Plant Soil
https://doi.org/10.1007/s11104-022-05818-2

RESEARCH ARTICLE

Transpiration response to soil drying and vapor pressure deficit is soil texture specific

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Received: 22 September 2022 / Accepted: 23 November 2022

Abstract

Aims Although soil water deficit is the primary constraint on transpiration globally, the mechanisms by which soil drying and soil properties impact transpiration and stomatal regulation remain elusive. This work aimed to investigate how soil textures and vapor pressure deficit (VPD) impact the relationship between transpiration rate, canopy conductance, and leaf water potential of maize (*Zea mays* L.) during soil drying. We hypothesize that the decrease in soil–plant hydraulic conductance (K_{sp}) triggers stomatal closure and the latter is soil specific.

Methods Plants were grown in two contrasting soil textures (sand and loam) and exposed to two consecutive VPD levels (1.8 and 2.8 kPa). We measured transpiration rate, canopy conductance, soil and leaf water potentials during soil drying.

Results Transpiration rate decreased at higher soil matric potential in sand than in loam at both VPD levels. In sand, high VPD generated a steeper drop in canopy conductance with decreasing leaf water potential. The decrease in canopy conductance was well correlated with the drop in K_{sp}, which was significantly affected by soil texture.

Conclusions Our results demonstrated that variations in canopy conductance were not simply a function of leaf water potential but largely affected by soil hydraulics. These results reinforce a model of stomatal closure

Responsible Editor: Janusz J. Zwiazek.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-022-05818-2.

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Published online: 28 November 2022

driven by a loss in soil hydraulic conductivity. Further studies will determine if soil-specific stomatal regulation exists among species.

Keywords Canopy conductance · Drought · Leaf water potential · Maize · Soil–plant hydraulic conductance · Stomatal regulation · VPD

Introduction

Low water availability in the soil and high vapor pressure deficit (VPD) in the atmosphere are the two primary drivers of water stress. Water stress, especially due to soil drying (Liu et al. 2020a), is a ubiquitous and unavoidable problem in agriculture worldwide. It is one of the main causes of impairment of plant development and substantial declines in crop production (Santini et al. 2022). In the future, the negative effect of water stress could be exacerbated by projected drought events (Dai 2013; Ben-Ari et al. 2018). Although numerous studies have investigated the mechanisms of plant responses to water stress during the last few decades, our understanding of how plants respond to soil and atmospheric drought is, as yet, incomplete (Bray 1997; Chaves et al. 2003; Osakabe et al. 2014; Lamers et al. 2020; Lynch 2022).

Plants regulate stomatal opening to varying VPD so that water transport from soil matches the hydraulics of the soil–plant system (Attia et al. 2015; Ranawana et al. 2021). When VPD is high, stomata partially close to counteract the high water demand and avoid excess water loss through limiting transpiration at the cost of reduced gas exchange (Oren et al. 1999; Lendzion and Leuschner 2008; McAdam and Brodribb 2015; Sinclair et al. 2017; Grossiord et al. 2020a). On the other hand, soil water potential (mainly matric potential) and soil hydraulic conductivity determine the water supply to the root system, and it is well documented that a decrease in soil matric potential triggers stomatal closure and thus results in reduction in transpiration rate (Gardner 1960; Passioura 1980; Sinclair and Ludlow 1986; Ray and Sinclair 1997; Carminati and Javaux 2020; Abdalla et al. 2021). However, disentangling the effect of these two factors is challenging because both soil moisture (Liu et al. 2020a) and rising VPD (Sulman et al. 2016; Novick et al. 2016; Kimm et al. 2020) have been identified as the dominant factor affecting transpiration at local or global scales. Hydraulic frameworks allow one to mechanistically link soil water availability and transpiration demand to leaf water potential and thus identify the key limits to transpiration (Gollan et al. 1985, 1989; Sperry et al. 2002; Sperry and Love 2015; Carminati and Javaux 2020).

In wet soils, the soil hydraulic conductivity is much higher than that of roots, and water flow is mainly controlled by root hydraulic conductivity (Passioura 1980; Hopmans and Bristow 2002; Draye et al. 2010; Cai et al. 2022). As the soil dries, its conductivity drops by a few orders of magnitude, thereby limiting the water flow towards the root surface (Gardner 1960; Passioura 1988), and hence the maximum transpiration could not be maintained and decreases continuously (Fig. 1A) (Sinclair and Ludlow 1986; Ray and Sinclair 1997). Plant response to soil drying can be described and predicted through the relationships between transpiration rate, soil matric potential, and leaf water potential (Sperry et al. 2002; Sperry and Love 2015). Carminati and Javaux (2020) used a soil–plant hydraulic model to propose that, during drought, the loss in soil hydraulic conductivity, especially at the root-soil interface, is the primary trigger for stomatal closure. The rationale is that, at a given soil matric potential, stomata would close when the relationship between transpiration and leaf water potential becomes nonlinear (Fig. 1A inset, leaf view). This concept was empirically tested in a series of experiments with different species (Hayat et al. 2020; Abdalla et al. 2021, 2022; Cai et al. 2021). Following the model rationale, plants exposed to a relatively high VPD would decrease transpiration at less negative soil matric potential compared to plants exposed to a relatively low VPD (Fig. 1A). This earlier drop at a high VPD was recently reported in tomato (Li and Liu 2022) and potato plants (Liu et al. 2022). When transpiration rate is normalized by leaf area and VPD, it represents stomatal conductance at plant scale, i.e., canopy conductance (Jarvis and McNaughton 1986). We hypothesize that variations in canopy conductance follow stomatal conductance. During soil drying, plants regulate stomata and canopy conductance would decrease earlier and faster at high VPD (Fig. 1B).

Soil texture determines soil hydraulic properties, which is expected to affect plant hydraulics and thus plant response to drought (Sinclair 2005; Draye et al. 2010; Dodd et al. 2010; Javaux and Carminati 2021; Cai

