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Discussions

The influence of leaf photosynthetic efficiency and stomatal closure on canopy carbon uptake and evapotranspiration – a model study in wheat and sugar beet

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Abstract

In this study two crop species, winter wheat (*Triticum aestivum*) and sugar beet (*Beta vulgaris*), were monitored over the course of five days during the entire season. We investigated the link of the main physiological leaf-level mechanisms, stomatal conductance and efficiency of photosynthetic energy conversion on canopy transpiration and photosynthetic CO_2 uptake. The physiological status of 900 leaves of different plants in a natural canopy was characterized on the leaf level using chlorophyll fluorescence. Gas exchange measurements were performed at leaves of 12 individual plants of each species. Eddy covariance flux measurements provided information on CO_2, water and energy fluxes on the field scale. The diurnal pattern of stomatal resistance on the leaf level was especially for sugar beet similar to the canopy resistance, which indicates that stomatal resistance may have a large impact on the bulk canopy resistance. The diurnal changes in canopy resistance appeared to have less effect on the evapotranspiration, which was mainly dependent on the amount of incoming radiation. The similar diurnal pattern of water use efficiency on the leaf level and on the canopy level during the day, underline the influence of physiological mechanisms of leaves on the canopy. The greatest difference between water use efficiency on leaf and canopy occurred in the morning, mainly due to an increase of stomatal resistance. Limitation of CO_2 uptake occurred in the afternoon when water vapor pressure deficit increased. Maxima of net ecosystem productivity corresponded to the highest values of photosynthetic capacity of single leaves, which occurred before solar noon. Within the course of a few hours, photosynthetic efficiency and stomatal resistance of leaves varied and these variations were the reason for diurnal variations in the carbon fluxes of the whole field. During the seasonal development, the leaf area index was the main factor driving carbon and water exchange, when both crops were still growing. During senescence of winter wheat these structural parameters did not account for changes in canopy fluxes and remaining high green leaf material of sugar beet did not present the reduction in canopy fluxes due to beginning dormancy. We thus hypothesize that the

functional status of plants is also important to correctly predict carbon and water fluxes throughout the season. We propose to additionally include the physiological status of plants in carbon flux models in order to improve the quality of the simulation of diurnal patterns of carbon fluxes.

1 Introduction

Photosynthesis is the dominant process determining carbon dioxide (CO_2) and water vapor (H_2O) fluxes between the terrestrial biogeosphere and the atmosphere. The physiology of a plant adapts dynamically to fast changes of environmental conditions such as light, temperature and water vapor pressure deficit of the air. Stomatal conductance and the efficiency of photosynthetic energy conversion are the main physiological control mechanisms. They are influenced by intrinsic and extrinsic stimuli and interactively regulate the rate of transpiration and photosynthetic CO_2 uptake (Farquhar and Sharkey, 1982; Willmer and Fricker, 1996). In general, photosynthetic CO_2 uptake is limited from its theoretical maximum and depends on availability of resources, mainly water and nitrogen when no disease or pest are involved. Environmental factors which influence plant performance are greatly variable on various time scales, ranging from seconds to seasons. Thus, photosynthesis almost never operates at a steady state, but continuously adapts to changing environmental conditions like light, temperature and changes in humidity (Rascher and Nedbal, 2006; Schurr et al., 2006).

Photosynthesis is commonly characterized in single leaf measurements to derive the carboxylation efficiency, which is then used to project to the ecosystem carbon fluxes (Collatz et al., 1991). However, scaling from the leaf to the canopy is challenging because of the large variability of the environment, plant and leaf properties within different patches of the ecosystem. Leaves within the canopy are exposed to rapidly changing spatio-temporal light conditions as well as gradients of meteorological parameters such as temperature and vapor pressure deficit inside and above the canopy (Arain et al., 2000; Bauerle et al., 2007; Hirose and Werger, 1987).

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀◀ ▶▶
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Feedback mechanisms within canopies are thought to decrease the impact of single leaves and stomata on the bulk canopy exchange of water and carbon, and it is postulated that with increasing scale the exchange processes between terrestrial vegetation and the atmosphere are increasingly driven by the atmospheric boundary layer (Jarvis and McNaughton, 1986).

In many models, photosynthetic CO_2 uptake and plant evapotranspiration is estimated by accounting for different levels of complexity from mechanistic soil-vegetation-atmosphere transfer models (SVAT) to empirical formulations, where photosynthesis is simply modeled as a function of plant functional group, temperature and light (see Cramer et al., 1999 for an overview). In the few past years, it has been recognized that ignoring the physiological responses of plant ecosystems to environmental constraints may introduce substantial uncertainties in modeling terrestrial carbon and water fluxes (Gerbig et al., 2009; Hanan et al., 2005; Sarrat et al., 2009).

Despite the importance of applying plant physiological processes from the leaf to the canopy and ultimately to the ecosystem, up to now only limited data is available on the contribution of physiological processes of single leaves to canopy exchange under field conditions (Hoyaux et al., 2008). The combination of measurements on the leaf and canopy scale is mostly based on theoretical assumptions (Collatz et al., 1991). One reason for this gap might be the lack of a suitable methodology for measurements on different scales.

On the leaf level, it is possible to determine the physiological status of photosynthesis by using fluorescence measurements (Baker, 2008; Genty et al., 1989; Krause and Weis, 1991) or gas exchange measurements, which can separate the photosynthetic CO_2 uptake, respiration and transpiration rate of a single leaf (Long and Bernacchi, 2003).

On the canopy level, eddy covariance (EC) measurements provide a powerful tool to determine CO_2 and water fluxes (Baldocchi, 2003). EC is a bulk measurement of the exchange processes of the entire ecosystem and provides little constraint on the bottom-up scaling approaches. More targeted measurements of the performance of many individual leaves in the context of their diverse natural environments in the canopy are necessary. It should be kept in mind that the total of the individuals matches the top-down constraint provided by EC measurements. Unfortunately, limited access to the leaves of many canopies and the impossibility of accurately measuring many leaves under naturally fluctuating conditions put major constraints on combined leaf and canopy level measurements. Agricultural systems provide a unique opportunity to perform important field measurements. Monocropping and potential access to plant individuals provide the opportunity to compare the performance of single leaves and bulk canopies.

In this study, we compared the characteristics of the photosynthetic efficiency of two agricultural C_3-plants, winter wheat and sugar beet, on the timescale of a day as well as seasonal changes. The detailed leaf-level characterization of the physiology of winter wheat and sugar beet was carried out in close combination with integrated CO_2 and water flux measurements performed by the EC method on the canopy level. The interpretation of characteristic diurnal and seasonal patterns of leaf-level gas exchange and fluorescence measurements can help to interpret the diurnal pattern of CO_2 and water fluxes on the canopy scale.

2 Materials and methods

2.1 Study site

The measurements were embedded in the FLUXPAT campaign, an experimental study of spatio-temporal structures in atmosphere-land surface energy, water and CO_2 exchange. For an overview of all measurements during the FLUXPAT field campaigns see Schween et al. (2009).

The test sites are located in a region dominated by agriculture within the Rur catchment (North Rhine-Westphalia, Germany). The main crops in this area are cereals and sugar beet; rape and corn can also be found in some scattered areas. Two intensive

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀I ▶I
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

measurement fields, a winter wheat field (*Triticum aestivum* "Raspail") near Selhausen (50°52′12.82″ N, 6°26′59.59″ E, 105 m a.s.l.) and a sugar beet field (*Beta vulgaris* "Lucata") near Merken (50°50′46.93″ N, 6°23′48.99″ E, 114 m a.s.l.) were chosen for the measurements.

While the sugar beet field had a maximum altitude difference of less than 1 m within the field the winter wheat field crossed a gentle terrain step with an altitude difference of about 4 m between the lower and the higher part. This led to a marked difference in stone content (particles >2 mm) from more than 55% in the higher to less than 5% in the lower part of the fields. The texture of the soil (<2 mm) was silt loam at both sites according to the USDA classification.

Winter wheat was sown at day of the year (DOY) 323 in 2007 and harvested at DOY 219 in 2008. Sugar beet was sown at DOY 112 in 2008, later than usual because of a prolonged rainy period. The plants were harvested in October 2008. Even though sugar beet is a biannual plant it is usually harvested at the end of the first growing year. Thus, sugar beet did not show any senescence or reduction of green leaf material at the time of harvest.

