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Characterisation of ecosystem water-use efficiency of european forests from eddy covariance measurements

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Abstract

Water-use efficiency (WUE) has been recognized as an important characteristic of vegetation productivity in various natural scientific disciplines for decades, but only recently at the ecosystem level, where different ways exist to characterize water-use efficiency. Hence, the objective of this research was (a) to systematically compare different ways of calculating ecosystem water-use efficiency (WUEe) from eddy-covariance measurements, (b) quantify the diurnal, seasonal and interannual variability of WUEe in relation to meteorological conditions, and (c) analyse between-site variability of WUEe as affected by vegetation type and climatic conditions, across sites in European forest ecosystems.

Day-to-day variability of gross primary productivity (GPP) and evapotranspiration (ET) were more strongly coupled than net ecosystem production (NEP) and ET, obviously because NEP also depends on the respiration that is not heavily coupled to water fluxes. However, the slope of daytime NEP versus ET (m_{NEP}) from half-hourly measurements of a single day may also be used as a WUEe-estimate giving very similar results to those of the GPP-ET slope (m_{GPP}), since the diurnal variation is dominated by GPP. Since ET is the sum of transpiration (linked to GPP) and evaporation from wet vegetation and soil surfaces (not linked to GPP) we expected that WUEe is increasing when days after rain are excluded from the analysis. However only very minor changes were found, justifying an analysis of WUEe related to vegetation type.

In most of the studied ecosystems the instantaneous WUE_{GPP} was quite sensitive to diurnally varying meteorological conditions and tended to decline from the morning to the afternoon by more than 50% because of increasing vapour pressure deficits (VPD).

Seasonally, WUE_{GPP} increased with a rising monthly precipitation sum and rising average monthly temperatures up to a threshold of 11, 14 and 18°C in boreal, temperate and Mediterranean ecosystems, respectively. Across all sites, the highest monthly WUE_{GPP}-values were detected at times of positive anomalies of summer-precipitation. During drought periods with high temperatures, high VPD, little precipitation and low soil water content, the water-use efficiency of gross carbon uptake (WUE_{GPP}) tended to decrease in all forest types because of a stronger decline of GPP compared to ET.

However the largest variation of growing season WUE_{GPP} was found between-sites and significantly related to vegetation type: WUE_{GPP} was highest in ecosystems dominated by deciduous trees ranging from 5.0 g CO_2 kg H_2O^{-1} for temperate broad-leaved deciduous forests (TD), to 4.5 for temperate mixed forests (TM), 3.5 for temperate evergreen conifers (TC), 3.4 for Mediterranean broad-leaved deciduous forests (MD), 3.3 for Mediterranean broad-leaved evergreen forests (Mbeg), 3.1 for Mediterranean evergreen conifers (MC), 2.9 for boreal evergreen conifers (BC) and only 1.2 g CO_2 kg H_2O^{-1} for a boreal wetland site (BT). Although vegetation type and meteorology co-vary, the WUEGPP variation was hardly related to meteorology, as we could show by comparing similar meteorological conditions only. Furthermore we compared across-site WUE_{GPP} only under conditions when the 10% high GPP rates were exhibited. The between site differences remained, and at all sites ecosystem reached higher WUE_{GPP} levels under this condition. This means when vegetation is most productive usually it also maximises the amount of carbon gained per water lost.

Overall our results show that water-use efficiency exhibits a strong time-scale dependency in the sense that at longer time-scale meteorological conditions play a smaller role compared to shorter time scale. Moreover, we highlight the role of vegetation in determining carbon-water relation at ecosystem level. Consequently, all predictions of changing carbon-water cycle under changing climate should take into this role and the differences between vegetation types. These results show the strong time-scale dependency of water-use efficiency

1 Introduction

Ecosystem carbon and water fluxes are intimately linked in vegetated ecosystems, since photosynthesis carbon fixation and transpiration are often limited by stomatal conductance at the leaf level. The question of how much water a plant transpires to assimilate a certain amount of carbon has received attention both from plant physiological and from more applied scientific disciplines such as applied hydrology, irrigation science, agronomy and agroecology (de Wit, 1958).

As shown in Fig. 1, water-use efficiency (WUE) can be calculated in very different ways depending on the temporal and spatial scales of interest, as well as on the scientific question of interest. Although various definitions of WUE are applied in different scientific disciplines, the common characteristic is that WUE is always a ratio of carbon gain to water loss.

Biologists and plant physiologists consider WUE usually on leaf and plant scales and are mainly interested in relations between total or above ground biomass (B), stem biomass (S) and net CO_2 assimilation (A) to transpiration (T) or evapotranspiration (ET). ε may represent both T and ET (Loomis and Connor, 1992; Denmead et al., 1993). ET is defined as the total water vapour flux between the canopy and the atmosphere consisting of evaporation from soil (E), plant transpiration and evaporation of the intercepted fraction. Agricultural scientists appreciate WUE mostly as a relation of yield (Y) or B to ε, the total water provided to the crop, including precipitation (W) or the amount of irrigated water (W_U), which is mainly of interest for irrigation purposes (Jones, 2004). To estimate the WUE of whole ecosystems (WUEe) geoscientists and ecologists commonly use the ratio of the main ecosystem fluxes such as net primary production (NPP), net ecosystem production (NEP), or gross ecosystem production (GEP) to the water losses (ET or T) (Law et al., 2002; Reichstein et al., 2002).

In general, major ecozones with typical dominant plant functional types are often characterized by differing water availability (Woodward, 1987). Thus we expect ecosystems to have different water-use efficiencies because of inherent physiological variation in leaf gas exchange characteristics and because of differences in environmental conditions among habitats (Farquhar et al., 1989). Therefore comparative studies of WUEe are crucial to our understanding on how future climate change accompanied by hydrological changes will affect the carbon and energy budgets of ecosystems.

The application of the eddy covariance technique for the continuous determination of carbon and water fluxes is deployed as a network throughout the world thus enabling scientists to study both, the temporal and the large-scale spatial variability of WUEe. However, one major problem is that both fluxes directly measured by the eddy covariance method (NEP and ET), are not directly related to the canopy function (GPP and T), but are confounded by respiration and evaporation from soil and wet surfaces, respectively. Consequently, there are different ways to calculate WUEe that have potentially different interpretations. These different options have not been systematically compared across sites until now.

Hence, in this study we take advantage of a large and harmonised flux dataset from the Carboeurope-IP project, covering a large range of forest types and climate zones and aim at: (1) comparing and interpreting different ways of calculating ecosystem water-use efficiency from eddy covariance data, and (2) summarizing the overall magnitude as well as the temporal and spatial variability of WUEe and the relevant driving factors (e.g. meteorology and vegetation type) for European flux sites.

2 Material and methods

2.1 Sites, data and processing

In this study flux measurements of 23 sites from the CARBOEUROFLUX/CARBOEUROPE-IP projects (http://gaia.agraria.unitus.it/database) were analyzed (22 forests and one boreal treeless wetland site) with 1–10 years of data collected from 1996 to 2005, resulting in a total of 135 unique site-year combinations. The geographic range of these sites varies in latitude from 39° N to 70° N and in longitude from 0° W to 28° E, covering the Mediterranean, temperate and boreal parts of Europe. All sites were categorized by one of the following eight plant functional types: (1) Boreal treeless wetland (BT), (2) Boreal evergreen conifers (BC), (3) Temperate evergreen conifers (TC), (4) Temperate mixed forests (TM), (5) Temperate broad-leaved deciduous (TD), (6) Mediterranean evergreen conifers (MC), (7) Mediterranean broad-leaved deciduous (MD) or (8) Mediterranean broad-leaved evergreen (Mbeg). The detailed characteristics and codes for the sites are shown in Table 1.

The carbon, water and energy exchange between the atmosphere and the vegetation was measured with the eddy covariance technique (for details see e.g. Aubinet et al., 2000) from towers above the vegetation canopies. Three-axis sonic anemometers measured wind speed and virtual temperature, infrared gas analyzers measured concentrations of water vapor and CO_2 and a suite of software was needed for real-time and post-processing analysis. The data were quality checked, and data gaps due to system failure or data rejection were filled using standardized methods (for details see Papale et al., 2006; Reichstein et al., 2005a; Moffat et al., 2007) to provide complete and standardized data sets. The measured NEP fluxes has been partitioned in the two main components GPP and Reco using the method described by Reichstein et al. (2005b) that is based on night-time data extrapolation using nonlinear regressions with temperature.

