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Responses of field-grown maize to different soil types, water regimes, and contrasting vapor pressure deficit

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Abstracts

Drought is a serious constraint to crop growth and production of important staple crops such as maize. Improved understanding of the responses of crops to drought can be incorporated into cropping system models to support crop breeding, varietal selection and management decisions for minimizing negative impacts. We investigate the impacts of different soil types (stony and silty) and water regimes (irrigated and rainfed) on hydraulic linkages between soil and plant, as well as root: shoot growth characteristics. Our analysis is based on a comprehensive dataset measured along the soil-plant-atmosphere pathway at field scale in two growing seasons (2017, 2018) with contrasting climatic conditions (low and high VPD). Roots were observed mostly in the topsoil (10-20 cm) of the stony soil while more roots were found in the subsoil (60-80 cm) of the silty soil. The difference in root length was pronounced at silking and harvest between the soil types. Total root length was 2.5 - 6 times higher in the silty soil compared to the stony

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soil with the same water treatment. At silking time, the ratios of root length to shoot biomass in the rainfed plot of the silty soil (F2P2) were 3 times higher than those in the irrigated silty soil (F2P3) while the ratio was similar for two water treatments in the stony soil. With the same water treatment, the ratios of root length to shoot biomass of silty soil was higher than stony soil. The observed minimum leaf water potential (ψ_{leaf}) varied from around -1.5 MPa in the rainfed plot in 2017 to around -2.5 MPa in the same plot of the stony soil in 2018. In the rainfed plot, the mimimum ψ_{leaf} in the stony soil was lower than in silty soil from -2 to -1.5 MPa in 2017, respectively while these were from -2.5 to -2 MPa in 2018, respectively. Leaf water potential, water potential gradients from soil to plant roots, plant hydraulic conductance (K_{soil_plant}), stomatal conductance, transpiration, and photosynthesis were considerably modulated by the soil water content and the conductivity of the rhizosphere. When the stony soil and silt soil are compared, the higher 'stress' due to the lower water availability in the stony soil resulted in less roots with a higher root tissue conductance in the soil with more stress. When comparing the rainfed with the irrigated plot in the silty soil, the higher stress in the rainfed soil resulted in more roots with a lower root tissue conductance in the treatment with more stress. This illustrates that the 'response' to stress can be completely opposite depending on conditions or treatments that lead to the differences in stress that are compared. To respond to water deficit, maize had higher water uptake rate per unit root length and higher root segment conductance in the stony soil than in the silty soil, while the crop reduced transpired water via reduced aboveground plant size. Future improvements of soil-crop models in simulating gas exchange and crop growth should further emphasize the role of soil textures on stomatal function, dynamic root growth, and plant hydraulic system together with aboveground leaf area adjustments.

Key words: irrigation, plant hydraulic conductance, transpiration, root length, soil types, soil to leaf water potential, stomatal regulation

Abbreviations: DOY: day of the year; DAS: day after sowing; TUE: transpiration use efficiency; SF: sap flow; LAI: green leaf area index; PAR: photosynthetically active radiation; VPD: vapor pressure deficit; An: net

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leaf photosynthesis; E: leaf transpiration; ψ_{leaf}: leaf water potential; $\psi_{sunlitleaf}$: leaf water potential of sunlit leaf; $\psi_{shadedleaf}$: leaf water potential of shaded leaf; K_{soil}: hydraulic conductance of soil; K_{root}: root hydraulic conductance; K_{stem}: stem hydraulic conductance; ψ_{soil_effec}: effective soil water potential; $\psi_{difference}$: difference between effective soil water potential and sunlit leaf water potential; K_{soil_root}: root system hydraulic conductance (includes soil and root hydraulic conductance); K_{soil_plant}: whole plant hydraulic conductance (includes below and aboveground components).

1. Introduction

Maize (*Zea mays L.*) is a major staple crop throughout the world. Drought stress, which negatively affects crop growth and yield, is of increasing concern in several important maize cultivating regions (Daryanto et al., 2016). Increases in frequency and severity of drought events due to climate change have been recently reported (IPCC, 2022). Thus, field observations and understanding on how maize responds to water stress are necessary to suggest promising traits for breeding programs (Vadez et al., 2021) as well as irrigation schemes (Fang and Su, 2019; Q. Cai et al., 2017). Improved understanding of crops' response to drought can be incorporated into soil-crop models (e.g. crop modelling and soil-vegetation-atmosphere transfer modelling).

Stomatal regulation is often considered as a key aboveground hydraulic variable in regulating water use of crops. Maize was considered as isohydric plant in which stomata are closed in response to sensing drought conditions to maintain leaf water potential (ψ_{leaf}) above critical levels ($\psi_{threshold}$ or minimum ψ_{leaf}) (Tardieu and Simonneau, 1998). Investigations of how stomatal controls differ among species and genotypes commonly observed minimum ψ_{leaf} or analyzed of genetic variability of stomatal control in response to varying soil water content. Analyzing measurements of ψ_{leaf} from 400 lines of maize of tropical and European origins under greenhouse and growth chamber conditions, Welcker et al. (2011) reported values of minimum ψ_{leaf} from -0.8 to -1.5 MPa, indicating genetic variability of stomatal responses. The isohydric behavior is due to different mechanisms including hydraulic and/or chemical (e.g. abscisic acid

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[ABA]) signals (Tardieu, 2016). The degree to which these underlying mechanisms interact and differ among genotypes and/or environmental scenarios in explaining the stomatal regulation is still debated (Tardieu, 2016, Hochberg et al., 2018). Field evidence in variation of the minimum ψ_{leaf} of maize due to soil water availability is rarely reported.

Water flow along the soil-plant-atmosphere continuum is determined by a series of hydraulic conductivities and gradients in water potential. Hydraulic conductance of soil (K_{soil}), root hydraulic conductance (K_{root}), and stem hydraulic conductance (K_{stem}) determine water potential from soil to root and root xylem water, and thus magnitude of ψ_{leaf}. There are two main resistances to water flow from the soil to the shoot, namely the soil and the root resistances, often expressed as their inverse, K_{soil} and K_{root} (Nguyen et al., 2020; Cai et al., 2018). In wet soils, the soil hydraulic conductivity is much higher than that of roots, and water flow is mainly controlled by root hydraulic conductivity (Hopmans and Bristow, 2002; Draye et al., 2010). It is well-known that a decrease in soil matric potential and soil hydraulic conductivity triggers stomatal closure and thus results in reduction in transpiration rate (Sinclair and Ludlow, 1986; Carminati and Javaux 2020; Abdalla et al., 2021). For the root water uptake and controlling stomata, the location where soil and roots are in close contact (rhizosphere) is most important, because when this thin layer of rhizosphere is disconnected (i.e. soil-root contact is lost), the water movement from soil toward the roots is reduced, which might trigger stomatal closure to maintain hydraulic integrity of plant (Carminati et al., 2016; Rodriguez-Dominguez and Brodribb, 2019; Abdalla et al., 2022). The magnitude of the drop of water potential between bulk soil and soil-root interface increases considerably at different levels of soil dryness for different soil types (Carminati and Javaux, 2020; Abdalla et al., 2022). Hydraulic limits in the soil (Carminati and Javaux, 2020), or in the root–soil interface [as measured for olive trees by Rodriguez-Dominguez and Brodribb, 2019 or tomato (Abdalla et al., 2022)], or in the root properties (Bourbia et al., 2021; Cai et al., 2022; Nguyen et al., 2020; Cai et al., 2018) or due to both soil textures and root phenotypes (Cai et al., 2022b) emphasized the importance of belowground hydraulics (Carminati and

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Javaux, 2020). However, also the shoot hydraulic conductance could be limiting in some crop plants (Gallardo et al., 1996) or in trees (Domec and Pruyn, 2008; Tsuda and Tyree, 1997). Stomatal conductance and shoot hydraulic conductance showed close links to each other in pine trees (Hubbard et al., 2001). This summary illustrates three points: (i) current studies have often focused either on above or on below hydraulic limits, but rarely consider both (ii) it is unclear the roles and relations of soil hydraulic properties to root and plant hydraulic conductance (thus influences on stomatal conductance) (iii) the role of different hydraulic processes across the soil - plant - atmosphere continuum i.e. soil to roots, stem, and soil-plant hydraulic conductance in controlling stomatal conductance remains unclear.

Simultaneous measurements of atmospheric conditions (light intensity and vapor pressure deficit), leaf water potential, and transpiration rates, coupled with measurements of root, stem and whole soil-plant hydraulic conductance, root architecture, and soil water potential distribution could reveal the relative importance of rhizosphere, shoot and root growth, and hydraulic conductance vulnerability, especially under progressive soil drying at field conditions (Carminati and Javaux, 2020; Tardieu et al., 2017). For the soil water conditions, soil texture and hydraulic characteristics are very important that influence soil water movement and thus affect infiltration, surface and sub-surface runoff, and ultimately plant available soil water (Vereecken et al., 2016). Soil texture properties, characterized by different fractions of clay, silt, and sand particles, are important drivers in determining the soil water retention properties (Scharwies and Dinneny, 2019; Stadler et al., 2015; Zhuang et al., 2001). Soil with higher water holding capacity (here the silty soil with low stone content) have a larger amount of plant available water which in turn enables crops to better meet the evaporative demand and facilitates better crop growth as compared to the soil with high stone content (Nguyen et al., 2020; Cai et al., 2018). Estimations of hydraulic conductance (different organs and whole plant hydraulic conductance) were done for crop plants and maize mainly under controlled environment or pot conditions e.g. for different species and genotypesduring soil drying (Sunita et al., 2014; Choudhary and Sinclair, 2014; Abdalla et al., 2022; Meunier et al., 2018; Wang et al., 2017; Li

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et al., 2016) or various species and genotypes together with different soil textures (Cai et al., 2022a), or soil texture with different vapor pressure deficit (VPD) (Cai et al., 2022b). Compared to the substantial effect of soil texture, there was no evidence of an effect of VPD on both soil–plant hydraulic conductance and on the relation between canopy stomatal conductance and soil–plant hydraulic conductance in pot-grown maize (Cai et al., 2022b). Contrast results were found in winter wheat where plant hydraulic conductance increased with rising VPD for some genotypes in wet conditions (Ranawana et al., 2021). Vadez et al., (2021) examined the effects of soil types together with increasing VPD on transpiration efficiency (TE) and yield under pot conditions for several C_4 species (maize, sorghum, and millet). The interpretation of differences in TE was attributed to soil types, more specifically, to the differences in soil hydraulic properties and soil hydraulic conductance However, experimental evidence linking root hydraulics to stomatal regulation was lacking in these two Vadez's studies (Vadez et al., 2021). Extrapolation and use of results obtained in pots or under greenhouse conditions to the field scale are difficult due to the fact that soil substrates in pots might not represent natural soil in the field (Passioura, 2006). There is often greater evaporative demand and considerable fluctuation and interactions of climatic variables in the field as compared to experiments under controlled or semi-controlled conditions. Recent field studies have aimed at quantification of root hydraulic conductance and it linkages with crop growth (leaf area and biomass) under different soil types (in wheat Cai et al., 2017; Cai et al., 2018; Nguyen et al., 2020 or maize in Nguyen et al., 2022; Jorda et al., 2022). However, field studies that consider both below (soil-root hydraulic conductance) and above (stem hydraulic conductance), or soil-plant hydraulic conductance (includes below and above-ground parts) and their roles in stomatal regulation as well as crop growth (leaf area and biomass) are rarely carried out.

This study aims at further understanding of the hydraulic linkages between soil and plant and responses of plants to drought stress in relation to root: shoot growth characteristics at field scale. We hypothesize that, in field-grown maize, (1) soil-plant hydraulic conductance depends on soil hydraulic properties,

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especially under dry soil conditions (2) minimum leaf water potential of maize is similar across soil types, water treatments and climatic conditions. The hypotheses will be tested through three objectives: (i) to investigate the effects of soil types, water application, and climatic condition on root growth and (ii) on stomatal conductance, leaf photosynthesis, transpiration, leaf water potential, different components (root, stem and whole soil-plant hydraulic conductance), and (iii) to analyze the relative contribution of root and shoot growth (leaf area and biomass) on the water uptake capacity of maize. These three objectives will be achieved based on a comprehensive dataset covering the whole soil-plant continuum over two growing maize seasons with contrasting climatic conditions (low and high VPD) under two water treatments (rainfed and irrigated) and two different soil types (stony and silty soil).

2. Materials and methods

2.1. Location and experimental set-up

We carried out a field experiment at two rhizotron facilities in Selhausen, North Rhine-Westphalia, Germany (50°52'N, 6°27'E). The field is slightly inclined with a maximum slope of around 4°. One rhizotrone facility was located upslope (F1) with around 60% gravel by weight in the 10-cm topsoil while the second rhizotrone facility was at downslope (F2) with silty soil (stone content is around 4% by weight).

Each experimental site was divided into three subplots of 7.25 m by 3.25 m: two rainfed plots (P1, P2), and one irrigated plot (P3). In rainfed plots P1, other sowing densities and dates were used than in the other plots and we excluded therefore these plots. Silage maize *cv.* Zoey was sown on 4 May and 8 May in 2017 and 2018, respectively, with a plant density of 10.66 seeds m^{-2} (Figure 1a; Table 1). Detailed information of crop management practices is provided in Table 1.

