

1 Responses of field-grown maize to different soil types, water regimes, and 2 contrasting vapor pressure deficit

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12 Abstracts

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

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

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

45 **Abbreviations:** DOY: day of the year; DAS: day after sowing; TUE: transpiration use efficiency; SF: sap flow;
46 LAI: green leaf area index; PAR: photosynthetically active radiation; VPD: vapor pressure deficit; An: net
47 leaf photosynthesis; E: leaf transpiration; ψ_{leaf} : leaf water potential; $\psi_{\text{sunlitleaf}}$: leaf water potential of sunlit

48 leaf; $\psi_{\text{shadedleaf}}$: leaf water potential of shaded leaf; K_{soil} : hydraulic conductance of soil; K_{root} : root hydraulic
49 conductance; K_{stem} : stem hydraulic conductance; $\psi_{\text{soil_effec}}$: effective soil water potential; $\psi_{\text{difference}}$:
50 difference between effective soil water potential and sunlit leaf water potential; $K_{\text{soil_root}}$: root system
51 hydraulic conductance (includes soil and root hydraulic conductance); $K_{\text{soil_plant}}$: whole plant hydraulic
52 conductance (includes below and aboveground components).

53 **1. Introduction**

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

62 Stomatal regulation is often considered as a key aboveground hydraulic variable in regulating water use
63 of crops. Maize is ~~considered as known as an~~ isohydric plant. ~~Maize in which~~ stomata are closed in response
64 ~~to sensing to~~ drought conditions to maintain leaf water potential (ψ_{leaf}) above critical levels ($\psi_{\text{threshold}}$ or
65 minimum ψ_{leaf}) (Tardieu and Simonneau, 1998). The isohydric behavior is due to different mechanisms
66 including hydraulic and/or chemical (e.g. abscisic acid [ABA]) signals (Tardieu, 2016). The degree to which
67 these underlying mechanisms interact and differ among genotypes and/or environmental scenarios in
68 explaining the stomatal regulation is still debated (Tardieu, 2016, Hochberg et al., 2018). Field evidence in
69 variation of the minimum ψ_{leaf} of maize due to soil water availability and soil hydraulics is rarely reported.

70 Water flow along the soil-plant-atmosphere continuum is determined by a series of hydraulic
71 conductivities and gradients in water potential. Hydraulic conductance of soil (K_{soil}), root hydraulic

72 conductance (K_{root}), and stem hydraulic conductance (K_{stem}) determine water potential from soil to root
73 and root xylem water, and thus magnitude of ψ_{leaf} . There are two main resistances to water flow from the
74 soil to the shoot, namely the soil and the root resistances, often expressed as their inverse, K_{soil} and K_{root}
75 (Nguyen et al., 2020; Cai et al., 2018). In wet soils, the soil hydraulic conductivity is much higher than that
76 of roots, and water flow is mainly controlled by root hydraulic conductivity (Hopmans and Bristow, 2002;
77 Draye et al., 2010). It is well-known that a decrease in soil matric potential and soil hydraulic conductivity
78 triggers stomatal closure and thus results in reduction in transpiration rate (Sinclair and Ludlow, 1986;
79 Carminati and Javaux 2020; Abdalla et al., 2021). For the root water uptake and controlling stomata, the
80 location where soil and roots are in close contact (rhizosphere) is most important, because when this thin
81 layer of rhizosphere is disconnected (i.e. soil-root contact is lost), the water movement from soil toward
82 the roots is reduced, which might trigger stomatal closure to maintain hydraulic integrity of plant
83 (Carminati et al., 2016; Rodriguez-Dominguez and Brodribb, 2019; Abdalla et al., 2022). The magnitude of
84 the drop of water potential between bulk soil and soil-root interface increases considerably at different
85 levels of soil dryness for different soil types (Carminati and Javaux, 2020; Abdalla et al., 2022). Hydraulic
86 limits in the soil (Carminati and Javaux, 2020), or in the root–soil interface [as measured for olive trees by
87 Rodriguez-Dominguez and Brodribb, 2019 or tomato (Abdalla et al., 2022)], or in the root properties
88 (Bourbia et al., 2021; Cai et al., 2022; Nguyen et al., 2020; Cai et al., 2018) or due to both soil textures and
89 root phenotypes (Cai et al., 2022b) emphasized the importance of belowground hydraulics (Carminati and
90 Javaux, 2020). However, also the shoot hydraulic conductance could be limiting in some crop plants
91 (Gallardo et al., 1996) or in trees (Domec and Pruyn, 2008; Tsuda and Tyree, 1997). Stomatal conductance
92 and shoot hydraulic conductance showed close links to each other in pine trees (Hubbard et al., 2001).
93 This summary illustrates three points: (i) current studies have often focused either on above or on below
94 hydraulic limits, but rarely consider both (ii) ~~it is unclear~~ the roles and relations of soil hydraulic properties
95 to root and plant hydraulic conductance (thus influences on stomatal conductance) remain unclear (iii) the

96 role of different hydraulic processes across the soil - plant - atmosphere continuum i.e. soil to roots, stem,
97 and soil-plant hydraulic conductance in controlling stomatal conductance remains unclear.

98 Simultaneous measurements of atmospheric conditions (light intensity and vapor pressure deficit), leaf
99 water potential, and transpiration rates, coupled with measurements of root, stem and whole soil-plant
100 hydraulic conductance, root architecture, and soil water potential distribution could reveal the relative
101 importance of rhizosphere, shoot and root growth, and hydraulic conductance vulnerability, especially
102 under progressive soil drying at field conditions (Carminati and Javaux, 2020; Tardieu et al., 2017). For the
103 soil water conditions, soil texture and hydraulic characteristics are very important because they influence
104 soil water movement and thus affect infiltration, surface and sub-surface runoff, and ultimately plant
105 available soil water (Vereecken et al., 2016). Soil texture properties, characterized by different fractions of
106 clay, silt, and sand particles, are important drivers in determining the soil water retention properties
107 (Scharwies and Dinnyen, 2019; Stadler et al., 2015; Zhuang et al., 2001). Soil with higher water holding
108 capacity (here the silty soil with low stone content) have a larger amount of plant available water which in
109 turn enables crops to better meet the evaporative demand and facilitates better crop growth as compared
110 to the soil with high stone content (Nguyen et al., 2020; Cai et al., 2018). Estimations of hydraulic
111 conductance (different organs and whole plant hydraulic conductance) were done for crop plants and
112 maize mainly under controlled environment or pot conditions e.g. for different species and genotypes
113 during soil drying (Sunita et al., 2014; Choudhary and Sinclair, 2014; Abdalla et al., 2022; Meunier et al.,
114 2018; Wang et al., 2017; Li et al., 2016) or various species and genotypes together with different soil
115 textures (Cai et al., 2022a), or soil texture with different vapor pressure deficit (VPD) (Cai et al., 2022b).
116 Compared to the substantial effect of soil texture, there was no evidence of an effect of VPD on both soil-
117 plant hydraulic conductance and on the relation between canopy stomatal conductance and soil-plant
118 hydraulic conductance in pot-grown maize (Cai et al., 2022b). Contrast results were found in winter wheat
119 where plant hydraulic conductance increased with rising VPD for some genotypes in wet conditions

120 (Ranawana et al., 2021). Vadez et al., (2021) examined the effects of soil types together with increasing
121 VPD on transpiration efficiency (TE) and yield under pot conditions for several C₄ species (maize, sorghum,
122 and millet). The interpretation of differences in TE was attributed to soil types, more specifically, to the
123 differences in soil hydraulic properties and soil hydraulic conductance. However, experimental evidence
124 linking root hydraulics to stomatal regulation was lacking in these two Vadez's studies (Vadez et al., 2021).
125 Recent field studies have aimed at quantification of root hydraulic conductance and its linkages with crop
126 growth (leaf area and biomass) under different soil types (in wheat Cai et al., 2017; Cai et al., 2018; Nguyen
127 et al., 2020 or maize in Nguyen et al., 2022; Jorda et al., 2022). However, field studies that consider both
128 below (soil-root hydraulic conductance) and above (stem hydraulic conductance), or soil-plant hydraulic
129 conductance (including below and above-ground parts) and their roles in stomatal regulation as well as
130 crop growth (leaf area and biomass) are rarely carried out.