2.2 Calculation of water-use efficiency

As mentioned in Sect. 1, water-use efficiency can be calculated in very different ways depending on the scientific discipline and the temporal and spatial scale of interest. For calculating WUEe we analyzed both, the ratio of daily integrals between NEP (g CO_2) and ET (kg H_2O) as well as the ratio between GPP (g CO_2) and ET (kg H_2O), calculated from half-hourly measurements, which provide a temporally highly resolved basis for calculating WUE_{NEP} and WUE_{GPP} (g CO_2 kg H_2O^{-1}).

Considering only days with active canopy during the growing season we used a filter to exclude daily NEP-, GPP- and ET-values, when mean daily latent heat flux (LE)<20 W m^{-2}, global radiation (Rg)<150 W m^{-2} and mean air temperature <0°C. Moreover we made use of a gap-filling quality measure of aggregated daily values that indicates which fraction of the data was original or most reliably filled (cf. Reichstein et al., 2005a). Only if more than 80% of the half-hourly data were original and reliably filled the data were used in the analysis.

An analysis was performed of how the exclusion of rainy days and the first, second and third day after, respectively, affects WUEe. Grelle et al. (1997) highlighted the need for eliminating days with high evaporation and interception causing underestimated WUEe which occur basically on day after precipitation events.

After these preparatory steps WUEe was calculated in different ways:

1. As ratio between daily integrals of GPP and ET (WUE_{GPP})
2. As ratio between daily integrals of NEP and ET (WUE_{NEP})
3. As slope from a linear regression between half-hourly values of GPP and ET calculated for each day (cf. Fig. 2) (m_{GPP})
4. As slope from a linear regression between half-hourly values of NEP and ET calculated for each day (cf. Fig. 2) (m_{NEP})

WUE_{GPP}, WUE_{NEP}, m_{GPP} and m_{NEP} ($g\,CO_2\,kg\,H_2O^{-1}$) were estimated for each day which was not excluded by the filter (mentioned before).

Half-hourly binned GPP, NEP ($g\,CO_2$) and ET ($kg\,H_2O$) values were used to estimate (1) the instantaneous WUEe (WUE_{GPP},WUE_{NEP}) and their mean daily course between 04:00 and 21:30 and (2) to estimate the mean daily WUEe (m_{GPP}, m_{NEP}) as the slope between GPP and ET or NEP and ET, respectively. Furthermore the ratio of daily sums of GPP, NEP and ET were used to estimate daily WUE_{GPP} and WUE_{NEP}. The monthly WUE_{GPP} and WUE_{NEP} was calculated by the ratio of monthly integrals of GPP divided by the respective H_2O flux integrals ($WUE_{GPPmonth}=GPP_{month}/ET_{month}$). The seasonal trend of WUEGPP is characterized by the mean monthly WUEGPP. The seasonal progress of GPP and ET is represented by normalized data such that the mean monthly maximum equals 100%. The standard error, SD_x,

where σ_n is the standard deviation and n is the number of months, was calculated for each calendar month. The mean annual or long-term WUEe is the median of all available daily averages.

3 Results and discussion

3.1 Comparison of different calculations of WUEe

Since NEP and GPP are differently related to ET an evaluation of these two parameters has to be done. The filtered (see Sect. 2 for details) NEP-, GPP- and ET-values for FI-Hyy are shown in Fig. 3, and demonstrate a much higher correlation between ET and GPP than between ET and NEP, a pattern which occurred at all investigated sites.

Furthermore, we expected to observe lower WUE_{NEP}- and WUE_{GPP}-values on precipitation days and the day after due to enhanced evaporation from surfaces that has never been part of the plant metabolism (cf. Grelle et al., 1997). However, a comparison of WUE_{GPP}-values calculated from all data or data excluding rainy and subsequent days, revealed that the evolution of WUE_{GPP} after rain events is quite conservative (Fig. 4). Only coniferous forests and the DE-Hai site (TD) show a WUE_{GPP}-decrease up to the second day after the rain event. The same results were found for WUE_{NEP} (not shown).

In a further step we performed a correlation analysis of different forms of daily WUEe-values, such as m_{GPP}, m_{NEP}, which represent the slope between half-hourly carbon fluxes, WUE_{GPP} and WUE_{NEP}, and ET for each day (see Sect. 2).

The plots for three coniferous sites of the boreal (FI-Hyy), temperate (DE-Tha) and Mediterranean zone (IT-SRo) are shown in Fig. 5a–d and demonstrate that correlations are remarkably high between the daily slopes from half-hourly measurements, m_{NEE} and m_{GPP} ($r>0.99$; see Fig. 5a). Therefore these measures seem to represent a similar water-use efficiency at the ecosystem level.

Correlation coefficients of m_{GPP}:WUE_{GPP} (Fig. 5b), WUE_{NEP}:WUE_{GPP} (Fig. 5c) and m_{NEP}:WUE_{NEP} (Fig. 5d) are quite similar for most of the sites, especially for the coniferous forests mentioned, on average the correlation coefficient is 0.56–0.65 (FI-Hyy), 0.74–0.84 (DE-Tha) and 0.64–0.68 (IT-SRo), and reach their maximum in most of the temperate and Mediterranean sites in WUE_{NEP}:WUE_{GPP} (see Table 2). In boreal ecosystems the highest correlations are found in m_{GPP}:WUE_{GPP} and m_{NEP}:WUE_{NEP}.

WUE_{GPP}-values are always highest in comparison to WUE_{NEP}-, m_{GPP}- and m_{NEP}-values. A summary of the slopes and r-values for all sites is presented in Table 2.

The mean long-term WUE_{NEP}-, m_{NEP}-, m_{GPP}- and WUE_{GPP}-values, summarized in Fig. 6, shows highest medians for WUE_{GPP} at all sites and lowest medians for WUE_{NEP} at most of the sites. Highest WUE_{GPP}-values of 4 g CO_2 kg H_2O^{-1} and more arise in temperate mixed (TM) and temperate broad-leaved deciduous forests (TD). In contrast, WUE_{NEP}-values are only 50% and less of WUE_{GPP}-values.

Remarkably high WUE_{NEP}-values can be observed particularly in some temperate (DE-Hai, FR-Hes) and Mediterranean broad-leaved deciduous forests (IT-Col, IT-Ro2, IT-PT1), which may indicate lower respiration-assimilation ratios in these ecosystems.

The Water-use efficiencies calculated from diurnal slopes (m_{GPP}, m_{NEP}) are quite similar, however WUEe from m_{GPP} is always slightly higher than WUEe from m_{NEP}. The reason for this similarity with the slopes is that the slope of NEP versus ET is much less influenced by respiration, because the diurnal variation is dominated by the GPP, while the ratio of NEP to ET is influenced by more important background values of respiration.

3.2 Seasonal water-use efficiency

Seasonal patterns of WUE_{GPP} GPP and ET are shown for selected sites from Table 1 of each vegetation functional type in Fig. 7.

In all ecosystems we found a remarkable high correspondence between the monthly amount of GPP and ET which both peak between May in Mediterranean conifers (MC) and August in temperate mixed forests (TM). As a result of year-round active assimilation in temperate conifers (TC), Mediterranean conifers (MC) and Mediterranean broad-leaved evergreen forests (Mbeg), WUE_{GPP} can be estimated for all seasons. Even some maritime influenced boreal conifers show a surprisingly long potential assimilation period due to the fact that they can even assimilate during days when mean daily temperatures are slightly below 0°C. This characteristic was also reported by Suni et al. (2003) and Sevanto et al. (2006). However, boreal ecosystems and temperate deciduous forests (TD) show a more confined season compared to Mediterranean sites.