[Insert Table 1 here]

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2.2. Water applications

Weather variables (global radiation, temperature, relative humidity, precipitation, and wind speed) were recorded every 10 minutes by a nearby weather station (approx. 100 m from the experiment). Drip lines (T-Tape 520-20-500, Wurzelwasser GbR, Müzenberg, Germany) were installed for irrigation at 0.3 m intervals parallel to the crop rows. In 2017, maize received a total amount of 230 mm precipitation during the growing period (136 days). Average, minimum and maximum daily air temperature were 17.6, 8.3, and 25.3 °C, respectively (Fig. 1b). The crop on P3 was irrigated (in total 130 mm) every 5-7 days (in total 10 times) using 13 mm of irrigation water per event between mid June to end of August for the irrigated plots (2017F1P3 and 2017F2P3) (Fig. 1b). In 2018, average, minimum, and maximum daily air temperature were 19.2, 10.85, and 27.3 °C, respectively (Fig. 1b) and exceeded those of 2017. Characterized by exceptionally hot and dry weather conditions, the summer season 2018 can be classified as an extreme year with respect to plant growth at our site. Maize experienced high temperatures and VPD, especially around tasseling and silking. In 2018, only 91.3 mm of rain were recorded in the growing period of 2018 (107 days). The maize crop was irrigated every 5-7 days (in total 13 times), with a total amount of irrigation of 257 mm and 239 mm between mid- June and mid- August for the irrigated plots 2018F1P3 and 2018F1P3, respectively (Fig. 1d). In contrast to 2017, the rainfed plot in the stony soil (2018F1P2) had to be irrigated (in total 66 mm) in four times (using 13, 22, 13, and 18 mm, respectively) to avoid a crop failure due to severe drought (Fig. 1d).

[Insert Figure 1 here]

2.3. Measurements

2.3.1. Soil water measurement and root growth

At soil depths of 10, 20, 40, 60, 80, and 120 cm, MPS-2 matrix water potential and temperature sensors (Decagon Devices Inc., UMS GmbH München, Germany) were installed to measure half-hourly soil water potential and soil temperature. The range of the water potential measurements is form -9 kPa to

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approximately -100000 kPa (pF 1.96 to pF 6.01). In addition to MPS-2, soil water potential was measured by pressure transducer tensiometers (T4e, UMS GmbH, München, Germany) where the minimum detectable suction is -85 kPa to +100 kPa. A detailed description of sensor installation, calibration and data post processing can be found in Cai et al., (2016).

Minirhizotubes (7 m long clear acrylic glass tubes with outer and inner diameters of 6.4 and 5.6 cm, respectively) were installed horizontally at six different depths of 10, 20, 40, 60, 80, and 120 cm below the soil surface in each facility. There are three replicate tubes at each depth, accounting for 54 tubes in each facility. Root measurements were taken manually by Bartz camera (Bartz Technology Corporation) (23 June 2017 – 12 September2017) and VSI camera (Vienna Scientific Instruments GmbH) (08 June 2017 – 22 June 2017) in 2017 while only VSI was used in 2018 (23 May2018 - 23 August 2018). Root images were repeatedly taken from both left and right sides at 20 locations along horizontally installed minirhizotubes. The root images were analyzed by automated minirhizotube image analysis pipeline for segmentation and automated feature extraction (Bauer et al., 2021). Two-dimensional root length density (RLD, in units of cm cm^{-2}) was estimated from the total root length observed in the image and the image surface area. The overview of camera system, minirhizotube images acquisition, and post-processing of the root data were described in detail in Bauer et al. (2021).

2.3.2. Crop growth measurement

The phenology, plant height, stem diameter, green and brown leaf area, dry matter of different organs, and total aboveground dry matter were observed and measured bi-weekly. Plant height was measured of 15 randomly selected plants. The diameters of five randomly selected stems were measured. Due to the limited number of plants in each plot, only two plants per measurement date were sampled to determine total aboveground dry matter and leaf area (7 and 8 times in 2017 and 2018, respectively). Green and brown leaf area was measured by a LI-3100C (Licor Biosciences, Lincoln, Nebraska, USA). At harvest, five

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separate replicates (1m^2 each) were harvested. The dry matter of separate organs was determined after drying at 105 °C for 48 hours (Nguyen et al., 2020).

2.3.3. Leaf gas exchange, leaf water potential, and sap flow measurements

Hourly leaf stomatal conductance (Gs), net photosynthesis (An), and leaf transpiration (E) were measured every two weeks under clear sky conditions. Observations from 8 AM to 5 PM on four days and from 10 AM to 4 PM on six days were carried out in 2017. In 2018, measurements were carried out on 6 days from 8 AM to 7 PM and on 5 days from 10 AM to 4 PM (Nguyen et al., 2022a). The Gs, An, and E of two sunlit leaves (uppermost fully developed leaves) and one shaded leaf of different plants were measured at steady-state using a LICOR 6400 XT device (Licor Biosciences, Lincoln, Nebraska, USA). After leaf gas exchange measurements, leaves were quickly detached using a sharp knife to measure leaf water potential (ψ_{leaf}) with a digital pressure chamber (SKPM 140/ (40-50-80), Skye Instrument Ltd, UK) with the working air pressure ranging from 0 to 35 bars. To study the diurnal course of ψ_{leaf} under dry and re-wetted soil conditions, in 2018, measurements were undertaken for three additional days with predawn measurements two days before and one day after irrigation. Further detail of measurement dates, range of real time records of PAR, VPD and soil water status could be found in (Nguyen et al., 2022a).

In 2017 (from 7 July 2017 until harvest) and 2018 (from 28 June 2018 until harvest), 20 sap flow sensors (SGA 13, SGB 16, and SGB 19 types) were installed (one sensor per plant and 5 maize plants per plot) based on stem diameter size. Sensor data, in particular the partitioning of energy, electricity supply, sap flow, and the temperature difference between upper and lower thermocouples (dT) of each sensor were recorded at 10 minute intervals using a CR1000 data logger and two AM 16/32 multiplexers (Campbell Scientific, Logan, Utah). The sap flow in the plant (g h^{-1}) was monitored directly by the data loggers (Dynamax, 2007) and used as a surrogate for canopy transpiration based on the number of plants per square meter.

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2.4. Calculation of total root length, root system conductance, stem, and whole plant hydraulic conductance

To estimate the total root length from minirhizotubes, we adopted the option 2 which was described in Cai et al., (2017). Total root length per square meter soil surface area within each soil layer (m m^{-2}) was computed by multiplying the root length density with the corresponding soil layer thickness. The root length density was determined in each depth by dividing the measured root length per minirhizotron image by the assumed volume the roots would have occupied in absence of the tube, i.e., W * L * tube radius (see Cai et al., 2017).

Following Nguyen et al., (2020), the effective soil water potential was calculated based on hourly measured soil water potential (ψ_i) and normalized root length density at six depths (10, 20, 40, 60, 80, and 120 cm) ($NRLD_i$), and soil layer thickness (Δz_i) in the soil profile (Equation 1).

$$\psi_{soil\_effec} = \sum_{i=1}^{N} \psi_i NRLD_i \, \Delta z_i \tag{1}$$

We followed Ohm's law analogy by dividing the hourly sap flow by the difference between effective soil water potential and shaded leaf water potential to estimate root system conductance (K_{soil_root} - Equation 2), between shaded leaf water potential and sunlit leaf water potential to estimate stem hydraulic conductance (K_{stem} - Equation 3), and between effective soil water potential and sunlit leaf water potential to estimate whole plant hydraulic conductance (K_{soil_plant} - Equation 4).

$$K_{soil\_root} = Sapflow/(\psi_{soil\_effec} - \psi_{shadedleaf}) \tag{2}$$

$$K_{stem} = Sapflow/(\psi_{shadedleaf} - \psi_{sunlitleaf}) \tag{3}$$

$$K_{soil\_plant} = Sapflow/(\psi_{soil\_effec} - \psi_{sunlitleaf}) \tag{4}$$

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During one measurement day, four values of the K_{soil_root}, K_{stem}, and K_{soil_plant} were obtained from measurements between 11AM and 2 PM. The average and standard deviation of these hourly measurements were calculated for each measurement day in order to present the seasonal dynamics of those variables. To capture the diurnal and seasonal variations of sap flow and sunlit leaf water potential, in addition, we plotted the hourly sap flow and hourly difference of effective soil water potential and sunlit leaf water potential for three measurement days starting from predawn and whole seasons, respectively, to derive the slope which is also K_{soil_plant}.

2.5. Statistical analysis

Regression analysis was performed to understand the relationship between the sap flow volume and the difference of effective soil water potential and sunlit leaf water potential as well as the relationship between the total aboveground biomass and cumulated water transpired (sap flow volume). These analyses allow to derive the slope as proxy of K_{soil_plant} and transpiration use efficiency, respectively. Since all measured data have their own measurement errors, the generalized Deming regression was employed. We performed relationships (via correlation coefficient and statistical significant levels) of midday leaf An, Gs, and E with midday K_{stem}, K_{soil_plant}, K_{soil_root}, sunlit leaf potential, ψ_{soil_effec}, and the difference of ψ_{soil_effec} and sunlit leaf water potential ($\psi_{difference}$). All data processing and analysis were conducted using the R statistical software (R Core Team, 2022).

3. Results

3.1. Root growth under different water treatments, soil types and climatic conditions

Observed root length (cm cm^{-2}) from the minirhizotubes in different soil depths at the first week of June (stem elongation), around silking, and at harvest in two growing seasons are shown in the Figure 2. Root length was similar among water treatments at the start of stem elongation in both years (Fig. 2a & 2d). The difference in root length was pronounced at silking and harvest between the soil types. More root growth was observed in the silty soil compared to the stony soil with the same water treatment (i.e. 2.5 -

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6 times higher at depth 40 cm). This indicated the strong negative effects of stone content on root development. In the stony soil, root length in the irrigated plot (F1P3) was slightly higher than in the rainfed plot (F1P2). In contrast, the rainfed treatment (F2P2) in the silty soil showed much higher root length, especially from 40 to 120 cm depths as compared to the irrigated plot (F2P3) in both growing seasons. Much lower stone content and deep soil cracks in the silty soil (Morandage et al., 2021) allow root extension to the subsoil, particularly in the rainfed plot F2P2. Root length in the rainfed treatment (F2P2) in 2018, is higher than in 2017 which implies that root further developed to exploit the water in the soil under the rainfed condition to meet the higher evaporative demand.

[Insert Figure 2 here]

Total root length (m m^{-2}) estimated from minirhizotubes and its ratio to shoot dry matter (m kg^{-1}) at three measured dates (as in Figure 2) are shown in the Figure 3. Total root length was much higher for the silty plots as compared to stony plots. In 2017, the highest total root length was observed in the rainfed plot of the silty soil (F2P2) with approximately 9166 m m^{-2} and 9878 m m^{-2} around silking and harvest, respectively, which was almost two times higher than in the irrigated plot (F2P3). These figures were higher in 2018 than 2017 where total root length of F2P2 was 10188 m m^{-2} and 13750 m m^{-2} at silking and harvest time, respectively. For the rainfed stony soil (F1P2), soil water depletion around the beginning of June in 2017 (Supplementary material 1a) and from the first two weeks of June to harvest in 2018 (Supplementary material 2a) caused the strong reduction of shoot biomass. In the stony soil, the shoot dry matter of the irrigated plot (F1P3) and the rainfed plot (F1P2) were 1275 and 536 g m^{-2} at silking time (e.g. 19 July 2018 –DOY 200, Supplementary material 3a and 3b). However, there was a minor difference between F1P2 and F1P3 in terms of the ratio of root length to shoot dry matter. In the silty soil, a decrease of soil water potential was not pronounced (compared to stony soil) in both years 2017 and 2018 (Supplementary material 1b and 2b). In 2018, shoot biomass in the irrigated stony soil (F1P3) and silt soil (F2P3) were similar (1275 and 1299 g m^{-2}, respectively on 19 July 2018 – DOY 200) while the shoot biomass of the

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rainfed silty soil (F2P2) was 876 g m^{-2} (Supplementary material 3a & 3b). However, the ratios of root length to shoot biomass in the rainfed plot of the silty soil (F2P2) were 3 and 6 times higher than those in the irrigated silty soil (F2P3) and stony soil (F1P3), respectively (e.g. 18 July, DOY 199). Moreover, total root length was relatively equal among treatments at the start of set elongation (DOY 159, first week of June) in both years, while this was the opposite for the ratio of root length to shoot dry matter. This firstly illustrated that the finer soil texture without stones and with soil cracks could favor the root growth which indicates strong interactions of root and soil conditions. Secondly, the larger root length and higher atmospheric evaporative demand in 2018 than 2017 indicates also the interaction of root growth and climatic conditions.

[Insert Figure 3 here]

3.2. Stomatal conductance, photosynthesis, transpiration, and K_{soil_plant}

3.2.1. Diurnal course of stomatal conductance, photosynthesis, transpiration, and water potential at leaf level

After a long period with high temperatures and no rainfall, soil water reduction in the rainfed plot of the stony soil (F1P2) on 17 July 2018 (Supplementary material 2) resulted in three times lower net photosynthesis (An), stomatal conductance (Gs), transpiration (E) and leaf water potential (ψ_{leaf}) as compared to the remaining treatments (Fig. 4). This indicates that the soil water content strongly affected the stomatal conductance. Stomatal closure was much pronounced around midday in F1P2 while this was not the case in the F2P2, indicating the soil type strongly affected the stomatal conductance and leaf gas exchange.

