

Relationship of leaf elongation rate of young wheat leaves, gross primary productivity and environmental variables in the field with hourly and daily temporal resolution

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ABSTRACT

Plant growth is controlled by an interplay of internal and external factors. The production of biomass via photosynthesis is dependent on the plant response to environmental variables such as temperature, vapour pressure deficit and light intensity. Short-term responses of plant growth to these variables at fine temporal scales of hours are not well investigated, especially under field conditions. The present study explores the relationship between leaf elongation rate (LER) of young wheat leaves in the field in very high temporal resolution (minutes). Turbulent fluxes of CO₂ were measured with the eddy covariance technique and used to derive GPP, and environmental variables such as air and soil temperature, short wave radiation and vapour pressure deficit were simultaneously measured.

The analysis revealed the importance of different variables on different temporal scales (hourly, daily). On an hourly scale, GPP and shortwave radiation explain most of the variance of LER, however on a daily scale, air temperature is the main driver. A cross-correlation analysis confirmed that the strongest immediate relationship can be found between LER and GPP and incoming shortwave radiation; variables that are determining photosynthesis. In principal, LER also shows the same diurnal patterns as air temperature and soil temperature, however air and soil temperature lag behind LER. Multivariate growth models show that combinations with GPP or incoming shortwave radiation and air temperature perform best. These results indicate that short term growth processes in young wheat leaves in the field are mainly controlled by incoming shortwave radiation, while the magnitude of growth is controlled by temperature.

1. Introduction

Plant growth is controlled by an interplay of internal and external factors. Photosynthesis is the primary process that ensures the autotrophic production of biomass in plants and finally governs the gross primary production (GPP) of entire ecosystems. Providing food, fuel, and fiber, plants contribute enormously to the very foundations of human society. Thus, experiments to understand growth under realistic field conditions are important to establish the basis for models that can be combined with modern information and communication technology to implement improved field management practices, e.g. in the context of smart farming (Walter et al., 2017). The production of biomass involves

a substantial number of responses to temperature, vapour pressure deficit and light intensity (Poorter et al., 2012c). The dependence of photosynthesis on environmental factors has been analysed thoroughly over the past decades, improving the precise understanding of physiology and molecular control of these processes in a wide range of plant species (e.g. Gallagher et al., 1979.; Gallagher and Biscoe, 1979; Kronenberg et al., 2020). Plant growth has been studied on various spatial and temporal scales, ranging from satellites observing entire continents daily from space, to meteorological measurement stations towering over forests or fields providing measurements every second, to small field-installations or hand-held devices unraveling the secrets of a single plant (de Jong et al., 2013; Emmel et al., 2018; Nagelmüller et al., 2016;

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Walter et al., 2017). Experiments that closely analyse plant growth under real field conditions are scarce. In the field, a multitude of ever-changing factors fluctuate with a certain periodicity, which are difficult to reproduce under controlled conditions such as growth chambers (Kronenberg et al., 2020; Passioura, 2006; Poorter et al., 2016, 2012b, 2012a) or in even more artificial cultivation settings (Dhondt et al., 2014; Yazdanbakhsh et al., 2011). Whereas the dependence of plant growth on environmental variables at large temporal scales of weeks to seasons is well described and modelled, short-term effects of environmental variables on plant growth are still not well investigated, especially in the field. (Körner, 2015). This study aims to uncover proxies that allow to predict growth processes in the field, using a combination of techniques to investigate the timing of plant growth processes on different temporal and spatial scales.

Most modelling approaches have modelled leaf growth based on leaf assimilate availability, on temperature and on a combination of both approaches (Van Delden et al., 2001). A consensus among crop modellers' is that the growth rates of different organs is related to temperature (Parent and Tardieu, 2014) while some models also include radiation (Van Delden et al., 2001). However, most models base their calculations on daily averages. Previous studies exploring plant growth describe temperature as the most important driver for plant growth (Ben-Haj-Salah and Tardieu, 1995; Parent and Tardieu, 2014, 2012). For cereals, the influence of temperature to stem elongation rate has been investigated to estimate growth responses (Kronenberg et al., 2021, 2017) also in relationship to high temperatures and draft (Hlaváčová et al., 2018). Few studies also investigated leaf growth of wheat and barley plants in field environments in relationship to air and soil temperatures and to radiance based on daily averages or few diel cycles (Gallagher et al., 1979, 1976; Gallagher and Biscoe, 1979). These studies showed that when plants are well-watered, diel leaf growth (i.e. during sunlight hours) generally follows air and soil temperatures. In recent years, similar experiments have been undertaken with automated image based devices that allow measuring leaf elongation rate (LER) of multiple leaves simultaneously in the field with high precision (sub-millimeter scale) and high temporal resolution (minutes) over several days (Nagelmüller et al., 2016). Nagelmüller et al. (2016) showed that leaf growth largely corresponds to a diel temperature cycle, but it remained unclear how closely air temperature affected LER and how tightly leaf growth is coupled to other environmental factors and biological processes such as to incident shortwave radiation, vapour pressure deficit (VPD), turgor pressure or canopy gas exchange, especially under field conditions. In principle, the experiment by Nagelmüller et al. (2016) confirmed the importance of air and soil temperature as the dominant driver for LER and highlighted the contrasting responses of different varieties of the same plant species towards environmental variables such as temperature. Plant growth, respectively, the production of biomass can also be remotely assessed by partitioning net ecosystem carbon dioxide (CO₂) exchange (NEE) into gross primary productivity (GPP) and total ecosystem respiration. These fluxes are estimated based on measurements using the eddy covariance (EC) technique. Today, EC measurements are widely used to assess (GPP) of ecosystems with temporal resolutions between 30 min up to entire seasons (Baldocchi, 2003). Several studies investigated the relationship between net ecosystem productivity (NEP), GPP and plant growth. For trees, NEP and GPP were positively related to stem radius changes on annual and monthly scales, indicating that NEP or GPP can be used for growth estimations. For cereal crops, GPP estimates have been related to temperature, photosynthetic photon flux density and VPD (Buysse et al., 2017; Dufrenne et al., 2011; Schmidt et al., 2012). Wohlfahrt et al. (2008) e.g. found that light intensity (photosynthetically active photon flux density) was the most important factor determining NEE, especially during periods with high vegetation activity, whereas the variability of NEE could best be explained by temperature. Further they found that the carbon uptake potential (NEE at saturating PPFD) of the ecosystem could be explained best by the available assimilating plant area. However, on half-hourly

scale, the correlation was found to be negative (Zweifel et al., 2010). These contrasting results indicate that different drivers become apparent when observing the process of growth with different temporal resolutions. Consequently, investigating growth processes in very-high temporal resolution is important to understand the interplay of factors to estimate growth processes.