Unlike the summer maximum of GPP and ET, WUE_{GPP} can peak, site-dependently in any season. A summer maximum of WUE_{GPP} can only be observed for the boreal wetland site (FI-Kaa), even though the seasonal course is flat compared to the other sites. All forest sites show a decrease of WUE_{GPP} during summertime due to a stronger decline in GPP than in ET. The more southernly the site is located, the longer the summertime depression lasts. This summertime depression lasts longer, the more southernly the site is located. This trend can even be observed in boreal conifers, where the mean long-term WUE_{GPP}-max appears in September. This is very interesting since many investigations on leaf-level (e.g. Monteith, 1995; Maroco et al., 1997) showed that stomatal closure due to heat stress reduces transpiration more than assimilation and hence induces higher water-use efficiencies. For these reasons many ecosystems tend to develop two peaks in seasonal WUE_{GPP}. Temperate ecosystems exhibit for example with the exception of very oceanic-exposed conifers (e.g. NL-Loo), one maximum in June and one in September/October. During summer months WUE_{GPP} normally decreases by about $1\,g\,CO_2\,kg^{-1}\,H_2O$ and reaches a relative minimum in August. This progress is most pronounced in evergreen Mediterranean ecosystems (MC, Mbeg), where the long hot and dry summer season leads to a massive shift of the two WUE_{GPP}-peaks to early spring (February–March) and late fall (October–December). During summer months WUE_{GPP} normally decreases by more than $2\,g\,CO_2\,kg\,H_2O^{-1}$ and reaches its absolute minimum in July or August. Mediterranean deciduous forests (MD) achieve their maximum WUE_{GPP}-values later, in May-June and September-October due to foliation and non year-round assimilation restricted to the growing season.

On a monthly time scale mean WUE_{GPP} tends to increase with rising precipitation sum and rising temperatures until average temperatures reach a threshold of 11, 14 and 18°C in most of the boreal, temperate and Mediterranean ecosystems, respectively. Hence, highest monthly WUE_{GPP}-values due to relatively higher GPP- and lower ET-values usually arise in wet summer-months with high precipitation sums and low mean VPDs. The higher GPP during these months can be the result of an increase of diffuse radiation that might stimulate assimilation (Alton et al., 2007; Knohl and Baldocchi, 2008). Similar long-term trends, fluctuations and estival decreases were also published for WUEe from the ratio above-ground production to accumulated transpiration in willow plantations in southern Sweden by Lindroth et al. (1994).

Thus, the seasonal progress of WUE_{GPP} differs very strongly depending on site, climate, vegetation type including the understory and growing season length, which lasts at our investigated sites between six and twelve months. In some deciduous broad-leaved forests understory plays a major role and is largely responsible for the demonstrated WUEe during early spring and late autumn months.

The mean annual WUE_{GPP} is between 1.2 g CO_2 kg H_2O^{-1} for the boreal wetland site and up to 5.0 g CO_2 kg H_2O^{-1} for temperate deciduous forests (see Sect. 3). However it is difficult to allocate one specific WUE_{GPP}-value to each vegetation type, because it is conspicuous that the WUE_{GPP} of sites within one vegetation type can also differ quite considerably from each other. For instance in temperate conifers, mean annual WUE_{GPP} achieve values between 2.1 and 3.8 g CO_2 kg H_2O^{-1} depending on site, with the highest values in Central Europe. Nevertheless, between-vegetation type differences were clearly significant ($p<0.02$, repeated measures ANOVA).

In order to exclude direct climatic effects on WUEe we analyzed WUE_{GPP} also under similar meteorological conditions but at different sites. The range of mean daily temperature (T), mean daily global radiation (Rg) and mean daylight VPD was set to 17.5–22.5°C, 200–300 W m^{-2} and 5–15 hPa, respectively. The resulting WUE_{GPP} values correspond well with the mean annual WUE_{GPP}, indicating that water-use efficiency is more driven by vegetation functioning than by climate forcing. In an alternative approach, where WUE_{GPP} was multiplied by VPD to account for direct VPD effects, Beer et al. (2007) also found strong between-site variability of this meteorology-adjusted WUE_{GPP}. Also the differences between the vegetation types remain similar, when sites are compared with respect to their WUE_{GPP} under conditions when their maximum seasonal GPP is reached. Moreover, all sites reach their highest water-use efficiency when also their overall productivity is highest, indicating that these high carbon uptake rates are not only caused by increased stomatal conductance (which affects both carbon and water fluxes), but also increased carboxylation efficiency.

Few published data of long-term WUEe makes a thorough comparison with other studies difficult. Similar or some lower WUE_{GPP}-patterns due to plant functional types were reported by Law et al. (2002) who estimated 3.2 g CO_2 kg H_2O^{-1} for temperate deciduous forests, 2.4 g CO_2 kg H_2O^{-1} for temperate evergreen conifers and 1.5 g CO_2 kg H_2O^{-1} for tundra vegetation. However, their results are based on much shorter time series. Highest WUE_{GPP}-values for temperate deciduous forests were also estimated by Reichstein et al. (2007a). Furthermore there are some studies which do not represent ecosystem WUE_{GPP} but water-use efficiency of specific tree species. Polster (1950) reported comparable WUEe-values from a ratio of above-ground growth to transpiration of 5.9 and 3.3 g CO_2 kg H_2O^{-1} for *Fagus sylvatica* and *Pinus sylvestris*, plant species that also dominate our TD- (4.3–5.5 g CO_2 kg H_2O^{-1}) and TC-sites (2.1–3.8 g CO_2 kg H_2O^{-1}). Higher WUEe-estimations of 4.8 for *Pinus sylvestris* were published by Cienciala et al. (1994).

Moreover WUE_{GPP} also varies from year to year due to meteorological conditions, however diverse conditions affect WUE_{GPP} differently depending on site. The highest annual WUE_{GPP}-values due to higher GPP- and lower ET-values usually arise in wet years with a high annual precipitation sum and a low mean annual VPD. Only the mountainous Mediterranean deciduous broad-leaved site IT-Col shows a negative correlation between the annual precipitation sum and the mean annual WUE_{GPP} (not shown). On an annual time-scale the temperature effect does not seem to be significant. While the boreal coniferous site SE-Nor shows the highest WUE_{GPP} in the warmest years, the Mediterranean coniferous site IT-SRo shows the highest values in the coldest years. All other sites do not show dependencies between mean annual temperature and mean annual water-use efficiency.

A very similar interannual fluctuation range between 0.3 and 0.7 g CO_2 kg H_2O^{-1} (standard deviation, SD) can be found for most of the sites. The largest interannual fluctuations of more than 1 g CO_2 kg H_2O^{-1} (SD) are detected in some boreal conifers (e.g. SE-Nor) and Mediterranean broad-leaved deciduous forests (e.g. IT-Col). The lowest fluctuations of about 0.2 g CO_2 kg H_2O^{-1} (SD) occur at the boreal wetland site.

Furthermore the interannual WUE_{GPP}-fluctuations under similar meteorological conditions (Temperature: 17.5–22.5°C, Global radiation: 200–300 W m^{-2}, VPD: 5–15 hPa) are, as expected, not lower but showed consistently comparable values (data not shown), suggesting that instantaneous meteorological conditions were not responsible for between-year variability of water-use efficiency. However, higher fluctuations can be observed when WUE_{GPP} was only calculated for days with the 10% highest GPP per site, i.e. under "optimal" conditions. This might indicate that interannual variability of WUE is caused by the overall vegetation state and its development, respectively.

3.3 Instantaneous water-use efficiency

Unlike the seasonal cycle of WUE_{GPP}, the instantaneous WUE_{GPP} which was estimated for every half hour shows a similar diurnal cycle trend for different sites, with a primary WUE_{GPP}-maximum in the early morning and a secondary maximum in the evening (see Fig. 8).

WUE_{GPP} reaches values of 6 to 10 g CO_2 kg H_2O^{-1} in the morning and 4 to 6 g CO_2 kg H_2O^{-1} in the evening for most of the sites. More extreme values of 14 and 3 g CO_2 kg H_2O^{-1} in the morning and 8 and 1.7 g CO_2 kg H_2O^{-1} in the evening can only be found for temperate deciduous (DE-Hai) and mixed (BE-Vie) forests as well as for the boreal wetland site (FI-Kaa). During the day WUE_{GPP} decreases by about 50% to 70%, which is 1 g CO_2 kg H_2O^{-1} for the boreal wetland site and up to 9 g CO_2 kg H_2O^{-1} for temperate deciduous and mixed forests and reaches at all sites a minimum between 1 and 2 p.m. This WUE_{GPP}-decrease is largely attributed to an increase in solar radiation (max. between 1 and 2 p.m.) during daytime, which causes a shift between the earlier GPP- and the later ET-maximum and was detectable in all investigated ecosystems. The deferred increase of VPD, reaching its maximum at 4 p.m. seems to play a minor part in affecting water-use efficiency during the course of the day.