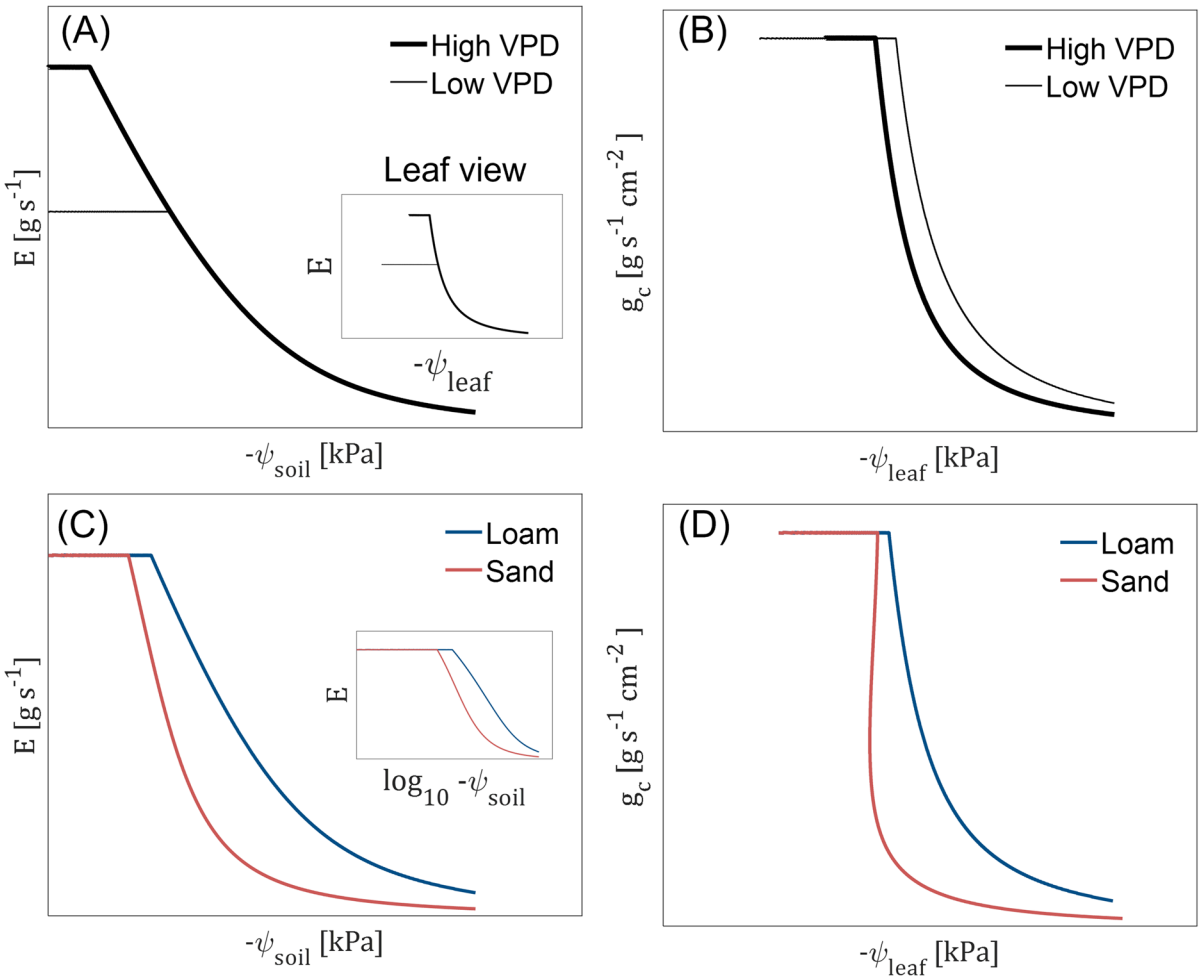

Fig. 1 Hypothetical effects of vapor pressure deficit (VPD) and soil texture on transpiration rate (E) and canopy conductance (g_c) during soil drying. The curves were generated using a soil–plant hydraulic model (Carminati and Javaux 2020) and data based on our recently published work (Abdalla et al. 2021; Cai et al. 2021). **A** Relationship between transpiration rate and soil matric potential (ψ_{soil}) at high and low VPD. The inset shows the leaf perspective, the relationship between transpiration rate and leaf water potential at high and low VPD during soil drying. **B** Relationship between g_c and leaf water potential (ψ_{leaf}) at high and low VPD. **C** Relationship between E and ψ_{soil} in sand and loam. The inset shows the same relationship but with a logarithm of the x-axis. **D** Relationship between g_c and ψ_{leaf} in sand and loam. In (**A**) and (**B**), the difference between the two curves results from the maximum transpiration rate, while in (**C**) and (**D**) it results from the soil hydraulic properties

et al. 2021, 2022). Cai et al. (2021, 2022) showed that, during soil drying, the loss in soil hydraulic conductivity leads to a steep, nonlinear drop in soil matric potential at the root-soil interface, and this drop was greater in sand than in loam. Therefore, we hypothesize that transpiration rate decreases more rapidly with decreasing leaf water potential, as well as with decreasing soil matric potential in sandy than in loamy soils (Fig. 1C). In other words, we hypothesize that transpiration response to drought is texture specific. We further hypothesize that the decline in canopy conductance, as a function of leaf water potential, is more prominent in coarser-textured soils, e.g., sand (Fig. 1D). Thus, the objective of this study is to explore plant response (including transpiration and canopy conductance) to increasing VPD and decreasing soil water content under two contrasting soil textures (sandy vs. loamy soils) from a hydraulic perspective.

We monitored transpiration rate, canopy conductance, and leaf water potential of maize (*Zea mays* L.) grown in sandy and loamy soils (refer to sand and loam for short in the following text). The plants were subjected to two consecutive VPD levels (1.8 and 2.8 kPa) during soil drying. We estimated the soil–plant hydraulic conductance from the relationship between transpiration rate and leaf water potential. The latter was compared with canopy conductance in both soils during soil drying.

Materials and methods

Plant growth and soil condition

The inbred line B73 of maize was used in this study (Hochholdinger et al. 2008). The seeds were germinated on saturated filter papers in darkness after being sterilized with 10% H_2O_2 for 10 min and in saturated $CaSO_4$ solution for three hours. Two days later, the seeds were sown in acrylic glass columns (7 cm in diameter, 25 cm in height) at 1-cm depth. The columns were filled with two contrasting soil textures: sand and loam, with a bulk density of 1.28 and 1.23 g cm^{-3}, respectively. The loamy substrate (Haplic Phaeozem) was collected in Schladebach, Germany. The sandy substrate was a mixture of 16.7% of the loamy soil by weight with quartz sand. The hydraulic properties of these two soils were reported by Vetterlein et al. (2021). The soil water retention and hydraulic conductivity curves for both soils are shown in Fig. 2.

Before being placed into the columns, the two soils were passed through a 1-mm sieve and mixed with nutrients (Table S1). The columns were covered with a layer of plastic beads (diameter: 3.5 mm) on the top to avoid evaporation, and the column walls were covered by an opaque sheath. Three 5-mm holes were made at 5-cm intervals along the column walls to enable soil moisture measurements.

Nine plants were grown in each soil in a walk-in climate chamber (ThermoTEC Weilburg GmbH & Co. KG, Weilburg, Germany). In the nighttime, plants were exposed to a temperature of 18.5 °C and relative humidity (RH) of 78% for eight hours. In the daytime, the plants were exposed to two consecutive VPD levels. The lower VPD (1.8 kPa) was set at