To our best knowledge, the relationship between highly resolved (hourly) growth dynamics and EC-based GPP estimates have not yet been investigated for cereals under field conditions. Therefore, this study examines proxies to predict plant growth based on environmental variables. Highly resolved *in-situ* growth measurements of winter wheat plants are investigated together with meteorological variables and CO₂ fluxes. This unique dataset is used to investigate i) how the diel patterns of environmental variables relate to LER, ii) whether the ranking of the explanatory variables for LER changes between highly resolved (hourly) and daily aggregated data, and iii) what variables or variable combinations allow modelling growth of winter wheat in the early season.

2. Material & methods

2.1. Field site

The experiment was conducted on a crop field of 1.55 ha in Oensingen, Switzerland, (47°17'11.1" N / 7°44'01.5" E, 452 m a.s.l.). The soil is classified as Eutric-Stagnic Cambisol of silty clay texture, with a particle size distribution of 43% clay, 47.5% silt, 9.5% sand, and a pH of 5.5 (Alaoui and Goetz, 2008). The field with a typical 3-year crop rotation is managed according to the rules of good agricultural practice followed by farmers for the label 'integrated production Switzerland' (IP Suisse) (Emmel et al., 2018). Winter wheat (*Triticum aestivum* L., var. Simano) was sown on 11.10.2018 and harvested on 19.07.2019. Annual mean air temperature is 9.8 °C and annual precipitation is 1155 mm (Emmel et al., 2018, based on data of 2004–2016). The wheat was in the tillering phase throughout the experiment and reached BBCH 21 at 28.02.2019 and BBCH 23 at 01.04.2019 (Lancashire et al., 1991).

2.2. Experimental set-up of leaf elongation measurements

Three leaf length tracker (LLT) panels were installed in the field on 14.03.2019 (see Fig. 1). LLTs are a novel method to track LER of monocots directly in the field. The panels had been built according to Nagelmüller et al. (2016). Briefly, LLTs consist of a black panel mounted on iron rods, which are rammed into the soil to ensure stability of the system. The panels were positioned in the field on the north-south axis. The experimental plants were south of the panels to avoid artificial shading. The front side of the panel holds black U-shaped aluminium rails. Behind the panels, plants can be selected for the leaf elongation measurements. Leaves are carefully attached to a hairpin, which is connected to a fishing rod (*Berkley Fireline 0.15 mm*). The rod is guided over reverse rollers underneath the panel, where it is running through the aluminium rails to the top of the panel and via another roller to the back of the panel again. At the end of the rod, a 20 g lead counter weight is attached to keep the rod straight. On the front side of the panel, where the fishing rod is running through the rails, a white acrylic bead of 20 mm diameter is mounted on the rod. Fishing rubber stoppers hinder the bead from sliding downwards. As the leaf expands, the bead moves upwards. A water-proof camera system (Lupusnet-LE933/934, Lupus electronics, Landau, Germany) photographed the panel every two minutes to track the movement of the beads. During the night, infrared light provided illumination for the camera to collect photographs. For each panel, ten young leaves from different plants were randomly selected to be measured. To account for tension in the soil or material elongation, one to three reference measurements were taken per panel by attaching the fishing rod to a nail pushed into the soil. A checker board was regularly installed in front of the panels and served as a geometric reference to correct for image distortion.

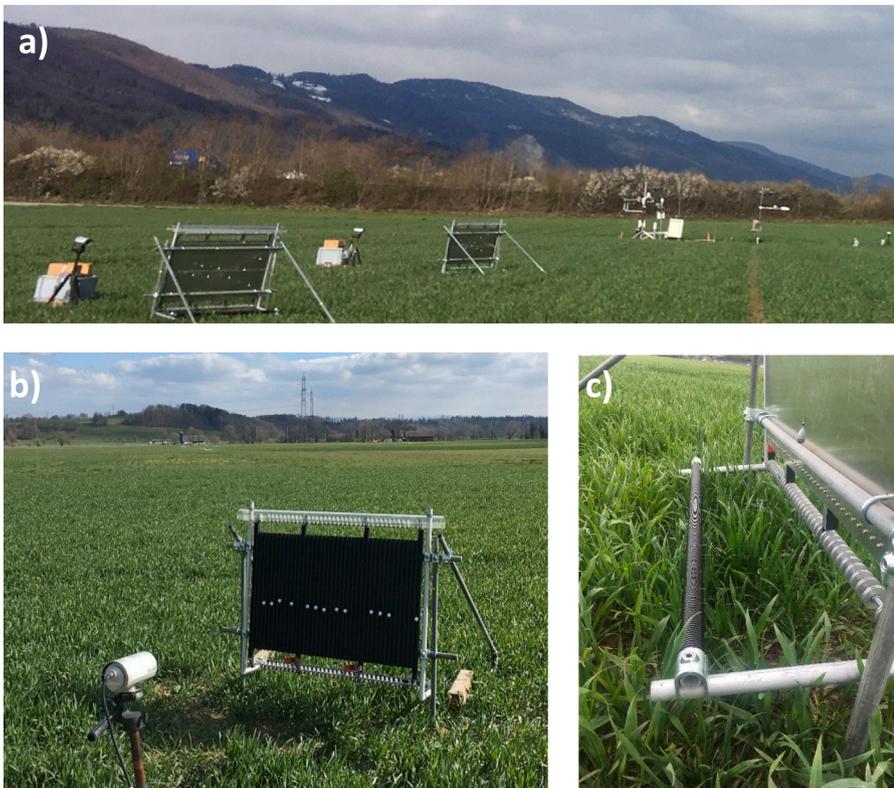


Fig. 1. Experimental set-up of the LLTs and the eddy covariance station.

a) Three LLT panels were positioned within the footprint of the eddy covariance station.
 b) The front side of the panel with the white beads is photographed every 2 min by the camera.
 c) At the back side of the panel, the fishing rod is guided from the plants over the cross tie to the first set of reverse rollers.