[Insert Figure 4 here]

Leaf gas exchange and leaf water potential in the F1P2 were still much lower than in other plots (Figure 5). On 18July 2018, after application of 22.75 mm of irrigation water (at 4 PM), photosynthesis, stomatal

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conductance, transpiration and leaf water potential were slightly increased in F1P2. However, these were still smaller than in F2P2 and the two irrigated plots.

[Insert Figure 5 here]

On the next day after irrigation, leaf gas exchange and water potential were considerably increased in the F1P2 (Figure 6). Leaf curling was also less pronounced as compared the two previous days. This indicated the recovery of plant after watering. Leaf water potential, photosynthesis, stomatal conductance, and leaf transpiration were almost similar to other plots from predawn throughout the day.

[Insert Figure 6 here]

3.2.2. Seasonal course of stomatal conductance, photosynthesis, transpiration, water potential, and plant hydraulic conductance at the leaf level

Seasonal stomatal conductance (Gs) and leaf water potential (ψ_{leaf}) are described in Figure 7. The relationship between two variables was rather noisy and non-linear. The leaf water potential showed distinct patterns among treatments in one growing season. Minimum ψ_{leaf} was maintained at around -1.5 MPa in the irrigated plot in stony soil (F1P3) and two plots in the silty soil (F2P2 and F2P3). Lower minimum ψ_{leaf} could be observed in the rainfed plot with stony soil (F1P2) but it did not go beyond -2 MPa. Minor leaf curling was observed only in the second week of June in the F1P2 in 2017. In 2018, the higher temperature and vapor pressure deficit resulted in lower minimum ψ_{leaf} in all treatments and soil types as compared to 2017. The minimum ψ_{leaf} was around -2 MPa in F1P3, F2P2, and F2P3 while ψ_{leaf} could drop below -2 MPa in F1P2 which was due to the severe soil water deficit. The low Gs and ψ_{leaf} associated with measurement dates when the substantial leaf curling was observed at mid of July to the end of growing season in F1P2 in 2018 (Supplementary material 3c & 3d and Supplementary material 4c & d).

[Insert Figure 7 here]

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The effective soil water potential ($\psi_{soil\_effect\ MD}$), sunlit leaf water potential ($\psi_{sunlitleaf\ MD}$), stomatal conductance (Gs_{MD}), and whole plant hydraulic conductance ($K_{soil\_plant\ MD}$) at midday at several times during the growing season are presented in Figures 8 and 9 for 2017 and 2018, respectively. As expected, there was not much difference in terms of $\psi_{soil\_effecMD}$ among F1P3, F2P2, and F2P3 from 02 August to one week before harvest in 2017. The lowest $\psi_{soil\_effec\ MD}$ was observed in the F1P2. Leaf water potential dropped drastically but also $K_{soil\_plant\ MD}$ increased strongly whereas $\psi_{soil\_effec\ MD}$ remained quite similar (e.g. 18 July). This is because sap flow have increased substantially in this day (e.g. from 2.34 mm d^{-1} on 17 July to 6.97 mm d^{-1} on 18 July for the F1P2). The stomatal conductance decreased a lot in this day which could be explained that the atmospheric demand increased (e.g. global radiation was 13.6 MJ m^{-2} on 17 July compared to 23.9 MJ on 18 July while daily VPD was 0.7 kPa and 1.2 kPa, respectively) even more than the sap flow. Midday sunlit leaf water potential was not distinctively different among treatments with the lowest $\psi_{sunlitleaf\ MD}$ around -1.6 MPa throughout season. Also, Gs_{MD} was rather similar among plots. The $K_{soil\_plant\ MD}$ ranged from 0.125 to 0.96 mm h^{-1} MPa^{-1} with a sharp reduction before harvest. In general, the lowest values of $K_{soil\_plant\ MD}$ were found in F1P2 which was consistent with the smaller overall seasonal K_{soil_plant} (as the slope of linear relationship between sap flow and difference of effective soil water potential and sunlit leaf water potential) (see Supplementary material 5).

[Insert Figure 8 here]

The $\psi_{soil\_effec\ MD}$ was substantially different in the two soil types and water treatments in 2018 (Figure 9a). Both F1P2 and F1P3 showed a gradual drop of $\psi_{soil\_effec\ MD}$ from 15 June until the third week of July then increased after irrigation events on 18 July (Supplementary material 2b). However, $\psi_{soil\_effec\ MD}$ of F1P2 was much lower than F1P3 toward the harvest. The $\psi_{soil\_effec\ MD}$ of F2P2 and F2P3 only decreased progressively from around 10 July till harvest even though there was water supply from the irrigation (Supplementary material 2b). The water applied by irrigation and coming in by rainfall were insufficient to wet up the deeper soil layers which remained dry. The low Gs_{MD} was corresponding to the lowest $\psi_{sunlitleaf\ MD}$ and

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$K_{soil\_plant\ MD}$ from the F1P2 (Figure 9c & 9d). The $K_{soil\_plant\ MD}$ from all plots was ranging from 0.12 to 0.91 mm h^{-1} MPa^{-1}.There was the drop in $K_{soil\_plant\ MD}$ (i.e. 3 to 9 July or 17-18 July) before irrigation in this plot. However, it increased after the irrigation (i.e. 10 July and 19 July). This suggests that K_{soil_plant} depends strongly on the soil water content and the conductivity of the rhizosphere.

[Insert Figure 9 here]

3.2.3. Relationships of stomatal conductance, transpiration, photosynthesis with plant hydraulic variables at the plant canopy level

The slope of linear relationship between sap flow and difference of ψ_{soil_effec} and $\psi_{sunlitleaf}$ is shown for three consecutive days (leaf water potential measurements from the predawn) and before and after irrigation applications (17, 18, and 19 July 2018 or DOY 198, 199 and 200, respectively) (Figure 10). On both DOYs 198 and 199, the difference between ψ_{soil_effec} and $\psi_{sunlitleaf}$ was around -1.6 MPa with very low transpiration rates in the treatment F1P2 which was associated with very low plant hydraulic conductance and leaf curling. The whole plant hydraulic conductance was disrupted on these two days (0.06 and 0.16 mm h^{-1} MPa^{-1} for DOY 198 and 199, respectively). Water was supplied on DOY 199 at 1 PM for the irrigated plots (F1P3, F2P3) as well as F1P2 at 4 PM (for saving plant from death due to severe drought stress). K_{soil_plant} was slightly changed (0.43 and 0.57 mm h^{-1} MPa^{-1} for F1P3 on DOY 199 and 200, respectively and 0.5 and 0.58 mm h^{-1} MPa^{-1} for F2P3 on DOY 199 and 200, respectively). However, the increase of K_{soil_plant} was substantial in the F1P2 after the irrigation. Soil water replenishment and an increase in the root - soil contact (Fig. 9a) allowed the K_{soil_plant} to recover overnight to 0.46 mm h^{-1} MPa^{-1}. This resulted in a narrower water potential gradient between root zone and sunlit leaf and in a higher transpiration rate on DOY 200.

[Insert Figure 10 here]

Seasonal average of different midday hydraulic conductance components (root system hydraulic conductance - K_{soil_root}, stem hydraulic conductance – K_{stem}, and whole plant hydraulic conductance –

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K_{soil_plant}) are shown in Figure 11. In the same year, the K_{stem} was not much different among F1P3, F2P2, and F2P3 plots. The K_{stem} of those plots was slightly higher than in the F1P2 in both years. In general, the K_{soil_root} was lower than the K_{stem}. The K_{soil_root} in the F1P2 in 2018 was much lower than the remaining plots while the K_{soil_root} was not much different among plots in 2017. Overall, the estimated K_{soil_plant} was around 1/ (1/K_{soil_root} +1/K_{stem}) regardless of soil types, years, and water treatments. Although there is a large difference in total root length between two soil types (e.g. F1P3 versus F2P2), K_{soil_root} and K_{soil_plant} in those two plots were not much different. The K_{soil_plant} and K_{soil_root} depend strongly on the soil water content and the soil hydraulic properties. Therefore, K_{soil_plant} and K_{soil_root} were not only a plant property but also a soil property.

[Insert Figure 11 here]

3.3. Relative importance of root and leaf area growth to transpiration and crop performance at canopy level

Drought stress was observed in the rainfed plot (F2P2) in the second week of June 2017 with mild leaf rolling. The crop then recovered due to sufficient rainfall and lower evaporative demand. Drought stress occurring again at the stem elongation phase caused reduction of plant size (height and stem diameter) (Supplementary material 4) as well as a slight reduction of leaf area and biomass in this plot (Supplementary material 3a & 3c). Transpiration per unit of leaf area did not differ much among water treatments and soil types in 2017 (Figure 12). The opposite was the case for the transpiration rate per unit of root length. The observed root length at different soil depths (Figure 2) and total root length for two plots in the stony soil was much smaller than in the silty soil (Figure 3). Therefore, transpiration per unit of root length in the stony soils (F1P2 & F1P3) was almost 3 times higher than transpiration in the silty soil. For the same soil, transpiration per unit root length of the irrigated treatment was slightly larger than in the rainfed plot.

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[Insert Figure 12 here]

The differences in sap flow per plant between water treatments and soil types were more pronounced in 2018 (Figure 13). The highest transpiration rate was observed in the irrigated plots (F1P3 & F2P3), followed by the rainfed plot of the silty soil (F2P2) and it was lowest in the rainfed plot of the stony soil (F1P2). These observations were in line with the differences in biomass and leaf area index between the treatments (Supplementary material 3b & 3d) and plant size (Supplementary material 4b-c-d). In 2018, severe leaf rolling was observed in the rainfed plot (F1P2) from the beginning of June until the end of the growing period in 2018 (Supplementary material 3d). Similar to 2017, transpiration per unit of root length was much higher in the stony plots as compared to silty plots. Also, for the silty soil, transpiration per unit of root length of the irrigated plot (F2P3) was higher than in the rainfed plot (F2P2).

[Insert Figure 13 here]

Higher cumulative transpiration in the irrigated plots did not result in higher transpiration use efficiency (TUE) in both soil types (Figure 14). For instance, TUE were 16.87 g mm^{-1} and 15.59 g mm^{-1} for F1P2 and F2P2, respectively, while they were 15.47 and 14.79 g mm^{-1} for F1P3 and F2P3, respectively, in 2017 (Figure 14A). For the same soil, the rainfed plot showed slightly higher TUE than the irrigated plot. When comparing the TUE of maize of the two soil types for the same water treatment, TUE at the stony soil was almost the same in silty soil. The TUE was not much different among treatments and soil types in 2018. Overall, TUE in 2017 was higher as compared to 2018 (Fig. 14b).

[Insert Figure 14 here]

4. Discussions

4.1. Effects of soil types, water application, and climatic condition on root growth

Our root observations showed that soil type considerably affected root growth more than water treatment (Figure 2). Root growth was strongly inhibited by the stony soil where much lower root length was

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observed than in the silty soil, especially in the deeper soil layers. This was consistent with the findings reported in (Morandage et al., 2021) where a linear increase of stone content resulted in a linear decrease of rooting depth across all stone contents and developmental stages. Also, both simulations and observations indicated that rooting depth was sensitive to the presence of cracks in the lower minirhizontron facility (Morandage et al., 2021) which could explain the high root length between 40 and 120 cm soil depths which was observed in the silty soil in both years. In the silty soil, root growth was favored towards deeper soil layers as also reported for the same field in 2016 for winter wheat (Nguyen et al., 2020). Observation in field grown maize, the higher root length density and root diameter were found in the sand than in the loam. This was attributed to the higher investment in nutrient exploration because the lower concentration of plant-available nutrients was in sand than in loam (Vetterlein et al., 2022). Also, the larger root diameters in sand than in loam are more likely explained by the need for soil contact of the roots (Jorda et al., 2022; Vetterlein et al., 2022).

Our total root length was in the reported range of Cai et al., (2018) who studied winter wheat roots on the same soil types in 2016. The total root length in our work was higher than the reported results from Cai et al., (2018) especially in the rainfed plot of the silty soil (F2P2) in 2018 (Fig. 3). In terms of the root: shoot ratio, our observations were in line with those reported in the same soil types for wheat in Cai et al., (2018). Ordóñez et al., (2020) has reported much larger figures of for instance 880 cm g^{-1} in different locations and under different N application rates in maize growing in the Midwest of US. Jorda et al., (2022) reported a wide range of root: shoot ratio from 200 to 1000 cm g^{-1} around flowering time of maize depending on the wild type and root hair mutant genotypes growing on either loamy or sandy soils. More roots and higher root: shoot ratios were found in the sand than in the loam in both wild type and root hair mutant genotypes (Jorda et al., 2022; Vetterlein et al., 2022). Cai et al., (2018) observed much larger root: shoot ratio in drought stressed plots than in irrigated plot in both soil types in winter wheat which indicated the alternation of sink: source relationships to cope with water stress. This study emphasized that more

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assimilates are used to promote root growth and extract more water under drought stress. However, this was not the case for the stony soil in our work where the drought stress was more pronounced, especially in 2018. A slightly higher root: shoot ratio in the F1P2 treatment compared to F1P3 (DOY 194 & 255) was observed in 2017 while the root: shoot ratio in the two treatments was almost the same on DOY 199 and 228 in 2018 (Fig. 3). We only observed much higher root: shoot ratio in the rainfed plot (F2P2) as compared to the irrigated plot on the silty soil (F2P3). Comas et al., (2013) has reported that maize increases the ratio of root to leaf surface area and relative distribution to deeper depths in responses to water deficit. Under drought stress, root growth of maize continues longer into the season than shoot and vegetative growth and even beyond the onset of reproduction. A drop of soil water potential (Supplementary material 2b), thus effective soil water potential (Figure 8a) was substantial from 10th July 2018 toward the harvest in the rainfed plot in the silty soil (F2P2) which was consistent with the reduction of leaf water potential (Fig. 8b), leaf area (Supplementary material 3c), total dry matter (Supplementary material 3d), and crop height (Supplementary material 4b) as compared the irrigated plot (F2P3). This indicates a mild water stress in 2018 in the rainfed plots on the silty soil. The larger root: shoot ratio in this F2P2 plot in 2018 as compared to F2P3 could be explained by the change of source: sink relations where more assimilates were devoted to root growth, even at a later growth stage. Moreover, the low stone content and soil cracks (Morandage et al., 2021) might favor root growth in the deeper soil layers which are close to the lower soil water table in the site with silty soil (Vanderborght et al., 2010).