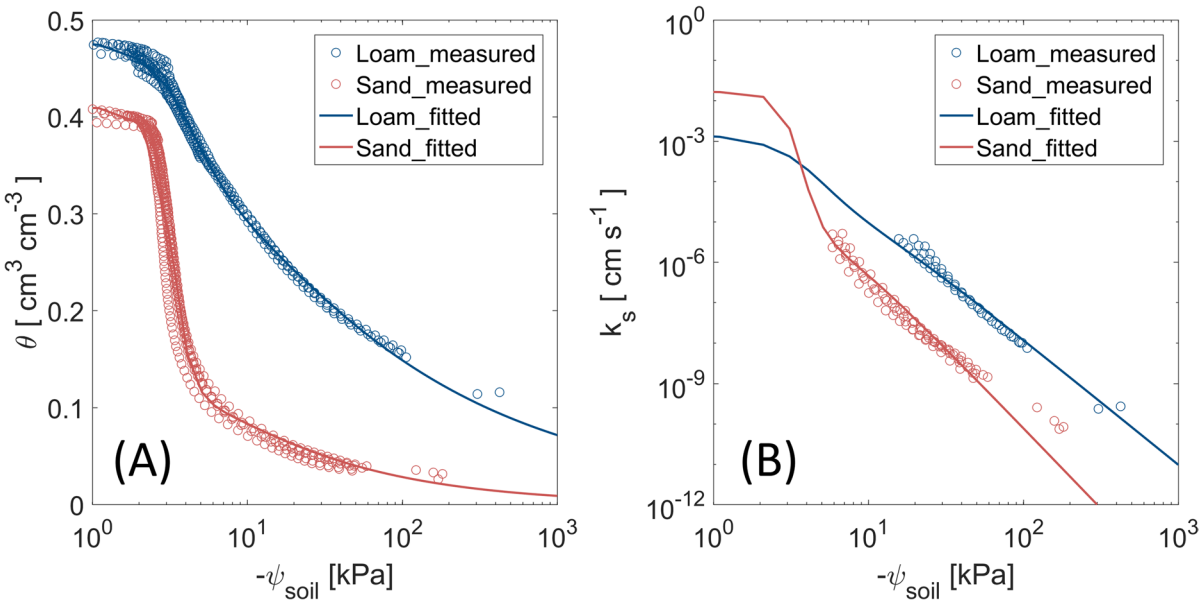

Fig. 2 Soil hydraulic properties of the two tested soils (sand and loam). **A** Soil water retention curves. **B** soil hydraulic conductivity curves. The curves were determined using a Hyprop apparatus (UMS GmbH, Munich, Germany) and the bimodal Mualem-van Genuchten model. The data are from Vetterlein et al. (2021). θ: soil water content, ψ_{soil}: soil matric potential, k_s: soil hydraulic conductivity. Statistics in (**A**): loam, $r^2 = 0.996$, root mean square error (RMSE) = 0.007; sand, $r^2 = 0.976$, RMSE = 0.019. Statistics in (**B**): loam, $r^2 = 0.937$, RSME = 0.347; sand, $r^2 = 0.751$, RMSE = 0. 002

29.5 °C and RH of 50% for 6.5 h, while the higher VPD (2.8 kPa) was set at 33.5 °C and RH of 40% for 6 h. Both VPD levels were set with an identical light intensity of 1100 µmol m^{-2} s^{-1}. VPD higher than 3 kPa is not considered in our study because high VPD is expected to induce stomatal closure and reduce transpiration rate (Kholová et al. 2010; Vadez et al. 2013; Devi et al. 2015; Medina et al. 2019). These two diurnal VPD levels are expected to induce a low and moderate atmospheric drought condition. Additionally, under these two diurnal VPD levels, plants are expected to have two transpiration levels and different leaf water potentials. The buffer time to raise VPD from the predawn condition was one and half hours. A one-hour interval was used to change the conditions between the two VPD levels and from the high VPD level to the nighttime condition thus allow plants to acclimate. The temperature and RH inside the chamber were monitored at canopy height every 10 min using a thermo-hygrometer (EL-USB-1, Lascar electronics, UK). The columns were watered every two to three days to maintain a soil water content of around 0.2 cm^3 cm^{-3} in sand and loam during the first 18 days.

Soil and plant measurements

Given the column volume (0.962 L) and to avoid having big plants (thus large leaves) that would result in rapid soil drying, plant and soil measurements started 18 days after sowing (DAS) in loam and 24 DAS in sand. During this growth stage, four leaves unfolded and adventitious roots were initiated (Cai et al. 2021). All measurements lasted around two weeks. Volumetric soil water content was measured daily using time domain reflectometer (TDR) (Easy Test, Poland) at predawn (i.e., before turning on lights). Soil matric potential (ψ_{soil}, kPa) and soil hydraulic conductivity (cm s^{-1}) were obtained from measured soil water content and soil water retention curves (Fig. 2). One day before the start of the measurements, plants were irrigated at the bottom of the columns. The columns were allowed to drip overnight (until no excess water was apparent at the bottom of the columns). The columns were then placed on balances (Platform Wägezelle H10A, Bosche, Germany, 8000 g×0.01 g) to monitor transpiration rate (E, g s^{-1}) every 10 min. Transpiration rate was calculated by the weight changes of the columns after each VPD level had stabilized (around 1.5 h after changing temperature and humidity). In the test, we observed that transpiration rate could be maintained at a constant level after each buffer time between different VPD levels (Figure S1). In this study, we did not measure stomatal conductance directly. Instead, we calculated stomatal conductance at the canopy level, canopy conductance, g_c (g s^{-1} cm^{-2}), which was determined according to Jarvis and McNaughton, 1986:

$$g_c = E_{norm} \times \frac{p_{atm}}{VPD} \quad (1)$$

where E_{norm} is E normalized by leaf area, and p_{atm} = 101.325 kPa. Leaf area was determined daily after the plant and soil measurements started by measuring leaves' length and width (McKee 1964; van Oosterom et al. 2001): LA = 0.7 ∑(length × width).

We measured leaf water potential (ψ_{leaf}, kPa) at predawn (defined as ψ_{leaf_PD}) and during two levels of VPD daily using a Scholander pressure bomb (model 3115, Soil Moisture Equipment Corp., US) (Scholander et al. 1965). As this is a destructive method, ψ_{leaf} was measured randomly on healthy excised leaves among the replicated plants to preserve leaf area. Three to four leaf samples were taken in each soil four hours after changing the VPD levels. Soil–plant hydraulic conductance (K_{sp}, g s^{-1} kPa^{-1}) was estimated from the measurements of E, ψ_{leaf_PD}, and ψ_{leaf} by:

$$K_{sp} = E/(\psi_{leaf\_PD} - \psi_{leaf}) \quad (2)$$

ψ_{leaf_PD} was used in Eq. 2 since the transpiration rate measured at predawn was minimum (close to 0).

Statistical analysis and fitting relations between parameters

Different nonlinear functions were used to describe the relationships between measured variables, which depend on the trends of the variables. The relationship between E and soil water content (θ) was fitted using a sigmoid function according to Muchow and Sinclair (1991):

$$E = \frac{c}{1 + a \times \exp(-b\theta)} \quad (3)$$

where a, b and c are fitting parameters. Additionally, we fitted the relation between E and ψ_{soil} with a modified sigmoid function as follows:

$$E = \frac{c}{1 + \exp(\frac{\psi_{soil}+a}{b})} \quad (4)$$

To avoid the impact of the difference in leaf area on E, we used E normalized leaf area (E_{norm}) instead of E in the fitting.

The relation between g_c and ψ_{leaf} was fitted according to Anderegg et al. (2017):

$$g_c = g_{c\_max} \times \exp(-(\frac{-\psi_{leaf}}{c})^{b}) \quad (5)$$

g_{c_max} is the maximum canopy conductance, b and c are fitting parameters. Note that the fitting parameters (a, b, and c) are dependent on the observed data and selected function in all the above equations. This function was also used to describe the relation between soil–plant hydraulic conductance and soil hydraulic conductivity and the relation between soil–plant hydraulic conductance and canopy conductance. However, the latter uses fitting parameter a instead of g_{c_max}. Equation 4 was also used to describe the relation between soil–plant hydraulic conductance and ψ_{soil}.

The impact of different factors (i.e., soil moisture, VPD, and soil texture) on plant growth, transpiration rate, and canopy conductance was evaluated using analysis of variance (ANOVA). We also evaluated the significance of the difference for the relationship of $E_{norm}(\psi_{soil})$, $E(\psi_{leaf})$, and $K_{sp}(\psi_{soil})$ between the two VPD levels and soil types using the analysis of covariance (ANCOVA). To do this analysis, we assumed that the variables above followed rough linear relationships. Statistical significance was justified when the p-value was lower than 0.05.