2.3. Calculation of leaf elongation rate

LERs were calculated using the LLT software (Nagelmüller et al., 2016). The software initially rectifies the image sequences by using the photograph of the checkerboard panel as a reference to account for camera distortion. The main part of the software tracks the white beads and calculates the relative displacement of every white bead on each panel for each photograph. Using the following equation Eq. (1):

$$LER = (L_1 - L_0)/(T_1 - T_0) \times 60 \quad (1)$$

where LER is the leaf elongation rate, L_1 corresponds to the total leaf elongation in mm at the time T_1 , and L_0 corresponds to the total leaf elongation in mm at the time T_0 (Nagelmüller et al., 2016). This equation yields hourly leaf elongation. Prior to the application of the equation, the daily growth of each leaf was carefully analysed, and outliers were removed from the data set. Outliers encompassed e.g. leaves that had died within the measurement period, showed significant amount of illness or had grown into the LLT panel and thereby had compromised measurements. The mean LER was calculated from the remaining leaves. During measurement period 1 (22.03.2019–28.03.2019), a total of seven leaves from one panel were used for the LER calculation, and during measurement period 2 (05.04.2019–09.04.2019), a total of 25 leaves from three different panels were used. The amount of samples is comparable to similar studies which observe plant growth in high temporal resolution (Muller et al., 2001; Nagelmüller et al., 2016; Zweifel et al., 2010).

2.4. Meteorological variables

The purpose of this investigation was to explore the relationship between environmental variables and single plant growth. Therefore, meteorological measurements were taken to represent the environmental conditions over the canopy of the entire field, rather than placing single sensors into the plant stand. Air temperature and relative humidity were measured at 2 m above the canopy (CS215, Campbell

Scientific, Logan, Utah, USA). Net radiation (CNR1, Kipp & Zonen, Delft, The Netherlands), total and diffusive PAR radiation (BF5, Delta-T Devices Ltd, Cambridge, UK) were also measured at 2 m above the canopy. Soil temperature and soil humidity were measured with four individual soil sensors (model 107, Campbell Scientific, Logan, Utah, USA) buried at 0.015 m depth in the field around the eddy flux station. All meteorological and soil measurements were logged in intervals of 1 min, and later aggregated to half-hourly and hourly averages.

2.5. Estimation of gross primary production

Turbulent fluxes were measured with the eddy covariance technique (Baldocchi, 2003). The set-up consisted of an ultrasonic anemometer for three-dimensional wind speed measurements (R3-50, Gill Instruments Limited, Lymington, Hampshire, UK) and an enclosed-path infrared gas analyser (LI-7200RS, LI-COR Biosciences, Lincoln, Nebraska, USA) for CO_2 and were recorded at 20 Hz. Half-hourly eddy covariance fluxes were processed with the EddyPro software (version 7.0.4, LI-COR), in accordance with established community guidelines (Aubinet et al., 2012). Eddy covariance raw data were despiked and screened following Vickers and Mahrt (1997). Wind data were rotated (2D rotation, after Wilczak et al., 2001), and time lags between the turbulent wind and CO_2 data were compensated using covariance maximization. For spectral corrections, fluxes were corrected for high-pass and low-pass filtering effects (Fratini et al., 2012; Moncrieff et al., 2004) and instrument separation (Horst and Lenschow, 2009). Processed fluxes were rejected from further analyses if (1) they were found outside a physically plausible range ($\pm 50 \mu mol m^{-2} s^{-1}$), (2) they failed to pass the tests for stationarity and well-developed turbulence (e.g., Foken et al., 2005), and (3) friction velocity (u_*) was below a detected threshold value (Reichstein et al., 2005). CO_2 storage fluxes were calculated within EddyPro following the approach of Aubinet et al. (2001). The net ecosystem exchange (NEE) was calculated by summing the half-hourly CO_2 flux and CO_2 storage, whereby NEE values outside of the monthly mean \pm three times its standard deviation were rejected (Rogiers et al.,

2005; Wohlfahrt et al., 2008). The detection of the u^* threshold and flux post-processing (i.e., gap-filling, partitioning of NEE into GPP and total ecosystem respiration) was conducted with the R package REdyProc (Wutzler et al., 2018). The flux footprint was estimated following Kljun et al. (2004).

2.6. Relationships of leaf elongation rate, GPP and meteorological variables

Data were aggregated and analysed using R (Version 3.6.3 with RStudio 1.2.5042). All data were transformed into UTC (for Fig. 2, CET was used). Civil dawn served as threshold to distinguish between day and night. When the sun reaches 6° below the horizon, we speak of civil dawn, or civil twilight. This time of the day has been shown to be important for the biological activity of both flora and fauna (Campbell and Norman, 2012). Any incoming shortwave radiation after civil dawn was zeroed in data post-processing.

In order to assess the ranking of the explanatory variables at different temporal resolutions, the data were aggregated to hourly means, based on the UTC timestamp. The diel period, ranging from sunrise to the next sunrise, thus encompassing a full day of sunlight as well as the following night, served as a basis for the daily means.

A cross-correlation analysis using a cross-correlation function (CCF) was performed to investigate the time lags between the response of the LER and the environmental variables. With CCF it is possible to compare entire time-series with each other. CCF computes the correlation between a given variable at a certain point in time ($t = 0$) and another given variable at another point in time ($t = 0 + h$) and thus allows to investigate time lags between time series data.