The hyperbolic relationship between WUE_{GPP} and VPD during the daylight period is shown for the three coniferous forests FI-Hyy, DE-Tha and IT-SRo in Fig. 9. These results confirm the effects of VPD on stomatal conductance, which is known on leaf level (Schulze and Hall, 1982) and also at ecosystem scale (Law et al., 2002). Increasing VPD until afternoon causes stomatal closure, thus decreasing stomatal conductance. Since stomatal conductance impacts both GPP and transpiration, but it is only the water flux which is proportional to VPD, the overall effect of VPD on GPP is higher than on transpiration. This leads to a decreasing WUE_{GPP}. However, we find a hysteresis, where WUE_{GPP} is higher in the evening than under similar VPD conditions during the day after VPD decreases again (cf. color scheme in Fig. 9). Since radiation is lower after 5 p.m., this phenomenon could be explained by two alternative hypotheses: (1) transpiration is lower because of lower leaf water potential and stomata react to these leaf water changes, and (2) leaf temperatures and thus the $VPD_{leaf-to-air}$ gradient is smaller in the evening when incoming shortwave radiation is less intense.

Similar trends but with some higher values of instantaneous WUEe were also detected for a short rotation *Salix viminalis* plantation by Lindroth and Cienciala (1996) and for boreal conifers in Norunda, Sweden, by Morén et al. (2001).

4 Concluding discussion

We identified and compared different methods to calculate ecosystem water-use efficiency (WUEe) at temporal scales of hours, days, months and years for European forest sites representing different biomes. The interpretation of daily-integral ratios of NEP versus ET are hampered by the fact that NEP is strongly influenced by respiration, which may obscure the coupling of canopy carbon and water fluxes. GPP derived from flux-partitioning algorithms should be preferred when calculating meaningful ecosystem level water-use efficiency, even though GPP is not directly measured and any possible biases in the flux-partitioning algorithm translate into WUEe biases.

The slopes of half-hourly measured daytime NEP/ET-(m_{NEE}) and GPP/ET-ratios

(m_{GPP}) were conspicuously consistent, offer an alternative for calculating ecosystem water-use efficiency and may be considered as the most direct physiological indicator of canopy water-use efficiency, in particular since both NEP and ET are directly measured. However, since m_{NEE} and m_{GPP} do not cross the origin (intercept>0), the slopes do not inform about the longer-term ratio of carbon gains versus water losses. Moreover, even the interpretation of WUE_{GPP}, as well as m_{NEE} and m_{GPP} in terms of canopy function, are in principle complicated by evaporation from soil and wet surfaces which is included in the ET and not related to the canopy function and the coupling of carbon and water fluxes therein, although we did not find changes after excluding rainy days. In this respect, a larger use of sap-flow measurements at flux sites could provide further insight of GPP and transpiration coupling. However, our analysis reveals that the soil and wet surface evaporation effect on WUEe calculation is not so large to compromise cross-site comparisons of WUEe from eddy covariance.

With between-site variability of WUEe being significantly larger than interannual variability, distinct groups of vegetation types with very similar mean annual WUE_{GPP}-values can be identified. The highest WUE_{GPP} with values of 4.5 to 5.0 g CO_2 kg H_2O^{-1} are found in temperate mixed and temperate deciduous forests. A second group includes the boreal and temperate conifers as well as the Mediterranean ecosystems with values between 3 and 3.5 g CO_2 kg H_2O^{-1}, while the boreal wetland site reached only values of around 1 g CO_2 kg H_2O^{-1}, probably caused by a combination of low photosynthetic capacities and open water evaporation. While it is known that WUEe strongly depends on the atmospheric conditions in the boundary layer (e.g. VPD), interestingly between site differences cannot be explained by such factors as we show by comparing WUEe under similar meteorological conditions. Hence, WUEe can be largely considered as a site or vegetation characteristic, hinting to adaptation of vegetation to their growing environment. Nevertheless, an abstraction of WUEe from meteorological conditions, the intrinsic water-use efficiency calculated as Assimilation/stomatal conductance (A/g) by Schulze and Hall (1982) or approximated as WUEe×VPD by Beer et al. (2007) remains very important, but was out of the scope of this study.

We also find very consistent behaviour of seasonal WUEe across sites: apart from some high-boreal and high-oceanic conifers, a decrease during summer months due to arising drought stress is observed. However, on a seasonal time scale the negative correlation between water-use efficiency and drought characteristics is no implicitness, and should be subject to additional scientific attention since investigations on a fast growing willow plantation in Sweden has shown increasing water-use efficiencies in response to reduced water availability and high VPD (Linderson et al., 2007).

In comparison to the seasonal trend, $\mathrm{WUE}_{\mathrm{GPP}}$ during the course of the day shows very similar changes with lowest values at times of highest VPD in the afternoon at all sites. This emphasizes the dependency of WUEe on daily varying meteorological conditions.

In summary, water-use efficiency is highly vegetation-dependent but also subject to short-term variation of meteorological conditions. Highest $\mathrm{WUE}_{\mathrm{GPP}}$-values arise at times of low VPDs under warm and humid conditions. While it is difficult to predict directly from our observations how WUEe will alter under global climate change, these generalized findings could be used as evalutation benchmarks for process-oriented dynamic global vegetation models (DGVMs) and Landsurface schemes (LSMs) which are used to predict trajectories of carbon and water cycle under a changing climate. In particular the role of vegetation compared to long-term meteorological conditions should be more strongly emphasized. Extensions of our analysis to other regions world wide and corroboration of our results with simultaneous sap-flow measurements will provide further insight in the coupling of carbon and water fluxes in forest ecosystems.

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Table 1. Site information for 23 forest and one boreal wetland site from the Carboeurope-IP project.

Site	Abb.	Country	Period	Coordinates	Elevation (mNN)	Dominant Species	Understory Species	Reference
Boreal treeless wetland (BT)								
Kaamanen	FI-Kaa	Finland	2000–2005	69°08’N, 27°17’E	155	Sedges, Mosses Small shrubs		Tuomas Laurila, Tuomas.Laurila@fmi.fi, Finnish Meteorological Institute, Helsinki Mika Aurela, Mika.Aurela@fmi.fi, Finnish Meteorological Institute, Helsinki
Boreal evergreen conifers(BC)								
Hyytiälä	FI-Hyy	Finland	1996–2005	61°51′N, 24°17′E	181	Pinus sylvestris	evergreen shrubs (Calluna, Vaccinium)	Timo Vesala, Timo.Vesala@Helsinki.fi, University of Helsinki
Sodankylä	FI-Sod	Finland	2001–2005	67°22′N, 26°39′E	180	Pinus sylvestris	lichens, mosses, small shrubs	Tuomas Laurila, Tuomas.Laurila@fmi.fi, Finnish Meteorological Institute, Helsinki Mika Aurela, Mika.Aurela@fmi.fi, Finnish Meteorological Institute, Helsinki
Norunda	SE-Nor	Sweden	1996–1999, 2003–2004	60°05′N, 17°28′E	45	Picea abies, Pinus sylvestris		Anders Lindroth, Anders.Lindroth@natgeo.lu.se, Geobiosphere Science Centre Lund University Meelis Molder, Meelis.Molder@nateko.lu.se, Lund University Harry Lankreijer, Harry.Lankreijer@nateko.lu.se, Lund University Fredrik Lagergren, Fredrik.Lagergren@nateko.lu.se, Lund University
Temperate evergreen conifers (TC)								
Bayreuth	DE-Bay	Germany	1997–1999	50°08′N, 11°52′E	840	Picea abies	deciduous grasses (Deschampsia f.)	Corinna Rebmann, crebmann@bgc-jena.mpg.de, Max Planck Institute Jena Werner Kutsch, wkutsch@bgc-jena.mpg.de, Max Planck Institute Jena

Table 1. Continued.

Site	Abb.	Country	Period	Coordinates	Elevation (mNN)	Dominant Species	Understory Species	Reference
Temperate evergreen conifers (TC)								
Tharandt	DE-Tha	Germany	1997–2004	50°58′N, 13°34′E	820	Picea abies	deciduous grasses (Deschampsia f.)	Christian Bernhofer, bernhofer@forst.tu-dresden.de, TU Dresden Tharandt Thomas Grünwald, gruenwald@forst.tu-dresden.de, TU Dresden Tharandt Barbara Köstner, koestner@forst.tu-dresden.de, TU Dresden Tharandt
Renon	IT-Ren	Italy	1999–2005	46°35′N, 11°26′E	1730	Picea abies, Larix decidua	deciduous grasses (Deschampsia f.), evergreen shrubs (Vaccinium, Rhododendron)	Stefano Minerbi, stefano.minerbi@provincia.bz.it, Autonomous Province of Bolzano Leonardo Montagnani, leonar@inwind.it, Autonomous Province of Bolzano Luigi Minach, luigi.minach@provincia.bz.it, Autonomous Province of Bolzano
Loobos	NL-Loo	The Netherlands	1997–2005	52°10′N, 05°45′E	25	Pinus sylvestris	deciduous grasses (Deschampsia f.)	Eddy Moors, eddy.moors@wur.nl, Wageningen University Jan Elbers, jan.elbers@wur.nl, Wageningen University Wilma Jans, wilma.jans@wur.nl, Wageningen University
Temperate mixed forests (TM)								
Vielsalm	BE-Vie	Belgium	1997–2005	50°18′N, 06°00′E	450	Fagus sylvatica, Pseudotsuga m.	evergreen mosses	Marc Aubinet, aubinet.m@fsagx.ac.be, Faculté universitaire des Sciences agronomiques de Gembloux Bernard Heinesch, heinesch.b@fsagx.ac.be, Faculté universitaire des Sciences agronomiques de Gembloux

Table 1. Continued.