The core measurements were performed on five days in 2008, which were selected by the phenological status of the crops plus preferably cloudless weather conditions. Winter wheat was measured during different growth stages in spring and summer on DOY 127 and on DOY 176. While on DOY 127 the winter wheat was in the three knops development stage (code 33 according to the BBCH table of Meier, 1997) on DOY 176 flower was already over and the ears were fully developed but still green (BBCH-scale 75). Sugar beet measurements were performed on DOY 183, DOY 229 and DOY 253. On DOY 183 more than 9 leaves of the sugar beet pant were already developed (BBCH-scale 31) and DOY229 the canopy continued to close up (BBCH-scale 33). On the last measurement day the canopy was nearly closed (BBCH-scale code 39).

On each day, the total diurnal course was measured from 07:00 to 16:00 UTC.

2.2 Measurements at leaf level

Leaf chlorophyll content of the two species was determined frequently over the whole vegetation period to give information about the development status of leaves. Leaf-level measurements of diurnal change on photosynthesis, CO_2 and H_2O exchange on the five measurement days were performed using a pulse-amplitude-modulated (PAM) fluorometer and a gas exchange analyzer (Fig. 1).

2.2.1 Chlorophyll content

The leaf chlorophyll content was determined with a chlorophyll meter SPAD-502 (Spectrum Technologies Inc. Plainfield, IL, USA). By measuring the absorbance of the leaf in the red and near-infrared band the amount of chlorophyll present in the leaf tissue can be deduced. Earlier measurements showed that the chlorophyll content of leaves does not change in the course of a day (data not shown). Therefore 200 SPAD measurements, randomly distributed inside the canopy, were taken once a day.

SPAD readings were calibrated for each species using laboratory analysis methods. For calibration, leaf disks were cut with a cork borer and instantly stored in liquid nitrogen. Leaf pigments were later extracted and spectroscopically analyzed using the method described by Lichtenthaler (1987).

2.2.2 Fluorescence measurements

To characterize diurnal and seasonal changes of the light reaction of photosynthesis the fluorescence signal of chlorophyll *a* was used. Chlorophyll fluorescence is emitted from photosynthetic active leaves in the red and near-infrared spectrum and is indirectly correlated to the energy used for photosynthesis (see Baker, 2008 for an overview).

These chlorophyll fluorescence measurements were performed on the five measurement days with the miniaturized pulse-amplitude-modulated photosynthesis yield

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀| |▶
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

analyzer Mini-PAM (Heinz Walz GmbH, Eichenring, Effeltrich, Germany). Fluorescence was stimulated by pulsed-modulated red light from a light-emitting diode (LED).

Leaves inside the canopy were dark-adapted (> 30 min) to measure the initial fluorescence (F_0). Afterwards a saturating light pulse was applied to the leaf to determine the maximum fluorescence (F_m) of dark-adapted leaves and subsequently the potential quantum yield ($F_\mathrm{v}/F_\mathrm{m}$) of photosystem II (PS II) was determined according to

$$F_\mathrm{v}/F_\mathrm{m} = \frac{F_\mathrm{m} - F_0}{F_\mathrm{m}}. \tag{1}$$

Healthy leaves of higher plants have $F_\mathrm{v}/F_\mathrm{m}$ values of 0.83 while significantly lower potential quantum yield values indicate damage to PS II due to photoinhibition (Björkman and Demmig, 1987).

Light-adapted measurements over leaves exposed to ambient incident photosynthetic photon flux density (PPFD) were performed with a leaf clip holder described by Bilger et al. (1995). In the course of one day 900 light adapted measurements on randomly distributed leaves inside the canopy were measured to determine the fluorescence yield (F) at ambient light conditions, taking special care not to change the ambient conditions, e.g. the angle of the leaf or shading. To determine maximum fluorescence ($F_{\mathrm{m}'}$), a saturating pulse was superimposed on ambient light conditions. The effective quantum yield ($\Delta F/F_{\mathrm{m}'}$) of the light reaction of PS II was measured after Genty et al. (1989) according to

$$\Delta F/F_{\mathrm{m}'} = \frac{F_{\mathrm{m}'} - F}{F_\mathrm{m}}. \tag{2}$$

The photosynthetic electron transport rate (ETR) was derived from the fluorescence measurements as

$$\mathrm{ETR} = \Delta F/F_{\mathrm{m}'} \cdot \mathrm{PPFD} \cdot 0.5 \cdot 0.84, \tag{3}$$

the factor 0.5 assumes equal excitation of both PS II and PS I; 0.84 accounts for the standard ETR-Factor defining the fraction of incident light estimated to be absorbed by the sample.

Thus, ETR can be interpreted as the amount of exited chlorophyll electrons that are used for photochemistry. Non-photochemical quenching (NPQ) was calculated as after Bilger and Björkman (1990) according to

$$\mathrm{NPQ} = \frac{F_{\mathrm{m}'} - F_{\mathrm{m}}}{F_{\mathrm{m}'}}. \tag{4}$$

NPQ mechanisms protect the photosynthetic apparatus from photo-oxidative damage by degrading excess energy into heat.

2.2.3 Gas exchange measurements

Leaf-level gas exchange was measured using the LI-6400 (LiCor, Lincoln, NE, USA). This is an open measurement system, where air flow was moved through a controlled atmosphere surrounding a plant leaf enclosed in an assimilation chamber. The CO_2 and H_2O exchange was then measured with infrared gas absorbance. The CO_2 level of the air was maintained in a steady state at 390 ppm. The light response curves of the net CO_2 assimilation rate (*A*) and transpiration rate (Tr) were measured using the LED light source LI-6400-02B (LiCor, Lincoln, NE, USA). Radiation was set to 2000, 1000, 500, 200, 100, 50, 20, 10 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ and dark. Air humidity and temperature inside the measuring chamber were adjusted to ambient conditions. Since the determination of a light response curve took approximately 45 min, up to twelve measurements on individual plants were performed from 07:00 to 16:00 UTC on each observation day. On DOY 127 the fully developed leaf from the upper layer at this development stage was taken to perform gas exchange measurements. On DOY 176 lower layers already started to be senescent, thus, the flag leaf was used for the measurements. For sugar beet mature leaves were available on all days and gas-exchange measurements were performed on randomly selected mature leaves of the external ring of the sugar beet rosette.

2.3 Integrating leaf-level measurements to the canopy scale

Characterization of structural parameters was performed in a two weeks frequency over the whole vegetation period to obtain information about the development status of the plant canopy. Leaf-level measurements carried out with PAM fluorometry were used to achieve characteristic plant parameters, which represent the physiological plasticity of a species. Light curves of the gas exchange measurements allowed the estimation of maximum photosynthetic parameters to characterize the potential photosynthetic performance at saturating light intensity (Fig. 1).

2.3.1 Leaf area index and canopy height

The leaf area index (LAI) is the total one-sided area of leaf tissue per unit ground surface area. It is a key parameter in ecophysiology and in studies of plant growth. A destructive method was used to derive the LAI. Three spots were sampled for each field. At each spot the canopy height was measured three times. Afterwards for each spot the leaves of two rows of winter wheat, with a length of 60 cm, and three plants of sugar beet were harvested. The leaf area of the harvested leaf material was determined with a LI 3000A area meter (LiCor, Lincoln, NE, USA). Green and yellow leaf materials were treated separately. The LAI [$m^2\,m^{-2}$] was determined taking into account the row distance of winter wheat and plant closeness for sugar beet.

2.3.2 Maximum electron transport rate and non-photochemical quenching parameter at saturating light intensity

Additional information on characteristic plant parameters of a species, which are not related to the momentary ambient light conditions, but rather to the ontogeny of a leaf and to the range of physiological plasticity of a plant, can be derived from light response curves. Therefore all ETR versus PPFD values of a 1.5 h window (n=150) were fitted with an single exponential rise to maximum function

$$f(x) = a \cdot (1 - \exp^{-b \cdot x}) \tag{5}$$

in order to quantify the maximum electron transport rate (a=ETR$_{\max}$), which is an indicator of the photosynthetic capacity of the plant canopy (Fig. 1; Rascher et al., 2000). To eliminate the dependence of light intensity on NPQ, the mean for each 1.5-h window of all measured NPQ values between a PPFD of 900 and 1300 µmol m^{-2} s^{-1} was taken to give the non-photochemical quenching parameter at the saturating light intensity of 1100 µmol m^{-2} s^{-1} (NPQ$_{1100}$). Light-adapted measurements in May could not be used because of technical difficulties.