To investigate if a combination of variables would improve the prediction of LER, several linear regression models were run. Each model was run with either a single variable or a combination of variables attempting to predict LER on an hourly scale. Using variable importance decomposition the relative importance of each variable for the models was calculated (Grömping, 2015, 2006). To account for missing data, only complete entries were used in the model.

3. Results

3.1. Leaf elongation rates, CO_2 fluxes and meteorological variables

Close relationships between the variables (LER, GPP, air and soil temperatures, incoming shortwave radiation, and VPD) were observed. All investigated variables followed a diel pattern, with maxima around noon and minima during the night. However, variables varied in smoothness of diel cycle and in appearance of local maxima.

During the first measurement period (22.03.2019–28.03.2019, Fig. 2a–e), the diel patterns of LER, air and soil temperatures, and VPD were more pronounced than in the second measurement period (05.04.2019–09.04.2019, Fig. 2f–j). The LER varied during daytime, but usually peaked around noon. During the night, LER was usually low, but in some nights noticeable growth occurred (e.g. 25.03.2019, 07.04.2019, 08.04.2019, 09.04.2019). GPP (Fig. 2b and g) and SW (Fig. 2c and i) showed a similar diel pattern as LER. Air and soil temperatures (Fig. 2c and h) represented a very smooth diel cycle, reaching maximum values after noon. Air temperature was generally higher than soil temperature, except for three days when soil temperature was higher than air temperature (24.03.2019, 25.03.2019, and 08.04.2019). VPD in most cases resembled air temperature, as it is derived from air temperature together with air humidity.

3.2. Relationships of leaf elongation rate, GPP and meteorological measurements at different temporal scales

For the hourly diel data (Fig. 3a–e), all variables related positively to LER. GPP showed the strongest relationship with LER ($R^2 = 0.54$),

followed by shortwave radiation (SW) ($R^2 = 0.49$), and air temperature ($R^2 = 0.41$). Soil temperature only showed a weak relationship ($R^2 = 0.26$), and VPD was not related significantly with LER ($R^2 = 0.073$). When taking into account diurnal data (i.e., dawn until dusk) at hourly resolution (Fig. 3f–j), the results were comparable to the highly resolved diel data. GPP showed the strongest relationship with LER ($R^2 = 0.51$) followed by shortwave radiation ($R^2 = 0.44$) and air temperature ($R^2 = 0.32$). Again, soil temperature shows only a weak relationship ($R^2 = 0.16$) and VPD was not correlated with LER ($R^2 = 0.046$). It is notable that the coefficient of determination decreased for all investigated variables compared to the diel dataset. Overall, it is also notable that plants did always show growth even at temperatures close to 0°C .

A comparison between hourly and daily data revealed that the ranking between the explanatory variables changed. In both the diel (Fig. 3, k to o) and the diurnal (Fig. 3, p to t) dataset, air temperature shows the strongest relationship ($R^2 > 0.7$), which is also the strongest relationship of the entire analysis shown in Fig. 3. In the diel dataset, this is followed by soil temperature ($R^2 = 0.67$) and GPP ($R^2 = 0.44$), whereas shortwave radiation and VPD have weak relationships to LER ($R^2 = 0.08$, $R^2 = 0.017$, respectively). In the diurnal dataset, GPP showed the second strongest relationship ($R^2 = 0.48$), whereas the other variables were weakly related to LER ($p < 0.05$).

When inspecting the cross-correlation analysis of diel measurement of LER (both periods were taken together) at hourly resolution against incoming shortwave radiation, GPP, air temperature and soil temperature, a time lag between LER and air and soil temperature was observed (Fig. 4). The results showed that for the incoming shortwave radiation the strongest relationship ($R^2 = 0.54$) occurred without any temporal lag. Similarly, for GPP, the strongest relationship ($R^2 = 0.55$) was found without any temporal lag. On the other hand, the strongest relationship of LER with soil temperature ($R^2 = 0.7$) appeared at a lag of -3 h, and for air temperature ($R^2 = 0.68$) at lag -2 h. This indicates that the LER was related with soil temperatures and air temperatures measured 3 h, respectively 2 h later.

3.3. Linear regression model

To assess how plant growth can be best predicted under field conditions, we compared individual variables and combinations of variables to model LER at hourly scale (Fig. 5). Both measurement periods were combined and used as model input. For each model, the relative importance of each variable was calculated. Combining more than one variable improved the results in most cases, apart from the combination of VPD and soil temperature. Models which included incoming shortwave radiation, GPP and air temperature performed best. These were also the variables that yielded the best linear relationships when used in a single factor model. VPD had the lowest importance in all models. GPP and incoming shortwave radiation show similar performance, both as single variable and when used in multi-factorial models. The best two factorial model was air temperature with GPP, the best three factorial model air temperature, GPP and soil temperature, and the best four factorial model air temperature, GPP, soil temperature and VPD. It can also be seen that the two factorial models that include GPP or shortwave radiation and temperature perform nearly as well as the three to four factorial models.

4. Discussion

4.1. Diel patterns of leaf elongation rate, environmental variables, and gross primary production

The leaf elongation rates measured in this experiment range from 0 to 2.0 mm h^{-1} and comparable to the rates reported by Nagelmueller et al. (2016). The authors found leaf elongation rates for wheat in the tillering phase between 0.25 to 0.5 mm h^{-1} for temperatures under 5°C , and rates up to 2 mm h^{-1} for temperature above 5°C . The environmental