Site	Abb.	Country	Period	Coordinates	Elevation (mNN)	Dominant Species	Understory Species	Reference
Temperate mixed forests (TM)								
Brasschaat	BE-Bra	Belgium	1997–2004	51°19′N, 04°31′E	16	Pinus sylvestris, Quercus robur	deciduous and evergreen shrubs, herbs and grasses	Ivan Janssens, Ivan.Janssens@ua.ac.be, University of Antwerp Wilrijk Hans Verbeeck, Hans.Verbeeck@ua.ac.be, University of Antwerp Wilrijk Reinhard Ceulemans, Reinhard.Ceulemans@ua.ac.be, University of Antwerp Wilrijk Fred Kockelbergh, Fred.Kockelberg@ua.ac.be, University of Antwerp Wilrijk
Temperate broad-leaved deciduous (TD)								
Hainich	DE-Hai	Germany	2000–2005	51°05′N, 10°28′E	430	Fagus sylvatica, Fraxinus	deciduous herbs	Corinna Rebmann, crebmann@bgc-jena.mpg.de, Max Planck Institute Jena Werner Kutsch, wkutsch@bgc-jena.mpg.de, Max Planck Institute Jena
Sorö	DK-Sor	Denmark	1997–1999	55°29′N, 11°38′E	40	Fagus sylvatica	deciduous grasses and herbs (Anemone n., Mercurialis p.)	Ebba Delwik, ebba.delwik@risoe.dk, Risoe National Laboratory Roskilde Lotte Geern, lotte.geern@risoe.dk, Risoe National Laboratory Roskilde Andreas Ibrom, andreas.ibrom@risoe.dk, Risoe National Laboratory Roskilde Kim Pilegaard, kim.pilegaard@risoe.dk, Risoe National Laboratory Roskilde
Hesse	FR-Hes	France	1997–2005	48°40′N, 07°05′E	300	Fagus sylvatica, Quercus petraea	deciduous shrubs (Carpinus betulus)	Andre Granier, agranier@nancy.inra.fr, INRA Champenoux Bernhard Longdoz, longdoz@nancy.inra.fr, INRA Champenoux
Mediterranean evergreen conifers (MC)								
El Saler	ES-ES1	Spain	1999–2002	39°21′N, 00°19′W	10	Pinus halepensis, Pinus pinea	evergreen shrubs (Quercus c., Rhamnus a., l.)	Maria J. Sanz, mjose@ceam.es, Fundaciòn CEAM Valencia Arnaud Carrara, arnaud@ceam.es, Fundaciòn CEAM Valencia

Table 1. Continued.

Site	Abb.	Country	Period	Coordinates	Elevation (mNN)	Dominant Species	Understory Species	Reference
Mediterranean evergreen conifers (MC)								
Le Bray	FR-LBr	France	1996–1997, 2000–2003	44°42′N, 00°46′W	3	Pinus pinaster	evergreen grasses (Molinia c.)	Denis Loustau, Denis.Loustau@pierroton.inra.fr, INRA Pierroton Jean-Marc Bonnefond, bonnefon@bordeaux.inra.fr, INRA-Ephyse Bordeaux Nathalie Jaraosz, Nathalie.Jarosz@bordeaux.inra.fr, INRA-Ephyse Bordeaux
San Rossore	IT-SRo	Italy	1999–2004	43°44′N, 10°17′E	4	Pinus pinaster, Quercus ilex	evergreen shrubs (Erica a., Phillyrea a., Rhamnus a.)	Günther Seufert, guenther.seufert@jrc.it, JRC Ispra Giovanni Manca, giovanni.manca@jrc.it, JRC Ispra Maurizio Teobaldelli, maurizio.teobaldelli@jrc.it, JRC Ispra
Mediterranean broad-leaved deciduous (MD)								
Collelongo	IT-Col	Italy	1996–2001, 2004–2005	41°52′N, 13°38′E	1560	Fagus sylvatica	deciduous herbs (Galium)	Dario Papale, darpap@unitus.it, University of Tuscia Viterbo Giorgio Metteucci, g.matteucci@isafom.cnr.it, Istituto di Ecologia e Idrologia Forestale CNR Francesco Mazzenga, mazzenga@unitus.it, University of Tuscia Viterbo Giuseppe S. Mugnozza, gscaras@unitus.it, University of Tuscia Viterbo Paolo Stefani, pstefani@unitus.it, University of Tuscia Viterbo Nicola Arriga, arriga@unitus.it, Università of Tuscia
Roccaresp.1	IT-Ro1	Italy	2000, 2004–2005	42°23′N, 11°51′E	235	Quercus cerris	evergreen shrubs (Ruscus)	Dario Papale, darpap@unitus.it, University of Tuscia Viterbo Nicola Arriga, arriga@unitus.it, Università of Tuscia Francesco Mazzenga, mazzenga@unitus.it, University of Tuscia Viterbo Paolo Stefani, pstefani@unitus.it, University of Tuscia Viterbo Luca Belelli, belelli@unitus.it, University of Tuscia Viterbo

Table 1. Continued.

Site	Abb.	Country	Period	Coordinates	Elevation (mNN)	Dominant Species	Understory Species	Reference
Roccaresp.2	IT-Ro2	Italy	2002–2004	42°24′N, 11°56′E	224	Quercus cerris	deciduous shrubs (Crataegus)	Dario Papale, darpap@unitus.it, University of Tuscia Viterbo Nicola Arriga, arriga@unitus.it, Università of Tuscia Francesco Mazzenga, mazzenga@unitus.it, University of Tuscia Viterbo Paolo Stefani, pstefani@unitus.it, University of Tuscia Viterbo Luca Belelli, belelli@unitus.it, University of Tuscia Viterbo
Nonantola	IT-Non	Italy	2001	44°41′N, 11°02′E	25	Quercus robur, Fraxinus spp.		Franco Miglietta, f.miglietta@ibimet.cnr.it, IBIMET CNR Firenze Osvaldo Facini, O.Facini@ibimet.cnr.it, IBIMET CNR Firenze
Parco Ticino	IT-PT1	Italy	2002–2004	45°12′N, 09°04′E	60	Populus		Günther Seufert, guenther.seufert@jrc.it, JRC Ispra Michele Meroni, michele.meroni@unimib.it, University of Milano Bicocca Mirco Migliavacco, mirco.migliavacca@unimib.it, University of Milano Bicocca
Mediterranean broad-leaved evergreen (Mbeg)								
Puechabon	FR-Pue	France	2001–2005	43°44′N, 03°36′E	270	Quercus ilex	evergreen shrubs (Buxus s.)	Serge Rambal, serge.rambal@cefe.cnrs.fr, Centre d Ecologie Fonctionnelle et Evolutive Montpellier Jean-Marc Ourcival, jean-marc.ourcival@cefe.cnrs.fr, Centre d Ecologie Fonctionnelle et Evolutive Montpellier Laurent Misson, laurent.misson@cefe.cnrs.fr, CNRS

Table 1. Continued.

Site	Abb.	Country	Period	Coordinates	Elevation (mNN)	Dominant Species	Understory Species	Reference
Castelporziano	IT-Cpz	Italy	1997, 2000–2005	41°45′N, 12°22′E	68	Quercus ilex	evergreen shrubs	Dario Papale, darpap@unitus.it, University of Tuscia Viterbo Nicola Arriga, arriga@unitus.it, Università of Tuscia Francesco Mazzenga, mazzenga@unitus.it, University of Tuscia Viterbo Paolo Stefani, pstefani@unitus.it, University of Tuscia Viterbo Luca Belelli, belelli@unitus.it, University of Tuscia Viterbo

Table 2. Regression results for the daily filtered WUEe-values of all investigated Carboeurope-IP sites. Daily WUEe-data were excluded if mean daily latent heat flux (LE)<20 W m^{-2} and less than 80% of the half-hourly data of a single day were original or reliably filled.

