.g., Law et al., 2001], or effects of branches on the measurements are not taken into account. Second, measurements of these state variables may not be representative of the tower footprint [Göckede et al., 2007].

4. Conclusions

[47] The observation of carbon and water exchanges between a terrestrial ecosystem and the atmosphere by means of the eddy covariance technique is suited to derive proxies of intrinsic water use efficiency at the ecosystem and various timescales (inherent water use efficiency, IWUE*). $\frac{ET}{VPD}$ is a hydrological measure that approximates surface conductance at the ecosystem level. It reliably explains GPP at the ecosystem level independent of temperature or the amount of global radiation. IWUE* increased during a short-term drought period. In contrast, among-site variability of mean IWUE* was proportional to soil moisture at field capacity in forests independent of the half-saturating relationship to LAI, with differences between evergreen needle-leaved and deciduous broad-leaved forests. In herbaceous ecosystems, we only observed a correlation between IWUE* and LAI.

[48] These empirical findings indicate that different mechanisms are important for the ecosystem response to drought on different temporal scales. Rapid increases in IWUE* could be overridden on annual to decadal timescales. Decreasing soil moisture could lead to decreasing LAI through changing allocation patterns or decreasing maximum CO₂ assimilation as a function of canopy conductance. The consequence would be a decreasing IWUE*. In addition, the resulting increase of soil evaporation or runoff relative to transpiration potentially further decreased soil water availability to plants thus accelerating the effects on LAI and maximum CO₂ assimilation which would be a positive feedback mechanism.

[49] The empirical relationships to state variables like canopy light interception and soil moisture at field capacity allow an extrapolation of mean IWUE* to the entire land surface by using vegetation indices such as LAI derived from remote sensing observations. Such data-driven spatial details of IWUE* will enable a novel and important evaluation of process-based terrestrial ecosystem models and offers the potential for a diagnostic extrapolation of GPP to entire watersheds.

[50] **Acknowledgments.** This work is the outcome of the La Thuile FLUXNET workshop 2007, which would not have been possible without the financial support provided by CarboEuropeIP, FAO-GTOS-TCO, iLEAPS, Max Planck Institute for Biogeochemistry, National Science Foundation, University of Tuscia, and the U.S. Department of Energy. Moreover, we acknowledge data-basing and technical support from Berkeley Water Center, Lawrence Berkeley National Laboratory, Microsoft Research eScience, Oak Ridge National Laboratory, University of California, Berkeley, and University of Virginia. The following networks participated with flux data: AmeriFlux, AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, ChinaFlux, Fluxnet-Canada, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia, and USCCC. Support came from the Office of Science (BER), U.S. Department of Energy, grant DE-FG02-04ER63911 (AmeriFlux Measurement Network: Science Team Research). Funding for the AT-Neu site was provided by EC FP 5 project CarboMont (EVK2-CT2001-00125). We are grateful to Almut Ameth, Andrew Friend, Martina Mund, Ernst-Detlef Schulze, Stan Schymanski, and Sönke Zaehle for their valuable comments.