Results

Variation of transpiration rate at two VPD levels in sand and loam

Given the slight difference in shoot growth between sand and loam (9.1% smaller in loam, but the difference is not significant ($p > 0.05$)), transpiration was normalized by leaf area (E_{norm}) for both VPD levels and soil textures (Fig. 3). The decline in E_{norm} with decreasing soil matric potential (Fig. 3) and soil water content (Figure S2) fits well with the empirical equations, Eq. 4 and 3, for both soils and VPD levels. The reduction of E_{norm} varied between VPD levels and soil textures with decreasing soil matric potential. The $E_{norm}(\psi_{soil})$ relationship was significantly impacted not only by soil type but also by the interaction between soil texture and soil matric potential under both VPD levels (Table 1). When comparing VPD levels, E_{norm} was higher at high VPD but, during soil drying, it was constrained earlier (at less negative soil matric potential) under high VPD in both soil textures (Fig. 3A and B). When comparing soil textures, the decline in E_{norm} was more pronounced in sand than in loam at both VPD levels (Fig. 3C and D). The soil matric potential at the lowest level of E_{norm} was around -200 kPa in loam but around -50 kPa in sand. In loam, E_{norm} declined at around -10 kPa (0.3 cm^3 cm^{-3}, see Figure S2) at high VPD and around -50 kPa (0.2 cm^3 cm^{-3}) at low VPD. In sand, those matric potentials were around -4 kPa (0.2 cm^3 cm^{-3}) and -4.5 kPa (0.15 cm^3 cm^{-3}) at high and low VPD, respectively.

When comparing E_{norm} at the two VPD levels for different soil moisture levels, the reduction in E_{norm} at high VPD was more evident (Figure S3). Soil moisture and VPD showed a significant ($p < 0.001$) effect on E_{norm} (Table S2). The effect of soil moisture on E_{norm} interacted strongly ($p < 0.001$) with both soil types and VPD levels. This interaction has two implications: Firstly, in each soil type, E_{norm} differed across VPD levels; Secondly, the impact of VPD varied for different soil moisture levels. However, there was no significant interaction between soil type and VPD (Table S2), and hence VPD had a similar effect on E_{norm} in each soil texture.

Relation between canopy conductance and leaf water potential

Variations of canopy conductance and ψ_{leaf} at both VPD levels and soils during soil drying were well described by the empirical function (Eq. 5). In wet soils, canopy conductance was slightly higher at high VPD and did not differ between sand and loam (Fig. 4A and B). As the soil dried, canopy conductance dropped continuously with decreasing ψ_{leaf} but with a steeper slope at high VPD compared to low VPD in both soils. This was also supported by the comparison between the regression slopes (Table 1). When comparing the difference between the two soil

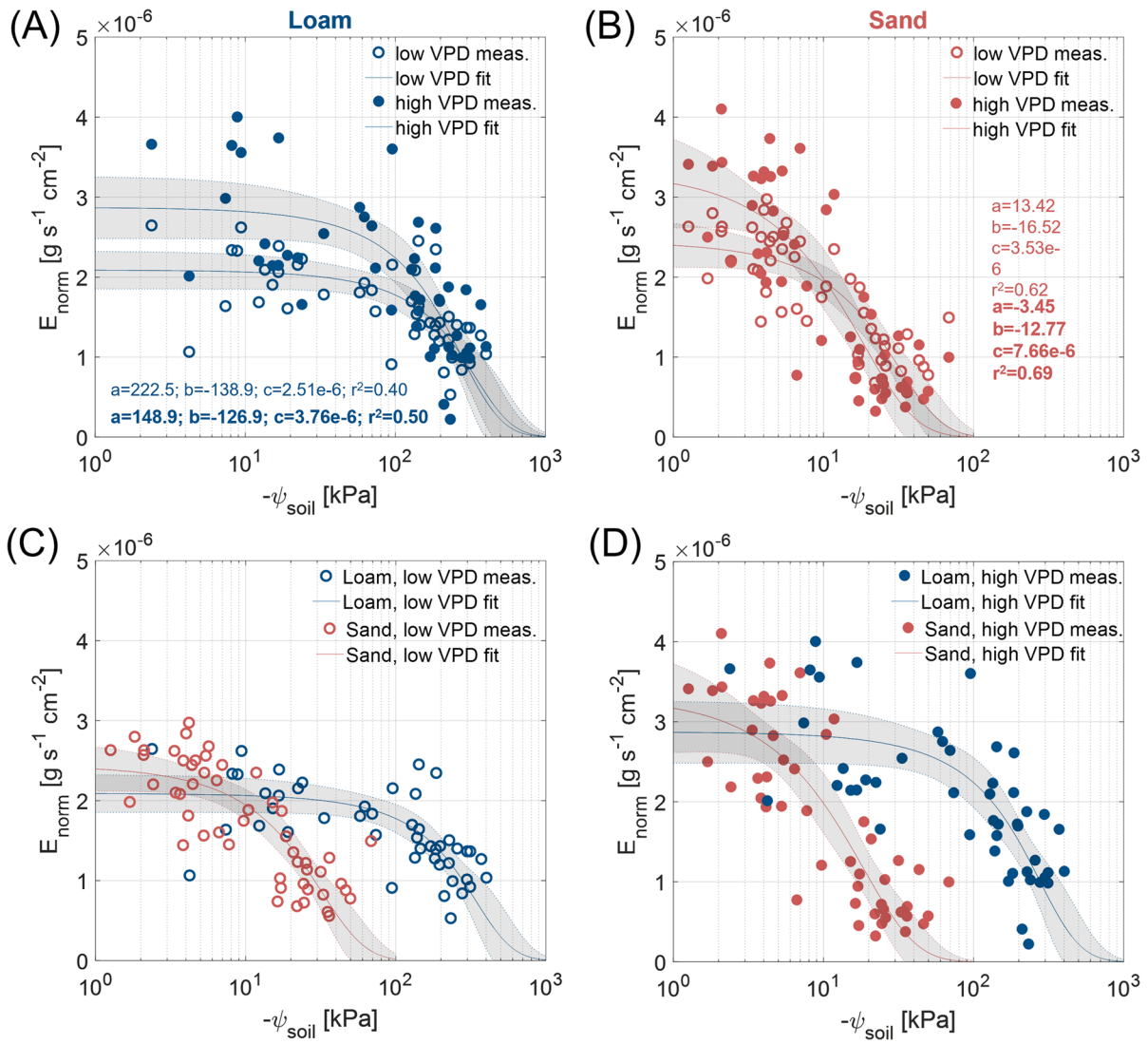

Fig. 3 Relationship between normalized transpiration rate (E_{norm}) and soil matric potential (ψ_{soil}) at low and high VPD levels. **A**, **B** The $E_{norm}(\psi_{soil})$ relationship in loam and in sand, respectively. **C**, **D** Comparison of the $E_{norm}(\psi_{soil})$ relationship between sand and loam at low and high VPD, respectively. The fitted parameters (a, b, and c) and fitting coefficient ($r.^2$) for each VPD level and soil texture are presented in the plots. The normal and bold font sizes are for low and high VPD, respectively. The gray areas are 95% functional prediction intervals. meas.: measured, fit: fitted. Data point N = 48 and 53 for loam and sand. Data shown in (**C**) and (**D**) are from (**A**) and (**B**)

textures, the reduction in canopy conductance over ψ_{leaf} was slightly steeper in sand compared to loam at low VPD (Fig. 4C), and this difference is more prominent at high VPD (Fig. 4D; $p < 0.05$, Table 1). The statistical analysis showed that the $g_c(\psi_{leaf})$ relationship was affected by the interaction between soil type and leaf water potential (Table 1). In sand, at both VPD levels, canopy conductance did not decrease with falling ψ_{leaf}, but fluctuated when the values reached a minimum canopy conductance (g_{min}) (Figure S4). Including g_{min}, a significant difference in the relationship of canopy conductance and leaf water potential between the two VPD levels remains in sand (Figure S4), as well as that between sand and loam at high VPD.