Site	m_{NEE}:m_{GPP}		m_{GPP}:WUE_{GPP}		WUE_{NEE}:WUE_{GPP}		m_{NEE}: WUE_{NEE}		m_{GPP}:WUE_{NEE}		m_{NEE}:WUE_{GPP}	
	r	slope	*r*	slope	*r*	slope	*r*	slope	*r*	slope	*r*	slope
Boreal treeless wetland (BT)												
FI-Kaa	0.99	1.03	0.93	1.36	0.83	1.46	0.75	0.68	0.75	0.66	0.86	1.37
Boreal evergreen conifers (BC)												
FI-Hyy	0.99	1.01	0.65	0.93	0.56	0.72	0.60	0.68	0.60	0.66	0.63	0.91
FI-Sod	0.93	0.95	0.55	0.91	0.34	0.54	0.68	0.72	0.55	0.57	0.42	0.71
FI-Nor	0.97	0.93	0.21	0.59	0.19	0.63	0.34	0.29	0.35	0.30	–0.01	–0.02
Temperate evergreen conifers (TC)												
DE-Bay	0.99	1.03	0.62	1.11	0.66	1.03	0.35	0.43	0.35	0.40	0.61	1.13
DE-Tha	1.00	1.01	0.74	0.95	0.84	1.08	0.75	0.76	0.74	0.74	0.74	0.96
IT-Ren	1.00	1.00	0.48	0.77	0.91	1.06	0.51	0.71	0.52	0.71	0.47	0.75
NL-Loo	1.00	1.01	0.76	0.92	0.82	1.07	0.73	0.69	0.72	0.68	0.74	0.92
Temperate mixed forests (TM)												
BE-Vie	1.00	1.00	0.79	1.10	0.81	1.01	0.80	0.90	0.80	0.89	0.77	1.08
BE-Bra	0.98	1.01	0.47	0.56	0.72	0.97	0.35	0.33	0.32	0.29	0.46	0.57
Temperate broad-leaved deciduous (TD)												
DE-Hai	1.00	1.00	0.82	1.14	0.82	1.00	0.69	0.87	0.68	0.86	0.74	1.14
DK-Sor	0.99	0.99	0.64	1.04	0.82	1.25	0.70	0.74	0.71	0.75	0.61	0.98
FR-Hes	1.00	0.99	0.59	0.92	0.68	1.00	0.61	0.64	0.59	0.62	0.56	0.87
Mediterranean evergreen conifers (MC)												
ES-ES1	1.00	1.03	0.51	0.71	0.80	1.29	0.58	0.52	0.56	0.49	0.52	0.74
FR-LBr	0.99	1.02	0.61	1.00	0.39	0.77	0.50	0.42	0.49	0.41	0.58	0.98
IT-SRo	1.00	1.02	0.64	0.94	0.67	1.05	0.68	0.65	0.68	0.64	0.62	0.93

Table 2. Continued.

Site	m_{NEE}:m_{GPP}		m_{GPP}:WUE_{GPP}		WUE_{NEE}:WUE_{GPP}		m_{NEE}: WUE_{NEE}		m_{GPP}:WUE_{NEE}		m_{NEE}:WUE_{GPP}	
	r	slope	*r*	slope	*r*	slope	*r*	slope	*r*	slope	*r*	slope
Mediterranean broad-leaved deciduous (MD)												
IT-Col	1.00	1.01	0.86	1.56	0.94	1.22	0.83	1.18	0.83	1.17	0.86	1.57
IT-Ro1	1.00	1.00	0.82	0.97	0.80	0.91	0.79	0.81	0.77	0.79	0.81	0.96
IT-Ro2	0.99	1.00	0.66	0.69	0.76	0.90	0.67	0.55	0.65	0.53	0.70	0.68
IT-Non	1.00	1.01	0.65	0.77	0.62	0.82	0.69	0.62	0.67	0.60	0.63	0.75
IT-PT1	1.00	0.99	0.79	1.10	0.82	0.98	0.80	0.93	0.79	0.93	0.79	1.09
Mediterranean broad-leaved evergreen (Mbeg)												
FR-Pue	0.97	0.98	0.70	0.76	0.74	1.00	0.63	0.56	0.62	0.55	0.60	0.72
IT-Cpz	1.00	1.01	0.69	0.74	0.78	1.12	0.67	0.51	0.67	0.51	0.67	0.74

Table 3. Mean WUEGPP ($\mathrm{g\,CO_2\,kg\,H_2O^{-1}}$) at GPP-max. (at highest 10% of GPP-values), under similar meteorological conditions (if mean daily temperature: 17.5–22.5°C, mean daily global radiation: 200–300 $\mathrm{W\,m^{-2}}$ and mean daily VPD: 5–15 hPa), as long-term average (all available data) and seasonal maximum (including month of year) for different functional vegetation types. The standard deviation (SD) is only reproduced if more than two sites within one vegetation type and if more than two years for calculating mean interannual variability were available, respectively. All daily WUEe-data were excluded if mean daily latent heat flux (LE) $<20\,\mathrm{W\,m^{-2}}$ and less than 80% of the half-hourly NEE-data of a single day were original or reliably filled.

Vegetation functional type	$\mathrm{WUE_{GPP}}$ ($\mathrm{g\,CO_2\,kg\,H_2O^{-1}}$)					
					Mean interannual variability (SD)	
	Mean at GPP-max. (SD)	Mean under similar meteorological conditions (SD)	Long-term average (SD)	Mean seasonal max. months)	From long-term average	From similar meteorological conditions
Boreal treeless wetland (BT)	1.8	1.3	1.2	1.8 (8)	0.2	0.4
Boreal evergreen conifers (BC)	4.2 (1.2)	3.4 (0.2)	2.9 (0.8)	3.7 (8–9)	0.8	0.9
Temperate evergreen conifers (TC)	4.6 (1.8)	3.3 (1.1)	3.5 (0.9)	4.1 (6–9)	0.5	0.3
Temperate mixed forests (TM)	5.1	3.9	4.5	5.2 (5–10)	0.6	0.6
Temperate broad-leaved deciduous (TD)	6.1 (0.8)	4.5 (0.4)	5.0 (0.6)	6.1 (6–10)	0.6	0.7
Mediterranean evergreen conifers (MC)	3.8 (0.4)	3.0 (0.5)	3.1 (0.7)	3.8 (10–2)	0.4	0.6
Mediterranean broad-leaved deciduous (MD)	4.6 (1.6)	3.4 (0.2)	3.4 (0.5)	4.3 (4–6, 10)	0.7	0.6
Mediterranean broad-leaved evergreen (Mbeg)	4.0	3.2	3.3	4.3 (3)	0.5	0.4

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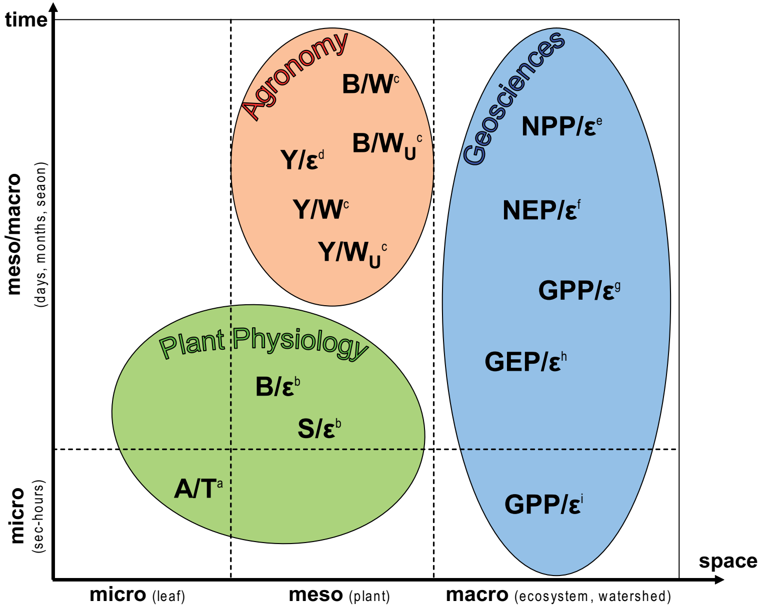

Fig. 1. Different calculation types of water-use efficiency depending on the scientific discipline (e.g. Plant Physiology, Agronomy, Geosciences) together with temporal and spatial scale. A=net CO_2 assimilation, B=total biomass or above ground biomass, S=stem biomass, Y=yield, NPP=net primary production, NEP=net ecosystem production, GPP=gross primary production, GEP=gross ecosystem production, T=transpiration, å=transpiration or evapotranspiration, W=total admitted water including precipitation, WU=amount of irrigated water. [a](e.g. Denmead et al., 1993), [b](e.g. Loomis and Connor, 1992), [c](e.g. Jones, 2004), [d](e.g. de Wit, 1958), [e](e.g. Schimel et al., 1997), [f](e.g. Mingkui and Woodward, 1998), [g](e.g. Reichstein et al., 2007), [h](e.g. Law et al., 2000), [i](e.g. Ponton et al., 2006).