131 This study aims at further understanding of the hydraulic linkages between soil and plant and responses
132 of plants to drought stress in relation to root: shoot growth characteristics at field scale. We hypothesize
133 that, in field-grown maize, (1) soil-plant hydraulic conductance depends on soil hydraulic properties,
134 especially under dry soil conditions (2) minimum leaf water potential of maize is similar across soil types,
135 water treatments and climatic conditions. The hypotheses will be tested through three objectives: (i) to
136 investigate the effects of soil types, water application, and climatic condition on root growth and (ii) on
137 stomatal conductance, leaf photosynthesis, transpiration, leaf water potential, different components of
138 the hydraulic conductance (root, stem, and whole soil-plant), and (iii) to analyze the relative contribution
139 of root and shoot growth (leaf area and biomass) on the water uptake capacity of maize. These three
140 objectives will be achieved based on a comprehensive dataset covering the whole soil-plant continuum
141 over two growing maize seasons with contrasting climatic conditions (low and high VPD) under two water
142 treatments (rainfed and irrigated) and two different soil types (stony and silty soil).

143

144 **2. Materials and methods**

145 **2.1. Location and experimental set-up**

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

150 Each rhizotrone facility was divided into three subplots of 7.25 m by 3.25 m: two rainfed plots (P1, P2),
151 and one irrigated plot (P3). In rainfed plots P1, other sowing densities and dates were used than in the
152 other plots and we excluded therefore these plots. Silage maize cv. Zoey was sown on 4 May and 8 May in
153 2017 and 2018, respectively, with a plant density of 10.66 seeds m⁻² (Figure 1a; Table 1). Detailed
154 information of crop management practices is provided in Table 1.

155 [Insert Table 1 here]

156 **2.2. Water applications**

157 The irrigation systems [T-Tape 520-20-500 drip lines (Wurzelwasser GbR, Müzenberg, Germany)] were
158 installed parallel to the crop rows with 0.3 m intervals. A nearby weather station (approx. 100 m from the
159 experiment) recorded every 10 minutes weather variables (global radiation, temperature, relative
160 humidity, precipitation, and wind speed). In addition, the precipitation amount was manually collected by
161 a plastic rain gauge next to each rhizotrone facility. The Penman-Monteith equation was employed to
162 estimate reference evapotranspiration. Daily crop evapotranspiration was calculated based on the single
163 crop coefficient and the reference evapotranspiration (Allen et al., 1998). Irrigation amounts were
164 estimated as the weekly sum of the calculated crop evapotranspiration. were recorded every 10 minutes
165 by a nearby weather station (approx. 100 m from the experiment). Drip lines (T-Tape 520-20-500,
166 Wurzelwasser GbR, Müzenberg, Germany) were installed for irrigation at 0.3 m intervals parallel to the
167 crop rows. A total amount of 230 mm precipitation was recorded during the growing period (136 days).

168 ~~2017, maize received a total amount of 230 mm precipitation during the growing period (136 days) while~~
169 ~~average, minimum and maximum daily air temperature were 17.6, 8.3, and 25.3 °C, respectively (Fig.~~
170 1b). The crop on ~~the irrigated plots (2017F1P3 and 2017F2P3)~~~~P3 was was received irrigated~~ (in total 130
171 mm) ~~(10 times, every 5-7 days (in days, total 10 times)~~ using 13 mm of irrigation water per event) between
172 mid June to end of August ~~for the irrigated plots (2017F1P3 and 2017F2P3)~~ (Fig. 1b). ~~In 2018,~~ average,
173 minimum, and maximum daily air temperature ~~in 2018~~ were ~~higher than in 2017 with~~ 19.2, 10.85, and
174 27.3 °C, respectively (Fig. 1b) ~~and exceeded those of 2017.~~ ~~Characterized by exceptionally hot and dry~~
175 ~~weather conditions,~~ ~~the summer season in 2018 could can be considered classified~~ as an extreme year with
176 respect to plant growth at our experimental location ~~due to exceptionally hot and dry weather conditions.~~
177 ~~Maize experienced high temperatures and VPD, especially around tasseling and silking. Crop in 2018,~~
178 ~~only received only~~ 91.3 mm of rain ~~were recorded in the during the~~ growing period of 2018 (107 days). The
179 ~~maize crop on the irrigated plots 2018F1P3 and 2018F2P3~~ was irrigated every 5-7 days (in total 13 times),
180 with a total amount of irrigation of 257 mm and 239 mm between mid- June and mid- August ~~for the~~
181 ~~irrigated plots 2018F1P3 and 2018F2P3,~~ respectively (Fig. 1d). ~~To avoid a crop failure due to severe drought~~
182 ~~in 2018, in contrast to 2017, t~~he rainfed plot in the stony soil (2018F1P2) had to be irrigated (in total 66
183 mm) four times (using 13, 22, 13, and 18 mm, respectively) ~~to avoid a crop failure due to severe drought~~
184 (Fig. 1d). Detailed estimates of irrigation amount and intervals could be found in Nguyen et al., (2022a).

185 [Insert Figure 1 here]

186 2.3. Measurements

187 2.3.1. Soil water measurement and root growth

188 ~~At soil depths of 10, 20, 40, 60, 80, and 120 cm,~~ MPS-2 matrix water potential and temperature sensors
189 (Decagon Devices Inc., UMS GmbH München, Germany) were installed ~~at soil depths of 10, 20, 40, 60, 80,~~
190 ~~and 120 cm~~ to measure half-hourly soil water potential and soil temperature. The range of the water
191 potential measurements is from -9 kPa to approximately -100000 kPa (pF 1.96 to pF 6.01). In addition to

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

195 Minirhizotubes (7 m long clear acrylic glass tubes with outer and inner diameters of 6.4 and 5.6 cm,
196 respectively) were installed horizontally at six different depths of 10, 20, 40, 60, 80, and 120 cm below the
197 soil surface in each facility. There are three replicate tubes at each depth, accounting for 54 tubes in each
198 facility. Root measurements were taken manually by Bartz camera (Bartz Technology Corporation) (23
199 June 2017 – 12 September 2017) and VSI camera (Vienna Scientific Instruments GmbH) (08 June 2017 – 22
200 June 2017) in 2017 while only VSI was used in 2018 (23 May 2018 - 23 August 2018). Root images were
201 taken at 20 fixed positions from the left- and right-hand sides of each tube weekly (or biweekly) during the
202 growing seasons. The root images were analyzed by automated minirhizotube image analysis pipeline for
203 segmentation and automated feature extraction (Bauer et al., 2021). Two-dimensional root length density
204 (RLD, in units of cm cm^{-2}) was estimated from the total root length observed in the image and the image
205 surface area. The overview of camera system, minirhizotube images acquisition, and post-processing of
206 the root data were described in detail in Bauer et al. (2021) and Lärm et al., (2023).

207 **2.3.2. Crop growth, leaf gas exchange, leaf water potential, and sap flow measurements**

208 The phenology, plant height, stem diameter, green and brown leaf area, dry matter of different organs,
209 and total aboveground dry matter were observed and measured bi-weekly. Dates of sowing, emergence,
210 tasseling, and silking for two growing seasons were observed. There was difference in emergence,
211 tasseling and silking dates for two growing seasons due to the differences of sowing dates and
212 temperature. However, the developmental stages were not different among water treatments and soil
213 types within one season. Measurements of green leaf area and aboveground dry matter were based on
214 the destructive method.

215 We performed leaf gas measurements under clear sky and sunny conditions. Hourly leaf stomatal
216 conductance (Gs), net photosynthesis (An), and leaf transpiration (E) of two sunlit leaves (uppermost fully
217 developed leaves) and one shaded leaf of different plants were measured every two weeks ~~under clear~~
218 ~~sky conditions.~~ The Gs, An, and E ~~of two sunlit leaves (uppermost fully developed leaves) and one shaded~~
219 ~~leaf of different plants~~ were measured at steady-state using a LICOR 6400 XT device (Licor Biosciences,
220 Lincoln, Nebraska, USA). Leaf water potential (ψ_{leaf}) was measured with a pressure chamber (SKPM 140/
221 (40-50-80), Skye Instrument Ltd, UK).