Table 1 Analysis of covariance (ANCOVA) for evaluating the difference in regression slopes of the relationship between different variables. ($p < 0.001$***, dark blue cells; $p < 0.01$**, blue cells; $p < 0.05$*, light blue cells)

Relationship	Source	Low VPD	high VPD	Combined VPD
$E_{norm}(\psi_{soil})$	Soil type	0.0043	<<0.001	-
	ψ_{soil}	<<0.001	<<0.001	-
	Soil type * ψ_{soil}	<<0.001	<<0.001	-
$g_c(\psi_{leaf})$	Soil type	0.8104	0.0276	-
	ψ_{leaf}	<<0.001	<<0.001	-
	Soil type *ψ_{leaf}	0.0179	0.0065	-
$K_{sp}(\psi_{soil})$	Soil type	0.8928	0.3832	0.4065
	ψ_{soil}	0.0929	0.076	0.0075
	Soil type * ψ_{soil}	0.0267	0.0703	0.002

Variations in soil–plant hydraulic conductance

Variation of transpiration rate (E) and leaf water potential (ψ_{leaf}), during soil drying, at both VPD levels and soils is shown in Fig. 5. Transpiration rate was higher at both VPD levels in sand at the beginning of the measurements due to a slightly larger leaf area. The $E(\psi_{leaf})$ relationship gives the soil–plant hydraulic conductance (see Eq. 1). In wet soil conditions, ψ_{leaf} decreased linearly with increasing E due to higher VPD in both soils (and the slope is it is equal to the plant conductance). There were no remarkable changes in soil–plant hydraulic conductance when the soil water content was higher than 0.2 $cm^3\ cm^{-3}$ in loam and 0.13 $cm^3\ cm^{-3}$ in sand (Fig. 5). As the soil dried, transpiration rate decreased, and the $E(\psi_{leaf})$ relation deviated continuously from the ones in wet soil conditions. Additionally, compared to sand, the mean ψ_{leaf} was less negative in loam at a similar level of E (both at predawn and both VPD levels). During soil drying, the decline in soil–plant hydraulic conductance between high and low VPD levels did not differ significantly ($p < 0.05$) in either soil. However, the values of soil–plant hydraulic conductance at both VPD levels decreased to around 1/4 of those in loam and 1/5 of those in sand in wet conditions.

Decreasing soil–plant hydraulic conductance during soil drying and relationship between soil–plant hydraulic properties and canopy conductance

In wet soil conditions, soil–plant hydraulic conductance remained fairly constant in both soils (Fig. 6A). During soil drying, soil–plant hydraulic conductance decreased in both soils, with an earlier decline in sand (ψ_{soil} was around -6 kPa in sand, and -150 kPa in loam). The relationship between $K_{sp}(\psi_{soil})$ was not significantly influenced by VPD levels but by the interaction between soil type and soil matric potential (Table 1). In both soils, the variations of soil–plant hydraulic conductance were well described ($r^2 = 0.53$ for sand and loam) by a sigmoid function similar to Eq. 4 (E was replaced with soil–plant hydraulic conductance in the equation). Given the great difference in soil water retention and hydraulic conductivity between the two soils (Fig. 2), the difference in the decline in soil–plant hydraulic conductance would be even larger when translating soil matric potential to soil hydraulic conductivity. In sand, the reduction in soil–plant hydraulic conductance occurred at a soil hydraulic conductivity three orders of magnitude larger than in loam (the red and blue dashed lines in Fig. 6B). However, variations of soil–plant hydraulic conductance at high and low VPD levels were not significantly different ($p > 0.05$), indicating that the decreases of E and ψ_{leaf} were similar at the two VPD levels in sand and loam.

During soil drying, both canopy conductance and soil–plant hydraulic conductance decreased, and the reduction of canopy conductance was steeper in sand when soil–plant hydraulic conductance decreased to around 2.5×10^{-6} g s^{-1} kPa^{-1}. The variation between canopy conductance and soil–plant hydraulic conductance was well ($r^2 = 0.73$ for sand and loam) characterized using an exponential function (Eq. 5) (Fig. 6C). In addition, a significant difference ($p < 0.05$) was identified for the relation of canopy conductance and soil–plant hydraulic conductance between sand and loam when combing the two VPD levels (Fig. 6D). No significant ($p > 0.05$) effect of VPD was identified in the relation between canopy conductance and soil–plant hydraulic conductance.