2.3.3 Maximum photosynthetic CO$_2$ uptake, maximum transpiration rate and maximum stomatal resistance to water vapor pressure

To characterize the potential photosynthetic performance of different plants during the day maximum net photosynthetic CO$_2$ uptake rate ($A_{\max}$) was estimated from each light response curve of gas exchange measurements (Fig. 1) using a single exponential rise to maximum function

$$f(x) = y_0 + a \cdot \exp^{-b \cdot x}. \tag{6}$$

Since the mean transpiration rate at high light intensities at 1000 µmol m^{-2} s^{-1} and 2000 µmol m^{-2} s^{-1} were not significantly different from each other but individual measurements still showed some variability, data points at 2000 µmol m^{-2} s^{-1} were excluded from the light curve for estimating maximum transpiration rates (Tr$_{\max}$) and maximum stomatal resistance (rs$_{\max}$) to water vapor pressure using Eq. (6).

2.3.4 Potential water use efficiency based on leaf-level measurements

According to the general definition, water use efficiency is given by the ratio of net assimilation and water loss. In this study we defined the potential water use efficiency at saturated light intensities but prevailing conditions of temperature and humidity, that was derived from the leaf-level measurements (${}_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}}$) according to

$$ {}_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}} = \frac{A_{\max}}{\mathrm{Tr}_{\max}} \tag{7} $$

with the maximum net photosynthetic CO_2 uptake rate ($A_{\max}$) divided by maximum transpiration rate ($\mathrm{Tr}_{\max}$).

2.4 Measurements above the canopy

2.4.1 Turbulent fluxes

A tower equipped with a CSAT3 sonic anemometer (Campbell Scientific, Inc., Logan, UT, USA) and an LI-COR 7500 open-path infrared gas analyzer for water vapor and CO_2 (LiCor, Lincoln, NE, USA) mounted between 1.45 m and 2.20 m, depending on station and measurement day, was installed on both fields to perform turbulence measurements during the whole vegetation season (Graf et al., 2010).

Additional measurements of air temperature (CS215, Campbell Scientific, Inc., Logan, UT, USA) and global radiation (SP-LITE, Kipp & Zonen, Delft, Netherlands) were taken on the winter wheat field (Fig. 1).

Gas analyzer data were logged at a temporal resolution of 20 Hz. CO_2 flux (net ecosystem exchange NEE=−NEP net ecosystem productivity) and evapotranspiration (E), as well as its energy equivalent, the latent heat flux (λE), were calculated at half-hour resolution from the turbulence data by the eddy covariance method (EC). The dataset from the winter wheat field was analyzed using the TK2 software (Mauder and Foken, 2004), whereas for the sugar beet field data the ECpack software (Van Dijk, 2004) was used. Analysis of a reference data set by both software programs provided similar results. Sensible heat flux (H) was corrected according to the method of Schotanus et al. (1983), the influence of density fluctuation on the other scalar fluxes according to Webb et al. (1980) and the spectral loss correction (revised after Moore, 1986). For the adjustments of the vector coordinate system the double rotation method (Kaimal and Finnigan, 1994) was applied for sugar beet and the planar fit method after Wilczak et al. (2001) for winter wheat.

2.4.2 Canopy resistance based on eddy covariance measurements

Bulk canopy resistance (rc) is defined as an integrated value of the leaf stomatal resistance of a canopy. According to the "big leaf" model of Penman–Monteith, rc presents the resistance of the entire vegetation canopy to the diffusion of water vapor from leaves to the atmosphere as a result of stomatal regulation. Therefore canopy resistance was calculated using a rearranged form of the Penman–Monteith equation (Kumagai et al., 2004; Monteith and Unsworth, 1990):

$$\mathrm{rc} = \left[\left(\frac{s}{\gamma}\right)\beta - 1\right] r_\mathrm{a} + \frac{\rho_\mathrm{a}\, c_\mathrm{p}}{\gamma}\frac{\mathrm{VPD}}{\lambda E} \tag{8}$$

where s [Pa K^{-1}] is the rate of change of saturation water vapor pressure with temperature, γ is the psychrometric constant [66.5 Pa K^{-1}], β is the Bowen ratio (H/λE), r_a is the aerodynamic resistance [m^{-1} s], ρ_a is the density of dry air [kg m^{-3}], c_p is the specific heat of air at constant pressure [J kg^{-1} K^{-1}] and VPD [kPa] is the vapor pressure deficit of the air, defined as the difference of saturation water vapor pressure and water vapor pressure at current air temperature.

The aerodynamic resistance was derived by the empirical equation of Thom and Oliver (1977):

$$r_\mathrm{a} = \frac{4.72[\ln((z-d)/z_0)]^2}{1+0.54u} \tag{9}$$

where u [m s^{-1}] is the wind speed at measurement height z [m] (winter wheat: 1.95 m; sugar beet: 1.45 m on DOY 183 and 2.20 m on DOY 229 and 253). The zero plane displacement (d) [m] and the roughness length (z_0) [m] were approximated as 0.63 and 0.13 times the vegetation height, respectively (Monteith and Unsworth, 1990).

2.4.3 Canopy water use efficiency

Canopy scale fluxes are the joint result of gas exchange in all plant organs as well as the non-stomatal components of plant and soil evaporation, and respiration. Nevertheless, we define the ratio between the total downward CO_2 and the total upward water vapor flux, which thus represents the actual water use efficiency ($\mathrm{WUE_C}$) of the whole canopy-soil system:

$$\mathrm{WUE_C} = \frac{\mathrm{NEP}}{E} \tag{10}$$

Half-hourly EC measurements were used to obtain $\mathrm{WUE_C}$. It was calculated by dividing the daytime net ecosystem productivity (NEP) by the corresponding evapotranspiration (E) values (see Sect. 2.4.1).

3 Result

3.1 Diurnal pattern

In the following, we will present the general diurnal pattern of different plant physiological parameters measured on the leaf and canopy level on five intensive measurement days: DOY 127 and 176 for the winter wheat field and DOY 183, 229 and 253 for the sugar beet field.

The main focus of this study was on a qualitative comparison of the diurnal pattern between parameters measured on the leaf and canopy level. All diurnal cycles were measured on days with no (Fig. 2Ba,Ca,Ea) or only minor cloud cover (Fig. 2Aa,Da) as can be deduced from the small variation of the global radiation in the first row of Fig. 2.

For all days, VPD increased from values of 0.5 kPa or lower to a maximum in the afternoon greater than 1.5 kPa (Fig. 2Aa–Ea) and decreased in a few cases in the late afternoon (Fig. 2Ea), thus in part reflecting the course of the temperature with a maximum in the afternoon. Maximum leaf transpiration rates ($\mathrm{Tr_{max}}$) did not follow VPD, but rather showed constant values of around 2–6 $\mathrm{mmol\,m^{-2}\,s^{-1}}$ all day for both species (Fig. 2Ab–Eb). Canopy evapotranspiration (E) reached a maximum of 6–8 $\mathrm{mmol\,m^{-2}\,s^{-1}}$ shortly after solar noon (11:30 UTC) on clear days (Fig. 2Bb,Cb,Eb) or the highest values of global radiation on days with few clouds (Fig. 2Ab,Db;Aa,Da). Stomatal resistance ($\mathrm{rs_{max}}$) at saturating light intensity on the leaf level showed no daily course for winter wheat (Fig. 2Ac,Bc) whereas for sugar beet $\mathrm{rs_{max}}$ increased over the day (Fig. 2Cc–Ec). It should be noted that temperature in the leaf chamber of the LI-Cor 6400 was set to match the external ambient air temperature (see Sect. 2.2.3). On DOY 127, low temperatures in the morning hours significantly affected leaf stomatal resistance, hence, $\mathrm{rs_{max}}$ values were highest (Fig. 2Ac). Canopy resistance (rc) of winter wheat and sugar beet was similar with rather constant values of rc in the morning when both evapotranspiration and VPD increased and an increase of rc in the afternoon (Fig. 2Ac–Ec) when only VPD still increased. On the early morning of DOY 127 and 183, dew led to unrealistically high values of rc. As in such cases the Penman–Montheith equation is no longer valid and as the Bowen ratio may generate a large bias, we excluded these values.