222 ~~In 2017 (from 7 July 2017 until harvest) and 2018 (from 28 June 2018 until harvest)~~ Based on stem diameter
223 size, 20 sap twenty sap flow sensors (SGA 13, SGB 16, and SGB 19 types) were installed (one sensor per
224 plant and 5 maize plants per ~~plot treatment~~) - in each year based on stem diameter size. The sensors were
225 operated from 7 July 2017 and- from 28 June 2018 until harvest for the 2017 and 2018 growing season,
226 respectively. The calculated sap flow in the plant (g h^{-1}) ~~was estimated directly by from~~ the data loggers
227 (Dynamax, 2007) ~~and was~~ used to compute as a surrogate for canopy transpiration based on ~~the number~~
228 ~~of plants~~ the plant density per square meter. Further detail of developmental stages, crop growth, leaf gas
229 exchange, leaf water potential, and sap flow measurements could be found in Nguyen et al., (2024),
230 Nguyen et al., (2022a), and Nguyen et al., (2020).

231 **2.4. Calculation of total root length, root system conductance, stem, and whole plant hydraulic** 232 **conductance**

233 To estimate the total root length from minirhizotubes, we adopted the option 2 which was described in
234 Cai et al., (2017). Total root length per square meter soil surface area within each soil layer (m m^{-2}) was
235 computed by multiplying the root length density with the corresponding soil layer thickness. The root
236 length density was determined in each depth by dividing the measured root length per minirhizotron

237 image by the assumed volume the roots would have occupied in absence of the tube, i.e., $W * L * \text{tube}$
238 radius (see Cai et al., 2017).

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

$$\psi_{soil_effec} = \sum_{i=1}^N \psi_i NRLD_i \Delta z_i \quad (1)$$

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

$$K_{soil_root} = Sapflow / (\psi_{soil_effec} - \psi_{shadedleaf}) \quad (2)$$

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

$$K_{soil_plant} = Sapflow / (\psi_{soil_effec} - \psi_{sunlitleaf}) \quad (4)$$

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

254 **2.5. Statistical analysis**

255
256 Regression analysis was performed to understand the relationship between the sap flow volume and the
257 difference of effective soil water potential and sunlit leaf water potential as well as the relationship
258 between the total aboveground biomass and cumulated water transpired (sap flow volume). These
259 analyses allow to derive the slope as proxy of $K_{\text{soil_plant}}$ and transpiration use efficiency, respectively. Since
260 all measured data have their own measurement errors, the generalized Deming regression was employed.
261 We performed relationships (via correlation coefficient and statistical significant levels) of midday leaf A_n ,
262 G_s , and E with midday K_{stem} , $K_{\text{soil_plant}}$, $K_{\text{soil_root}}$, sunlit leaf potential, $\psi_{\text{soil_effec}}$, and the difference of $\psi_{\text{soil_effec}}$
263 and sunlit leaf water potential ($\psi_{\text{difference}}$). All data processing and analysis were conducted using the R
264 statistical software (R Core Team, 2022).

265 **3. Results**

266 **3.1. Root growth under different water treatments, soil types and climatic conditions**

267 Observed root length (cm cm^{-2}) from the minirhizotubes in different soil depths at the first week of June
268 (stem elongation), around silking, and at harvest in two growing seasons are shown in the Figure 2. Root
269 length was similar among water treatments at the start of stem elongation in both years (Fig. 2a & 2d).
270 The difference in root length was pronounced at silking and harvest between the soil types. More root
271 growth was observed in the silty soil compared to the stony soil with the same water treatment (i.e. 2.5 -
272 6 times higher at depth 40 cm). This indicated the strong negative effects of stone content on root
273 development. In the stony soil, root length in the irrigated plot (F1P3) was slightly higher than in the rainfed
274 plot (F1P2). In contrast, the rainfed treatment (F2P2) in the silty soil showed much higher root length,
275 especially from 40 to 120 cm depths as compared to the irrigated plot (F2P3) in both growing seasons.
276 Much lower stone content and deep soil cracks in the silty soil (Morandage et al., 2021) allow root
277 extension to the subsoil, particularly in the rainfed plot F2P2. Root length in the rainfed treatment (F2P2)

278 in 2018, is higher than in 2017 which implies that root further developed to exploit the water in the soil
279 under the rainfed condition to meet the higher evaporative demand.

280 [Insert Figure 2 here]

281 Total root length (m m^{-2}) estimated from minirhizotubes and its ratio to shoot dry matter (m kg^{-1}) at three
282 measured dates (as in Figure 2) are shown in the Figure 3. Total root length was much higher for the silty
283 plots as compared to stony plots. In 2017, the highest total root length was observed in the rainfed plot of
284 the silty soil (F2P2) with approximately 9166 m m^{-2} and 9878 m m^{-2} around silking and harvest, respectively,
285 which was almost two times higher than in the irrigated plot (F2P3). These figures were higher in 2018
286 than 2017 where total root length of F2P2 was 10188 m m^{-2} and 13750 m m^{-2} at silking and harvest time,
287 respectively. For the rainfed stony soil (F1P2), soil water depletion around the beginning of June in 2017
288 ([Supplementary material Figure S1a](#)) and from the first two weeks of June to harvest in 2018
289 ([Figure Supplementary material S2a](#)) caused the strong reduction of shoot biomass. In the stony soil, the
290 shoot dry matter of the irrigated plot (F1P3) and the rainfed plot (F1P2) were 1275 and 536 g m^{-2} at silking
291 time (e.g. 19 July 2018 – DOY 200, [Figure Supplementary material S3a](#) and [S3b](#)). However, there was a
292 minor difference between F1P2 and F1P3 in terms of the ratio of root length to shoot dry matter. In the
293 silty soil, a decrease of soil water potential was not pronounced (compared to stony soil) in both years
294 2017 and 2018 ([Figure Supplementary material S1b](#) and [S2b](#)). In 2018, shoot biomass in the irrigated stony
295 soil (F1P3) and silt soil (F2P3) were similar (1275 and 1299 g m^{-2} , respectively on 19 July 2018 – DOY 200)
296 while the shoot biomass of the rainfed silty soil (F2P2) was 876 g m^{-2} ([Figure Supplementary material S3a](#)
297 & [S3b](#)). However, the ratios of root length to shoot biomass in the rainfed plot of the silty soil (F2P2) were
298 3 and 6 times higher than those in the irrigated silty soil (F2P3) and stony soil (F1P3), respectively (e.g. 18
299 July, DOY 199). Moreover, total root length was relatively equal among treatments at the start of set
300 elongation (8 June - DOY 159) in both years, while this was the opposite for the ratio of root length to
301 shoot dry matter. This firstly illustrated that the finer soil texture without stones and with soil cracks could

302 favor the root growth which indicates strong interactions of root and soil conditions. Secondly, the larger
303 root length and higher atmospheric evaporative demand in 2018 than 2017 indicates also the interaction
304 of root growth and climatic conditions.

305 [Insert Figure 3 here]

306 **3.2. Stomatal conductance, photosynthesis, transpiration, and $K_{\text{soil_plant}}$**

307 **3.2.1. Diurnal course of stomatal conductance, photosynthesis, transpiration, and water potential at leaf** 308 **level**

309 After a long period with high temperatures and no rainfall, soil water reduction in the rainfed plot of the
310 stony soil (F1P2) on 17 July 2018 (~~FigureSupplementary material-S2~~) resulted in three times lower net
311 photosynthesis (A_n), stomatal conductance (G_s), transpiration (E) and leaf water potential (ψ_{leaf}) as
312 compared to the remaining treatments (~~FigureSupplementary material-S4~~). This indicates that the soil
313 water content strongly affected the stomatal conductance. Stomatal closure was much pronounced
314 around midday in F1P2 while this was not the case in the F2P2, indicating the soil type strongly affected
315 the stomatal conductance and leaf gas exchange. Leaf gas exchange and leaf water potential in the F1P2
316 were still much lower than in other plots (Figure 4). On 18 July 2018, after application of 22.75 mm of
317 irrigation water (at 4 PM), photosynthesis, stomatal conductance, transpiration and leaf water potential
318 were slightly increased in F1P2. However, these were still smaller than in F2P2 and the two irrigated plots.