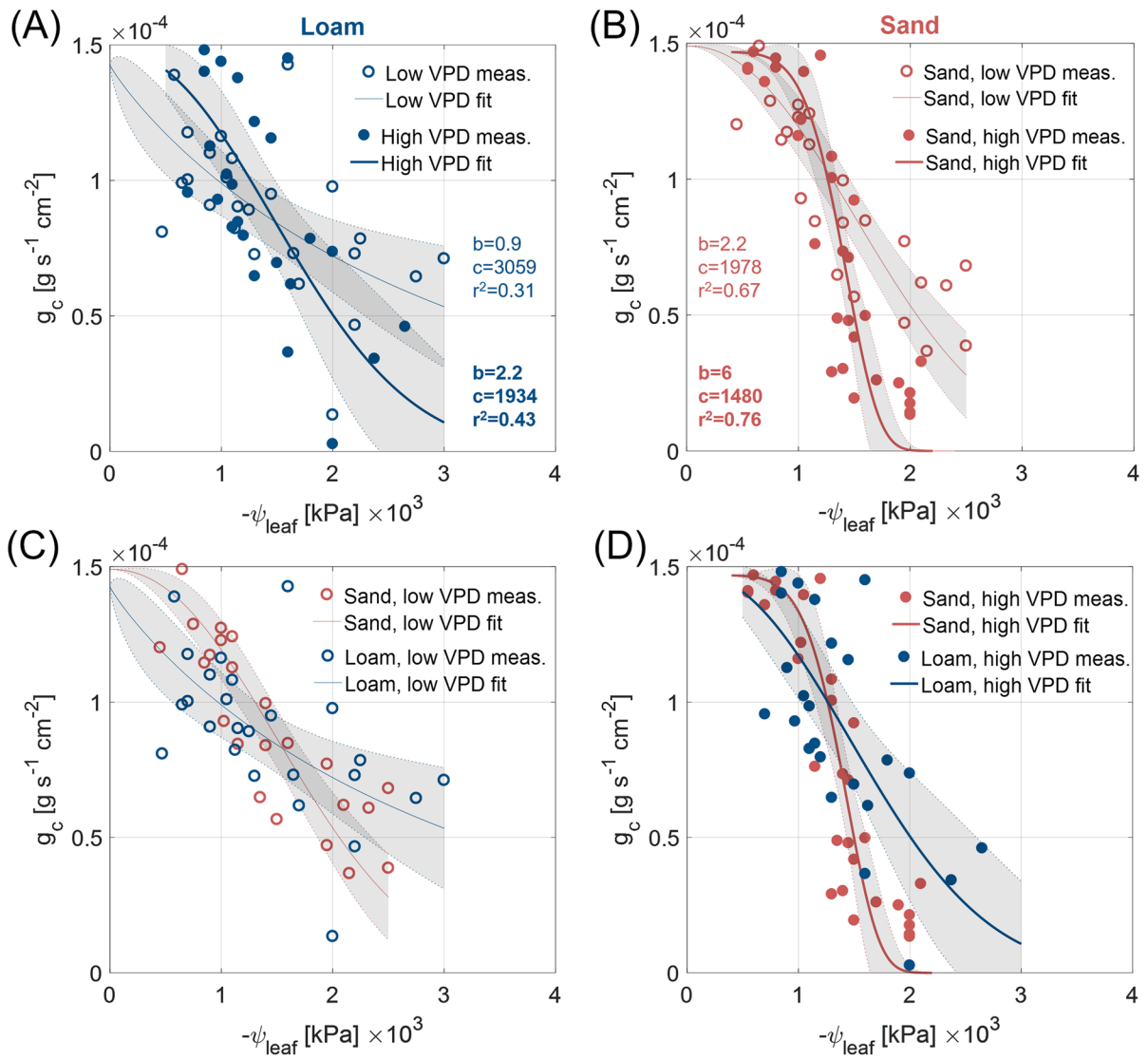

Fig. 4 Relation between canopy conductance (g_c) and leaf water potential (ψ_{leaf}). **A**, **B** The $g_c(\psi_{leaf})$ relation at low and high VPD in sand and loam, respectively. **C**, **D** Comparison of $g_c(\psi_{leaf})$ relation between sand and loam at low and high VPD, respectively. The data and fittings in (**C**) and (**D**) are from (**A**) and (**B**). Note that the data in sand do not include the fraction of g_c not decreasing with reduced ψ_{leaf} (which was considered as minimum leaf conductance g_{min}) at both VPD levels. The data including g_{min} are shown in Figure S4. The $g_c(\psi_{leaf})$ relation was fitted with 95% functional prediction intervals. The fitted parameters (b and c) in Eq. 5 and the fitting coefficient ($r.^2$) for each VPD level and soil texture are presented in the plots. The bold text refers to high VPD. meas.: measured, fit: fitted. Data point N = 27 and 26 for low and high VPD in (**A**), 23 and 30 for low and high VPD in (**B**)

Discussion

We showed that, during soil drying, the decline in transpiration rate at high VPD differed between sand and loam (Fig. 3). Transpiration rate declined at more negative soil matric potential in loam than in sand (Fig. 3). A much steeper drop in canopy conductance was observed in sand compared to loam, especially at high VPD (Fig. 4). Additionally, the decrease in canopy conductance was well correlated with the drop in soil–plant hydraulic conductance in both soils (Fig. 6). We provide the experimental evidence that,

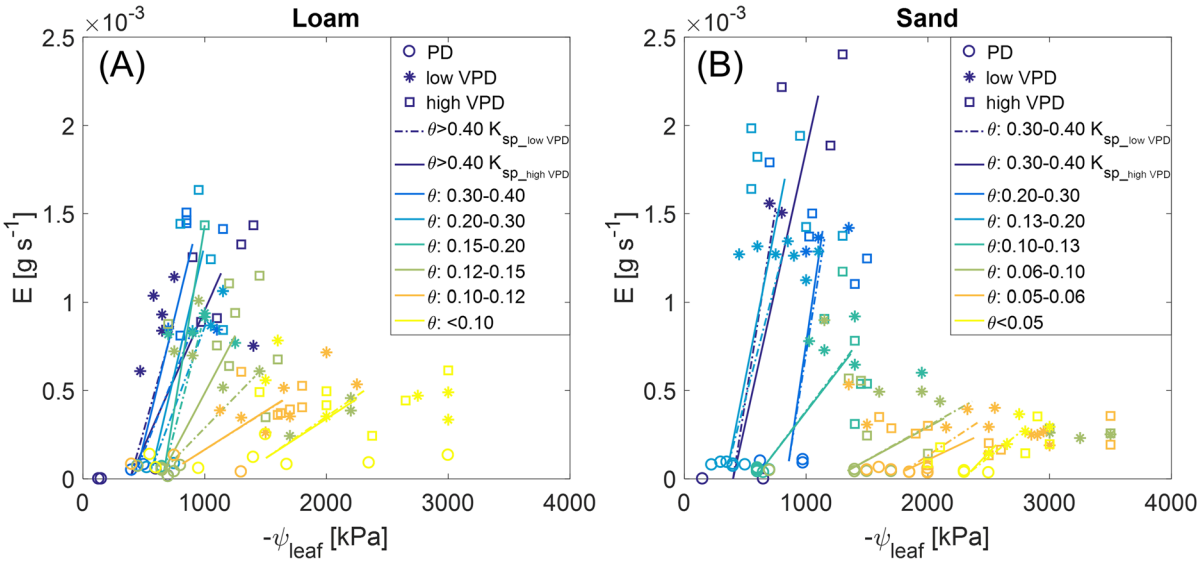

Fig. 5 Relation between transpiration (E) and leaf water potential (ψ_{leaf}) at predawn (PD), low and high VPD levels during soil drying. **A**, **B** The $E(\psi_{leaf})$ relation in loam and sand at different soil water contents (θ). θ was measured on consecutive days. The legend shows the θ range measured in the replicated columns. The linearly fitted slope of $E(\psi_{leaf})$ relation in (**A**) and (**B**) is the soil–plant hydraulic conductance (K_{sp}). The linear fitting for low VPD (dashed line) and high VPD (solid line) was conducted using the mean E and ψ_{leaf} at each soil moisture. Data point N = 3 ~ 8 for each VPD and soil water content in sand and loam. Uneven replicates were necessary to preserve as much leaf area as possible

during drought, canopy conductance was not simply a function of leaf water potential but was affected by soil hydraulics (Fig. 4) in a predictable way (see the hypothesis in Fig. 1). The results supported our hypothesis that stomatal regulation varied with varying soil hydraulic properties.

Impact of rising vapor pressure deficit and soil drying on transpiration

Both VPD and soil drying reduce transpiration rate. Similar to previous findings in trees (Will et al. 2013; Flo et al. 2021) and maize (Ray et al. 2002), we observed a more prominent decrease in transpiration rate at higher VPD than at lower VPD (Fig. 3). Moreover, we found that the reduction in transpiration rate and canopy conductance occurred earlier at higher VPD, which is in line with the studies on tomato (Liu et al. 2022; Li and Liu 2022) and potato (Zhang et al. 2022). In this study, we explained the different responses to VPD during soil drying using soil–plant hydraulics. According to soil–plant hydraulic models (Sperry and Love 2015; Carminati and Javaux 2020), plants exposed to relatively high evaporation demand would experience a higher loss in water potential at the soil-root interface and hence a lower (more negative) leaf water potential during soil drying. Thus, the relation between transpiration and leaf water potential of those plants becomes nonlinear at less negative soil matric potential. On the other hand, for plants exposed to a relatively low evaporation demand, the drop in leaf water potential and the reduction in transpiration will occur at a more negative soil matric potential (Fig. 1A).

Ray et al. (2002) showed a linear relationship between transpiration rate and VPD in wet and dry conditions. However, we did not observe a similar relationship, and the transpiration was even lower at higher VPD when soil water content decreased to 0.13 cm^3 cm^{-3} in sand (Figure S3). This apparent contradiction could be due to the difference in soil textures (sandy loam in the above study; see discussion below) and varieties (hybrid in the above study; inbred in our study) (Kholová et al. 2010; Schoppach and Sadok 2012; Gholipoor et al. 2013; Devi and Reddy 2018).