In particular for sugar beet, highest maximum electron transport rates ($\mathrm{ETR_{max}}$) were observed in the morning before solar noon (Fig. 2Cd–Ed). The potential quantum yield of PS II of dark-adapted leaves ($F_\mathrm{v}/F_\mathrm{m}$) for both species showed neither a significant diurnal variation nor changes in seasonal characteristics, which indicates there was no chronic or serious damage due to photoinhibition (Fig. 2Ad–Ed; Dodd et al., 1998). Maximum leaf net $\mathrm{CO_2}$ uptake rates (A_max) of winter wheat showed no distinct diurnal cycle but constant values of A_max around 10–30 $\mathrm{\mu mol\,m^{-2}\,s^{-1}}$ (Fig. 2Ae,Be). In contrast, values of A_max for sugar beet decreased over the day (Fig. 2Ce–Ee). A_max was found to be sensitive to stomatal resistance on the leaf level ($\mathrm{rs_{max}}$) with a pronounced negative correlation for both species (Table 1). On the canopy level, the net ecosystem productivity (NEP) obtained from the eddy covariance method reached maxima at solar noon for winter wheat (Fig. 2Ae,Be) and before solar noon for sugar beet (Fig. 2Ce–Ee).

For both species water use efficiency on the leaf level ($_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}}$) and actual water use efficiency on the canopy level ($\mathrm{WUE}_{\mathrm{C}}$) (Fig. 2Af–Ef) showed highest values in the morning and decreased throughout the day. In general, values of $_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}}$ were higher or in the same range than $\mathrm{WUE}_{\mathrm{C}}$. Only at DOY 127 one value in the morning and two $_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}}$ values in the afternoon were slightly lower than $\mathrm{WUE}_{\mathrm{C}}$.

On the leaf level $_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}}$ was measured as the potential maximum water use efficiency under saturating light intensities inside a clip-on leaf chamber under the prevailing temperature and humidity conditions. The $_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}}$ was higher in the morning than in the afternoon for both species (Fig. 2Af–Ef). This decrease was due to lower humidity and higher temperature in the afternoon and the increase of stomatal resistance throughout the day, especially for sugar beet. On the canopy level, values of $\mathrm{WUE}_{\mathrm{C}}$ were calculated as the ratio between the molar fluxes of water vapor and CO_2 and thus they are the actual water use efficiency of the canopy-soil system including the non-stomatal components of plant and soil evaporation and respiration. In the morning, photosynthesis enhanced more rapidly than evapotranspiration under increasing solar radiation and led to high $\mathrm{WUE}_{\mathrm{C}}$ in the morning for both species (Fig. 2Af–Df). Thereafter $\mathrm{WUE}_{\mathrm{C}}$ decreased gradually because declining photosynthesis and increasing respiration led to a decrease in NEP in the afternoon.

The feedback of VPD on stomatal resistance indicates the strong decrease of $_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}}$ and influences $\mathrm{WUE}_{\mathrm{C}}$. The negative correlation between VPD, $_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}}$ and $\mathrm{WUE}_{\mathrm{C}}$, respectively, can be described with a single exponential decay decreasing function (Fig. 3, Table 2).

Maximum photosynthetic electron transport rate ($\mathrm{ETR}_{\mathrm{max}}$) and non-photochemical quenching parameters at saturating light intensity (NPQ_{1100}) were negatively correlated and showed a dynamic adaptation of the photosynthesis in the seasonal cycle of the sugar beet crop which can be described by a linear fitting function (Fig. 4; axis interception $b=2.69$, the slope $m=-0.00578$, correlation coefficient $r=-0.93$, number of data points $n=18$ and the significance of correlation p-value<0.0001).

This indicates a regulation of photosynthetic and non-photosynthetic energy conversion of light reaction throughout the season. NPQ_{1100} increased during the season whereas the $\mathrm{ETR}_{\mathrm{max}}$, which is indicator of photosynthetic capacity, declined. In addition to the dynamics of the regulation of photosynthetic energy conversion an increase of leaf chlorophyll content during the season was detected, which indicated that changes of the physiological status of photochemistry due to beginning dormancy which was not accompanied with reduction of leaf chlorophyll content in sugar beet leaves (Fig. 4).

There was only one day with full daily coverage in winter wheat (DOY 176) which showed rather low NPQ_{1100} values (Fig. 4). During this measurement, winter wheat had already finished flowering and grain filling was in progress. Thus the reduced non-photochemical protection with still high photosynthetic electron transport could be interpreted as a strategy to maximize carbon uptake for grain filling by reduced long-term photo-protection, which is acceptable for leaves that will soon be senescent.

3.2 Seasonal variation

The two crops showed differences in their development stages during the vegetation period that greatly influenced CO_2 and water fluxes on leaf and canopy level during the season. After the vernalization of winter wheat, the vegetation height increased to a maximum of 80 cm. Simultaneously, green LAI increased to a maximum of $5.5\,\mathrm{m}^2\,\mathrm{m}^{-2}$ (DOY 136; Fig. 5a). The canopy reached maturity at the end of May (DOY 150) when flowering was already finished and grain filling began. At this time the amount of yellow leaf material increased, while green leaf material was reduced (Fig. 5a). Senescence of the wheat started at the bottom and advanced upwards to the flag leaves during the developmental stages.

During the growing phase of winter wheat from the beginning of March (DOY 62) to the middle of May (DOY 136), the increase of green LAI corresponded to a constant rise of E and NEP (Fig. 5a,e,g). After the highest LAI had been reached, the wheat canopy still showed high photosynthetic activity (Fig. 5g) until mid June (DOY

166), although yellowing already started at the lower leaves. The seasonal development of water fluxes at the winter wheat field was more variable than the CO_2 flux (Fig. 5e). After harvesting in the first half of August (DOY 218), evapotranspiration still displayed values of up to 2–3 mmol m^{-2} s^{-1} due to evaporation from the soil (Fig. 5e). The mean apparent maximum transpiration rate (Tr_{max}) on leaf level was always lower than the canopy measurements because non-stomatal components like evaporation from soil and plants contribute to water loss of the field (Fig. 5e). The maximum net CO_2 uptake rate (A_{max}) of single leaves of winter wheat was lower than NEP during the growing period (DOY 127) when green LAI was up to 5.6 m^2 m^{-2} (Fig. 5a) and approximately similar to NEP on DOY 176 because of the already strongly reduced green LAI (2 m^2 m^{-2}; Fig. 5a). On this measurement day only the upper leaves of the canopy which are exposed to the sunlight showed high leaf chlorophyll content and photosynthetic activity. In this case, A_{max} on the leaf level could be seen as an approximation of the NEP of the whole canopy.

Sugar beet was sown on DOY 112. The vegetation height of sugar beet stagnated at around 65 cm from DOY 200 on (Fig. 5b), but the green LAI still rose until the end of September (Fig. 5b). Since sugar beet is a biannual crop no senescence or reduction of green leaf material but dormancy can be expected at the end of summer. Sugar beet EC measurements showed large gaps during the season, because the measurements were performed with a roving station that was used on other fields between the insensitive measurement periods on this sugar beet field. Nevertheless, the development of sugar beet E and NEP followed the green LAI during the growing period (Fig. 5b,f,h). Even tough LAI rose until the end of measurements the canopy CO_2 and water fluxes showed a decrease towards the end of the measurement period (Fig. 5f,h). Mean daily A_{max} values were larger than NEP values while Tr_{max} values were lower than E (Fig. 5f,h).

4 Discussion

In the present study, we investigated the structural and functional properties of two important crop species, winter wheat (*Triticum aestivum*) and sugar beet (*Beta vulgaris*), by monitoring their performance on the leaf and canopy level over the course of five days and the entire season. The analysis of structural parameters allowed an evaluation of the growth status of both plant species (see Sect. 2.2), the physiological status of plants was intensively characterized on the level of leaves (see Sect. 2.3), and the entire canopy by carbon and water flux measurements with the eddy covariance method (see Sect. 2.4).