References

- Allard, V. (2007), The role of grazing management for the net biome productivity and greenhouse gas budget (CO₂, N₂O and CH₄) of semi-natural grassland, *Agric. Ecosystems Environ.*, *121*, 47–58, doi:10.1016/j.agee.2006.12.005.
- Ammann, C., C. Flechard, J. Leifeld, A. Neftel, and J. Fuhrer (2007), The carbon budget of newly established temperate grassland depends on management intensity, *Agricu. Ecosystems Environ.*, *121*, 5–20.
- Anthoni, P., A. Knohl, C. Rebmann, A. Freibauer, M. Mund, W. Ziegler, O. Kolle, and E. Schulze (2004a), Forest and agricultural land-use-dependent CO₂ exchange in Thuringia, Germany, *Global Change Biol.*, *10*, 2005–2019.
- Anthoni, P. M., M. H. Unsworth, B. E. Law, J. Irvine, D. D. Baldocchi, S. V. Tuyl, and D. Moore (2004b), Winter wheat carbon exchange in Thuringia, Germany, *Agric. For. Meteorol.*, *121*, 55–67.
- Ameth, A., E. M. Veenendaal, C. Best, W. Timmermans, O. Kolle, L. Montagnani, and O. Shibistova (2006), Water use strategies and ecosystem-atmosphere exchange of CO₂ in two highly seasonal environments, *Biogeosciences*, *3*, 421–437.
- Aubinet, M., B. Heinesch, and B. Longdoz (2002), Estimation of the carbon sequestration by a heterogeneous forest: Night flux corrections, heterogeneity of the site and inter-annual variability, *Global Change Biol.*, *8*, 1053–1072.
- Aurela, M., T. Laurila, and J.-P. Tuovinen (2004), The timing of snow melt controls the annual CO₂ balance in a subarctic fen, *Geophys. Res. Lett.*, *31*, L16119, doi:10.1029/2004GL020315.
- Baldocchi, D. D., and D. R. Bowling (2003), Modelling the discrimination of ¹³CO₂ above and within a temperate broad-leaved forest canopy on hourly to seasonal time scales, *Plant Cell Environ.*, *26*, 231–244.
- Baldocchi, D. D., S. B. Verma, and N. J. Rosenberg (1985), Water use efficiency in a soybean field: Influence of plant water stress, *Agric. For. Meteorol.*, *34*, 53–65.
- Baldocchi, D., et al. (2001), FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities, *Bull. Am. Meteorol. Soc.*, *82*(11), 2415–2434.
- Beer, C., M. Reichstein, P. Ciais, G. D. Farquhar, and D. Papale (2007), Mean annual GPP of Europe derived from its water balance, *Geophys. Res. Lett.*, *34*, L05401, doi:10.1029/2006GL029006.
- Berbigier, P., J. M. Bonnefond, and P. Mellmann (2001), CO₂ and water vapour fluxes for 2 years above Euroflux forest site, *Agric. For. Meteorol.*, *108*, 183–197.
- Bierhuizen, J., and R. Slatyer (1965), Effect of atmospheric concentration of water vapor and CO₂ in determining transpiration-photosynthesis relationships of cotton leaves, *Agric. Meteorol.*, *2*, 259–270.
- Bouguer, P. (1729), *Essai d'optique sur la gradation de la lumière*, 164 pp., Claude Jombert, Paris.
- Carrara, A., I. A. Janssens, J. Curiel Yuste, and R. Ceulemans (2004), Seasonal changes in photosynthesis, respiration and NEE of a mixed temperate forest, *Agric. For. Meteorol.*, *126*, 15–31.
- Clark, K., H. Gholz, and M. Castro (2004), Carbon dynamics along a chronosequence of slash pine plantations in north Florida, *Ecol. Appl.*, *14*, 1154–1171.
- Cosby, B. J., G. M. Hornberger, R. B. Clapp, and T. R. Ginn (1984), A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils, *Water Resour. Res.*, *20*(6), 682–690.
- Cowan, I. R., and G. D. Farquhar (1977), Stomatal function in relation to leaf metabolism and environment, in *Integration of Activity in the Higher Plant*, edited by D. H. Jennings, pp. 471–505, Cambridge Univ. Press, Cambridge, U. K.
- Desai, A. R., et al. (2008), Cross-site evaluation of eddy covariance GPP and RE decomposition techniques, *Agric. For. Meteorol.*, *148*(6–7), 821–838.
- Dolman, A. J., E. J. Moors, and J. A. Elbers (2002), The carbon uptake of a mid latitude pine forest growing on sandy soil, *Agric. For. Meteorol.*, *111*, 157–170.