319 [Insert Figure 4 here]

320 On the next day after irrigation, leaf gas exchange and water potential were considerably increased in the
321 F1P2 (~~FigureSupplementary material-S5~~). Leaf curling was also less pronounced as compared the two
322 previous days. ~~This indicated the recovery of plant after watering.~~ Predawn and midday leaf water
323 potential, were around -0.4 MPa and -1.6 MPa for all plots, respectively. Leaf photosynthesis transpiration
324 rate was around 3.1 millimole $\text{m}^{-2} \text{s}^{-1}$ for all water treatments and soil types at 12 AM. ~~stomatal~~

325 ~~conductance, and leaf transpiration were almost similar to other plots from predawn throughout the day.~~

326 This indicated the recovery of plant after watering at the rainfed plot with stony soil (F1P2).

327 **3.2.2. Seasonal course of stomatal conductance, photosynthesis, transpiration, water potential, and** 328 **plant hydraulic conductance at the leaf level**

329 Seasonal stomatal conductance (G_s) and leaf water potential (ψ_{leaf}) are described in Figure 5. The
330 relationship between two variables was rather noisy and non-linear. The leaf water potential showed
331 distinct patterns among treatments in one growing season. Minimum ψ_{leaf} was maintained at around -1.5
332 MPa in the irrigated plot in stony soil (F1P3) and two plots in the silty soil (F2P2 and F2P3). Lower minimum
333 ψ_{leaf} could be observed in the rainfed plot with stony soil (F1P2) but it did not go beyond -2 MPa. Minor
334 leaf curling was observed only in the second week of June in the F1P2 in 2017. In 2018, the higher
335 temperature and vapor pressure deficit resulted in lower minimum ψ_{leaf} in all treatments and soil types as
336 compared to 2017. The minimum ψ_{leaf} was around -2 MPa in F1P3, F2P2, and F2P3 while ψ_{leaf} could drop
337 below -2 MPa in F1P2 which was due to the severe soil water deficit. The low G_s and ψ_{leaf} associated with
338 measurement dates when the substantial leaf curling was observed at mid of July to the end of growing
339 season in F1P2 in 2018 (~~FigureSupplementary material S3c & S3d and FigureSupplementary material S6c~~
340 & d).

341 [Insert Figure 5 here]

342 The effective soil water potential ($\psi_{\text{soil_effect MD}}$), sunlit leaf water potential ($\psi_{\text{sunlitleaf MD}}$), stomatal
343 conductance (G_{sMD}), and whole plant hydraulic conductance ($K_{\text{soil_plant MD}}$) at midday at several times during
344 the growing season are presented in Figures 6 and 7 for 2017 and 2018, respectively. As expected, there
345 was not much difference in terms of $\psi_{\text{soil_effecMD}}$ among F1P3, F2P2, and F2P3 from 02 August to one week
346 before harvest in 2017. The lowest $\psi_{\text{soil_effec MD}}$ was observed in the F1P2. Leaf water potential dropped
347 drastically but also $K_{\text{soil_plant MD}}$ increased strongly whereas $\psi_{\text{soil_effec MD}}$ remained quite similar (e.g. 18 July).

348 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
349 mm d⁻¹ on 18 July for the F1P2). The stomatal conductance decreased a lot in this day which could be
350 explained that the atmospheric demand increased (e.g. global radiation was 13.6 MJ m⁻² on 17 July
351 compared to 23.9 MJ on 18 July while daily VPD was 0.7 kPa and 1.2 kPa, respectively) even more than the
352 sap flow. Midday sunlit leaf water potential was not distinctively different among treatments with the
353 lowest $\psi_{\text{sunlitleaf MD}}$ around -1.6 MPa throughout season. Also, G_{SMD} was rather similar among plots. The
354 $K_{\text{soil_plant MD}}$ ranged from 0.125 to 0.96 mm h⁻¹ MPa⁻¹ with a sharp reduction before harvest. In general, the
355 lowest values of $K_{\text{soil_plant MD}}$ were found in F1P2 which was consistent with the smaller overall seasonal
356 $K_{\text{soil_plant}}$ (as the slope of linear relationship between sap flow and difference of effective soil water potential
357 and sunlit leaf water potential) (see [FigureSupplementary material S7](#)).

358 [Insert Figure 6 here]

359 The $\psi_{\text{soil_effec MD}}$ was substantially different in the two soil types and water treatments in 2018 (Figure 7a).
360 Both F1P2 and F1P3 showed a gradual drop of $\psi_{\text{soil_effec MD}}$ from 15 June until the third week of July then
361 increased after irrigation events on 18 July ([FigureSupplementary material S2b](#)). However, $\psi_{\text{soil_effec MD}}$ of
362 F1P2 was much lower than F1P3 toward the harvest. The $\psi_{\text{soil_effec MD}}$ of F2P2 and F2P3 only decreased
363 progressively from around 10 July till harvest even though there was water supply from the irrigation
364 ([FigureSupplementary material S2b](#)). The water applied by irrigation and coming in by rainfall were
365 insufficient to wet up the deeper soil layers which remained dry. The low G_{SMD} was corresponding to the
366 lowest $\psi_{\text{sunlitleaf MD}}$ and $K_{\text{soil_plant MD}}$ from the F1P2 (Figure 7c & 7d). The $K_{\text{soil_plant MD}}$ from all plots was ranging
367 from 0.12 to 0.91 mm h⁻¹ MPa⁻¹. There was the drop in $K_{\text{soil_plant MD}}$ (i.e. 3 to 9 July or 17-18 July) before
368 irrigation in this plot. However, it increased after the irrigation (i.e. 10 July and 19 July). This suggests that
369 $K_{\text{soil_plant}}$ depends strongly on the soil water content and the conductivity of the rhizosphere.

370 [Insert Figure 7 here]

371 **3.2.3. Relationships of stomatal conductance, transpiration, photosynthesis with plant hydraulic**
372 **variables at the plant canopy level**

373 The slope of linear relationship between sap flow and difference of $\psi_{\text{soil_effec}}$ and $\psi_{\text{sunlitleaf}}$ is shown for three
374 consecutive days (leaf water potential measurements from the predawn) and before and after irrigation
375 applications (17, 18, and 19 July 2018) (Figure 8). On both dates 17 and 18 July, the difference between
376 $\psi_{\text{soil_effec}}$ and $\psi_{\text{sunlitleaf}}$ was around -1.6 MPa with very low transpiration rates in the treatment F1P2 which
377 was associated with very low plant hydraulic conductance and leaf curling. The whole plant hydraulic
378 conductance was disrupted on these two days (0.06 and 0.16 mm h⁻¹ MPa⁻¹ for 17 and 18 July, respectively).
379 Water was supplied on 18 July at 1 PM for the irrigated plots (F1P3, F2P3) as well as F1P2 at 4 PM (for
380 saving plant from death due to severe drought stress). $K_{\text{soil_plant}}$ was slightly changed (0.43 and 0.57 mm h⁻¹
381 MPa⁻¹ for F1P3 on 18 and 19 July, respectively and 0.5 and 0.58 mm h⁻¹ MPa⁻¹ for F2P3 on 18 and 19 July,
382 respectively). However, the increase of $K_{\text{soil_plant}}$ was substantial in the F1P2 after the irrigation. Soil water
383 replenishment and an increase in the root - soil contact (Fig. 7a) allowed the $K_{\text{soil_plant}}$ to recover overnight
384 to 0.46 mm h⁻¹ MPa⁻¹. This resulted in a narrower water potential gradient between root zone and sunlit
385 leaf and in a higher transpiration rate on 19 July.

386 [Insert Figure 8 here]

387 Seasonal average of different midday hydraulic conductance components (root system hydraulic
388 conductance - $K_{\text{soil_root}}$, stem hydraulic conductance - K_{stem} , and whole plant hydraulic conductance -
389 $K_{\text{soil_plant}}$) are shown in Figure 9. In the same year, the K_{stem} was not much different among F1P3, F2P2, and
390 F2P3 plots. The K_{stem} of those plots was slightly higher than in the F1P2 in both years. In general, the $K_{\text{soil_root}}$
391 was lower than the K_{stem} . Overall, the estimated $K_{\text{soil_plant}}$ was around $1 / (1/K_{\text{soil_root}} + 1/K_{\text{stem}})$ regardless of
392 soil types, years, and water treatments. The $K_{\text{soil_root}}$ and $K_{\text{soil_plant}}$ in the F1P2 in 2018 was much lower than
393 the remaining plots while the $K_{\text{soil_root}}$ and $K_{\text{soil_plant}}$ were not much different among plots in 2017. Our results

394 indicated that there was an impact of soil hydraulic conductance on $K_{\text{soil_root}}$ and $K_{\text{soil_plant}}$. Although there is
395 a large difference in total root length between the two soil types (e.g. F1P3 versus F2P2 or F2P3 versus
396 F2P2), $K_{\text{soil_root}}$ and $K_{\text{soil_plant}}$ in those two plots were not much different. This could be explained by the fact
397 that $K_{\text{soil_plant}}$ was not only depended on root length but also depended on the variability of root segment
398 hydraulic conductance.