Our analysis showed that the effects of VPD and soil drying, and their interaction on transpiration,

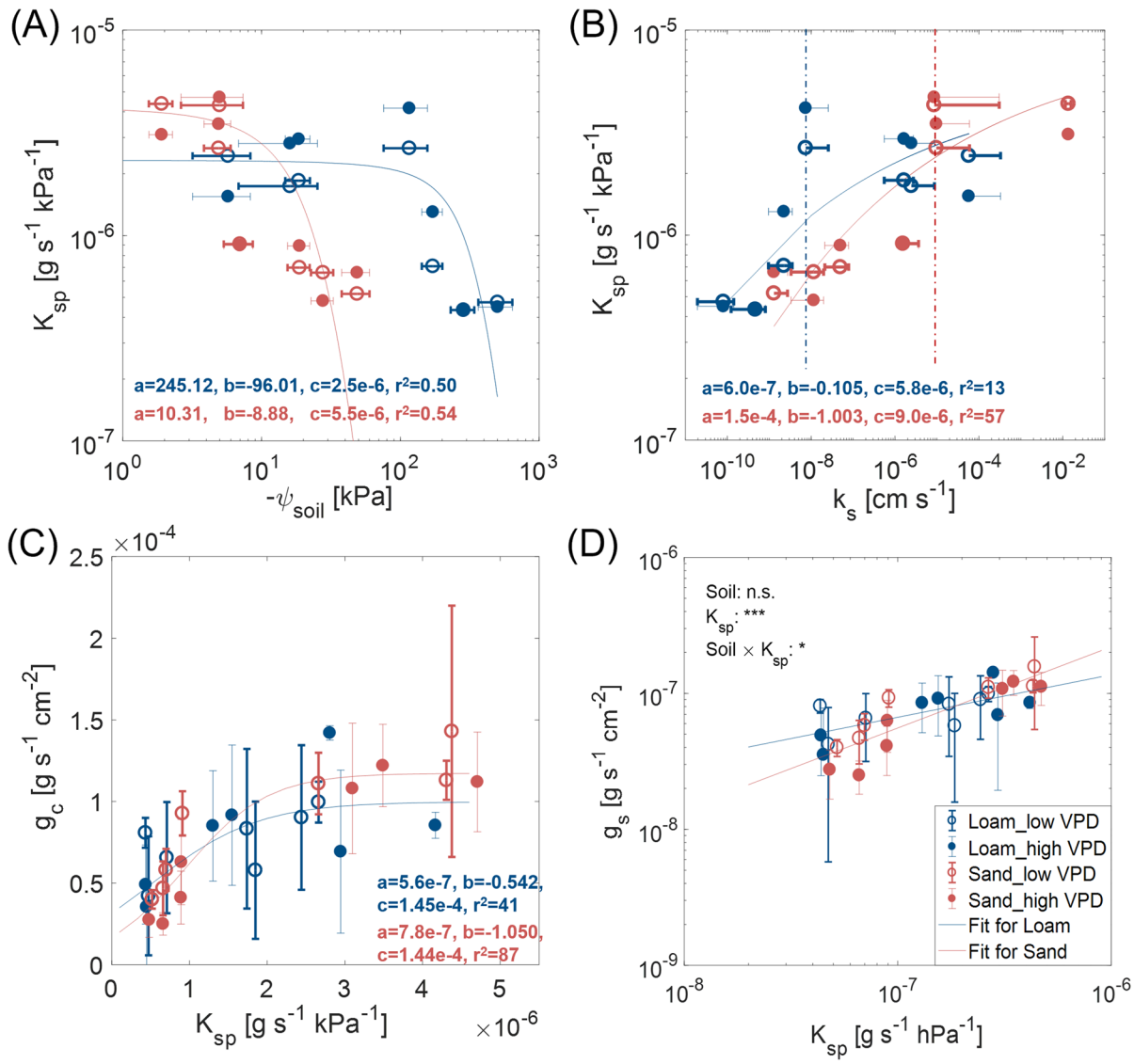

Fig. 6 Relation between soil and plant hydraulic properties and canopy conductance (g_c). **A** Soil–plant hydraulic conductance (K_{sp}) and soil matric potential (ψ_{soil}) at low and high VPD levels in sand and loam. **B** K_{sp} and soil hydraulic conductivity (k_s) in sand and loam. The two vertical dashed lines show the highest K_{sp} before declining with decreasing k_s. **C** Canopy conductance (g_c) and K_{sp} in sand and loam. The standard deviation of K_{sp} is not shown due to inconsistent measurements of ψ_{leaf} at predawn and two VPD levels from each plant. This was to conserve leaf tissue throughout the duration of the experiment, given the repeated destructive sampling required for Scholander bomb measurements. Therefore, the fitting was performed without showing the confidence interval. **D** The same data as (**C**) but with a logarithmic scale. The linear fitting was to compare the difference of g_c-K_{sp} relations between sand and loam. The significance of the impact of soil texture, K_{sp}, and the interaction between them (i.e., Soil × K_{sp}) on g_c was justified using the analysis of covariance (ANCOVA) for sand and loam. n.s.: not significant

were significant (Table 1, and S2). During soil drying, the larger reduction in transpiration rate (Fig. 3 and Figure S3) and canopy conductance (Fig. 4) at higher VPD implies that plant water use is more sensitive to the changes in VPD (especially at the higher level). Disentangling these two factors has been investigated in different species. Previous studies on trees and crops suggest that rising VPD showed a greater

effect on transpiration and canopy conductance than decreasing soil water content, given that the time scale of changing VPD is shorter than that of soil drying (Sulman et al. 2016; Novick et al. 2016; Flo et al. 2021). These results were supported by Kimm et al. (2020), who showed a dominant role of VPD in limiting canopy conductance over soil moisture in two- to ten-year studies of maize and soybean. It is worth noting that the highest VPD in those studies was 4 to 5 kPa (higher than the 2.8 kPa in this study), which may have caused stomatal closure in wet conditions (Fletcher et al. 2007; Gholipoor et al. 2013; Ryan et al. 2016). Note that in the above studies, the effect of soil texture was not considered. During soil drying, the decrease in transpiration rate was shown to be soil texture specific (Koehler et al. 2022). Because the difference in soil texture can result in remarkable variations in soil hydraulic conductivity, soil–plant hydraulic conductance (Cai et al. 2022; Koehler et al. 2022), and stomatal regulation (Carminati and Javaux 2020). Additionally, a recent study showed that longer root systems postponed the impact of soil drying on transpiration rate (Abdalla et al. 2022). Accounting for soil and plant hydraulics will be crucial in exploring the main limiting factor on plant water use under different conditions (Liu et al. 2020b).