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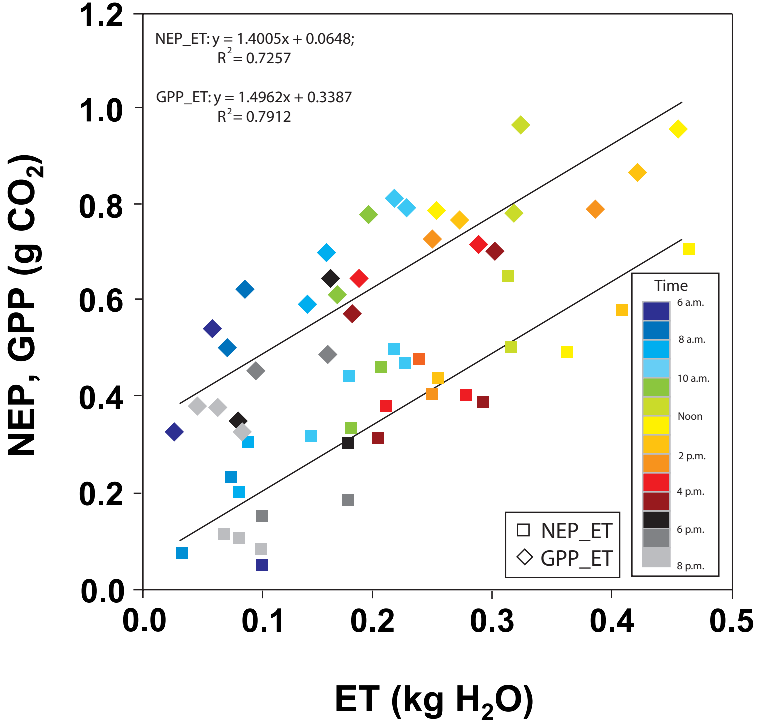

Fig. 2. Half-hourly sums of NEP and GPP versus ET between 6 a.m. and 8 p.m. on an average summer day, 15 July 2002, in the boreal coniferous forest Hyytiälä, Finland (FI-Hyy).

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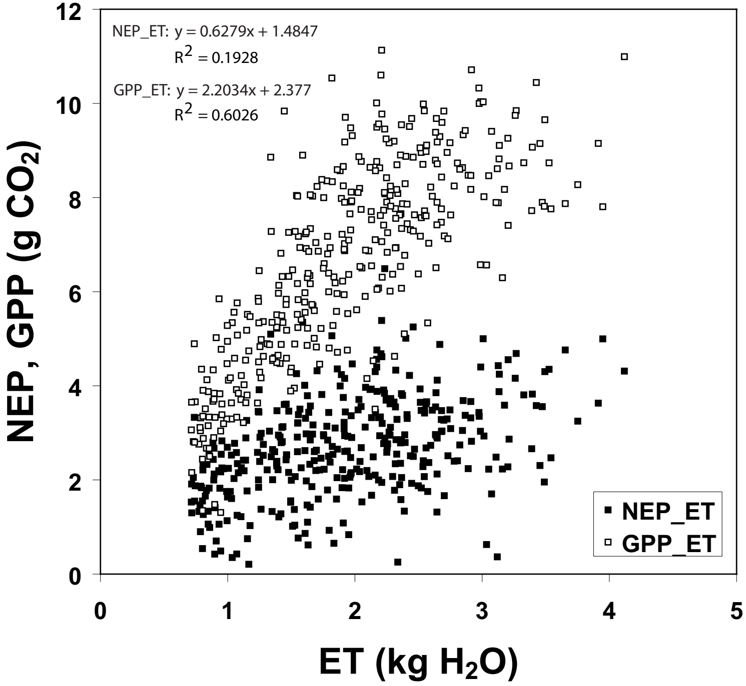

Fig. 3. Daily sums of NEP and GPP versus ET from half-hourly measurements for the boreal coniferous forest Hyytiälä, Finland (FI-Hyy).

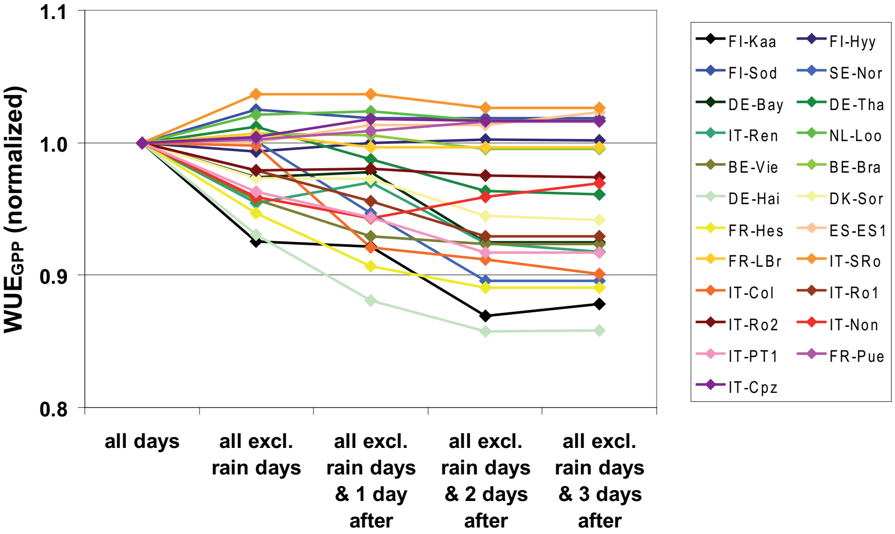

Fig. 4. Normalized medians of long-term water-use efficiency for each study site regarding the exclusion of days with potentially wet surfaces, i.e. no exclusion (=1), exclusion of rain days, exclusion of rain days and subsequent one, two and three days.

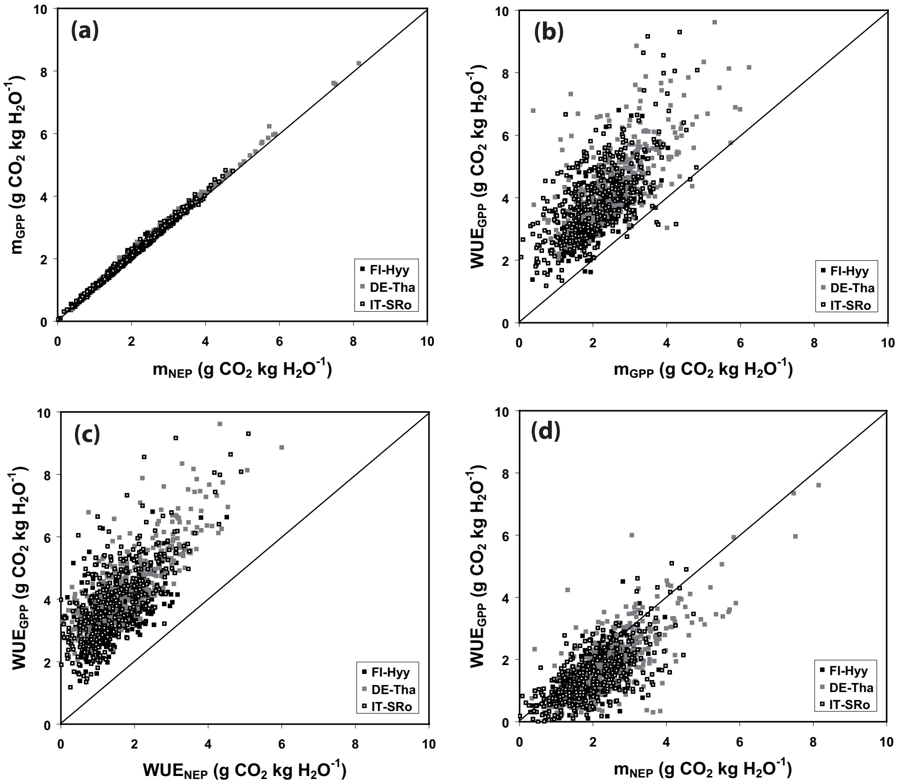

Fig. 5. Normalized medians of long-term water-use efficiency for each study site regarding the exclusion of days with potentially wet surfaces, i.e. no exclusion (=1), exclusion of rain days, exclusion of rain days and subsequent one, two and three days.