- Farquhar, G. D., S. V. Caemmerer, and J. A. Berry (1980), A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ plants, *Planta*, *149*(1), 78–90.
- Farquhar, G. D., M. H. O'Leary, and J. A. Berry (1982), On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves, *Aust. J. Plant. Physiol.*, *9*, 121–137.
- Fessenden, J. E., and J. R. Ehleringer (2003), Temporal variation in δ¹³C of ecosystem respiration in the Pacific Northwest: Links to moisture stress, *Oecologia*, *136*, 129–136.
- Fick, A. (1855), Ueber diffusion, *Ann. Phys. Chem.*, *94*, 59–86.
- Fischer, M. L., D. Billesbach, W. Riley, J. A. Berry, and M. S. Torn (2007), Spatiotemporal variations in growing season exchanges of CO₂, H₂O, and sensible heat in agricultural fields of the southern Great Plains, *Earth Interact.*, *11*(17), 1–21, doi:10.1175/EI231.1.
- Gallé, A., and U. Feller (2007), Changes of photosynthetic traits in beech saplings (*Fagus sylvatica*) under severe drought stress and during recovery, *Physiol. Plantarum*, *131*, 412–421.
- Gilmanov, T., et al. (2007), Partitioning European grassland net ecosystem CO₂ exchange into gross primary productivity and ecosystem respiration using light response function analysis, *Agric. Ecosystems Environ.*, *121*, 93–120.
- Göckede, M., C. Thomas, T. Markkanen, M. Mauder, J. Ruppert, and T. Foken (2007), Sensitivity of Lagrangian stochastic footprints to turbulence statistics, *Tellus, Ser. B*, *59*, 577–586.
- Granier, A. (1987), Mesure du flux de sève brute dans le tronc du douglas par une nouvelle méthode thermique, *Ann. Sci. For.*, *44*, 1–14.
- Granier, A., et al. (2000), The carbon balance of a young beech forest, *Funct. Ecol.*, *14*, 312–325.
- Grelle, A., A. Lundberg, A. Lindroth, A.-S. Moren, and E. Cienciala (1997), Evaporation components of a boreal forest: Variations during the growing season, *J. Hydrol.*, *197*, 70–87.
- Grier, C., and W. Running (1977), Leaf area of mature northwestern coniferous forests: Relation to site water balance, *Ecology*, *58*, 893–899.
- Grünwald, T., and C. Bernhofer (2007), A decade of carbon, water and energy flux measurements of an old spruce forest at the Anchor Station Tharandt, *Tellus, Ser. B*, *59*, 387–396.
- Hollinger, D. Y., et al. (2004), Spatial and temporal variability in forest-atmosphere CO₂ exchange, *Global Change Biol.*, *10*, 1689–1706.
- Humphreys, E. R., T. A. Black, K. Morgenstern, Z. Li, and Z. Niesic (2005), Net ecosystem production of a Douglas-fir stand for 3 years following clearcut harvesting, *Global Change Biol.*, *11*, 450–464.
- Irvine, J., B. E. Law, M. R. Kurpius, P. M. Anthoni, D. Moore, and P. A. Schwarz (2004), Age-related changes in ecosystem structure and function and effects on water and carbon exchange in ponderosa pine, *Tree Physiol.*, *24*, 753–763.
- Jacobs, C. M. J., et al. (2007), Variability of annual CO₂ exchange from Dutch grasslands, *Biogeosciences*, *4*, 803–816.
- Jarvis, P. G., and K. G. McNaughton (1986), Stomatal control of transpiration: Scaling up from leaf to region, *Adv. Ecol. Res.*, *15*, 1–49.
- Jassal, R. S., T. A. Black, M. D. Novak, D. Gaumont-Guay, and Z. Niesic (2008), Effect of soil water stress on soil respiration and its temperature sensitivity in an 18-year-old temperate Douglas-fir stand, *Global Change Biol.*, *14*, 1–14.
- Katul, G. G., D. S. Ellsworth, and C. Lai (2000), Modelling assimilation and intercellular CO₂ from measured conductance: a synthesis of approaches, *Plant Cell Environ.*, *23*, 1313–1328.
- Knohl, A., E.-D. Schulze, O. Kolle, and N. Buchmann (2003), Large carbon uptake by an unmanaged 250-year-old deciduous forest in central Germany, *Agric. For. Meteorol.*, *118*, 151–167.