Impact of soil hydraulics on plant hydraulics and stomatal regulation

Although there was no difference in E_{norm} between sand and loam in wet conditions, during soil drying, a clear reduction in E_{norm} occurred at both VPD levels, around -95 kPa higher in sand (Fig. 3). This was in line with the results that canopy conductance declined more prominently with decreasing leaf water potential in sand, especially at high VPD (Fig. 4). This is not surprising considering the steep shape of the soil hydraulic conductivity curve of sand (Fig. 2). During soil drying, soil hydraulic conductivity dropped by seven orders of magnitude in sand and by six orders of magnitude in loam (Fig. 2 and Figure S3C). The curves for sandy soil suggest a sharp drop in water potential at the soil-root interface (Dodd et al. 2010), particularly at higher levels of transpiration demand (Cai et al. 2021, 2022). Indeed, this would be in line with the soil–plant hydraulic model, which predicts that stomata close when the water potential around the roots drops more rapidly than the increase in transpiration in drying soil (Carminati and Javaux 2020). In other words, stomatal closure would prevent a further decrease in water potential at the soil-root interface (Carminati et al. 2020; Cai et al. 2021).

In addition, the effect of soil texture on transpiration response to soil drying manifests in the relation between soil–plant hydraulic conductance, soil hydraulic conductivity (Fig. 6B), and canopy conductance (Fig. 6C). The reduction in soil hydraulic conductivity of sand at less negative soil matric potential causes a more rapid decline in soil–plant hydraulic conductance (Fig. 6A), which limits water flow from soil to root, triggering earlier stomatal closure (Fig. 6C) (Carminati and Javaux 2020). Furthermore, there is a good match between the decline in canopy conductance and the drop in soil–plant hydraulic conductance (Fig. 6C). Our results support the soil–plant hydraulic model concept, and also indicate that during soil drying canopy conductance was not simply a function of leaf water potential (Fig. 1).

Stomatal closure was also shown to be closely related to declines in leaf hydraulics (leaf water potential or leaf conductance) (Brodribb and Holbrook 2003; Torres-Ruiz et al. 2015; Scoffoni et al. 2018) or outside-xylem pathways (Scoffoni et al. 2018; Albuquerque et al. 2020). Nevertheless, Corso et al. (2020) found that stomatal closure in wheat was not induced by the decline in leaf hydraulic conductance but might be hastened by a reduction in the whole plant or root hydraulic conductance. Recent studies showed that stomatal closure was triggered by drought-induced changes in belowground hydraulics, e.g., the drop in the hydraulic conductance of roots, soil and/or their interface (Rodriguez-Dominguez and Brodribb 2020; Bourbia et al. 2021; Cai et al. 2021), or decrease in soil–plant hydraulic conductance (Abdalla et al. 2021). Note that we are not identifying the mechanism of stomatal closure in this study, but rather exploring the link between soil–plant hydraulics and stomatal regulation in different soils. Interestingly, in this study, the earlier decrease in canopy conductance indicated that plants closed stomata earlier in sand despite having a higher soil–plant hydraulic conductance in wet conditions (Fig. 6). This is in line with the findings by Cai et al. (2022) who analyzed the relationship between maximum plant hydraulic conductance and critical soil matric potential where stomatal closure was induced across different species and soil textures. The higher soil–plant

hydraulic conductance was related to higher transpiration (Fig. 5), which indicates a larger capacity for water uptake in the root zone. Besides the drop in soil hydraulic conductivity, earlier stomatal closure in plants with higher soil–plant hydraulic conductance might be a conservative strategy to avoid dehydration, which is similar to the hydraulic/stomatal efficiency safety tradeoff (Nardini et al. 2012; Henry et al. 2019; Grossiord et al. 2020b). The generalization of this result needs further investigation with contrasting species grown in different soils.

Impact of vapor pressure deficit on soil–plant hydraulic conductance

Compared to the effect of soil texture, there was no evidence of an effect of VPD on soil–plant hydraulic conductance, nor on the relation between canopy conductance and soil–plant hydraulic conductance (Fig. 6). This is not in line with a recent study in wheat (*Triticum aestivum*) in which plant hydraulic conductance (soil–plant hydraulic conductance in this study) slightly increased with rising VPD, particularly for some genotypes in wet conditions, such that ψ_{leaf} showed a more conspicuous decline with rising VPD (Ranawana et al. 2021). Note that soil–plant hydraulic conductance depends on transpiration rate and leaf water potential at a specific soil matric potential (Eq. 2). In wet soils, the transpiration rate increased with rising VPD, and the corresponding leaf water potential decreased proportionally with transpiration across both VPD levels (Fig. 5). During drought, both transpiration rate and leaf water potential dropped rapidly at both VPD levels (Fig. 5), and the drop in transpiration was larger at high VPD and lower soil matric potential (ca. -20 kPa in sand and -200 kPa in loam, Fig. 3). Similarly, the decrease in canopy conductance with the drop in soil–plant hydraulic conductance was visible only around 0.5×10^{-4} g s^{-1} cm^{-2} (Fig. 6C). Therefore, this difference in canopy conductance and soil–plant hydraulic conductance due to VPD levels was masked by fewer data points in very dry soils. However, more measurements in the drier soils may not help because the canopy conductance reached a minimum and then continued to fluctuate, especially in sand (Figure S4). Higher VPD that constrains transpiration rate under wet or less dry conditions could be useful to disentangle the impact of VPD on soil–plant hydraulic conductance.

Conclusions

In this study we showed that, during soil drying, transpiration rate and canopy conductance dropped at less negative soil matric potential in sand than in loam, particularly at high VPD. The earlier drop in sandy soil is explained by a steeper drop in soil hydraulic conductivity of sand compared to loam. We demonstrated that soil hydraulic properties play an important role in transpiration responses to soil and atmospheric drought. Additionally, in the context of climate change, an increase in global temperature and VPD is likely to happen (Park Williams et al. 2013; Xu et al. 2018; IPCC 2021). Our results showed that rising temperature/VPD caused an earlier reduction in water use in both soils during soil drying. This reduction could suggest positive feedback to increasing temperature/VPD, by adopting a more conservative water use strategy (Ahmed et al. 2018). Earlier stomatal closure prevents further drops in leaf water potential (Carminati et al. 2020), which might also avoid the risk of embolism (hydraulic failure), but at the cost of lower carbon assimilation and lower yields (Hsiao et al. 2019). Taken together, our results demonstrated that variations in canopy conductance were not simply a function of leaf water potential but largely affected by soil hydraulics. Determining how different VPD levels and any associated feedback responses may affect plant growth and productivity of different species over the long term requires additional investigation, with particular attention to different soil textures.

Acknowledgements The authors acknowledge the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) for funding of the priority program 2089, project number 403670197 "*Emerging effects of root hairs and mucilage on plant scale soil water relations*", and the Federal Ministry of Education and Research (BMBF), Project 02WIL1489 (Deutsch-Israelische Wassertechnologie-Kooperation).

Author contributions MAA and AC acquired the funding and conceived the study; MK, MAA, FW and MA conducted the measurements; MK and GC did the data analysis; GC wrote the text with inputs from MAA, AC, and MJ. All authors contributed to editing and revising the manuscript.

Data availability The data presented in this study are available from the first and corresponding authors upon reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Appendix

Parameters and units used in the text, figures, and table:

E: transpiration rate, g s^{-1}
E_{norm}: transpiration rate normalized by leaf area, g s^{-1} cm^{-2}
g_c: canopy conductance, g s^{-1} cm^{-2}
ψ_{soil}: soil matric potential, kPa
ψ_{leaf}: leaf water potential, kPa
ψ_{leaf_PD}: predawn leaf water potential, kPa
k_s, soil hydraulic conductivity, cm s^{-1}
K_{sp}, soil–plant hydraulic conductance, g s^{-1} kPa^{-1}
θ: soil water content, cm^3 cm^{-3}
VPD: vapor pressure deficit, kPa

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