4.2. Effects of soil types, water application, and climatic condition on stomatal conductance, photosynthesis, transpiration, leaf water potential, and plant hydraulic conductance

4.2.1. Leaf water potential and stomatal conductance as affected soil water conditions

In our study, stomata closed earlier and at more negative soil and leaf water potentials in stony soil than in silty soil (see Fig. 4, 5, 6 and 7). In other work, Koehler et al., (2022) reported that maize stomata closed at lower negative leaf water potentials in sand than in loam growing under controlled environment. Cai et

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al., (2022b) investigated transpiration response of pot-grown maize in two contrasting soil textures (sand and loam) and exposed to two consecutive VPD levels (1.8 and 2.8 kPa). Transpiration rate decreased at less negative soil matric potential in sand than in loam at both VPD levels. In sand, high VPD generated a steeper drop in stomatal conductance with decreasing leaf water potential which indicated the transpiration and stomatal responses depend on soil hydraulics.

Stomatal control is an early and effective response to water stress to prevent the plant from water loss and dehydration. Maize is considered as an isohydric plant which closes its stomata to maintain leaf water potential above critical levels (Tardieu and Simonneau, 1998). Our results showed that minimum leaf water potential varied among treatments (-1.5 MPa for F1P3, F2P2, and F2P3 and up to -2 MPa for F1P2 in 2017, while in 2018 minimum values were -2 MPa for F2P3, F2P2, and F2P3 and -2.7 MPa for F1P2) (Fig. 7 and Fig. 8, Fig. 9). Large variability of minimum LWP has been reported for maize genotypes. Leaf water potential can be limited at quite high values, for instance -0.8 MPa in some lines of maize, while values as low as -1.5 MPa have also been recorded (Welcker et al., 2011). Some drought-tolerant maize genotypes close stomata at less negative leaf water potential under soil water depletion than more sensitive ones, which is associated with their ability to avoid xylem embolism and hydraulic failure (Cochard, 2002; Tyree et al., 1986; Li et al., 2009). However, our results show that the leaf water potential threshold can vary within the same genotype depending on soil types, climatic conditions and water management. It should be noted the constant ψ_{leaf} level (around -1.8 MPa) under different soil water regimes reported in Tardieu and Simonneau (1998) that was associated with high VPD values, was based on observations from a single day. Measurements on ψ_{leaf} and Gs for different days during several growing seasons have been rarely reported for maize. The results of our study confirmed that maize appears to maintain its ψ_{leaf} at around -1.5 to -2 MPa which depended on evaporative demand and levels of soil moisture (Fig. 1, Fig. 7, Fig. 8, and Fig. 9). This has been reported recently in Nguyen et al. (2022a). Our current study, which investigates the drivers of the modifications of ψ_{leaf} during the growing season, also confirmed that such stomatal

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regulation and the ψ_{leaf} were mediated by soil hydraulics. Cochard, (2002) reported that stomatal closure is complete between -1.6 and -2 MPa. In our study, the observed ψ_{leaf} was below -2 MPa for several days. Similar values were also reported by Li et al. (2002) for field-grown maize in semiarid conditions. In our study, leaf water potential dropped below -2 MPa in the rainfed plots to levels much lower than those observed in the irrigated plots in 2018. This could imply different degrees of isohydry in maize. A continuum exists in the degree to which stomata regulate the ψ_{leaf} for trees (Domec and Johnson, 2012; Klein, 2014) or in grape-vine (Schultz, 2003). Also, cultivars of grape vine show large differences in minimum ψ_{leaf} indicating differing degrees of isohydric behavior (Coupel-Ledru et al., 2014). When comparing different herbaceous species, Turner et al., (1984) showed that there was a range of isohydric behavior among the species in terms of the response to increasing vapor pressure deficit (VPD) under sufficient soil moisture. However, conclusions concerning contrasting minimum ψ_{leaf} between 2017 and 2018 should not be overemphasized. Observed extremely low ψ_{leaf} correspond with the extremely low Gs and were further accompanied by complete leaf curling in rainfed treatment under stony soil in 2018 (Fig. 4, 5, and Fig. 9) due to the extremely dry and hot summer and severe soil dryness.

4.2.2. Hydraulic conductance components as affected by soil water conditions

Estimates of hydraulic components in soil-plant-atmosphere continuum are important not only to understand its underlying relationship to other crop characteristics (stomatal conduction, transpiration, and photosynthesis) but also to provide modeling parameters in process-based soil-root-shoot models (Nguyen et al., 2020; Sulis et al., 2019; Nguyen et al., 2022b). Measurement of the components of hydraulic conductance are challenging under field conditions because it requires the estimate of transpiration and root to leaf water potential gradients. To our knowledge, our results were unique with regard to the dynamics of K_{soil_plant} for field-grown maize on two soil types and under contrasting water, and climate conditions. Our seasonal K_{soil_plant} ranged from 0.12 mm h^{-1} MPa^{-1} to 0.9 mm h^{-1} MPa^{-1} (Fig. 8 & Fig. 9; Fig. 10, and Supplementary material 5). Root system hydraulic conductance ranged from 0.26 to 1.47 mm h^{-1}

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MPa $^{-1}$ (Figure 11). Note that the unit of K_{soil_plant} as mm h^{-1} MPa $^{-1}$ could be equivalent to the unit of 10^{-5} h^{-1} if one assumes 1MPa is approximately 10^5 mm in terms of pressure head. Cai et al., (2018) reported root hydraulic conductance in winter wheat from 0.05 x 10^{-5} h^{-1} to 0.5 x 10^{-5} h^{-1} in two similar soil types. Nguyen et al., (2020) also reported K_{soil_plant} in winter wheat from 0.0625 x 10^{-5} h^{-1} to 0.461 x 10^{-5} h^{-1}. Meunier et al., (2018) focused on estimating the root system hydraulic conductance of maize in a container experiment where the range of K_{soil_plant} was much larger from 0.37 x 10^{-5} h^{-1} to 36 x 10^{-5} h^{-1} for the plant density of 10 plant m^{-2}. Jorda et al., (2022) estimated root system hydraulic conductance of 0.5 to 1.5 10^{-3} d^{-1}which would be roughly between 2 to 6 10^{-5} h^{-1}. To simulate leaf water potential in the modeling work for field maize, Nguyen et al., (2022b) based on assumption that K_{soil_plant} was 0.53 x K_{soil_root}. Such fraction (0.53) was consistent with the reported range in our work (0.3-0.8) with average K_{soil_plant} was at half of root system hydraulic conductance across treatments. In our work, except the F2P2 in 2018, the stem hydraulic conductance was 10% to 60% higher than root system hydraulic conductance. Gallardo et al., (1996) reported that stem hydraulic conductance of wheat was lower than root system conductance at around 71 to 91 days after sowing (DAS), but they were similar at 102 DAS. In lupine, stem hydraulic conductance was two times higher than root system conductance regardless of measured days. The larger root length in wheat than lupine did not necessarily result in higher root conductance in wheat. Together with this study, our study emphasizes the values of stem hydraulic conductance compared to the root hydraulic conductance in maintaining water potential gradient from shaded leaf or plant color to the sunlit leaf.

Our results showed clear differences in K_{soil_plant} among treatments where much lower K_{soil_plant} was observed in the F1P2 as compared to F2P2 (see Figure 10 for 2018; Figure 8 and 9 and Supplementary material 5 for both years). This indicated the soil texture dependence for whole plant hydraulic conductance. Maize plants with the shorter root system (i.e. rainfed plot in the stony soil in 2018) (Fig. 3) had lower plant hydraulic conductance. Our results indicated that there was an impact of soil hydraulic conditions on K_{soil_plant} via the reduction of root system hydraulic conductance. Our analysis for three

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consecutive measurement days in 2018 (Fig 10) showed that in the silty soil, K_{soil_plant} decrease when soil water potentials are becoming more negative. For instance, in the silty soil in 2018 when the soil water potentials were considerably lower in the rainfed than in the irrigated plot (e.g. after 10th July), K_{soil_plant} was lower in the rainfed than in the irrigated plot. In the stony soil, the K_{soil_plant} and leaf water potentials seems to decrease more considerably (compared to the silty soil) when the soil water potentials become more negative. In other words, K_{soil_plant} increased considerably when the soil water potentials in the stony soil increased. Koehler et al., (2022) analyzed the maize plant responses to soil drying under controlled climate conditions with three soil types (sand, sandy loam, and loam). This study confirmed the impact of soil texture on plant response to soil drying in various relationships. In their work, the soil-plant conductance decreased in both sand and loam but at less negative water potentials in the sand than in the loam. Root system hydraulic conductance decreased at less negative bulk soil water potential in the coarse soil than in the fine soil (Vanderborght et al., 2023).In our work, K_{soil_plant} increased slowly after irrigation mainly for the severe water stress plot (see F1P2 on 19 July in Fig 9d and 10c). This implied that added soil water by irrigation took some time for recovery the soil-root contact within the rhizophere.

4.2.3. Relationships of stomatal conductance, transpiration, photosynthesis with plant hydraulic variables

In 2017, our estimated midday effective soil water potential ($\psi_{soil\_effec\ MD}$) did not vary much (between soil types and treatments) which was consistent with the low variability in midday sunlit leaf water potential ($\psi_{sunlitleaf\ MD}$) and K_{soil_plant} among water treatments (Fig. 8). The $\psi_{soil\_effecMD}$ was high (around -0.35 MPa) while $\psi_{sunlitleaf\ MD}$ was around -1.5 MPa (Fig. 8c). In contrast, the difference of $\psi_{soil\_effec\ MD}$, $\psi_{sunlitleaf\ MD}$, and K_{soil_plant} was higher among water treatments and soil types in 2018 as compared to 2017. Moreover, the high VPD and air temperature in combination with the small precipitation in the main growing season in 2018 led to a stronger reduction of $\psi_{soil\_effec\ MD}$ up to -0.75 MPa (i.e. in F1P2 in the stony soil on 17 and 18 July in 2018, Figure 9) and $\psi_{sunlitleaf\ MD}$ to -2.5 MPa. This low $\psi_{soil\_effec\ MD}$ in F1P2 was associated with low

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stomatal conductance (Fig. 9c), low K_{soil_plant} (Fig. 9d), and strong transpiration reduction (Fig. 10a-b, Fig. 12, and Supplementary material 5). Our results were in line with the analysis from Cai et al., (2022a) which revealed that water uptake depended on effective soil water potential which in turn depended on soil water potential which differed between plots with different textures.

The transpiration rate and K_{soil_plant} (slope of linear regression lines in Fig. 10a and b) were very low in the rainfed plot under the stony soil (F1P2) which was associated with the large $\psi_{difference}$ (Fig. 10a & b) and the lower stomatal conductance as compared to other plots (Fig. 9c). The K_{soil_plant} slightly increased after irrigation (DOY 199 in Fig. 10b) corresponding with the smaller $\psi_{difference}$ (Fig. 10b) and an increase in stomatal conductance (Fig. 9c). Seasonal K_{soil_plant} was low in the rainfed plot under stony soil (F1P2) with the larger $\psi_{difference}$ (Supplementary material 5). In addition, our study showed that the midday stomatal conductance, photosynthesis, and transpiration were significantly correlated only with midday K_{soil_plant} in the rainfed plot on the stony soil (F1P2) in 2018 where high VPD and temperature occurred (Supplementary material 6, 7, and Supplementary material 8). Maize plant had lower plant hydraulic conductance in the rainfed plot in stony soil required the larger gradients in soil water pressure to sustain the same transpiration rate (thus exhibited earlier stomatal closure) as compared to the same plot in the silty soil. This was in line with a study from Abdalla et al., (2022) which suggested that during soil drying, stomatal regulation of tomato is controlled by root and soil hydraulic conductance. Recent work from Müllers et al., (2022) on faba bean and maize suggested that differences in the stomatal sensitivity among plant species can be partly explained by the sensitivity of soil-plant hydraulic conductance to soil drying. The loss of conductance has immediate consequences for leaf water potential and the associated stomatal regulation. Cai et al., (2022b) also showed that the decrease in sunlit leaf stomatal conductance was well correlated with the drop in soil-plant hydraulic conductance, which was significantly affected by soil texture. This was confirmed in our work where the stony soil strongly impacted on root growth, modulated K_{soil_plant}, and consequently influenced the leaf stomatal conductance, photosynthesis, and transpiration.