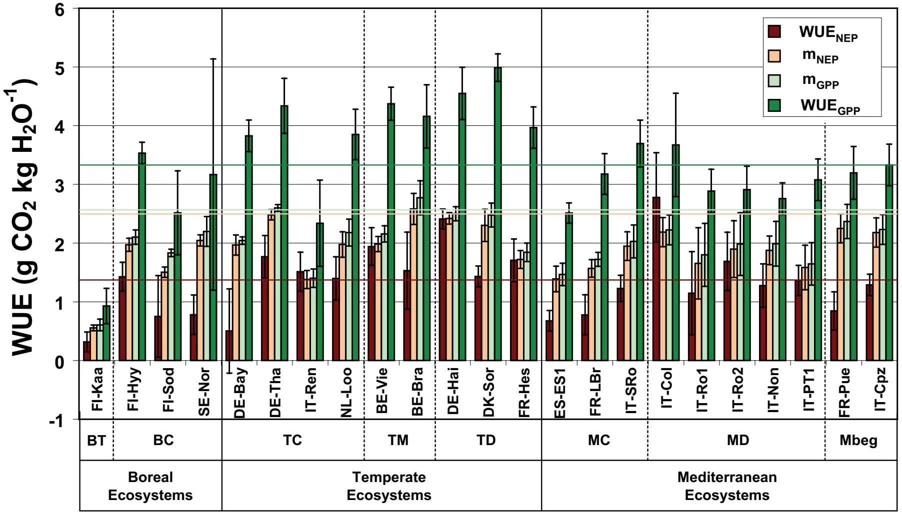

Fig. 6. Medians of long-term water-use efficiency from filtered daily values and different modes of calculation for all investigated Carboeurope-IP sites. Horizontal lines indicate means over all sites. The interannual variability of a single site is represented by the standard error bar.

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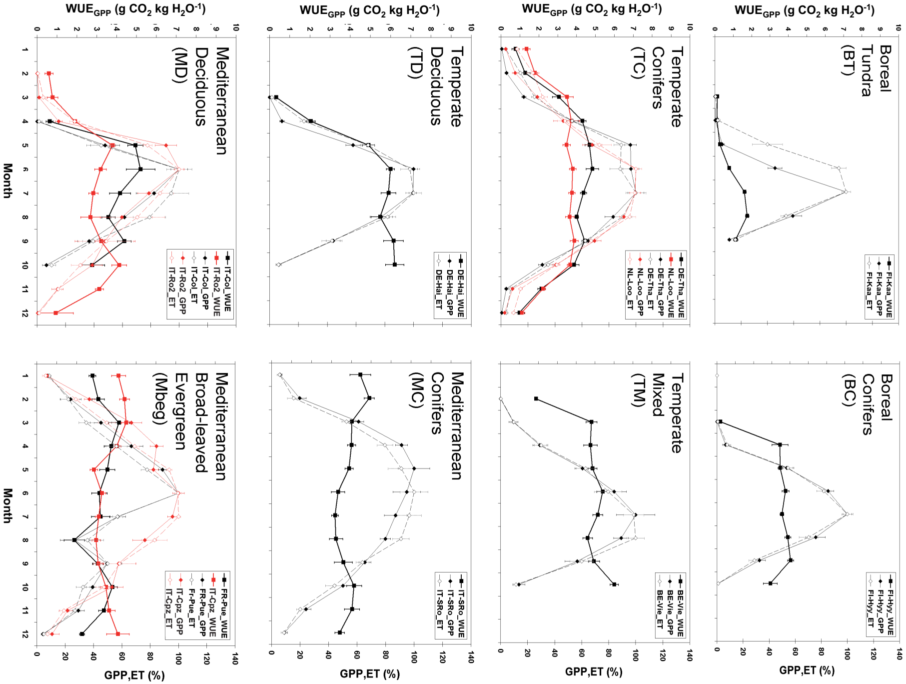

Fig. 7. Seasonal development of mean monthly WUEGPP, GPP and ET, for selected sites from Table 1. GPP and ET data are normalized such that the mean maximum monthly value equals 100%. The interannual variability is represented for every month by the standard error bar.

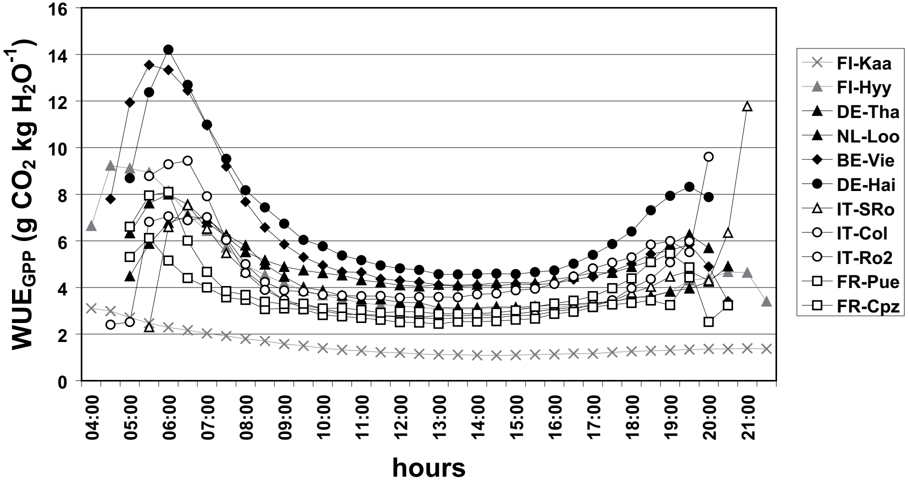

Fig. 8. Mean diurnal cycle of instantaneous WUEGPP for selected sites of each vegetation functional type.

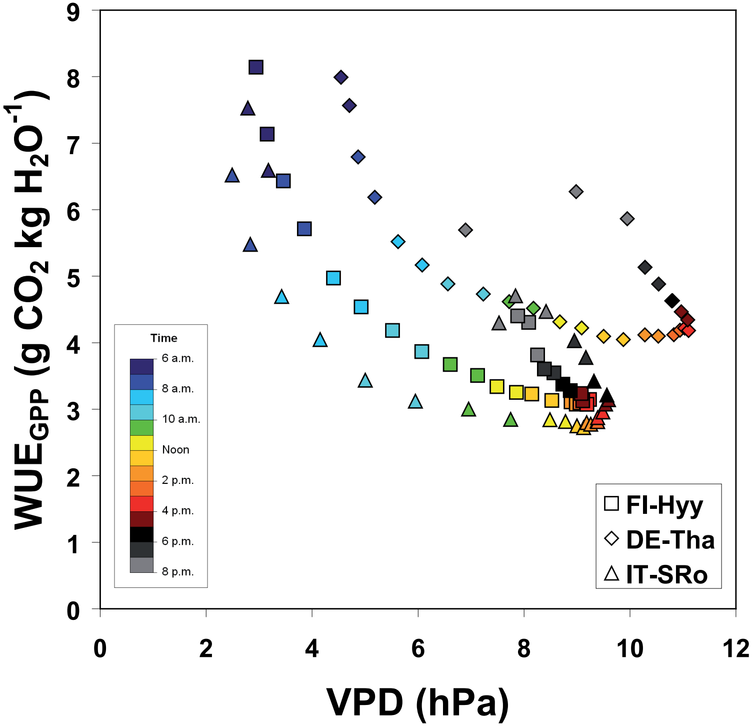

Fig. 9. Relations between half-hourly means of WUEGPP and VPD (hPa) between 6 a.m. and 8 p.m. for the three coniferous forests Hyytiälä, Finland (FI-Hyy), Tharandt, Germany (DE-Tha) and San Rossore, Italy (IT-SRo) that represent the boreal, temperate and Mediterranean zone.