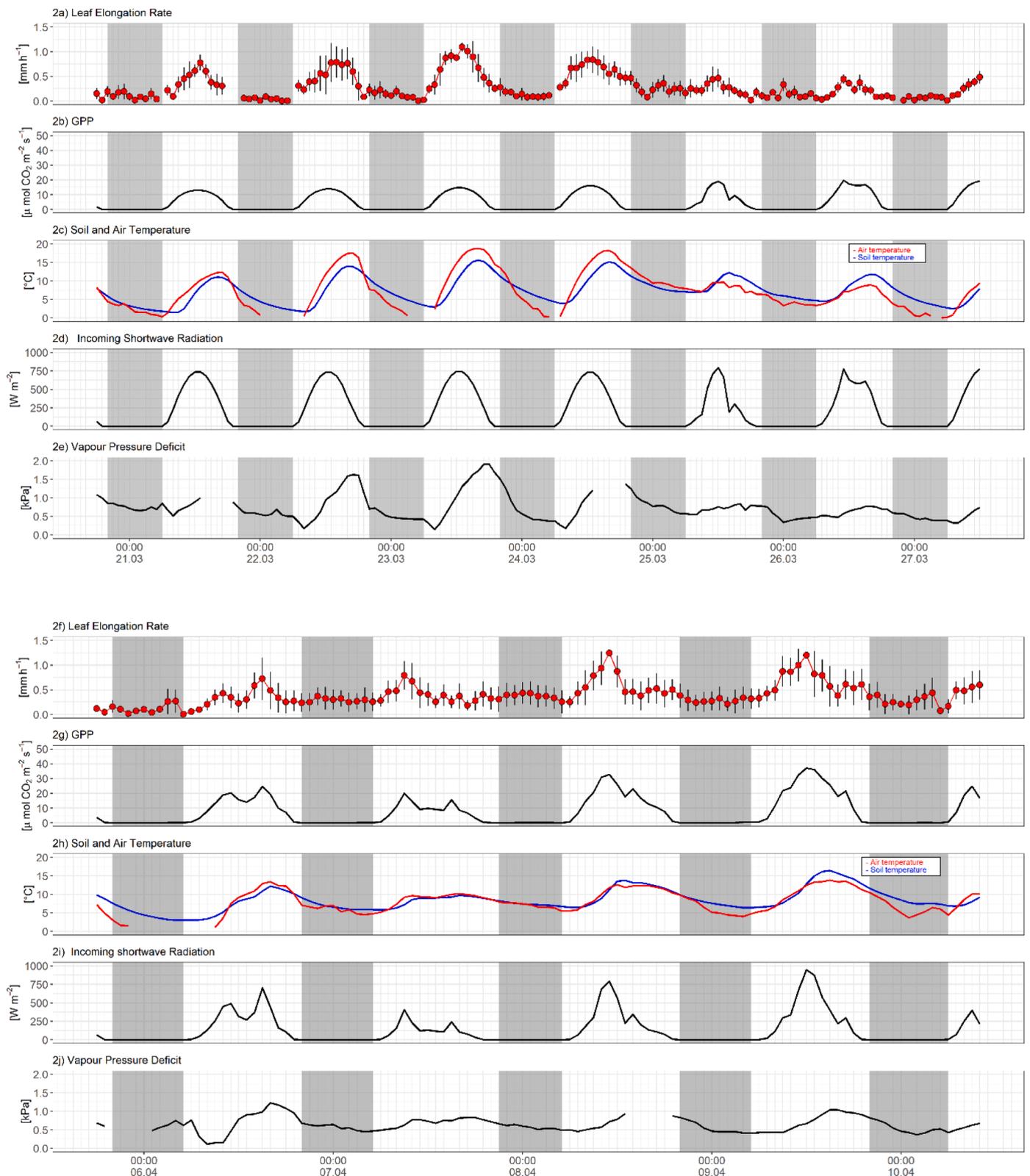


Fig. 2. Time series of LER and environmental variables for two measurement periods (22.03.2019–28.03.2019, a–e, with seven leaves from one panel; 05.04.2019–09.04.2019, f–j, with 25 leaves from three panels). Mean LER (red) with standard deviation (black) are shown in panels a, f; GPP in b, g; soil temperature at –1.5 cm below ground (red) and air temperature (blue) at 2 m above ground in a, h; incoming shortwave radiation in d, i and VPD is shown in e, j. Gray areas indicate night hours. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