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4.3. Relative contribution of water control by leaves and roots on transpiration and transpiration use efficiency

Responses of crops via stomatal control to reduce water loss at leaf scale while maintaining leaf photosynthesis and water use efficiency were reported earlier (Nguyen et al., 2022a; Vitale et al., 2007). In addition to that, in the maize experiments in 2017 and 2018 leaf rolling was observed in both rainfed plots on the stony and the silty soil in the second week of June 2017 and from the beginning of June until the end of the growing period in 2018. This indicates another dehydration avoidance mechanism resulting from morphological adjustments which is an effective mechanism for delaying senescence (Aparicio-Tejo and Boyer, 1983; Richards et al., 2002). Stomatal closure resulted in more reduction of transpiration and assimilation in the rainfed plots than irrigated plots with the same soil type (Fig. 5, Fig. 6, Fig. 7, and Fig. 13A). There was reduction of shoot biomass (also stem size and leaf size adjustments) in F1P2 as compared to other plots. However, the TUE was not smaller in this plot than the remaining plots. These observations confirm that plant size adjustments through reduction of height, leaf width and length are efficient responses to reduce water loss at canopy scale in addition to stomatal control at the leaf level.

Relative contribution of leaf area to transpiration has been highlighted in wheat where reduction of tiller number resulted in significantly (lower LAI, thus lower canopy transpiration (Cai et al., 2018; Trillo and Fernández, 2005; Nguyen et al., 2022a). However, root system conductance per unit of leaf area and per unit root mass were strongly reduced and eventually more than reduction of leaf area under water stress (Trillo and Fernández, 2005). In our work, expressing the transpiration per unit of root length on the one hand allowed to analyze the role of total root length to water uptake. However, on the other hand, the lower total root length did not necessarily result in a lower root water uptake and vice versa. For instance, the rainfed plot of the treatment F2P2 had the larger total root length which could postpone the effect of soil water limitations in drying soils due to greater ability to extract water from subsoils. Therefore, transpiration was very similar between F2P2 and F2P3. Despite of the much lower total root length in the

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stony soil, K_{soil_plant} in the irrigated plot (F1P3) was not much lower than in the same water treatment in the silty soil (F2P3, Fig. 8c, 9c, Fig. 10, and Supplementary material 5). This could be explained by the fact that the K_{soil_plant} variability was not only depended on root architecture (here the root length and distribution) but also depended on the variability of root segment hydraulic properties which has also been illustrated and discussed in Zwieniecki et al. (2002), Frensch and Steudle (1989), Meunier et al. (2018), Couvreur et al. (2014), and Ahmed et al. (2018). Meunier et al. (2020) showed that more than 65% of the variability of root system conductance of maize plants could be attributed to variability in root architecture, which includes root length, whereas only 25% of the variability was attributed to root segment hydraulic properties. However, the analysis of Meunier et al., (2020) neither included the impact of root hairs nor the impact of rhizosphere conductivity but only focused on the root system hydraulic conductance. Moreover, the contribution of shoot hydraulic conductance could be large in plants (Gallardo et al., 1996; Trillo and Fernández, 2005; Sunita et al., 2014) which also confirmed in our work. In our work, K_{soil_plant} comprised root and shoot conductance which are directly influenced by soil hydraulics. Our estimates of K_{soil_plant} varied with transpiration and gradients of $\psi_{sunlitleaf}$ and ψ_{soil_effec}. Thus, any change of soil hydraulic conductance will change the root to shoot water potential. Consequently, it will affect the gradients between shoot and root rhizosphere (Carminati and Javaux, 2020). Thus, our study is revealing the importance of both soil texture characteristics and root phenotypic traits (here root length) in regulating plant transpiration (Cai et al., 2022a). Other traits like root hair density (Cai et al., 2022a) or higher root length density (Vadez, 2014) could contribute to the soil to root water potential and root-zone hydraulic conductance where dense root hairs are delaying soil water deficit in drying soils. However, contrast results have shown that root hairs did not have an effects on root water uptake (see Jorda et al. 2022). The role of root hairs could not be analyzed in our work which based on the root data from minirhizotron images.

5. Conclusion

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We presented plant hydraulic characteristics and crop growth from root to shoot of maize under field-grown conditions with two soil types (silty and stony), each soil with two water regimes (irrigated and rainfed) for two growing seasons (2017, 2018). Our results confirmed that root length and root: shoot ratio was modulated by soil types and water treatment but less by seasonal evaporative demand. Increase root: shoot ratio has been an important response of maize that allows plants to extract more water under drought stress that occurred rather in the silty soil but less in the stony soil due to the higher content of stony material. Despite of lower root length in the stony irrigated plot, transpiration rate was not much lower than in the silty irrigated plot. This could be related to another property of the root such as root segment conductance or other root traits (e.g. root hair). Further investigation with extensive measurements of roots including axial and radial root conductance at field scale will be required to better explain the observed results.

Another conclusion is that stomatal regulation maintains leaf water potential at certain thresholds which depends on soil types, soil water availability, and seasonal atmospheric demand. The stomata conductance was smaller and at more negative leaf water potentials in stony soil than in silty soil. The leaf water potentials are affected by the soil-plant plant hydraulic conductance. In addition to stomatal regulation, leaf growth and plant size adjustments are important to regulate the transpiration that water use efficiency was not different among treatments and soil types in the same year.

The lowest soil-plant hydraulic conductance was observed in the stony soil with severe drought stress as compared to silty soil while its variation depends also on the soil water variation (before and after irrigation). Root system and soil-plant hydraulic conductance depended strongly on soil hydraulic properties. In the stony soil, which has a considerably smaller water holding capacity than the silty soil, root length was considerably smaller than in the silty soil. Nevertheless water uptake per unit root length was much larger than in the fine soil. This also means that the hydraulic conductance per unit root length must have been much larger in the stony soil than in the fine soil. Cai et al., (2018) observed a similar effect

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for winter wheat but they found much smaller differences in the root length normalized root conductance. The higher root length normalized root conductance means that the anatomy of the root tissues must have been influenced by the soil texture and compensated the considerably smaller root length in the stony soil. Looking at the effect of water treatments in the silt soil, the non-irrigated plot had more roots than the irrigated one and both had more roots in the year with high VPD. But the soil-root conductance was higher in the irrigated plot than in the rainfed plot. This means that in the irrigated plot, the soil-root conductance per unit root length was higher than in the rainfed plot. This could either be due to wetter soil conditions and higher soil conductance or it could be due to a larger conductance of the root tissues. Especially in 2017 when the silty soil was wetter, the slightly larger soil-root conductance in the irrigated plot is most likely the result of larger root tissue conductance in the irrigated plot. Thus, how root architecture (here represented simply by the total root length) and root tissue conductivities 'respond' to drought stress might be opposite depending on the comparisons that are made. When the stony soil and silt soil are compared, the higher 'stress' due to lower water availability in the stony soil resulted in less roots with a higher root tissue conductance in the soil with more stress. When comparing the rainfed with the irrigated plot in the silty soil, the higher stress in the rainfed soil resulted in more roots with a lower root tissue conductance in the treatment with more stress. This illustrates that the 'response' to stress can be completely opposite depending on conditions or treatments that lead to the differences in stress that are compared. Therefore, it cannot be the 'stress' alone that defines how a plant will react and adapt its root system. Modelling the impact of stress and the feedback between drought stress and plant development is likely controlled by other properties or parameters that change with changing soil water availability and atmospheric water demand then the plant stress level. Results from this study show that soil-crop models should focus not only on simulating stomatal regulations to capture the response to drought stress, but also require adequate representations of leaf growth and adjustments.

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Table 1. Crop phenology and management information for different treatments in 2017 and 2018.

	2017				2018			
Soil types	Stony (F1)	Stony (F1)	Silty (F2)	Silty (F2)	Stony (F1)	Stony (F1)	Silty (F2)	Silty (F2)
Water treatments	Rainfed (P2)	Irrigated (P3)	Rainfed (P2)	Irrigated (P3)	Rainfed (P2)	Irrigated (P3)	Rainfed (P2)	Irrigated (P3)
Plot names	F1P2	F1P3	F2P2	F2P3	F1P2	F1P3	F2P2	F2P3
Growing season (days)[¥]	136	136	136	136	107	107	107	107
Cumulative rainfall (mm)[*]	248.7	248.7	248.7	248.7	91.3	91.3	91.3	91.3
Irrigation (mm)	0	130	0	130	66	257.6	0	257.6
Fertilizer application (mm/dd) (per hectare)	05/09:100 kg N + 40kg P_2O_5 07/06: 80 kg N + 40 kg K_2O				05/22: 100 kg N 05/30: 40 kg P_2O_5 + 40 kg K_2O 06/27: 80 kg N			
Sowing date (mm/dd)	05/04				05/08			
Emergence date	05/09				05/13			
Tasseling date	07/09				07/09			
Silking date	07/14				07/11			
Harvest date	09/12				08/22			

Notes: [¥] from sowing to harvest; [*] for rainfall for whole growing season;

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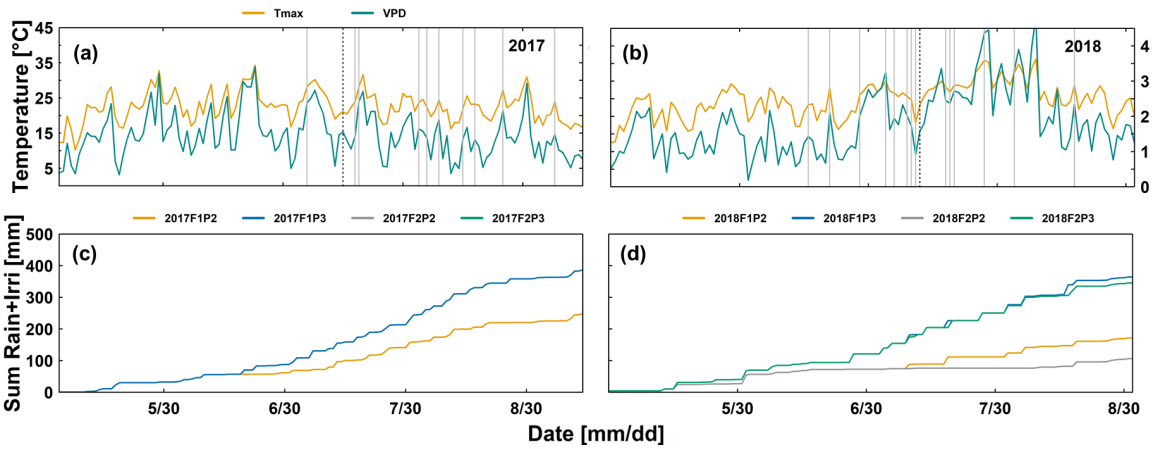

Figure 1: Daily maximum air temperature (Tmax) (°C), daily maximum air vapor pressure deficit (VPD) (kPa) in the two growing seasons (a) 2017 and (b) 2018 and cumulative (sum) of rainfall and irrigation from the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2) in the two growing seasons (c) 2017 and (d) 2018. The black dashed vertical lines (a) and (b) indicate silking time. Grey vertical lines in (a) and (b) indicate the measured days for leaf gas exchange and leaf water potential. Two lines for 2017F2P2 and 2017F2P3 were overlapped by the lines from 2017F1P2 and 2017F1P3, respectively

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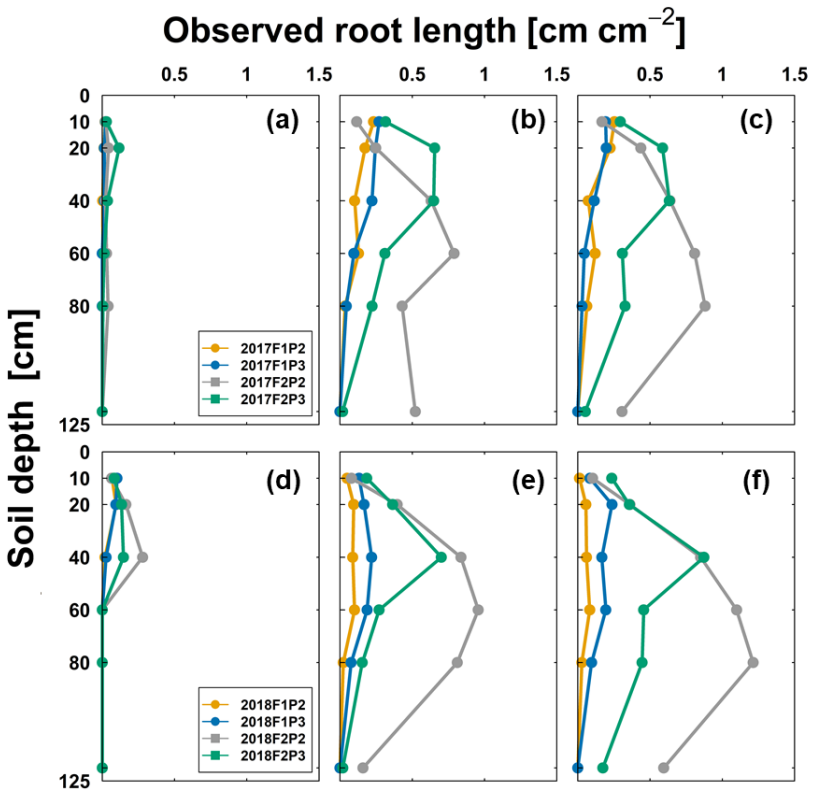

Figure 2: Observed root length from minirhizotubes (cm cm^{-2}) from 10, 20, 40, 60, 80, and 120 cm soil depth from the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2) in the two growing seasons in 2017 (a - 8 June, b - at silking on 13 July, c - at harvest on 12 September) and in 2018 (d - 7 June, e - at one week after silking - 18 July, f - one week before harvest - 16 August).