399 [Insert Figure 9 here]

400 **3.3. Relative importance of root and leaf area growth to transpiration and crop performance at canopy** 401 **level**

402 Drought stress was observed in the rainfed plot (F2P2) in the second week of June 2017 with mild leaf
403 rolling. The crop then recovered due to sufficient rainfall and lower evaporative demand. Drought stress
404 occurring again at the stem elongation phase caused reduction of plant size (height and stem diameter)
405 ([FigureSupplementary material S6](#)) as well as a slight reduction of leaf area and biomass in this plot
406 ([FigureSupplementary material S3a & S3c](#)). Transpiration per unit of leaf area did not differ much among
407 water treatments and soil types in 2017 ([FigureSupplementary material S8](#)). The opposite was the case for
408 the transpiration rate per unit of root length. The observed root length at different soil depths (Figure 2)
409 and total root length for two plots in the stony soil was much smaller than in the silty soil (Figure 3).
410 Therefore, transpiration per unit of root length in the stony soils (F1P2 & F1P3) was almost 3 times higher
411 than transpiration in the silty soil. For the same soil, transpiration per unit root length of the irrigated
412 treatment was slightly larger than in the rainfed plot.

413 The differences in sap flow per plant between water treatments and soil types were more pronounced in
414 2018 ([FigureSupplementary material S9](#)). The highest transpiration rate was observed in the irrigated plots
415 (F1P3 & F2P3), followed by the rainfed plot of the silty soil (F2P2) and it was lowest in the rainfed plot of
416 the stony soil (F1P2). These observations were in line with the differences in biomass and leaf area index
417 between the treatments ([FigureSupplementary material S3b & S3d](#)) and plant size ([FigureSupplementary](#)

418 ~~material~~ S6b-c-d). In 2018, severe leaf rolling was observed in the rainfed plot (F1P2) from the beginning
419 of June until the end of the growing period in 2018 (FigureSupplementary material_S3d). Similar to 2017,
420 transpiration per unit of root length was much higher in the stony plots as compared to silty plots. Also,
421 for the silty soil, transpiration per unit of root length of the irrigated plot (F2P3) was higher than in the
422 rainfed plot (F2P2).

423 Higher cumulative transpiration in the irrigated plots did not result in higher transpiration use efficiency
424 (TUE) in both soil types (Figure 10). For instance, TUE were 16.87 g mm⁻¹ and 15.59 g mm⁻¹ for F1P2 and
425 F2P2, respectively, while they were 15.47 and 14.79 g mm⁻¹ for F1P3 and F2P3, respectively, in 2017 (Figure
426 10A). For the same soil, the rainfed plot showed slightly higher TUE than the irrigated plot. When
427 comparing the TUE of maize of the two soil types for the same water treatment, TUE at the stony soil was
428 almost the same in silty soil. The TUE was not much different among treatments and soil types in 2018.
429 Overall, TUE in 2017 was higher as compared to 2018 (Fig. 10b).

430 [Insert Figure 10 here]

431 **4. Discussions**

432 **4.1. Effects of soil types, water application, and climatic condition on root growth**

433 Our root observations showed that soil type ~~considerably~~ affected root growth more than water treatment
434 (Figure 2). Root growth was strongly inhibited by the stony soil where much lower root length was
435 observed than in the silty soil, especially in the deeper soil layers. This was consistent with the findings
436 reported in (Morandage et al., 2021) where a linear increase of stone content resulted in a linear decrease
437 of rooting depth across all stone contents and developmental stages. Also, both simulations and
438 observations indicated that rooting depth was increased due to the presence of cracks in the lower
439 minirhizontron facility (Morandage et al., 2021) which could explain the high root length between 40 and
440 120 cm soil depths which was observed in the silty soil in both years.

441 In terms of the ratios of root length to shoot biomass, Ordóñez et al., (2020) has reported much larger
442 figures of for instance 880 cm g⁻¹ in different locations and under different N application rates in maize
443 growing in the Midwest of US. Jorda et al., (2022) reported a wide range of ratios of root length to shoot
444 biomass from 200 to 1000 cm g⁻¹ around flowering time of maize depending on the wild type and root hair
445 mutant genotypes growing on either loamy or sandy soils. More roots and higher ratios of root length to
446 shoot biomass were found in the sand than in the loam in both wild type and root hair mutant genotypes
447 (Jorda et al., 2022; Vetterlein et al., 2022). Cai et al., (2018) observed much larger ratios of root length to
448 shoot biomass in drought stressed plots than in irrigated plot in both soil types in winter wheat which
449 indicated the alternation of sink: source relationships to cope with water stress. This study emphasized
450 that more assimilates are used to promote root growth and extract more water under drought stress.
451 However, this was not the case for the stony soil in our work where the drought stress was more
452 pronounced, especially in 2018. A drop of soil water potential ([FigureSupplementary material_S2b](#)), thus
453 effective soil water potential (Figure 6a) was substantial from 10th July 2018 toward the harvest in the
454 rainfed plot in the silty soil (F2P2) which was consistent with the reduction of leaf water potential (Fig. 6b),
455 leaf area ([Figure Supplementary material_S3c](#)), total dry matter ([FigureSupplementary material_S3d](#)), and
456 crop height ([FigureSupplementary material_S6b](#)) as compared the irrigated plot (F2P3). This indicates a
457 mild water stress in 2018 in the rainfed plots on the silty soil. The larger ratios of root length to shoot
458 biomass in this F2P2 plot in 2018 as compared to F2P3 could be explained by the change of source: sink
459 relations where more assimilates were devoted to root growth, even at a later growth stage. Moreover,
460 the low stone content and soil cracks (Morandage et al., 2021) might favor root growth in the deeper soil
461 layers which are close to the shallow soil water table in the rhizotron facility with silty soil (Vanderborght
462 et al., 2010). In conclusion, both soil texture and water conditions influenced the root growth, however,
463 effects of the former on root length was more pronounced than the latter.

464 -In the stony soil, which has a considerably smaller water holding capacity than the silty soil, root length
465 was considerably smaller than in the silty soil. Nevertheless, water uptake per unit root length was much
466 larger than in the fine soil. This also means that the hydraulic conductance per unit root length must have
467 been much larger in the stony soil than in the fine soil. Cai et al., (2018) observed a similar effect for winter
468 wheat but they found much smaller differences in the root length normalized root conductance. The
469 higher root length normalized root conductance means that the anatomy of the root tissues must have
470 been influenced by the soil texture and compensated the considerably smaller root length in the stony
471 soil. Looking at the effect of water treatments in the silt soil, the non-irrigated plot had more roots than
472 the irrigated one and both had more roots in the year with high VPD. But the soil-root conductance was
473 higher in the irrigated plot than in the rainfed plot. This means that in the irrigated plot, the soil-root
474 conductance per unit root length was higher than in the rainfed plot. This could either be due to wetter
475 soil conditions and higher soil conductance or it could be due to a larger conductance of the root tissues.
476 Epecially in 2017 when the silty soil was wetter, the slightly larger soil-root conductance in the irrigated
477 plot is most likely the result of larger root tissue conductance in the irrigated plot. Thus, how root
478 architecture (here represented simply by the total root length) and root tissue conductivities 'respond' to
479 drought stress might be opposite depending on the comparisons that are made. When the stony soil and
480 silt soil are compared, the higher 'stress' due to lower water availability in the stony soil resulted in less
481 roots with a higher root tissue conductance in the soil with more stress. When comparing the rainfed with
482 the irrigated plot in the silty soil, the higher stress in the rainfed soil resulted in more roots with a lower
483 root tissue conductance in the treatment with more stress. This indicates that the response to water stress
484 can be different depending on soil conditions or water treatments.