In our study, maximum transpiration ($\mathrm{Tr_{max}}$) on the leaf level was quite variable during the course of the day for both species (Fig. 2Ab–Eb). This may be due to the variability of individual plants and leaves although leaves of the same order and development stage were chosen. Stomatal resistance ($\mathrm{rs_{max}}$) showed no pronounced diurnal pattern for winter wheat (Fig. 2Ac,Bc). Sugar beet, however, showed an increase of $\mathrm{rs_{max}}$ towards the afternoon when VPD increased (Fig. 2Cc–Ec). The higher sensitivity of stomatal resistance of the sugar beet leaves in contrast to winter wheat may be explained be the different construction of root distribution. Winter wheat roots can reach up to 1.5 m depth and are widely distributed in the soil while sugar beet roots can reach the same depth but are taproots, which are more locally attached. This may affect the water absorption and influence the sensitivity of stomatal resistance of sugar beet plants. Leaf and canopy architecture of both species is also different. Winter wheat leaves are long and narrow and are arranged in different layer. Hence most solar energy is absorbed by the upper layer of the canopy. The denseness of the canopy as well as the canopy height could cause a microenvironment with high humidity inside the canopy, which reduces the sensitivity of stomatal resistance of the winter wheat leaves. Sugar beet in contrast has larger leaves, which are in an erectophil position in the morning. Leaf inclination changes gradually through the day to a planophil position and the rosette arrangement of the leaves support an optimum supply with solar energy, already during the morning hours when sun angles are low. This might lead to a higher sensitivity of stomatal resistance of the sugar beet plant towards VPD than for winter wheat. The dependence of stomatal resistance on VPD has been discussed in numerous publications. However, Monteith (1995) reanalyzed a number of studies by regarding the interaction of stomatal resistance, transpiration and VPD and concluded, as did Mott and Parkhurst (1991), that the stomata respond to the rate of transpiration rather than directly to VPD or humidity. Our results support this view and show a negative correlation for both species between $\mathrm{Tr}_{\mathrm{max}}$ and $\mathrm{rs}_{\mathrm{max}}$ (Fig. 2Ab–Eb,Ac–Ec; Table 1), but no consistent relationship between $\mathrm{rs}_{\mathrm{max}}$ and VPD. Sugar beet indicated a positive response of $\mathrm{rs}_{\mathrm{max}}$ to an increasing VPD (Fig. 2Cc–Ec,Ca–Ea; Table 1), while for winter wheat (Fig. 2Ac,Aa; Table 2) no dependency or only a slightly negative but not significant response was detected (Fig. 2Bc,Ba; Table 1). Previous studies with winter wheat also showed no consistent response of stomatal resistance to VPD. While Bunce (1998) found that stomata of wheat may respond to the changes of VPD, Condon et al. (1992) showed a different response of stomata to VPD, which was related to different cultivars. Inoue et al. (1989) and Rawson et al. (1977) reported no response of leaf stomatal resistance to an increase of VPD, but an increase of transpiration rate related to VPD changes as observed in the present study (DOY 176; Fig. 2Bc,Ba; Table 2).

Canopy resistance (rc) for both species started to increase in the afternoon, when VPD was already high. For winter wheat this did not correspond to $\mathrm{rs}_{\mathrm{max}}$ values which did not show a constant diurnal pattern (Fig. 2Ac,Bc). For sugar beet maximum stomatal resistance on the leaf level showed an increase over the day, which was also presented on canopy level by an increase of rc in the afternoon (Fig. 2Ac–Ec). This indicates that stomatal resistance may have a large impact on the bulk canopy resistance. On the canopy level, evapotranspiration (E) showed less fluctuation than single leaf measurements. The correlation of stomatal resistance and maximum transpiration discovered on the leaf level was not presented on the canopy scale. Diurnal changes in rc appear to have less effect on the evapotranspiration since E was mainly dependent on the incoming solar energy (Table 1) thus supporting previous studies that showed a correlation between E and available energy (Dekker et al., 2000; Douglas et al., 2009; Priestley and Taylor, 1972). McNaughton and Jarvis (1991) showed that feedback mechanisms within a canopy can cause the canopy response to the environment to be more stable than an individual leaf which could explain the difference between the response of rs_{max} respectively rc to the transpiration

Our data also confirm a negative correlation between rs_{max} and A_{max} as already described in several studies (e.g., Guo et al., 2002; Steduto et al., 1997; Fig. 2Ac–Ec; Ae–Ee). On DOY 127, low temperatures in the morning hours significantly affected leaf stomatal resistance, hence, rs_{max} values were highest in the morning (Fig. 2Ac). This influenced the correlation between rs_{max} and A_{max} leading to an extremely low slope and a poor correlation (Fig. 2; Table 1). NEP and stomatal resistance on the canopy level were also negatively correlated.

Maximum values of NEP were reached at solar noon for winter wheat (Fig. 2Ae,Be) and before solar noon for sugar beet (Fig. 2Ce–Ee). Thus, sugar beet did not respond to the highest incoming radiation (Fig. 2Ca–Ea; Ce–Ee). A previous study by Pingintha et al. (2010) in a peanut canopy stated that up to 89% of daytime NEE variations are primarily controlled by the incoming radiation. Since canopy resistance usually started to increase around noon the reduced canopy CO_2 uptake in the afternoon might also be related to progressive stomatal closure and therefore diffusional limitations of CO_2 (Fig. 2Cc–Ec). Additionally, the maximum electron transport rate (ETR_{max}) showed highest values in the morning hours before solar noon, which corresponded to NEP maxima, especially for sugar beet (Fig. 2Cd–Ed). Thus, the efficiency of photosynthetic light reactions was not constant during the day, but followed a pattern with the highest values in the photosynthetic capacity of sugar beet in the morning, which also influences the diurnal pattern of canopy CO_2 uptake. While other studies, e.g., Flexas et al. (1999), often reported a midday depression of ETR_{max}, such a decrease was not observed in the present study, which points to well-irrigated conditions of the studies crops during the whole season.

Since the crops were well watered carbon uptake could, theoretically, be maximized if stomatal resistance and thus canopy resistance were reduced in the afternoon. However, this strategy would result in a large and uncontrolled loss of water. The studied crops showed highest WUE in the morning. The potential water use efficiency on the leaf level ($_{\text{pot}}\text{WUE}_\text{L}$) and actual water use efficiency on the canopy level (WUE_C) were highest before solar noon (Fig. 2Af–Ef) when the evaporative demand was lowest and rather high light intensities stimulate photosynthesis. The diurnal pattern of WUE was similar to other reports on cropland (Baldocchi, 1994; Tong et al., 2009) and forest (Scanlon and Albertson, 2004). Increasing evaporative demand caused stomatal resistance to increase. Stomatal control is generally thought to facilitate an optimum between CO_2 uptake and water loss (Farquhar and Sharkey, 1982). In agreement with previous studies, in general the $_{\text{pot}}\text{WUE}_\text{L}$ was higher than WUE_C (Steduto et al., 1997; Tong et al., 2009). While $_{\text{pot}}\text{WUE}_\text{L}$ depends mainly on stomatal control of photosynthetic CO_2 uptake and transpiration, WUE_C is additionally influenced by non-stomatal components like soil respiration and soil evaporation. An earlier study showed that for an LAI larger than two the influences of non-stomatal components became small (Tong et al., 2009). In our study, the largest difference between WUE_C and $_{\text{pot}}\text{WUE}_\text{L}$ occurred during the first hours of the day when the light intensity was lower than the light intensity inside a leaf chamber where $_{\text{pot}}\text{WUE}_\text{L}$ was measured. Additional evaporation from soil would decrease WUE_C compared to the actual apparent average water use efficiency of all leaves in the canopy. Thus, soil fluxes could account for the difference between WUE_C and $_{\text{pot}}\text{WUE}_\text{L}$ and not only photosynthetic exchange But the relation between WUE_C and $_{\text{pot}}\text{WUE}_\text{L}$ changed during the course of the day, and it cannot be deduced whether the diminishing difference between WUE_C and $_{\text{pot}}\text{WUE}_\text{L}$ during the day reflects only an increase of stomatal resistance (underestimation of WUE_C) or also increasing non-stomatal soil fluxes. This demonstrates once more the complexity of photosynthetic exchange processes in the whole canopy and the difficulties of scaling from the leaf to the canopy. But the similar diurnal pattern of $_{\text{pot}}\text{WUE}_\text{L}$ and WUE_C provides an indication that stomatal closure on leaf and canopy is the main process which largely affects WUE. This is supported by the fact that a correlation of the actual canopy and potential leaf WUE with VPD was found for all measurement days. While on a seasonal base the WUE of well-watered crops depends only on VPD (Baldocchi et al., 1985), on the diurnal timescale the relationship is indicated because of an increase of stomatal closure in the afternoon (Baldocchi, 1994; Steduto et al., 1997). For winter wheat the ${}_{\text{pot}}\text{WUE}_\text{L}$ at DOY 127 is lower than on DOY 176 which is not mirrored in WUE_C of the species. Lower values of VPD on DOY 229 led to a higher ${}_{\text{pot}}\text{WUE}_\text{L}$ value in the morning (Fig. 3b). Slightly cloudy condition (Fig. 2Da) on this day caused higher absolute ${}_{\text{pot}}\text{WUE}_\text{L}$ values. While Tr_max was a comparable range to the other days A_max values were higher resulting in higher absolute ${}_{\text{pot}}\text{WUE}_\text{L}$ values. The decline on DOY 253 is generated by lower A_max and Tr_max values at this time of the year due to reduced photosynthetic activity. This is also presented in the down regulation of the ETR_max throughout the season due to beginning dormancy (Fig. 4).