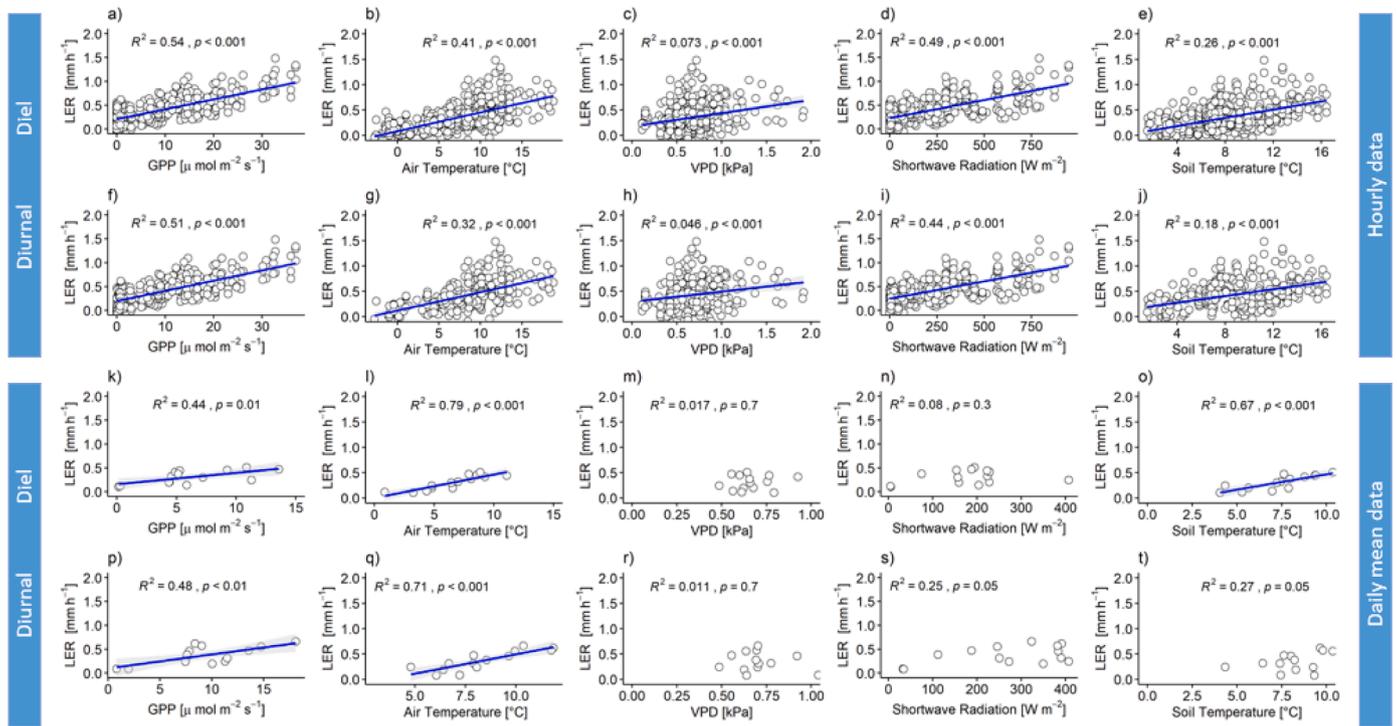


Fig. 3. Relationships of LER and environmental variables shown for two different temporal resolutions and two different time frames considering both measurement periods: hourly values for 24 h (a–e) and for diurnal (dawn until dusk) data (f–j) as well as daily mean values for a full day (k–o) and the daily mean, considering only diurnal data (p–t).

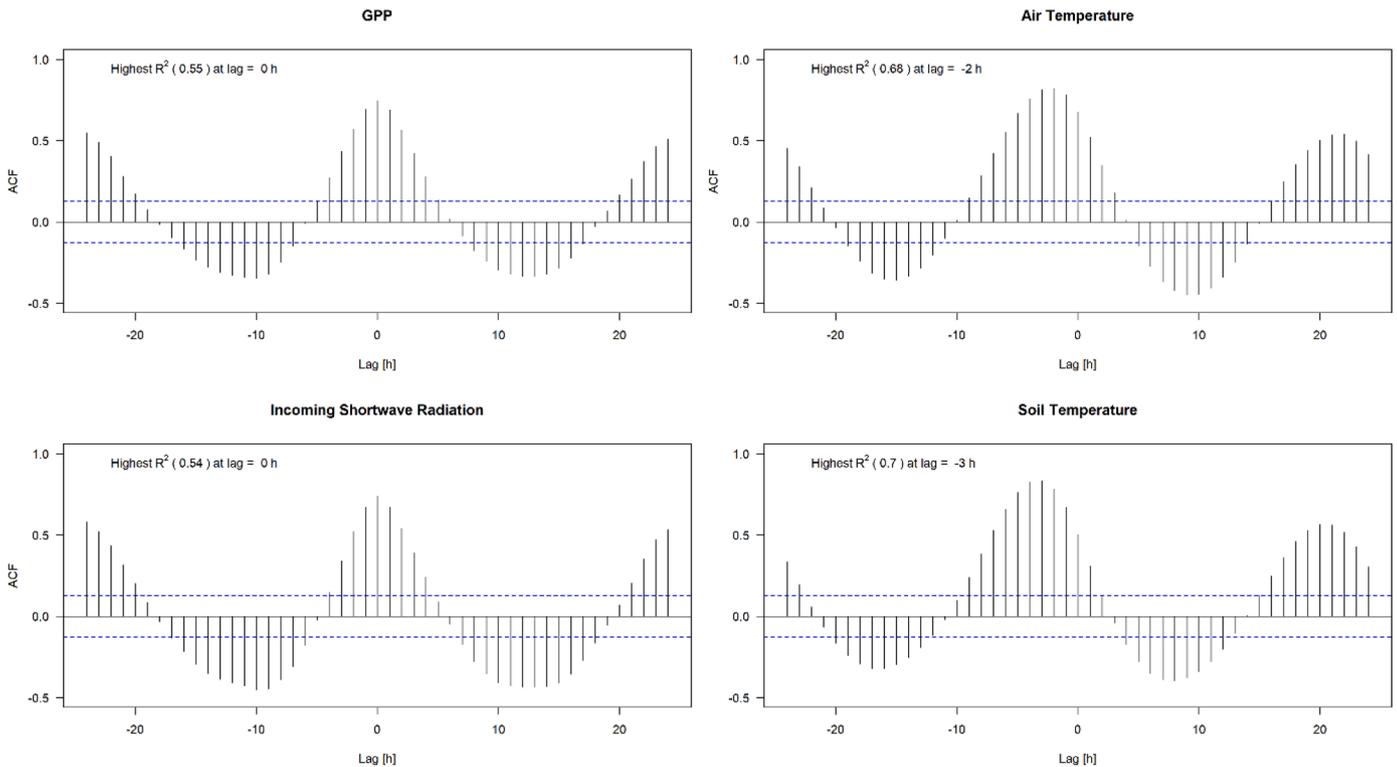


Fig. 4. Correlograms for LER versus SW, GPP, air temperature and soil temperature for both periods. The dashed blue line corresponds to the 95% confidence interval. The auto-correlation function (ACF) is shown at a respective lag. Maximum R² values were calculated separately and are shown with their respective lag on top. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

parameters reported are also comparable to parameter reported for this long-term field research site (Emmel et al., 2018). Soil water content remained at field capacity throughout the experiment.

We observed similar diel patterns of LER, GPP and environmental variables. LER seems to be closely connected to SW and GPP (Fig. 2f–j). If SW decreases abruptly, LER also decreases and there is a decline in GPP.