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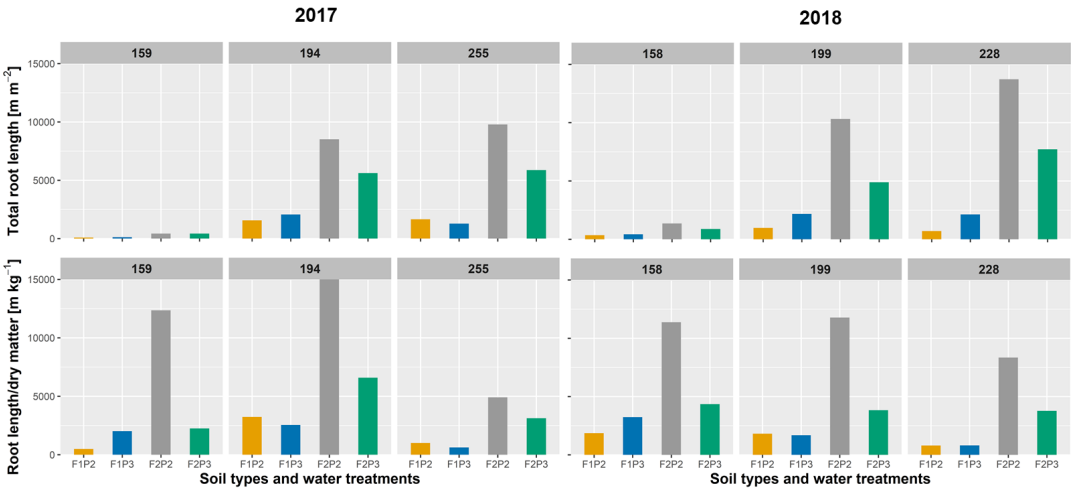

Figure 3: Observed root length from minirhizotubes (m m^{-2}) and ratio of root length per shoot dry matter (m kg^{-1}) from the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2) in the two growing seasons (DOY 159, 194, and 255, left panel) in 2017 and in 2018 (DOY 158, 199, and 228, right panel) where on 8 June (DOY 159) at silking on 13 July (DOY194) 2017; and at harvest on 12 September (DOY 255) in 2017; 7 June (DOY 158), one week after silking on 18 July (DOY 199); and one week before harvest on 16 August (DOY 228) in 2018 (see also Figure 2).

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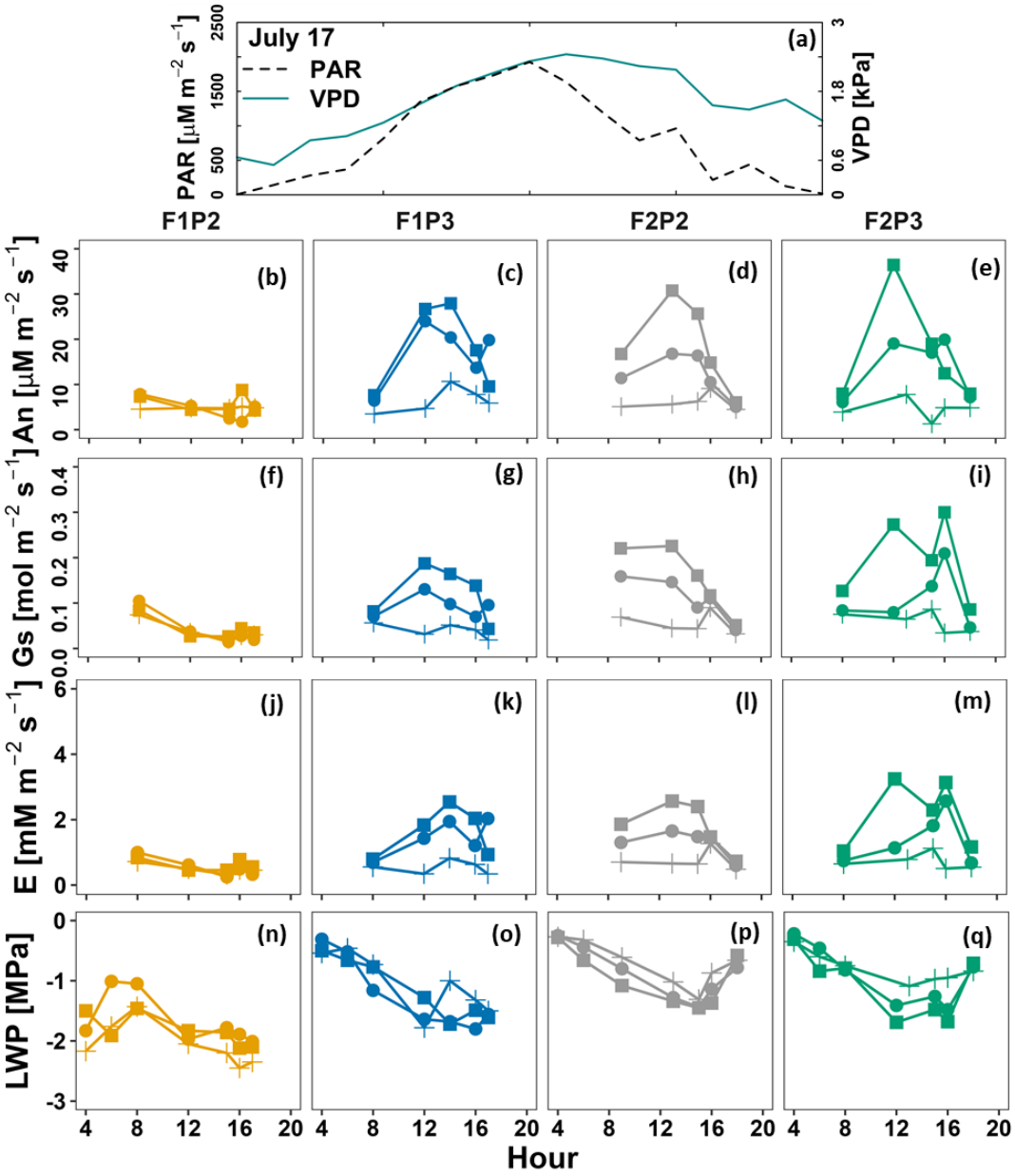

Figure 4. Diurnal course of (a) photosynthetically active radiation (PAR) and vapor pressure deficit (VPD), (b –e) leaf net photosynthesis (An), (f –i) leaf stomatal conductance (Gs), (j –m) leaf transpiration (E), and (n –q) leaf water potential (LWP) on 17 July in maize in 2018 before irrigation at the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2). Measurement was carried out from shaded leaf (plus symbol with lines) and two sunlit leaves (solid dot - lines and solid square - lines).

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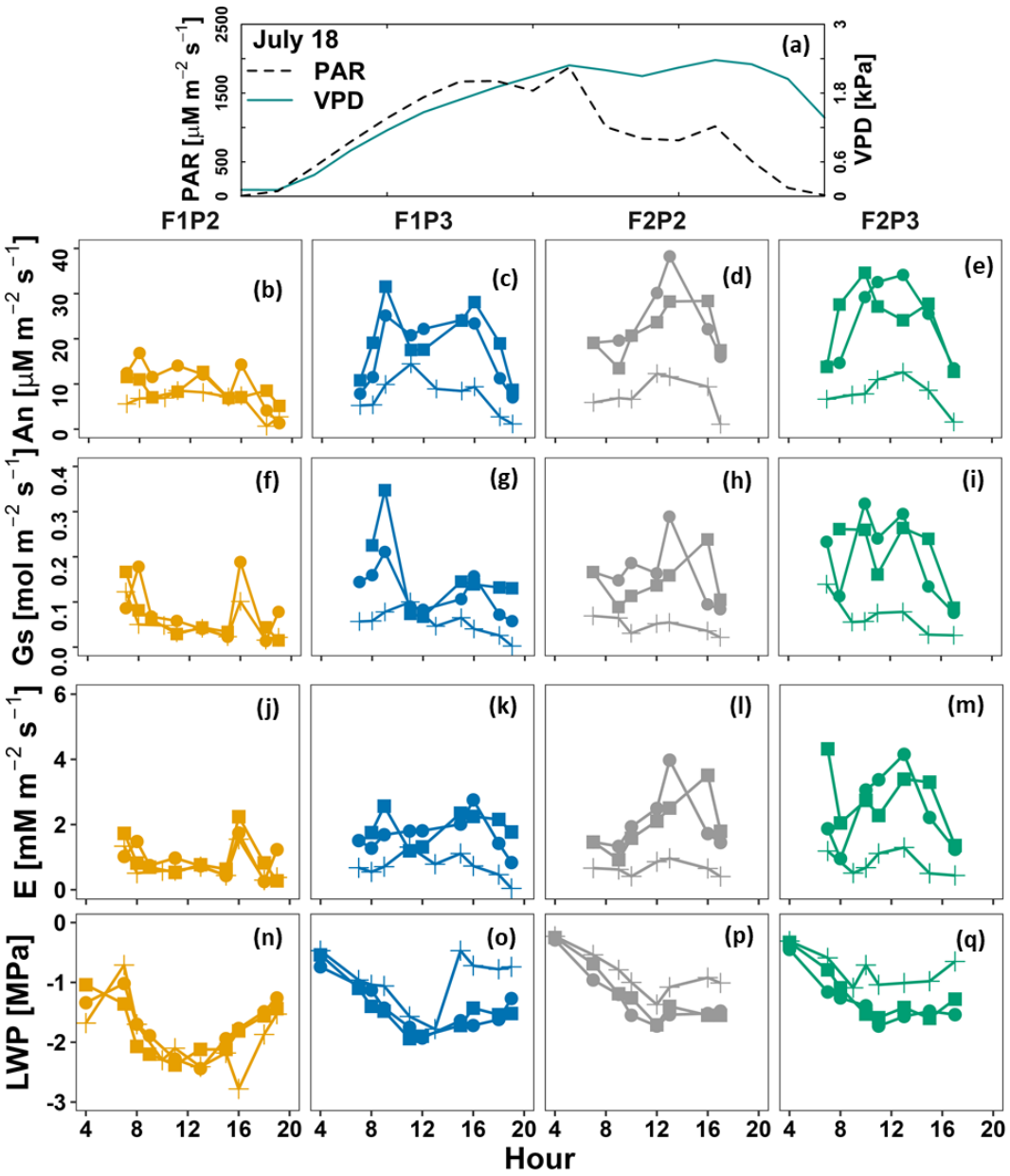

Figure 5. Diurnal course of (a) photosynthetically active radiation (PAR) and vapor pressure deficit (VPD), (b –e) leaf net photosynthesis (An), (f –i) leaf stomatal conductance (Gs), (j –m) leaf transpiration (E), and (n –q) leaf water potential (LWP) on 18 July in maize in 2018 before irrigation at the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2). Measurement was carried out from shaded leaf (plus symbol with line) and two sunlit leaves (solid dot - lines and solid square - lines). Crop was irrigated at 1 PM, 1 PM, 4 PM for F1P3, F2P3, and F1P2, respectively (22.75 mm for each plot) (Supp. 2).

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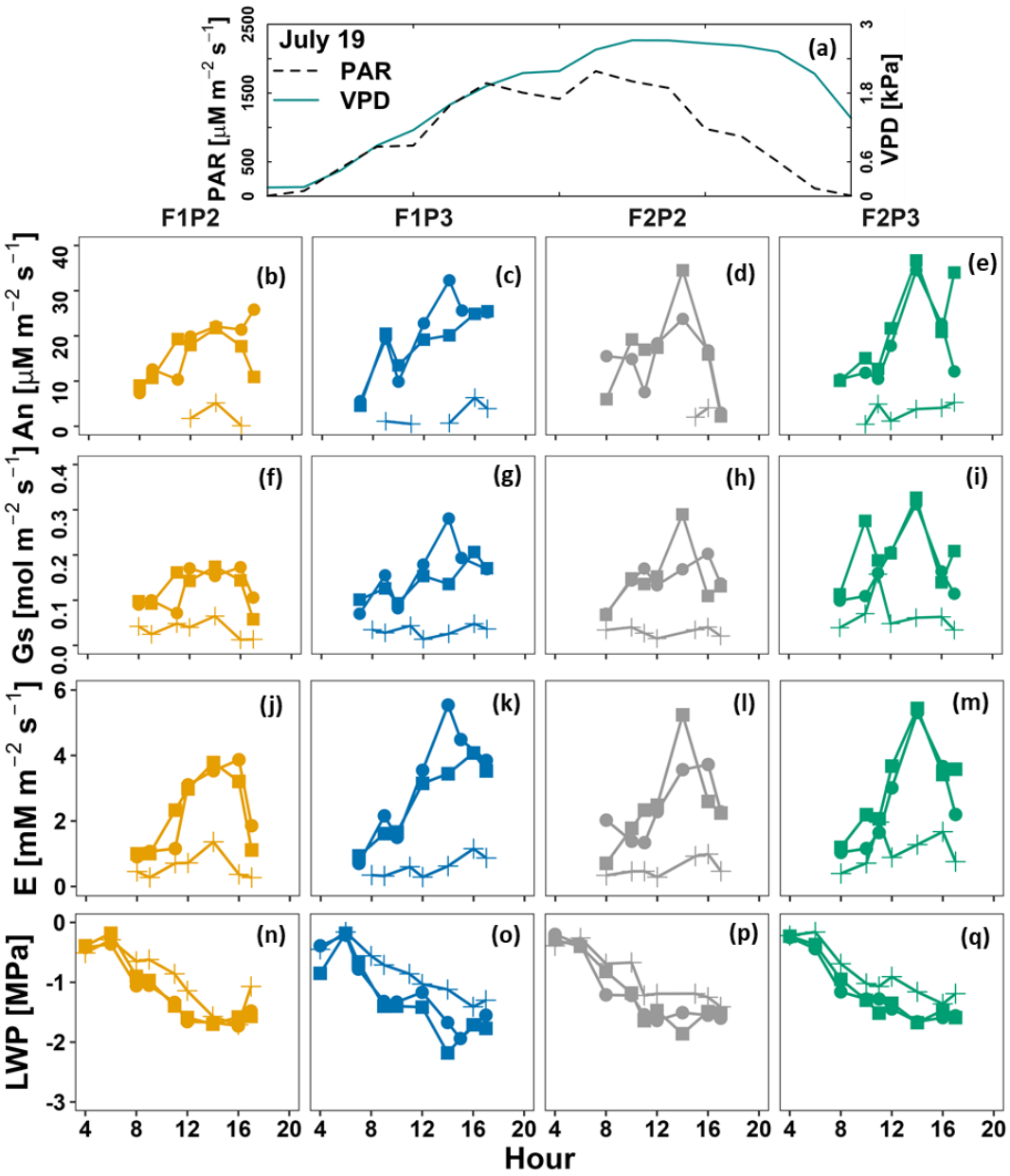