- Krishnan, P., T. A. Black, N. J. Grant, A. G. Barr, E. H. Hogg, R. S. Jassal, and K. Morgenstern (2006), Impact of changing soil moisture distribution on net ecosystem productivity of a boreal aspen forest during and following drought, *Agric. For. Meteorol.*, *139*, 208–223.
- Krishnan, P., T. A. Black, A. G. Barr, N. J. Grant, D. Gaumont-Guay, and Z. Nestic (2008), Factors controlling the interannual variability in the carbon balance of a southern boreal black spruce forest, *J. Geophys. Res.*, *113*, D09109, doi:10.1029/2007JD008965.
- Kuglitsch, F. G., et al. (2008), Characterisation of ecosystem water-use efficiency of European forests from eddy covariance measurements, *Biogeosci. Disc.*, *5*, 4481–4519.
- Kutsch, W., O. Kolle, C. Rebmann, A. Knohl, W. Ziegler, and E.-D. Schulze (2008), Advection and resulting CO₂ exchange uncertainty in a tall forest in central Germany, *Ecol. Appl.*, *18*, 1391–1405.
- Lai, C. T., J. R. Ehleringer, A. J. Schauer, P. P. Tans, D. Y. Hollinger, K. T. Paw U, J. W. Munger, and S. C. Wofsy (2005), Canopy-scale δ¹³C of photosynthetic and respiratory CO₂ fluxes: Observations in forest biomes across the United States, *Global Change Biol.*, *11*(4), 633–643.
- Lambers, H., F. Chapin III, and T. Pons (1998), *Plant Physiol. Ecol.*, 540 pp., Springer, New York.
- Lange, O. L., R. Lösch, E.-D. Schulze, and L. Kappen (1971), Responses of stomata to changes in humidity, *Planta*, *100*, 76–86.
- Larcher, W. (1969), The effects of environmental and physiological variables on the carbon dioxide gas exchange of trees, *Photosynthetica*, *3*, 167–198.
- Law, B. E., S. Van Tuyl, A. Cescatti, and D. D. Baldocchi (2001), Estimation of leaf area index in open-canopy ponderosa pine forests at different successional stages and management regimes in Oregon, *Agric. For. Meteorol.*, *108*, 1–14.
- Law, B., et al. (2002), Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation, *Agric. For. Meteorol.*, *113*, 97–120.
- Lindroth, A., L. Klemedtsson, A. Grelle, P. Weslien, and O. Langvall (2007), Measurement of net ecosystem exchange, productivity and respiration in three spruce forests in Sweden shows unexpectedly large soil carbon losses, *Biogeochemistry*, *89*, 43–60, doi:10.1007/s10533-007-9137-8.
- Lloyd, J., O. Shibistova, D. Zolotoukhina, O. Kolle, A. Arneth, C. Wirth, J. M. Styles, N. M. Tchebakova, and E. Schulze (2002), Seasonal and annual variations in the photosynthetic productivity and carbon balance of a central Siberian pine forest, *Tellus, Ser. B*, *54*(5), 590–610.
- Monsi, M., and T. Saeki (1953), Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion, *Jpn. J. Bot.*, *14*, 22–52.
- Monteith, J. L. (1986), How do crops manipulate water supply and demand?, *Philos. Trans. R. Soc. London Ser. A*, *316*, 245–259.
- Moureaux, C., A. Debacq, B. Bodson, B. Heinesch, and M. Aubinet (2006), Carbon sequestration by a sugar beet crop, *Agric. For. Meteorol.*, *139*, 25–39.
- Nagy, Z., et al. (2007), The carbon budget of a semiarid grassland in a wet and a dry year in Hungary, *Agric. Ecosystems Environ.*, *121*, 21–29.
- Ogeé, J., Y. Brunet, D. Loustau, P. Berbigier, and S. Delzon (2003), MuSICA, a CO₂, water and energy multilayer, multileaf pine forest model: Evaluation from hourly to yearly time scales and sensitivity analysis, *Global Change Biol.*, *9*, 697–717.
- Papale, D., et al. (2006), Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation, *Biogeosciences*, *3*, 1–13.
- Ponton, S., L. Flanagan, K. Alstad, B. Johnson, K. Morgenstern, N. Klyun, T. Black, and A. Barr (2006), Comparison of ecosystem water-use efficiency among douglas-fir forest, aspen forest and grassland using eddy covariance and carbon isotope techniques, *Global Change Biol.*, *12*(12), 294–310.
- Prentice, I. C., A. Bondeau, W. Cramer, S. P. Harrison, T. Hickler, W. Lucht, S. Sitch, B. Smith, and M. T. Sykes (2007), Dynamic global vegetation modeling: Quantifying terrestrial ecosystem responses to large-scale environmental change, in *Terrestrial Ecosystems in a Changing World, IGBP Book Ser.*, edited by J. Canadell, D. E. Pataki, and L. F. Pitelka, pp. 175–192, Springer, Berlin, isbn:978-3-540-32729-5.