Non-linearity of the correlation of VPD and actual WUE_C was due to low light conditions in the morning limiting photosynthetic rate and influence actual WUE_C values (Fig. 3c,d). While absolute values of WUE_C for sugar beet do not differ significantly but range between 3 $\mu\text{mol}\,\text{mmol}^{-1}$ and 11 $\mu\text{mol}\,\text{mmol}^{-1}$ at all three measurement days (Fig. 3d). Winter wheat WUE_C on DOY 127 was higher than on DOY 176, which is in contrast to ${}_{\text{pot}}\text{WUE}_\text{L}$. An earlier study showed that the highest WUE_C values appeared at the end of April and beginning of May as the main growing phases of winter wheat (Tong et al., 2009).

Winter wheat NEP (Fig. 5g) showed similar magnitudes during the seasonal development in accordance with the results of (Anthoni et al., 2004) who monitored the carbon exchange of a winter wheat canopy in Thuringia, Germany. During the growing phase of winter wheat, an increase of green LAI and vegetation height corresponded to a rise of E and NEP (Fig. 5a,e,g). After the highest green LAI was reached, the wheat canopy still showed a high photosynthetic activity during grain filling, although yellowing had already started at the lower leaves. Characterization of the photosynthetic efficiency of light reaction (Fig. 3) illustrated that the reduced non-photochemical protection leading to a high maximum electron transport rate of the canopy could be interpreted as a strategy to maximize carbon uptake for grain filling. A significant reduction of NEP values of the canopy was detected during a 2–3 week period from the beginning of July (DOY 182) when green LAI dropped below 2 $m^2 m^{-2}$ and plant senescence constantly reduced green leaf material until the second half of July (DOY 200) which is in accordance with similar crop studies of winter wheat in Belgium (Aubinet et al., 2009).

For sugar beet the increase of green LAI corresponded with a rise of daily E and NEP (Fig. 5b,f,h). The reduction of NEP and E in August and September (DOY 213–270) did not correspond to a significant decrease in LAI (Fig. 5b), which is in line with observations by Moureaux et al. (2006). Neither leaf chlorophyll content (Fig. 3) nor leaf level measurements of potential quantum yield (F_v/F_m; Fig. 2Cd–Ed) gave any indication of the senescence of sugar beet leaves. The photosynthetic capacity of the light reaction (ETR_{max}), however, decreased during the season while energy conversion was balanced by increased non-photochemical quenching (NPQ_{1100}) parameters (Fig. 3). This reduction of photosynthetic capacity of light reaction over the season on sugar beet leaves was pronounced compared to the downward trend of leaf-level gas exchange measurements of A_{max} (Fig. 2Ce–Ee and Fig. 5h) which was previously reported in Monti et al. (2007). In our study high values of A_{max} at DOY 229 do not answer the general lower NEP values at this time a year. Seasonal development of global radiation (Fig. 5) limited the available energy for photosynthesis in August and September. Therefore the decrease of daily NEP values of the sugar beet canopy was caused by a combination of the limitation of maximum photosynthetic CO_2 uptake rate on the leaf level and the concurrent reduction in solar radiance in August and September. This is supported by earlier studies where natural canopy photosynthesis did not operate at its maximum potential rate and may have been reduced under prevailing environmental conditions (Bergh et al., 1998; Rascher et al., 2004).

The photosynthetic efficiency of leaves varies largely within hours and these variations as well as changes in stomatal resistance are most likely the reason for the fluctuations of carbon fluxes of the whole field. On the basis of our study, we propose to additionally include the physiological status of plants in carbon flux models in order to improve the quality of the simulation of diurnal patterns of carbon fluxes and represent plant ecosystems more reliably. One way to achieve this is to use the chlorophyll fluorescence of photosynthetically active leaves as it was done for many years. The intensity of the re-emitted fluorescence is indirectly correlated to the energy used for photosynthesis and thus can serve as an indicator of photosynthetic light conversion (Baker, 2008). However, most fluorescence techniques rely on active excitation of leaves with saturating pulses and are therefore not applicable for remote ecosystem monitoring. Modern remote sensing approaches deriving the fluorescence from hyperspectral reflectance measurement have the potential to measure the top-of-canopy fluorescence in the atmospheric oxygen absorption lines (Louis et al., 2005; Meroni et al., 2009; Rascher et al., 2009). Damm et al. (2010) showed that modeling of carbon fluxes on a timescale of one day could be improved by using the canopy fluorescence signal and this approach may become a powerful tool for better understanding the variation of photosynthetic efficiency and thus carbon uptake. However, this approach also provides some challenges since a range of different factors influence the fluorescence signal, such as canopy structural effects (LAI, chlorophyll content) and bidirectional effects (changing viewing illumination geometry), which are not completely understood yet.

Appendix A

Abbreviations

[A_{max}]	maximum photosynthetic net CO_2 uptake rate at saturating light intensity (µmol m^{-2} s^{-1})
[DOY]	day of year

[E]	evapotranspiration (mmol m^{-2} s^{-1})
[ETR]	photosynthetic electron transport rate (µmol m^{-2} s^{-1})
[ETR$_{\text{max}}$]	maximum photosynthetic electron transport rate (µmol m^{-2} s^{-1})
[F]	fluorescence yield of light-adapted leaf (a.u.)
[F_0]	initial fluorescence at dark-adapted leaf (a.u.)
[F_m]	maximum fluorescence of dark-adapted leaf (a.u.)
[$F_{\text{m}'}$]	maximum fluorescence of light-adapted leaf (a.u.)
[F_v]	variable fluorescence of dark-adapted leaf (a.u.)
[F_v/F_m]	maximum quantum yield of PS II of dark-adapted leaf (a.u.)
[H]	leaf area index (m^2 m^{-2})
[LED]	light-emitting diode
[NEE]	net ecosystem exchange (µmol m^{-2} s^{-1})
[NEP]	net ecosystem productivity (µmol m^{-2} s^{-1})
[NPQ]	non-photochemical quenching parameter
[NPQ$_{1100}$]	non-photochemical quenching parameter at saturating light intensity of 1100 µmol m^{-2} s^{-1}
[$_{\text{pot}}$WUE$_\text{L}$]	potential water use efficiency at saturating light intensity on leaf level scale (µmol mmol^{-1})
[PPFD]	photosynthetic photon flux density (µmol m^{-2} s^{-1})
[PS II]	photosystem II
[rc]	bulk canopy resistance (mol^{-1} m^2 s^1)

[rs_{max}]	stomatal resistance at saturating light intensity ($mol^{-1}\ m^2\ s^1$)
[Tr_{max}]	maximum transpiration rate at saturating light intensity ($mmol\ m^{-2}\ s^{-1}$)
[VPD]	water vapor pressure deficit of the air (kPa)
[WUE_C]	water use efficiency on canopy scale ($\mu mol\ mmol^{-1}$)
[λE]	latent heat flux

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Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀| |▶
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

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Table 1. Statistic parameters characterizing the relationship between rs_{max} and Tr_{max}, VPD and rs_{max}, rs_{max} and A_{max} at leaf level as well as Rg and E at canopy level. Given is the axis interception b, the slope m of the linear fitting line the correlation coefficient r, the number of data points n and the significance of correlation p-value.