Figure 6. Diurnal course of (a) photosynthetically active radiation (PAR) and vapor pressure deficit (VPD), (b –e) leaf net photosynthesis (An), (f –i) leaf stomatal conductance (Gs), (j –m) leaf transpiration (E), and (n –q) leaf water potential (LWP) on 19 July in maize in 2018 after irrigation at the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2). Measurement was carried out from shaded leaf (plus symbol with line) and two sunlit leaves (solid dot - lines and solid square -lines). Crop was irrigated on 18 July at 1 PM, 1 PM, 4 PM for F1P3, F2P3, and F1P2, respectively (22.75 mm for each plot) (Supp. 2).

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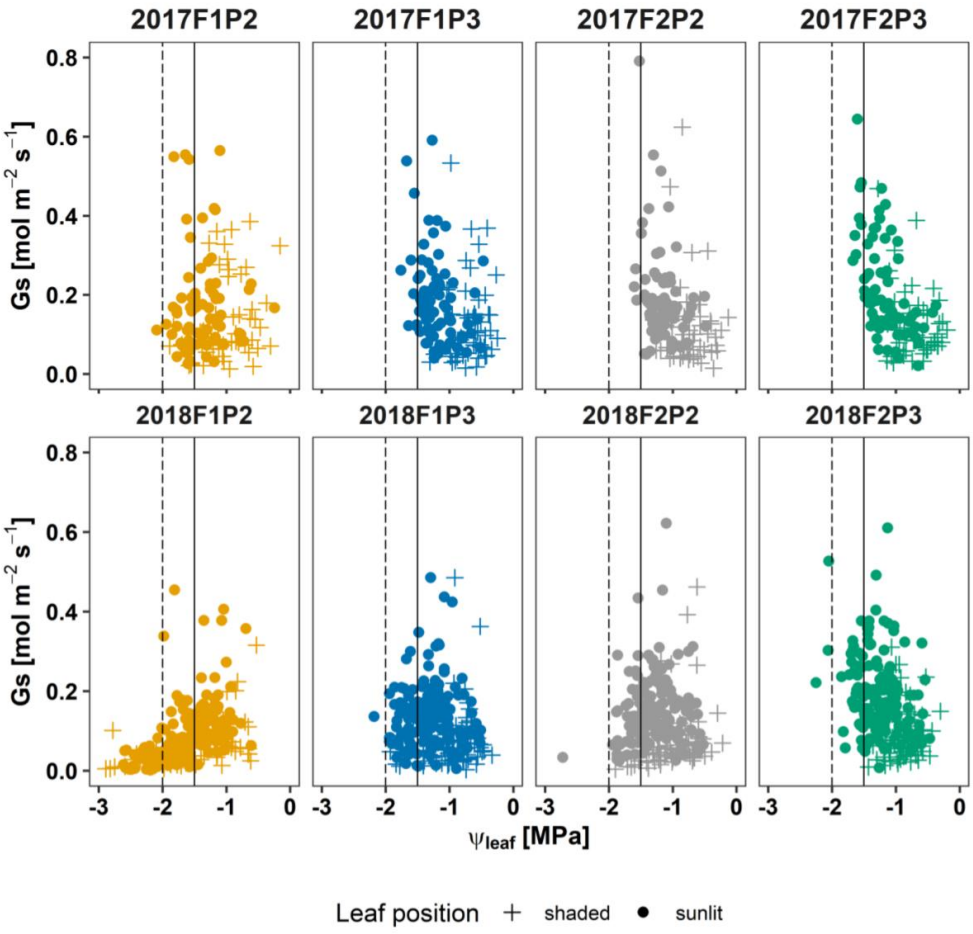

Figure 7: Seasonal stomatal conductance to water vapor (Gs) versus leaf water potential (ψ_{leaf}) in 2017 (top panel) and in 2018 (bottom panel) at the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2). Vertically continuous and dashed lines indicated ψ_{leaf} at -1.5 and -2 MPa, respectively. Measurement was carried out from shaded leaf (plus symbol) and two sunlit leaves (solid dots)

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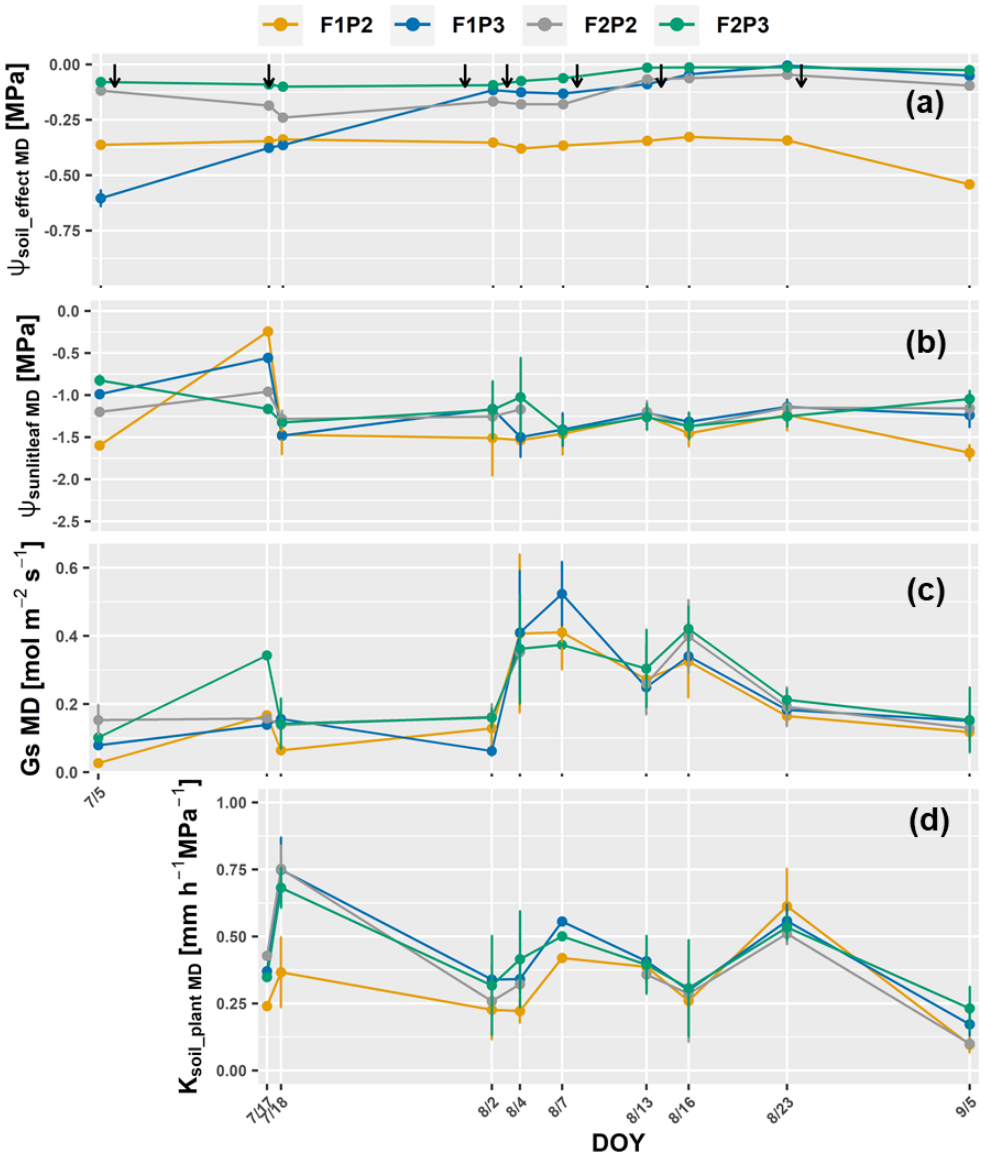

Figure 8: Dynamic of around midday (MD) of (a) the effective soil water potential ($\psi_{soil\_effec,\ MD}$) (b) sunlit leaf water potential ($\psi_{sunlitleaf\ MD}$), (c) stomatal conductance (Gs MD) and (d) whole soil-plant hydraulic conductance ($K_{soil\_plant\ MD}$) in the growing season 2017 from the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2). Error bars indicate the standard deviation of the different values taken around midday (11 AM, 12AM, 1PM, and 2 PM) of different sunlit leaves. Whole soil-plant hydraulic conductance was shown from 17 July when sap flow was measured. The black arrows indicates the irrigation events for the irrigated treatments F1P3 and F2P3 in the showing period.

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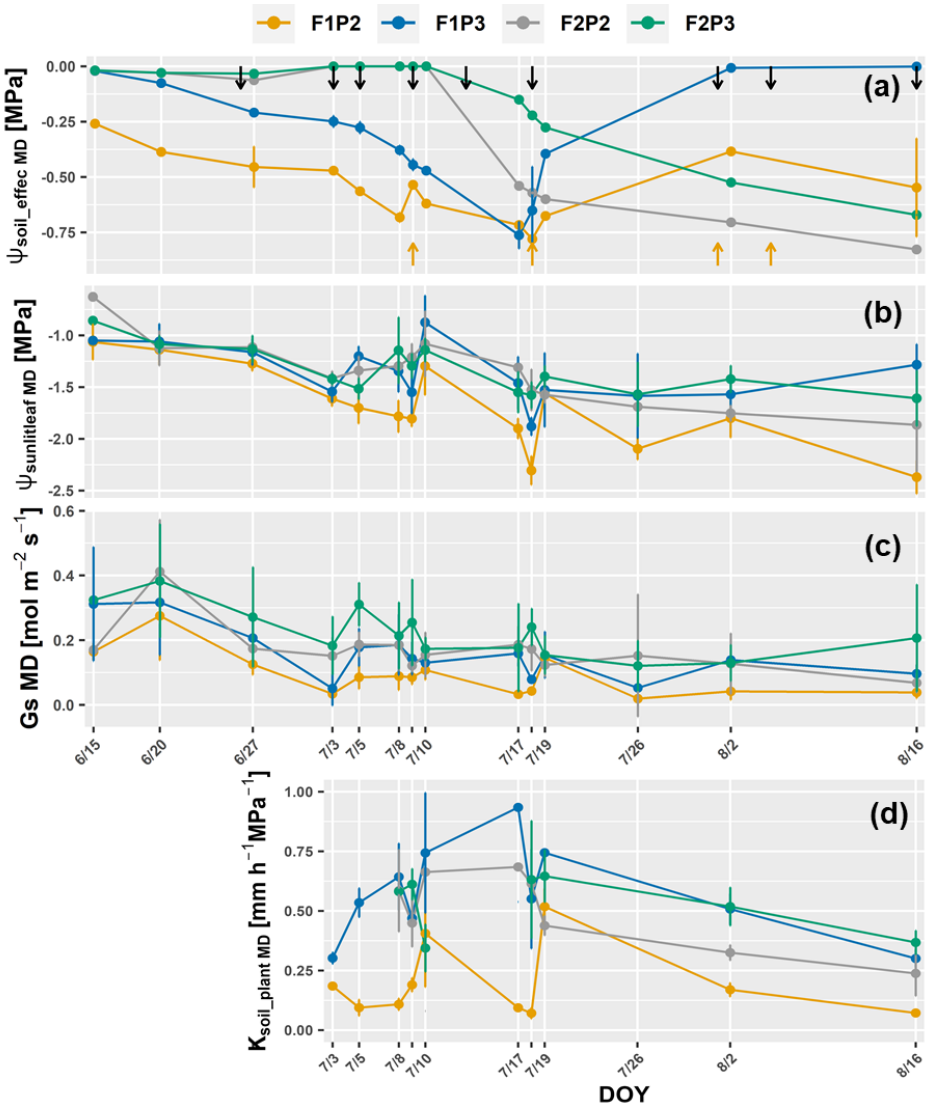

Figure 9: Dynamic of around midday (MD) of (a) the effective soil water potential ($\psi_{soil\_effec\ MD}$) (b) sunlit leaf water potential ($\psi_{sunlitleaf\ MD}$), (c) stomatal conductance (Gs MD) and (d) whole soil-plant hydraulic conductance ($K_{soil\_plant\ MD}$) in the growing season 2018 from the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2). Error bars indicate the standard deviation of the different values taken around midday (11 AM, 12AM, 1PM, and 2 PM) Leaf water potential and stomatal conductance were 2 sunlit leaves and one shaded leaf at each measured hour. Whole soil-plant hydraulic conductance was shown from 3 July when sap flow was measured. The black arrows indicates the irrigation events for the irrigated treatments F1P3 and F2P3 while the orange arrow indicates the irrigation application for the rainfed plot at the stony soil (F1P2).