- Rambal, S., J.-M. Ourcival, R. Joffre, F. Mouillot, Y. Nouvellon, M. Reichstein, and A. Rocheteau (2003), Drought controls over conductance and assimilation of a mediterranean evergreen ecosystem: scaling from leaf to canopy, *Global Change Biol.*, *9*, 1813–1824.
- Reichstein, M., et al. (2002), Severe drought effects on ecosystem CO₂ and H₂O fluxes at three mediterranean evergreen sites: Revision of current hypotheses?, *Global Change Biol.*, *8*, 999–1017.
- Reichstein, M., et al. (2005), On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm, *Global Change Biol.*, *11*, 1424–1439.
- Reichstein, M., et al. (2007), Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: A joint flux tower, remote sensing and modelling analysis, *Global Change Biol.*, *13*, 634–651.
- Roupsard, O., et al. (2006), Partitioning energy and evapo-transpiration above and below a tropical palm canopy, *Agric. For. Meteorol.*, *139*, 252–268.
- Running, S. W., R. R. Nemani, F. A. Heinsch, and M. Zhao (2004), A continuous satellite-derived measure of global terrestrial primary production, *Bioscience*, *54*, 547–560.
- Sanz, M. J., A. Carrara, G. Gimeno, A. Bucher, and R. Lopez (2004), Effects of a dry and warm summer conditions on CO₂ and energy fluxes from three mediterranean ecosystems, *Geophys. Res. Abstr.*, *6*, 3239.
- Schulze, E.-D., and A. E. Hall (1982), Stomatal responses and water loss and CO₂ assimilation rates of plants in contrasting environments, in *Encyclopedia of Plant Physiology*, vol. 12B, *Water Relations and Photosynthetic Productivity*, edited by O. Lange et al., pp. 181–230, Springer, Berlin.
- Sinclair, T. R., C. B. Tanner, and J. M. Bennett (1984), Water-use efficiency in crop production, *Bioscience*, *34*, 36–40.
- Suni, T., J. Rinne, A. Reissel, N. Altim, P. Keronen, U. Rannik, M. D. Maso, M. Kulmala, and T. Vesala (2003), Long-term measurements of surface fluxes above a Scots pine forest in Hyytiälä, southern Finland, 1996–2001, *Boreal Environ. Res.*, *4*, 287–301.
- Tedeschi, V., A. N. A. Rey, G. Manca, R. Valentini, P. G. Jarvis, and M. Borghetti (2006), Soil respiration in a mediterranean oak forest at different developmental stages after coppicing, *Global Change Biol.*, *12*, 110–121.
- Thum, T., T. Aalto, T. Laurila, M. Aurela, P. Kolari, and P. Hari (2007), Parametrization of two photosynthesis models at the canopy scale in a northern boreal Scots pine forest, *Tellus, Ser. B*, *59*, 874–890.
- Tirone, G., S. Dore, G. Matteucci, S. Greco, and R. Valentini (2003), Evergreen mediterranean forests: Carbon and water fluxes, balances, ecological and ecophysiological determinants, in *Fluxes of Carbon, Water and Energy of European Forests, Ecol. Stud. Ser.*, vol. 163, edited by R. Valentini, pp. 125–149, Springer, Berlin.
- Valentini, R., P. De Angelis, G. Matteucci, R. Monaco, S. Dore, and G. E. Scarascia Mucnozza (1996), Seasonal net carbon dioxide exchange of a beech forest with the atmosphere, *Global Change Biol.*, *2*, 199–207.
- Wohlfahrt, G., A. Hammerle, A. Haslwanter, M. Bahn, U. Tappeiner, and A. Cernusca (2008a), Seasonal and inter-annual variability of the net ecosystem CO₂ exchange of a temperate mountain grassland: effects of weather and management, *J. Geophys. Res.*, *113*, D08110, doi:10.1029/2007JD009286.
- Wohlfahrt, G., et al. (2008b), Biotic, abiotic and management controls on the net ecosystem CO₂ exchange of European mountain grasslands, *Ecosystems*, *11*, 1338–1351.
- Wong, S. C., I. R. Cowan, and G. D. Farquhar (1979), Stomatal conductance correlates with photosynthetic capacity, *Nature*, *282*, 424–426.
- Wu, J. H., C. Z. Fu, F. Lu, and J. K. Chen (2005), Changes in free-living nematode community structure in relation to progressive land reclamation at an intertidal marsh, *Appl. Soil Ecol.*, *29*, 47–58.

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