485 **4.2. Effects of soil types, water application, and climatic condition on stomatal conductance,** 486 **photosynthesis, transpiration, leaf water potential, and plant hydraulic conductance**

487 **4.2.1. Leaf water potential and stomatal conductance as affected by soil water conditions**

488 In the previous work, Koehler et al., (2022) reported that maize stomata closed at lower negative leaf
489 water potentials in sand than in loam growing under controlled environment. Cai et al., (2022b)
490 investigated transpiration response of pot-grown maize in two contrasting soil textures (sand and loam)
491 and exposed to two consecutive VPD levels (1.8 and 2.8 kPa). Transpiration rate decreased at less negative
492 soil matric potential in sand than in loam at both VPD levels. In sand, high VPD generated a steeper drop
493 in stomatal conductance with decreasing leaf water potential which indicated that the transpiration and
494 stomatal responses depend on soil hydraulics. In our study, stomata closed earlier and at more negative
495 soil and leaf water potentials in the stony soil than in the silty soil (see Fig. 4 & 7 and [FigureSupplementary](#)
496 [material-S4 & S5](#)). The lower soil water holding capacity of the stony soil compared to the silty soil resulted
497 in lower soil water potential and smaller total plant hydraulic conductance which in turn led to earlier
498 stomatal closure and to more negative soil water potential in the stony soil.

499 Stomatal control is an early and effective response to water stress to prevent the plant from water loss
500 and dehydration. Maize is considered as an isohydric plant which closes its stomata to maintain leaf water
501 potential above critical levels (Tardieu and Simonneau, 1998). Our results showed that minimum leaf
502 water potential varied among treatments (-1.5 MPa for F1P3, F2P2, and F2P3 and up to -2 MPa for F1P2
503 in 2017, while in 2018 minimum values were -2 MPa for F2P3, F2P2, and F2P3 and -2.7 MPa for F1P2) (Fig.
504 5, Fig. 6, and Fig. 7). In conclusion, our results confirmed that the minimum ψ_{leaf} not only depended on
505 genotypic differences but also was influenced by soil types, soil hydraulic conductance, and atmospheric
506 demand.

507 **4.2.2. Hydraulic conductance components as affected by soil water conditions**

508 Estimates of hydraulic components in soil-plant-atmosphere continuum are important not only to
509 understand its underlying relationship to other crop characteristics (stomatal conductance, transpiration,
510 and photosynthesis) but also to provide modeling parameters in process-based soil-root-shoot models
511 (Nguyen et al., 2020; Sulis et al., 2019; Nguyen et al., 2022b). Measurement of the components of hydraulic

512 conductance are challenging under field conditions because it requires the estimation of transpiration and
513 root to leaf water potential gradients. To our knowledge, our results were unique with regard to the
514 dynamics of $K_{\text{soil_plant}}$ for field-grown maize on two soil types and under contrasting water, and climatic
515 conditions. Our seasonal $K_{\text{soil_plant}}$ ranged from $0.12 \text{ mm h}^{-1} \text{ MPa}^{-1}$ to $0.9 \text{ mm h}^{-1} \text{ MPa}^{-1}$ (Fig. 6 & Fig. 7; Fig.
516 8, and [FigureSupplementary material S7](#)). Root system hydraulic conductance ranged from 0.26 to 1.47
517 $\text{mm h}^{-1} \text{ MPa}^{-1}$ (Figure 9). Note that the unit of $K_{\text{soil_plant}}$ as $\text{mm h}^{-1} \text{ MPa}^{-1}$ could be equivalent to the unit of
518 10^{-5} h^{-1} if one assumes 1MPa is approximately 10^5 mm in terms of pressure head. Cai et al., (2018) reported
519 root hydraulic conductance in winter wheat from 0.05 to $0.5 \text{ mm h}^{-1} \text{ MPa}^{-1}$ in two similar soil types.
520 Nguyen et al., (2020) also reported $K_{\text{soil_plant}}$ in winter wheat from 0.0625 to $0.461 \text{ mm h}^{-1} \text{ MPa}^{-1}$. Meunier
521 et al., (2018) focused on estimating the root system hydraulic conductance of maize in a container
522 experiment where the range of $K_{\text{soil_plant}}$ was much larger from 0.37 to $36 \text{ mm h}^{-1} \text{ MPa}^{-1}$ for the plant density
523 of 10 plant m^{-2} . Jorda et al., (2022) estimated root system hydraulic conductance of 0.5 to $1.5 \cdot 10^{-3} \text{ d}^{-1}$ which
524 would be roughly between 2 to $6 \text{ mm h}^{-1} \text{ MPa}^{-1}$. In our work, except the F2P2 in 2018, the stem hydraulic
525 conductance was 10% to 60% higher than root system hydraulic conductance. Gallardo et al., (1996)
526 reported that stem hydraulic conductance of wheat was lower than root system conductance at around
527 71 to 91 days after sowing (DAS), but they were similar at 102 DAS. In lupine, stem hydraulic conductance
528 was two times higher than root system conductance regardless of measured days. The larger root length
529 in wheat than lupine did not necessarily result in higher root conductance in wheat. Together with this
530 study, our study emphasizes the values of stem hydraulic conductance compared to the root hydraulic
531 conductance in maintaining water potential gradient from shaded leaf or plant color to the sunlit leaf.

532 Our results showed clear differences in $K_{\text{soil_plant}}$ among treatments where much lower $K_{\text{soil_plant}}$ was
533 observed in the F1P2 as compared to F2P2 (see Figure 8 for 2018; Figure 6 and 7 and [FigureSupplementary](#)
534 [material S7](#) for both years). This indicated the soil texture dependence for whole plant hydraulic
535 conductance. Maize plants with the shorter root system (i.e. rainfed plot in the stony soil in 2018) (Fig. 3)

536 had lower plant hydraulic conductance. Our results indicated that there was an impact of soil hydraulic
537 conditions on $K_{\text{soil_plant}}$ via the reduction of root system hydraulic conductance. Our analysis for three
538 consecutive measurement days in 2018 (Fig 8) showed that in the silty soil, $K_{\text{soil_plant}}$ decrease when soil
539 water potentials are becoming more negative. For instance, in the silty soil in 2018 when the soil water
540 potentials were considerably lower in the rainfed than in the irrigated plot (e.g. after 10th July), $K_{\text{soil_plant}}$
541 was lower in the rainfed than in the irrigated plot. In the stony soil, the $K_{\text{soil_plant}}$ and leaf water potentials
542 seems to decrease more considerably (compared to the silty soil) when the soil water potentials become
543 more negative. In other words, $K_{\text{soil_plant}}$ increased considerably when the soil water potentials in the stony
544 soil increased. In our work, $K_{\text{soil_plant}}$ increased slowly after irrigation mainly for the severe water stress plot
545 (see F1P2 on 19 July in Fig 7d and 8c). This implied that added soil water by irrigation took some time for
546 recovery the soil-root contact within the rhizosphere.

547 **4.2.3. Relationships of stomatal conductance, transpiration, photosynthesis with plant hydraulic** 548 **variables**

549 The transpiration rate and $K_{\text{soil_plant}}$ (slope of linear regression lines in Fig. 8a and b) were very low in the
550 rainfed plot under the stony soil (F1P2) which was associated with the large $\psi_{\text{difference}}$ (Fig. 8a & b) and the
551 lower stomatal conductance as compared to other plots (Fig. 7c). The $K_{\text{soil_plant}}$ slightly increased after
552 irrigation (18 July - DOY 199 in Fig. 8b) corresponding with the smaller $\psi_{\text{difference}}$ (Fig. 8b) and an increase in
553 stomatal conductance (Fig. 7c). Seasonal $K_{\text{soil_plant}}$ was low in the rainfed plot under stony soil (F1P2) with
554 the larger $\psi_{\text{difference}}$ (~~Figure Supplementary material S7~~). In addition, our study showed that the midday
555 stomatal conductance, photosynthesis, and transpiration were significantly correlated only with midday
556 $K_{\text{soil_plant}}$ in the rainfed plot on the stony soil (F1P2) in 2018 where high VPD and temperature occurred
557 (~~Supplementary material Table 4S1, Figure 4S10, and 4S11~~). Maize plants had lower plant hydraulic
558 conductance and more negative soil water potential in the rainfed plot in stony soil that and they exhibited
559 earlier stomatal closure as compared to the same plot in the silty soil. This was in line with a study from

560 Abdalla et al., (2022) which suggested that during soil drying, stomatal regulation of tomato is controlled
561 by root and soil hydraulic conductance. Recent work from Müllers et al., (2022) on faba bean and maize
562 suggested that differences in the stomatal sensitivity among plant species can be partly explained by the
563 sensitivity of soil-plant hydraulic conductance to soil drying. The loss of conductance has immediate
564 consequences for leaf water potential and the associated stomatal regulation. Cai et al., (2022b) also
565 showed that the decrease in sunlit leaf stomatal conductance was well correlated with the drop in soil-
566 plant hydraulic conductance, which was significantly affected by soil texture. This was confirmed in our
567 work where the stony soil strongly impacted on root growth, modulated $K_{\text{soil_plant}}$, and consequently
568 influenced the leaf stomatal conductance, photosynthesis, and transpiration.