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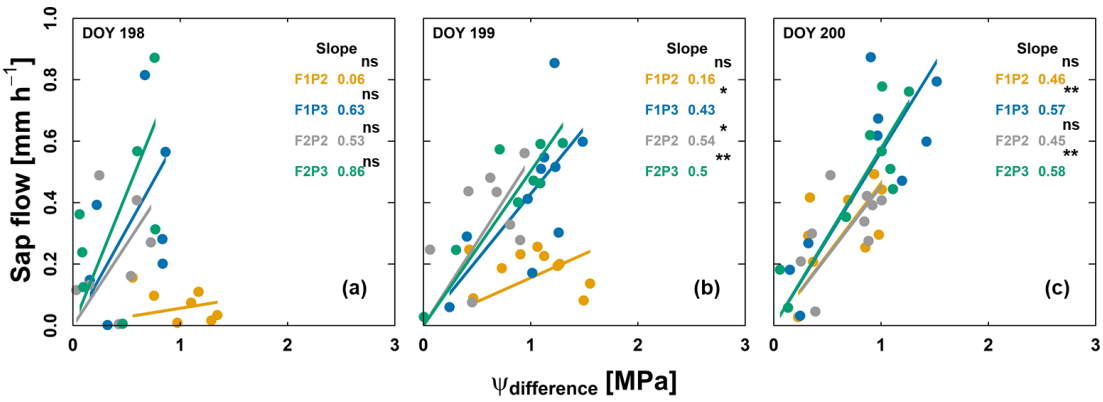

Figure 10: Relationship of sap flow and difference of effective soil water potential and sunlit leaf water potential ($\psi_{difference}$) from the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2) on three consecutive measurement days from predawn in 2018 (a) DOY 198, (b) DOY 199 and (c) DOY 200. Crop was irrigated on 18 July (DOY 199) at 1 PM, 1 PM, and 4 PM for F1P3, F2P3, and F1P2, respectively (22.75 mm for each plot). The unit of slope in the linear regression (or soil-plant hydraulic conductance) is mm h^{-1} MPa^{-1}. Regression was based on the DEMING approach. The asterisk which are next to the slopes indicate a significant correlation between two variables according to Pearson method (ns: non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

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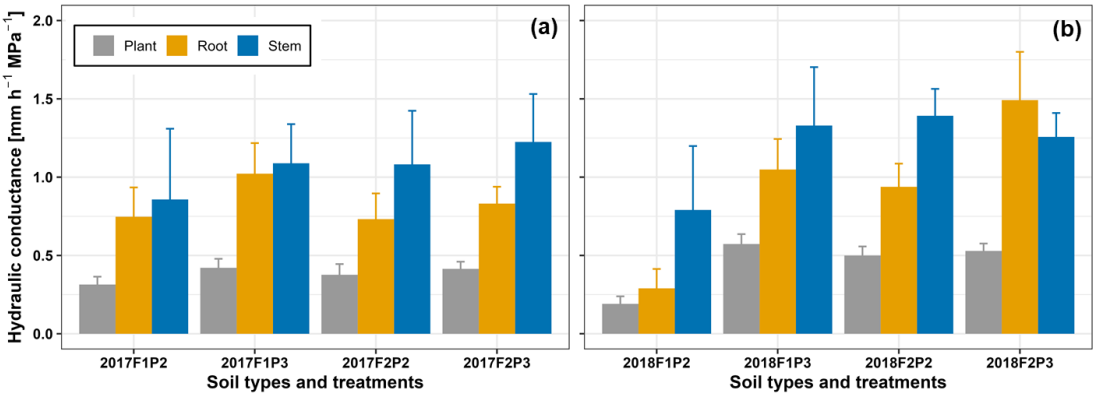

Figure 11: Comparison of different midday hydraulic components (mm h^{-1} MPa^{-1}): soil-plant (grey bars), soil-root (yellow bars), and stem (blue bars) from the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2) in the two growing seasons (a) in 2017 and (b) in 2018. The error bars indicate the standard deviation from measurements around midday (11 AM, 12AM, 1PM, and 2 PM) in different measured days (in 2017 with n = 4 x 9 days, Supplementary material 6, 7, and Fig. 8 and in 2018 with n = 4 x 10 days, Supplementary material 6, 8, and Fig. 9).

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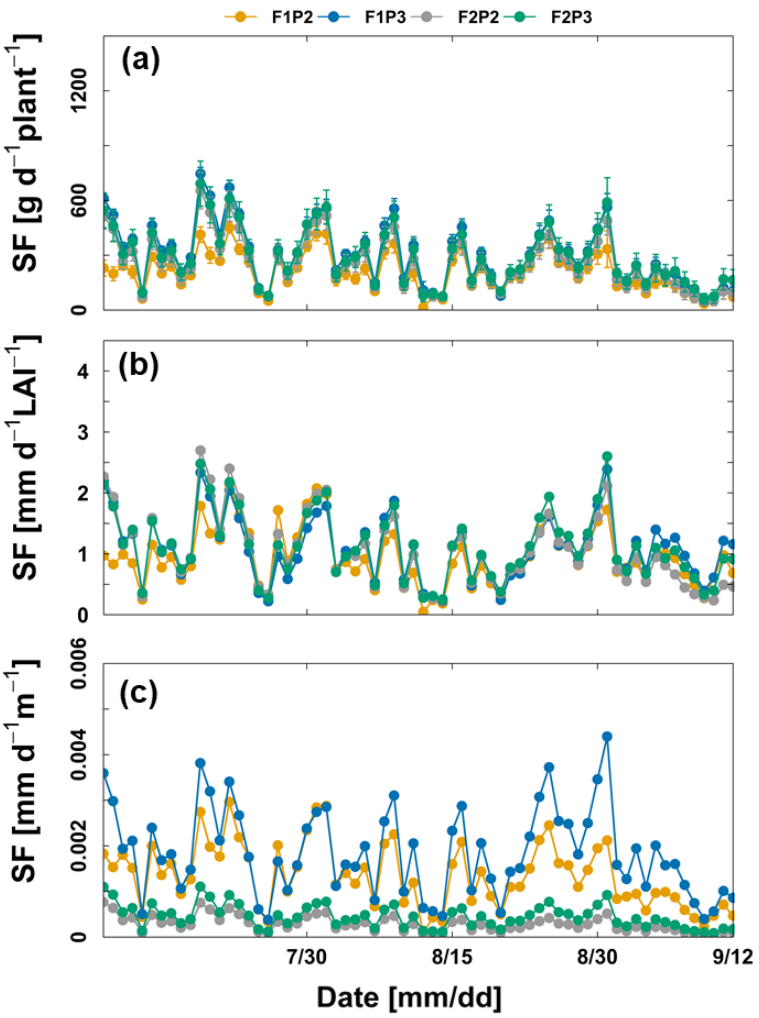

Figure 12: Comparison of sap flow (SF) in growing season 2017 from the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2) with (a) sap flow per single plant (b) sap flow per leaf area index (LAI) and (c) sap flow per total root length. Data is shown from 9 July to 12 September 2017. Error bars in (a) indicate the standard deviation of the sap flow measurements in the five different maize plants.

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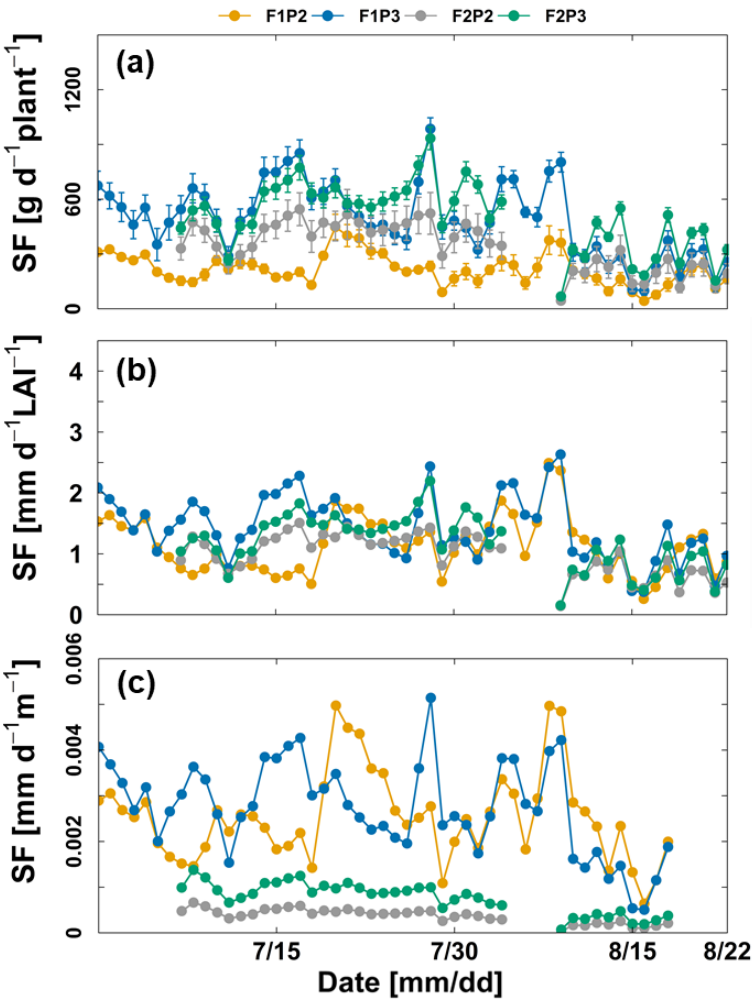

Figure 13: Comparison of sap flow (SF) in growing season 2018 from the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2) with (a) sap flow per single plant (b) sap flow per leaf area index (LAI) and (c) sap flow per total root length. Data is shown in (a, b) from 29 June and 6 July for the stony soil (F1) and silty soil (F2), respectively to 21 August, 2018. Missing values of the beginning of the growing season and from 3 August to 6 August 2018 in the F2P2 and F2P3 were due to the missing values of measured sap flow because of sensor disconnection. Missing values in (c) at the end of the growing season in F2P2 and F2P3 was due to no availability of root measurement. Error bars in (a) indicate the standard deviation of the sap flow measurements in the five different maize plants.

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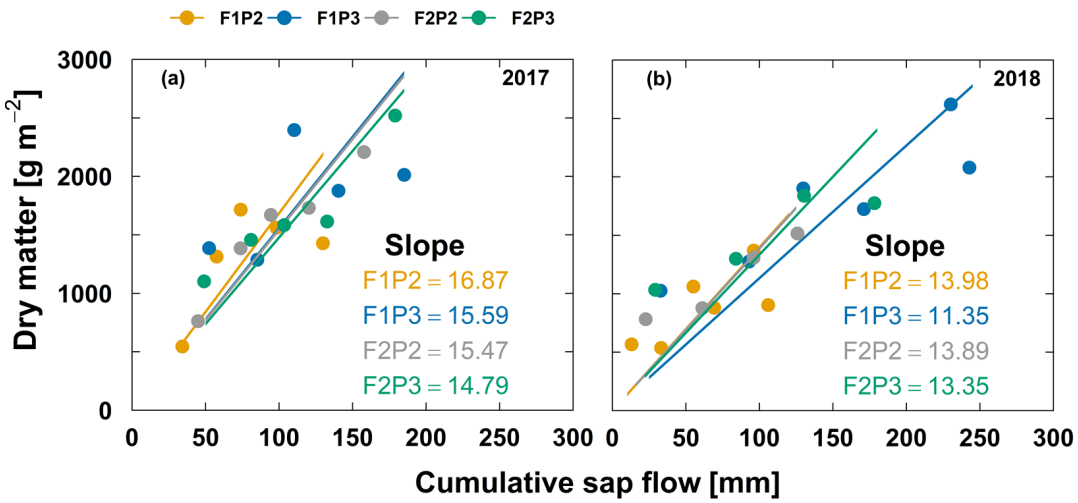

Figure 14: Relationship of aboveground dry matter and cumulative sap flow from the rainfed (P2) and irrigated (P3) plots of the stony soil (F1) and silty soil (F2) in the two growing seasons (a) 2017 and (b) 2018. The unit of slope linear relationship is g mm^{-1}. The less number of data points in (b) in 2018 from the F2P2 and F2P3 plots were due to the missing values of measured sap flow because of sensor disconnection.

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Author contribution

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Competing interests

This manuscript has not been published and is not under consideration for publication in any other journal. All authors agreed and approved the manuscript and its submission to this journal. We declare there is no conflict of interest.

Code/Data availability

The meteorological data were collected from a weather station in Selhausen (Germany) which belongs to the TERENO network of terrestrial observatories. Weather data are freely available from the TERENO data portal (https://www.tereno.net/ddp/dispatch?searchparams=freetext-Selhausen, last access: October 2020) (TERENO, 2020). The data which were obtained from the minirhizotron facilities (under- and aboveground) are available from the corresponding author on reasonable requests.