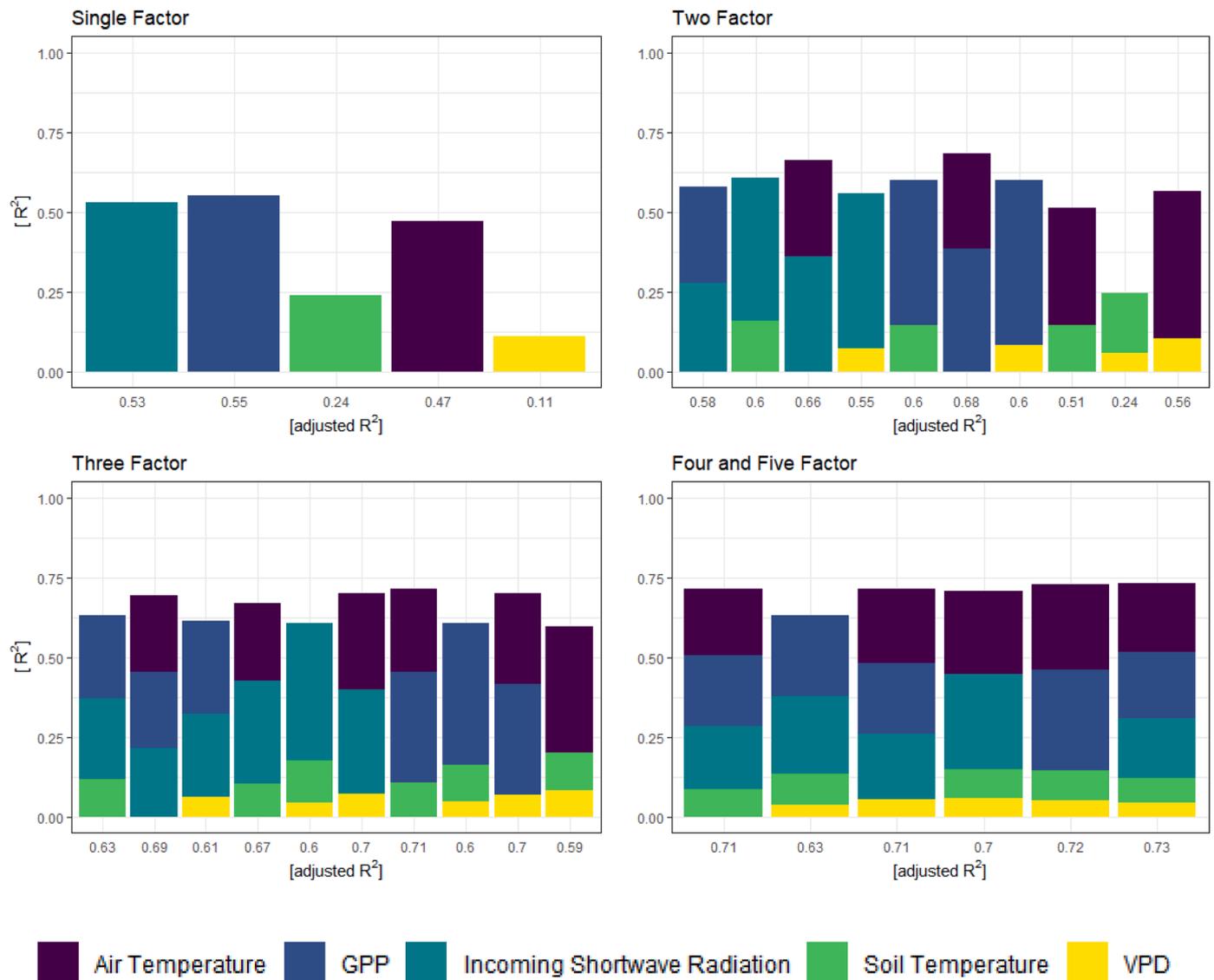


Fig. 5. Coefficients of determination for linear regression models for different sets of input variables. The coefficient of determination corresponds to the full height of the bar plot. The relative importance of a certain variable in multi factor models is shown in different colors. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

These findings are also supported by the negligible time lag between SW or GPP and LER (Fig. 4), however LER precedes increases in soil temperature or air temperature by two to three hours. Whereas GPP is closely connected to the assimilation of carbohydrates via photosynthesis, incoming shortwave radiation creates the potential for photosynthetic activity, and LER is a proxy of aboveground biomass increase (Briggs et al., 1920; Muller et al., 2001; Nagelmüller et al., 2016; Rajendran et al., 2009). In our study, we found that the maximum of growth activity coincides with the maximum of GPP production of the canopy, which happens at the time of highest light intensity. At this time, stomata are wide open, CO₂ is taken up and water vapour is released – if VPD permits and no water stress occurs (Yates et al., 2019). We found a strong temporal relationship between GPP or solar irradiance and LER (see e.g. Fig. 4.), which indicates that under the conditions prevalent during the experiment (a typical European spring 2019, moderate increase in temperature, moderate sun activity, and sufficient water availability) plant growth occurred indeed simultaneously to the assimilation of carbohydrates. This is remarkable, since the processes involved happen in tissues that are separated by a few centimeters from each other, connected by the phloem. Leaf growth happens in the meristematic tissue of the leaf sheath that is part of the pseudostem of

the plant and that is not exposed to sunlight. However, environmental changes can influence the phloem speed considerably (Kuz'yakov and Gavrichkova, 2010). While it can be assumed that the photosynthetically active tissue of the young leaves has its assimilation maximum at the same time as the other leaves in the canopy, the majority of CO₂ uptake will occur in fully grown, older leaves. This means that carbohydrates fostering growth in the elongation zone of the wheat leaf are immediately fed into the growth processes and thus into the elongation of cells and the extension of cell walls.

There has been little research on the temporal coincidence of LER in field environments with air temperature and soil temperature. We found that LER precedes soil and air temperature by 2 to 3 h. To our knowledge this study is the first one to report such a lag between growth rates and temperature. This can be accounted to the fact that there are almost no studies that have investigated growth pattern in such high temporal resolution in field environments. Still, when looking at Fig. 3 in Nagelmüller et al. (2016), a similar observation can be made, although the authors did not mention this in their manuscript.