Leaf level					
$A_{max} = m \cdot rs_{max} + b$					
DOY	b	m	r	n	p-value
127	19.34	−0.56	−0.34	5	0.5798
176	32.78	−2.12	−0.85	8	0.0078
183	48.75	−6.01	−0.92	11	<0.0001
229	48.69	−7.18	−0.81	11	0.0024
253	38.66	−4.03	−0.87	11	0.0005
$Tr_{max} = m \cdot rs_{max} + b$					
DOY	b	m	r	n	p-value
127	7.58	−0.74	−0.91	5	0.0238
176	7.32	−1.19	−0.79	8	0.0198
183	6.20	−0.39	−0.40	11	0.2252
229	4.90	−0.51	−0.66	11	0.0272
253	5.15	−0.39	−0.84	11	0.0006
$rs_{max} = m \cdot \mathrm{VPD} + b$					
DOY	b	m	r	n	p-value
127	9.20	−3.15	−0.77	5	0.1297
176	2.63	0.09	0.02	8	0.9634
183	0.05	2.76	0.75	11	0.0081
229	0.61	1.35	0.60	11	0.0509
253	1.95	1.59	0.50	11	0.1167
Canopy level					
$E = m \cdot \mathrm{Rg} + b$					
DOY	b	m	r	n	p-value
127	−2.45	0.010	0.78	18	0.00011
176	−0.13	0.007	0.71	16	0.00192
183	0.23	0.008	0.96	18	<0.0001
229	−0.26	0.007	0.94	18	<0.0001
253	0.74	0.006	0.89	16	<0.0001

Table 2. Statistic parameters characterizing the relationship between VPD, $_{\mathrm{pot}}\mathrm{WUE}_\mathrm{L}$ and WUE_C, respectively. Given are the independent parameters of the single exponential decay functions y_0, α and b, as well as the coefficient of determination r^2 and the number of data points n.

Leaf level					
		$_{\mathrm{pot}}\mathrm{WUE}_\mathrm{L}=y_0+a\cdot e^{-\frac{\mathrm{VPD}}{b}}$			
DOY	y_0	α	b	r^2	n
127	3.47598	22.88966	0.41113	0.83792	5
176	5.947	5558.36324	0.11945	0.76857	8
183	−2.06268	19.87179	1.50707	0.71849	11
229	7.9762	934.76862	0.12185	0.9014	11
253	2.68964	8.14007	1.55912	0.60842	11
Canopy level					
		$\mathrm{WUE}_\mathrm{C}=y_0+a\cdot e^{-\frac{\mathrm{VPD}}{b}}$			
DOY	y_0	α	b	r^2	n
127	3.99512	29.00188	0.44335	0.94118	18
176	0.55602	11.42832	0.87504	0.80396	15
183	2.26076	6.01692	1.01649	0.74316	18
229	2.85883	9.62848	0.71759	0.88738	18
253	3.61802	176.693	0.16897	0.87646	16

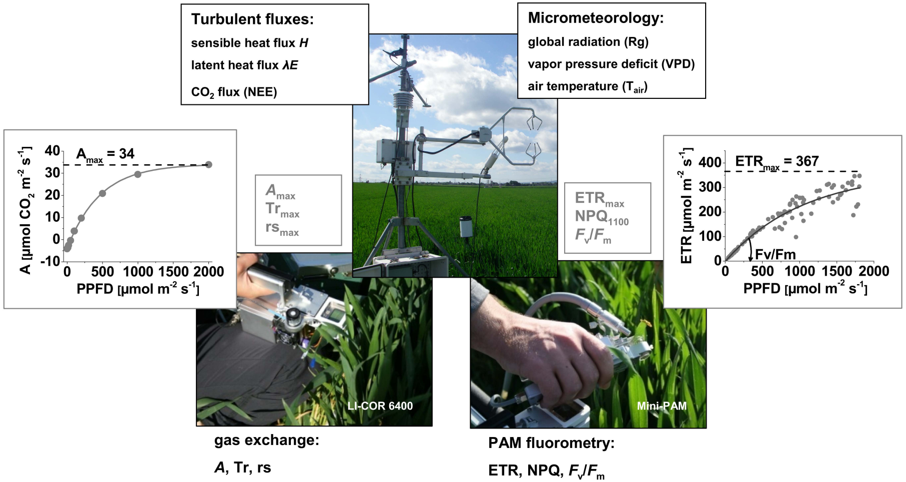

Fig. 1. Overview of the instrumentation and various measurements at different levels of the vegetation-atmosphere system. Gas exchange of single leaves was recorded to determine CO_2 assimilation rate (A), stomatal resistance to water vapor (rS) and transpiration rate (Tr). Light curves allowed the estimation of maximum net photosynthetic CO_2 uptake (A_{max}) and transpiration rate (Tr_{max}) as well as maximum stomatal resistance (rs_{max}) to characterize the potential photosynthetic performance at saturating light intensity. Apparent electron transport rate (ETR) and non-photochemical quenching (NPQ) processes were determined with PAM fluorometry. To achieve characteristic plant parameters independent of momentary light conditions, such as the maximum apparent electron transport rate (ETR_{max}) of the canopy, several hundred randomly distributed leaf measurements within the canopy were made and data were fitted using a photosynthesis model. Turbulence measurements above both canopies were used to derive sensible (H) and latent (λE) heat flux as well as CO_2 fluxes (net ecosystem exchange NEE). Additional measurements of global radiation (Rg), air temperature and water vapor pressure deficit (VPD) above the canopy describe the micrometeorological conditions during measurements.

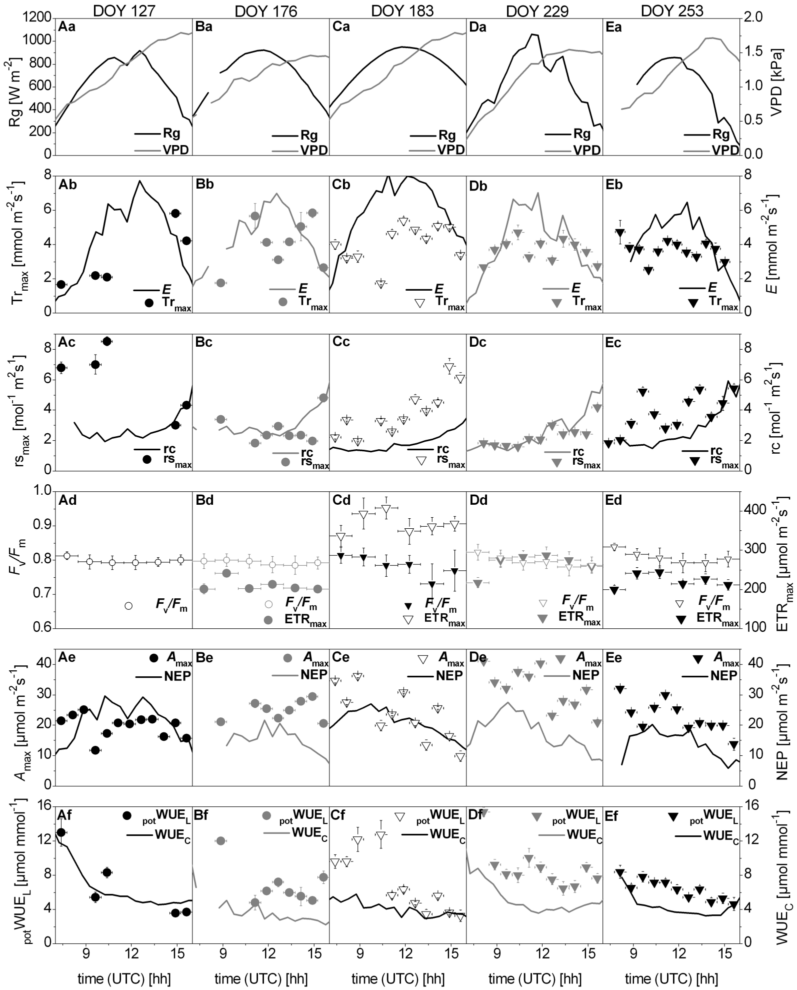

Fig. 2. Caption on next page.

Fig. 2. Diurnal patterns of plant physiological parameters and plant-mediated exchange on two days for winter wheat (DOY 127, 176) and three days for sugar beet (DOY 183, 229, 253). Lines indicate eddy covariance measurements and symbols leaf-level measurements, respectively. Circles represent values for winter wheat and triangles sugar beet. First row: **(Aa–Ea)**, global radiation (Rg) and vapor pressure deficit (VPD); second row: **(Ab–Eb)**, maximum transpiration on leaf level ($\mathrm{Tr}_{\mathrm{max}}$) and evapotranspiration (E) on canopy level; third row: **(Ac–Ec)**, maximum leaf stomatal resistance ($\mathrm{rs}_{\mathrm{max}}$) at light saturation and canopy resistance (rc); forth row: **(Ad–Ed)**, maximum potential quantum yield of photosynthesis ($F_{\mathrm{v}}/F_{\mathrm{m}}$) and maximum photosynthetic electron transport rate ($\mathrm{ETR}_{\mathrm{max}}$); fifth row: **(Ae–Ee)**, maximum net photosynthetic CO_2 uptake rate (A_{max}) on leaf level and net ecosystem productivity (NEP) on canopy level; sixth row: **(Af–Ef)**: potential water use efficiency on leaf level (${}_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}}$) and water use efficiency on canopy level ($\mathrm{WUE}_{\mathrm{C}}$). Vertical error bars: ±standard deviation besides $\mathrm{ETR}_{\mathrm{max}}$, $\mathrm{A}_{\mathrm{max}}$ and $\mathrm{Tr}_{\mathrm{max}}$ uncertainty value of the fitting function; horizontal error bars: period of measurement.