569 **4.3. Relative contribution of water control by leaves and roots on transpiration and transpiration use** 570 **efficiency**

571 Responses of crops via stomatal control to reduce water loss at leaf scale while maintaining leaf
572 photosynthesis and water use efficiency were reported earlier (Nguyen et al., 2022a; Vitale et al., 2007).
573 In addition to that, in the maize experiments in 2017 and 2018 leaf rolling was observed in both rainfed
574 plots on the stony and the silty soil in the second week of June 2017 and from the beginning of June until
575 the end of the growing period in 2018. This indicates another dehydration avoidance mechanism resulting
576 from morphological adjustments which is an effective [mechanism strategy for delaying to leaf](#) senescence
577 (Aparicio-Tejo and Boyer, 1983; Richards et al., 2002). Stomatal closure resulted in more reduction of
578 transpiration and assimilation in the rainfed plots than irrigated plots with the same soil type (Fig. 4,
579 [FigureSupplementary material S4](#) & [S5](#), Fig. 5, and [FigureSupplementary material S9a](#)). There was
580 reduction of shoot biomass (also stem size and leaf size adjustments) in F1P2 as compared to other plots.
581 However, the TUE was not smaller in this plot than the remaining plots. These observations confirm that
582 plant size adjustments through reduction of height, leaf width and length are efficient responses to reduce
583 water loss at canopy scale in addition to stomatal control at the leaf level.

584 Relative contribution of leaf area to transpiration has been highlighted in wheat where reduction of tiller
585 number resulted in significantly lower LAI, thus lower canopy transpiration (Cai et al., 2018; Trillo and
586 Fernández, 2005; Nguyen et al., 2022a). However, root system conductance per unit of leaf area and per
587 unit root mass were strongly reduced and eventually more than reduction of leaf area under water stress
588 (Trillo and Fernández, 2005). In our work, expressing the transpiration per unit of root length on the one
589 hand allowed to analyze the role of total root length to water uptake. However, on the other hand, the
590 lower total root length did not necessarily result in a lower root water uptake and vice versa. For instance,
591 the rainfed plot of the treatment F2P2 had the larger total root length which could postpone the effect of
592 soil water limitations in drying soils due to greater ability to extract water from subsoils. Therefore,
593 transpiration was very similar between F2P2 and F2P3. Despite of the much lower total root length in the
594 stony soil, K_{soil_plant} in the irrigated plot (F1P3) was not much lower than in the same water treatment in
595 the silty soil (F2P3, Fig. 6d, 7d, Fig. 8, and [FigureSupplementary material S7](#)). This could be explained by
596 the fact that the K_{soil_plant} variability was not only depended on root architecture (here the root length and
597 distribution) but also depended on the variability of root segment hydraulic properties which has also been
598 illustrated and discussed in Zwieniecki et al. (2002), Frensch and Steudle (1989), Meunier et al. (2018),
599 Couvreur et al. (2014), and Ahmed et al. (2018). Moreover, the contribution of shoot hydraulic
600 conductance could be large in plants (Gallardo et al., 1996; Trillo and Fernández, 2005; Sunita et al., 2014)
601 which also confirmed in our work. In our work, K_{soil_plant} comprised root and shoot conductance which are
602 directly influenced by soil hydraulics. Our estimates of K_{soil_plant} varied with transpiration and gradients of
603 $\psi_{sunlitleaf}$ and ψ_{soil_effec} . Thus, any change of soil hydraulic conductance will change the root to shoot water
604 potential. Consequently, it will affect the gradients between shoot and root rhizosphere (Carminati and
605 Javaux, 2020). Thus, our study is revealing the importance of both soil texture characteristics and root
606 phenotypic traits (here root length) in regulating plant transpiration (Cai et al., 2022a). Despite of lower
607 root length in the stony irrigated plot, transpiration rate was not much lower than in the silty irrigated plot
608 in our work. This could be related to another property of the root such as root segment conductance or

609 other root traits (e.g. root hair). Further investigation with extensive measurements of roots including axial
610 and radial root conductance at field scale will be required to better explain the observed results. Other
611 traits like root hair density (Cai et al., 2022a) or higher root length density (Vadez, 2014) could contribute
612 to the soil to root water potential and root-zone hydraulic conductance where dense root hairs are
613 delaying soil water deficit in drying soils. However, contrasting results have shown that root hairs did not
614 have an effect on root water uptake (see Jorda et al. 2022). ~~The role of root hairs could not be analyzed in~~
615 ~~our work which was based on the root data from minirhizotron images.~~ Despite of lower root length in the
616 stony irrigated plot, transpiration rate was not much lower than in the silty irrigated plot. This could be
617 related to another property of the root such as root segment conductance or other root traits (e.g. root
618 hair). ~~The role of root hairs could not be analyzed in our work which was based on the root data from~~
619 ~~minirhizotron images.~~ Further investigation with extensive measurements of roots including axial and
620 radial root conductance at field scale will be required to better explain the observed results.

~~. In the stony soil, which has a considerably smaller water holding capacity than the silty soil, root length~~
621 ~~was considerably smaller than in the silty soil. Nevertheless water uptake per unit root length was much~~
622 ~~larger than in the fine soil. This also means that the hydraulic conductance per unit root length must have~~
623 ~~been much larger in the stony soil than in the fine soil. Cai et al., (2018) observed a similar effect for winter~~
624 ~~wheat but they found much smaller differences in the root length normalized root conductance. The~~
625 ~~higher root length normalized root conductance means that the anatomy of the root tissues must have~~
626 ~~been influenced by the soil texture and compensated the considerably smaller root length in the stony~~
627 ~~soil. Looking at the effect of water treatments in the silt soil, the non irrigated plot had more roots than~~
628 ~~the irrigated one and both had more roots in the year with high VPD. But the soil-root conductance was~~
629 ~~higher in the irrigated plot than in the rainfed plot. This means that in the irrigated plot, the soil-root~~
630 ~~conductance per unit root length was higher than in the rainfed plot. This could either be due to wetter~~
631 ~~soil conditions and higher soil conductance or it could be due to a larger conductance of the root tissues.~~
632

633 Epecially in 2017 when the silty soil was wetter, the slightly larger soil-root conductance in the irrigated
634 plot is most likely the result of larger root tissue conductance in the irrigated plot. Thus, how root
635 architecture (here represented simply by the total root length) and root tissue conductivities 'respond' to
636 drought stress might be opposite depending on the comparisons that are made. When the stony soil and
637 silt soil are compared, the higher 'stress' due to lower water availability in the stony soil resulted in less
638 roots with a higher root tissue conductance in the soil with more stress. When comparing the rainfed with
639 the irrigated plot in the silty soil, the higher stress in the rainfed soil resulted in more roots with a lower
640 root tissue conductance in the treatment with more stress.

641 This study investigated soil-water-plant relations, more specifically the interactions of the root and shoot
642 growth processes and water fluxes under variations of soil water status and atmospheric demands. To the
643 best of our knowledge, the comprehensive data collected from soil to root, plant, and atmosphere under
644 field conditions in this work was unique. However, we acknowledged the lack of treatment replicates
645 which was due to the complex and expensive construction of the rhizotrone facilities. We also
646 acknowledged the small size of plots that did not allow the extensive destructive sampling (i.e. leaf area,
647 biomass, or determination of leaf water potential etc.). Each rhizotrone site originally contained the
648 irrigated, rainfed, and rain-out sheltered plots (Nguyen et al., 2022a; Cai et al., 2016). The overall aim of
649 the experiments was to investigate the root and shoot responses and gas fluxes (CO₂ and H₂O) of wheat
650 and maize to the variations of soil water and soil hydraulics. Note that the studies did not intend to
651 investigate the impacts of similar irrigation strategies on plant water status among seasons (i.e. in 2017
652 and 2018) because the irrigation practices were less common in the regions. The collapse of manual rain-
653 out shelters due to strong wind after the 2016 growing season resulted in only two water treatments
654 (rainfed and irrigated). Based on experiences from the previous seasons (wheat), we argued that such
655 combinations of two water treatments and two soil types, to some extent, could still create a wide range
656 of soil water conditions for the maize trial. For instance, the "rainfed" treatment at the stony soil in the

657 upper rhizotrone (F1P2) could lead to severe water stress compared to other treatments, especially in the
658 summer time when the atmospheric evaporative demand is high. In fact, mild water stress was observed
659 at the F1P2 around mid-June in 2017. In 2018, the sites were slightly modified to induce more severe water
660 stress (Nguyen et al., 2022a). One rainfed plot with the stony soil had late sowing while one rainfed plot
661 with the silty soil had the higher sowing density (data not shown in the study). Unprecedented weather
662 (extremely hot and dry) in 2018 resulted in severe drought stress at the rainfed plots with the stony soil.
663 To compare the effects of soil types and water treatments on crop, we presented here only data from two
664 plots (rainfed and irrigated) for two soil types. In spite of the experimental limitations, the relative
665 differences among the treatments, soil types, and seasons as well as measured dates were clearly
666 illustrated which ultimately supported the overall aim of our study.