Comparing the results to growth chamber or green house experiments is challenging, since microclimatic conditions strongly differ to the open field. Besides, studies that investigated growth patterns in such

detail focused on meristem temperature or general relationships rather than temporal lags (e.g. Ben-Haj-Salah and Tardieu, 1995.; Gallagher et al., 1979; Parent and Tardieu, 2012). However, this requires to penetrate the plant with sensors at the meristem (e.g. Gallagher et al., 1979.) which is barely feasible for field environments and thus was not carried out in this study. Unfortunately, this leaves some room for interpretation since the meristem is controlling plant growth. One assumption may be that water that is taken up from the soil and flows along the meristem is likely to have the same temperature as soil temperature, since this water originates from the soil, and consequently the temporal progression of meristem temperature did not deviate markedly from soil temperature. On the other hand, solar radiation may influence the air temperature close to the soil surface, and thus, the meristem temperature and consequently growth. While it is important to highlight the finding that the temporal pattern of LER on very high resolution corresponds closely to incoming SW radiation and precedes air and soil temperature, the study design does not allow to investigate the effect of meristem temperature due to the uncertainty outlined above. To investigate this further, using the LLT setup together with isotope tracers to follow the pathway of assimilated carbon (Kuz'yakov and Gavrichkova, 2010) or e.g. thermocouples to measure the temperature inside the plant meristem (Gallagher et al., 1979) would be necessary.

4.2. Relationship of leaf elongation rate, gross primary production and meteorological measurements at different temporal scales

The apparent relationship between LER and environmental variables depends on the investigated temporal scale. In contrast to the hourly data, where GPP as well as SW has the highest correlation with LER, the relationship between daily average values for leaf growth and air temperature (Fig. 3b and g) show a higher correlation of leaf growth with soil and air temperature. The correlations are even higher, when diel (Fig. 3l) and not only diurnal (Fig. 3q) data is taken into account. Overall, temperature seems to be the controlling factor when considering daily averages. This also corresponds to the paradigm of base temperatures for crops, e.g. Salazar-Gutierrez et al. (2013).

These results can also be interpreted in the recent discussion on the two main paradigms about how carbon uptake and growth is controlled in plants. The first line of argumentation suggests that carbon uptake controls the other drivers of plant growth, while the second one argues that other drivers control carbon uptake. This would thus imply that an increase in photosynthesis leads to an instantaneous increase in growth activity, in other words, as the 'source' is providing a stronger flow of carbohydrates, the uptake of carbohydrates at the 'sink' site of the plant growth zone is also increased (Körner, 2015). In our case the strong relation between temperature and LER for the daily averages would support that growth processes (i.e. the 'sink') are the major driver. However, the close relationship between SW radiation and growth on the hourly temporal scale and the lag between the temperatures and LER favour the 'source' hypothesis. Connecting these thoughts allow the interpretation that under field conditions in early growth of winter wheat (where leaf area is still limited) radiation controls the timing of growth while temperature controls the magnitude of growth. The ecophysiological explanation for this might be that solar radiation through photosynthesis delivers the carbohydrates, but higher (meristem) temperature enables faster (more) cell division and growth and consequently more absolute growth per day.

4.3. Combinations of gross primary productivity and meteorological measurements to model leaf elongation rate

For the modelling analysis as presented here, Fig. 5 shows that a combination of environmental variables improves the prediction of LER on short time scales. Models using air temperature as input performed better than models without air temperature, even though air temperature is not the strongest predictor in single factor models. Since the data

show (Fig. 3) that the plants investigated in this study continued to grow even at air temperatures below 5 °C, no base temperature was used in the modelling approach. Also Gallagher et al. (1979) found that not all cereals seem to show a clear base temperature. As expected, GPP relates well to LER, also on fine temporal scales. However, since the relation between LER and GPP has not been investigated for cereals, it is still notable. These results suggest that the photosynthesis related variable shortwave radiation complements tissue formation and cell growth related variables, such as temperature, in predicting leaf growth. Our findings do not contradict the previous studies on LER which identified temperature as the single most important driver (e.g. Nagelmüller et al., 2016). As most crop models focus on crop growth over entire seasons (e.g. Chenu et al., 2008; Sands, 1995), the results are not directly comparable. In practical applications (e.g. farm management sensors) a robust measurement of GPP is often not available, since the maintenance of an eddy flux tower is complex and expensive, - however, air temperature and soil temperature are easily measured and can be complemented with data from radiation sensors or VPD estimates. This would provide a robust estimate of how much and when plants actually grow. Overall, the results of this study give important insights into improving the modelling of LER. First, it confirmed that in the early season temperature is a good predictor for plant growth. These findings are particularly important for practical applications such as biomass estimation in the early season. Second, this study also demonstrates that for ecophysiological research and process understanding very high resolution measurements allow to reveal the importance of other drivers. Also, similar datasets as this one could be used to parameterize crop growth models for modelling crop growth beyond daily averages.

5. Conclusion

This study investigated the importance of gross primary production (GPP) and the environmental variables air temperature, soil temperature, shortwave radiation and vapour pressure on hourly to daily temporal resolution for the leaf elongation rate (LER) of young wheat leaves on a farmer's field.

The highly resolved data revealed that the highest activity in leaf elongation temporally coincides with the highest rates of incoming shortwave radiation and GPP, whereas the LER precedes increases of soil temperature or air temperature by 2–3 h. These findings imply that the observed increase in photosynthesis leads to an instantaneous increase in growth in the elongation zone of the wheat leaf and support a sink-centered view of photosynthesis. Further studies that give a better insight into processes that are within the plant (e.g. carbon metabolism, phloem speed or meristem temperature) could help to further disentangle the main driver for leaf elongation rate in cereals. The study presented here further shows that the temporal resolution strongly matters when investigating plant growth. Linear regressions on different subperiods demonstrated that temporal resolutions have an influence on the importance of predicting variables. Daily aggregates of the data confirmed air temperature as the most important variable, when using a coarser temporal scale whereas on a finer temporal scale LER is best explained by either radiation or GPP. Several linear models were run with different combinations of input variables and the relative variable importance was decomposed. This showed that the most robust predictor was shortwave radiation. The combination of GPP and air temperature was also robust and showed higher correlations. Overall, these findings suggest that light controlled the growing pattern in the early growth of winter wheat, but temperature controlled the magnitude of growth. These findings can support more sustainable agricultural management practices in the future by improving our understanding of crop growth under field conditions and thereby giving insights on how to refine crop growth models that may inform farmers.

Declaration of Competing Interest

The authors declare no conflicts of interest.

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