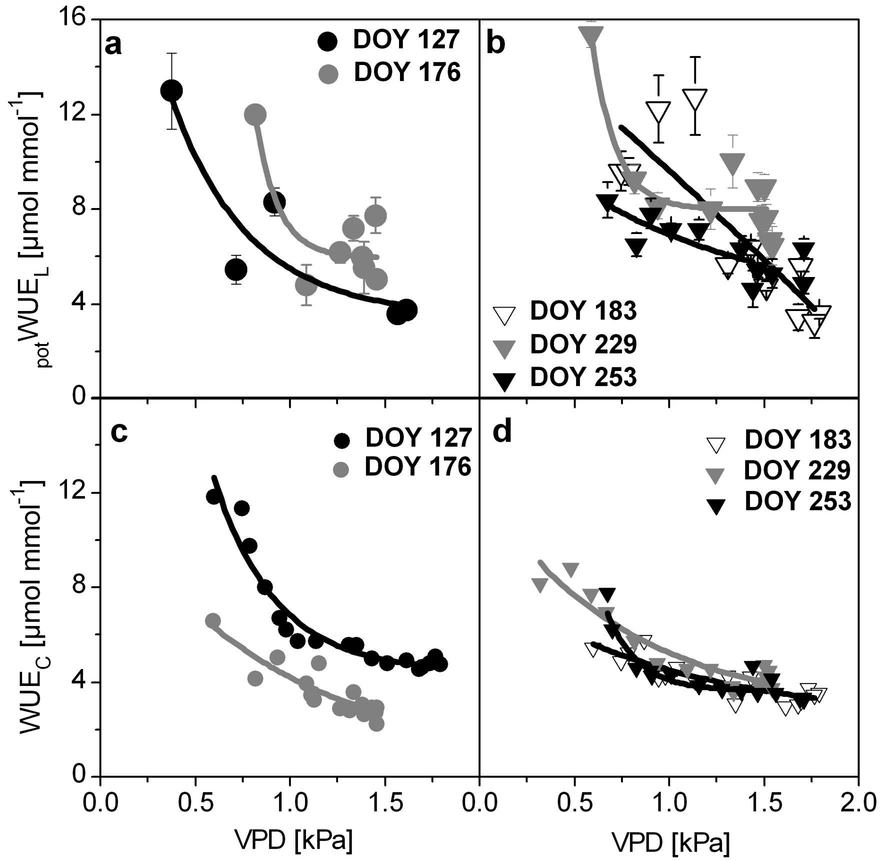

Fig. 3. (a, b) Correlation of vapor pressure deficit (VPD) and ${}_{\mathrm{pot}}\mathrm{WUE}_{\mathrm{L}}$ for wheat (A) and sugar beet (a). Vertical error bars: ±uncertainty value. **(c, d)** Correlation of vapor pressure deficit (VPD) and $\mathrm{WUE}_{\mathrm{C}}$ for wheat (c) and sugar beet (d). Data were fitted using a single exponential decay function (see Table 2).

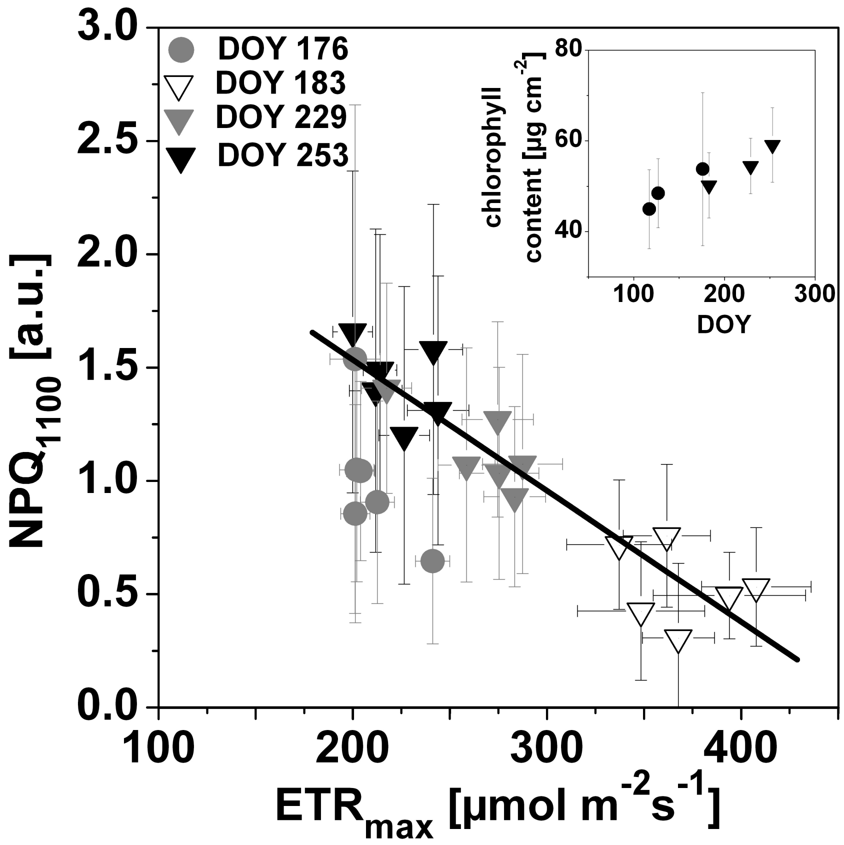

Fig. 4. Correlation of maximum electron transport rate (ETR_{max}) and non-photochemical quenching parameters NPQ_{1100} for winter wheat (DOY 176) and sugar beet (DOY 183, 229, 253). Thick line: linear fit to the seasonal development of sugar beet. Error bars: ±standard deviation or uncertainty value (see Sect. 2.3.2). The insert shows the seasonal development of leaf chlorophyll content. Circle=winter wheat, triangle=sugar beet.

Title Page
Abstract
Introduction
Conclusions
References
Tables
Figures
◀|
|▶
◀
▶
Back
Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

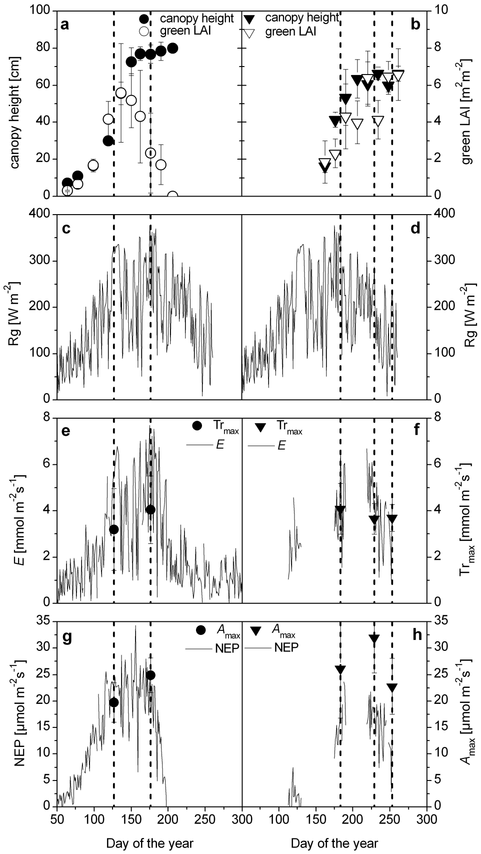

Fig. 5. Seasonal development of several parameters for winter wheat (left) and sugar beet (right). From top to bottom: canopy height and leaf area index (LAI) (mean±sd); daily means of global radiation (Rg), evapotranspiration (E) and maximum leaf transition rate (Tr_{max}); net ecosystem productivity (NEP) and maximum net photosynthetic CO_2 uptake (A_{max}). Dashed lines mark the five days of core measurements.