667 The simultaneous measurements of atmospheric conditions, leaf water potential, and transpiration rates,
668 coupled with measurements of root, stem and whole soil-plant hydraulic conductance, root architecture
669 (root length), and soil water potential distribution illustrated the complex responses of the shoot and root
670 growth and hydraulic conductance vulnerability to soil water availability. The different responses of crop
671 processes to soil hydraulics and climatic conditions suggest further field investigations for other soil types,
672 growing seasons, and water regimes. Future studies considering the effects of progressive soil drying or
673 irrigation strategies on plant water status and crop growth at field conditions will be necessary. This is very
674 relevant for those crop growing regions that require irrigation. Our results show that the leaf water
675 potential threshold can vary within the same genotype depending on soil types, climatic conditions, and
676 water management. Large variability of minimum leaf water potential has been reported for maize
677 genotypes under greenhouse conditions (Welcker et al., 2011). Field studies are required concerning the
678 stomatal functions, water relations, hydraulic vulnerability traits, and root: shoot responses, especially of
679 different maize cultivars in responding to drought stress. This will suggest implications for selecting
680 agronomic cultivars and traits under changing climates. [Results from this study show that soil-crop models](#)

681 should focus not only on simulating stomatal regulations to capture the response to drought stress, but
682 also require adequate representations of root and leaf growth and adjustments. The soil hydraulics
683 strongly influenced soil water availability and crop growths. Regional applications of soil-crop models for
684 simulating gas fluxes and crop growth processes and for estimating irrigation amounts must account for
685 the environmental heterogeneity within the spatial simulation unit whereas the soil heterogeneity is the
686 key variable.

687 **5. Conclusion**

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

699 Another conclusion is that stomatal regulation maintains leaf water potential at certain thresholds which
700 depends on soil types, soil water availability, and seasonal atmospheric demand. The stomata conductance
701 was smaller and decreased at more negative leaf water potentials in stony soil than in silty soil. The leaf
702 water potentials are affected by the soil-plant hydraulic conductance. In addition to stomatal regulation,
703 leaf growth and plant size adjustments are important to regulate the transpiration and water use efficiency
704 in the same year.

705 The lowest soil-plant hydraulic conductance was observed in the stony soil with severe drought stress as
706 compared to silty soil while its variation depends also on the soil water variation (before and after
707 irrigation). Root system and soil-plant hydraulic conductance depended strongly on soil hydraulic
708 properties. ~~In the stony soil, which has a considerably smaller water holding capacity than the silty soil,
709 root length was considerably smaller than in the silty soil. Nevertheless water uptake per unit root length
710 was much larger than in the fine soil. This also means that the hydraulic conductance per unit root length
711 must have been much larger in the stony soil than in the fine soil. Cai et al., (2018) observed a similar effect
712 for winter wheat but they found much smaller differences in the root length normalized root conductance.
713 The higher root length normalized root conductance means that the anatomy of the root tissues must
714 have been influenced by the soil texture and compensated the considerably smaller root length in the
715 stony soil. Looking at the effect of water treatments in the silt soil, the non-irrigated plot had more roots
716 than the irrigated one and both had more roots in the year with high VPD. But the soil root conductance
717 was higher in the irrigated plot than in the rainfed plot. This means that in the irrigated plot, the soil root
718 conductance per unit root length was higher than in the rainfed plot. This could either be due to wetter
719 soil conditions and higher soil conductance or it could be due to a larger conductance of the root tissues.
720 Especially in 2017 when the silty soil was wetter, the slightly larger soil root conductance in the irrigated
721 plot is most likely the result of larger root tissue conductance in the irrigated plot. Thus, how root
722 architecture (here represented simply by the total root length) and root tissue conductivities 'respond' to
723 drought stress might be opposite depending on the comparisons that are made. When the stony soil and
724 silt soil are compared, the higher 'stress' due to lower water availability in the stony soil resulted in less
725 roots with a higher root tissue conductance in the soil with more stress. When comparing the rainfed with
726 the irrigated plot in the silty soil, the higher stress in the rainfed soil resulted in more roots with a lower
727 root tissue conductance in the treatment with more stress. This illustrates that t~~The 'response' to stress
728 can be completely opposite depending on conditions or treatments that lead to the differences in stress
729 that are compared. Therefore, it cannot be the 'stress' alone that defines how a plant will react and adapt

730 its root system. Modelling the impact of stress and the feedback between drought stress and plant
 731 development is likely controlled by other properties or parameters that change with changing soil water
 732 availability and atmospheric water demand then the plant stress level. ~~Results from this study show that
 733 soil crop models should focus not only on simulating stomatal regulations to capture the response to
 734 drought stress, but also require adequate representations of leaf growth and adjustments.~~

735 **Acknowledgements**

736 This work has partially been funded by Federal Ministry of Education and Research (BMBF) through
 737 European SUSCAP project – 031B0170B and COINS project [- 01LL2204C](#) and the Deutsche
 738 Forschungsgemeinschaft (DFG, German Research Foundation) under Germany’s Excellence Strategy – EXC
 739 2070 – 390732324². We acknowledge the support by the SFB/TR32 “Pattern in Soil–Vegetation–
 740 Atmosphere Systems: Monitoring, Modelling, and Data Assimilation” funded by the Deutsche
 741 Forschungsgemeinschaft (DFG). Thuy Nguyen and Thomas Gaiser also thank the DETECT – CRC 1502
 742 research program which is funded by DFG. We thank Dr. Matthias Langensiepen for his supports and
 743 technical help in the TR32 project. We would like to thank all the student assistants and technicians for
 744 their considerable efforts to collect the data in the field and the laboratories.

745

746 **List of Tables**

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

| Soil types | 2017 | | | | 2018 | | | |
|------------------------------------|--------------|----------------|--------------|----------------|--------------|----------------|--------------|----------------|
| | 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 ₂ O ₅ 07/06: 80 kg N + 40 kg K ₂ O | | | | 05/22: 100 kg N 05/30: 40 kg P ₂ O ₅ + 40 kg K ₂ O 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 | | | |

748 Notes: † from sowing to harvest; * for rainfall for whole growing season;

749

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968 **Author contribution**

- 969 Huu Thuy Nguyen, Thomas Gaiser, Jan Vanderborght, and Frank Ewert: Conceptualization; Huu Thuy
970 Nguyen, and Hubert Hüging: Data curation and data quality check (aboveground measurements); Lena
971 Lärm, Felix Bauer, Anja Klotzsche, Jan Vanderborght, and Andrea Schnepf: data curation and data quality
972 check (belowground measurements); Huu Thuy Nguyen: Formal data analysis and visualization; Thomas

973 Gaiser, Jan Vanderborght, Andrea Schnepf, and Frank Ewert: Funding acquisition & Project administration;
974 Huu Thuy Nguyen: writing – original draft; all authors: review, editing, and finalizing the manuscript.

975 **Competing interests**

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

979 **Code/Data availability**

980 The meteorological data were collected from a weather station in Selhausen (Germany) which belongs to
981 the TERENO network of terrestrial observatories. Weather data are freely available from the TERENO data
982 portal (<https://www.tereno.net/ddp/dispatch?searchparams=freetext-Selhausen>, last access:
983 October 2020) (TERENO, 2020). The data which were obtained from the minirhizotron facilities (under-
984 and aboveground) are publicly available from the corresponding author on reasonable requests in Lärm et
985 al., (2023) and in Nguyen et al., (2024), respectively.

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