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Research

Drought effects on trait space of winter wheat are independent of land management

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Summary

- Investigating plant responses to climate change is key to develop suitable adaptation strategies. However, whether changes in land management can alleviate increasing drought threats to crops in the future is still unclear.
- We conducted a management × drought experiment with winter wheat (*Triticum aestivum* L.) to study plant water and vegetative traits in response to drought and management (conventional vs organic farming, with intensive vs conservation tillage). Water traits (root water uptake pattern, stem metaxylem area, leaf water potential, stomatal conductance) and vegetative traits (plant height, leaf area, leaf Chl content) were considered simultaneously to characterise the variability of multiple traits in a trait space, using principal component analysis.
- Management could not alleviate the drought impacts on plant water traits as it mainly affected vegetative traits, with yields ultimately being affected by both management and drought. Trait spaces were clearly separated between organic and conventional management as well as between drought and control conditions. Moreover, changes in trait space triggered by management and drought were independent from each other.
- Neither organic management nor conservation tillage eased drought impacts on winter wheat. Thus, our study raised concerns about the effectiveness of these management options as adaptation strategies to climate change.

Introduction

Reduced water availability to crops due to global warming is becoming progressively disturbing (IPCC, 2018, 2019) and highlights the need to better understand crop drought responses. Thus, detailed studies on plant water relations along the soil–plant–atmosphere continuum, from root water uptake, via xylem transport to leaf water use (Donovan & Sperry, 2000), are highly relevant to understand the physiological response of crop plants to water scarcity and safeguard crop growth as well as productivity (Boyer, 1985; Lambers & Oliveira, 2019).

Although aspects of crop water relations have been intensively investigated among species and across climates (Turner, 1997; Sourour *et al.*, 2017), in-depth studies for crops using multiple traits along the soil–plant–atmosphere continuum (SPAC) are scarce, for example as concluded for root water uptake of arable crops by Penna *et al.* (2020). Especially studies addressing a more integrated view on the trait space of plants are lacking, that is studies which combine multiple traits such as root water uptake depths (resource supply), stem length and anatomy (important for plant demand and internal water transport), and foliar ecophysiology (e.g. plant water potentials driving water uptake, leaf stomatal conductance regulating transpiration, leaf area driving water demand, Chl content as proxy for photosynthesis), the latter in turn modulating root water uptake (Schulze *et al.*, 2019).

In order to combine multiple traits in an integrative perspective, the trait space concept has been used on community scale (e.g. Lamanna *et al.*, 2014; Roscher *et al.*, 2018; Ajal *et al.*, 2021) and for species across different ecosystems (e.g. Lamy *et al.*, 2014; Schuldt *et al.*, 2016; Santiago *et al.*, 2018). However, studies on traits in arable crops mainly considered traits of different species or varieties and focused only on growth and yield (e.g. Peltonen-Sainio *et al.*, 2008; Nouri *et al.*, 2011), or on relationships between individual traits, for example hydraulic conductivity in different maize genotypes (Gleason *et al.*, 2019), root water uptake in different wheat genotypes (Nakhforoosh *et al.*, 2021), as well as soil properties and evapotranspiration in tomato (Chen *et al.*, 2015). None of these studies presented a comprehensive assessment of traits along the soil–plant–atmosphere continuum, which is surprising since coupled water–carbon exchange processes underpin plant growth and represent one of the most important links to better understand crop responses to changing climate and agricultural management.

Many benefits of organic as well as conservation tillage strategies for crop management have been reported for different arable cropping systems, such as improved soil physical and chemical properties (e.g. van Eerd *et al.*, 2014; Loaiza Puerta *et al.*, 2018; Colombi *et al.*, 2019) as well as microbial diversity and functionality (e.g. Mader *et al.*, 2002; Fliessbach *et al.*, 2007; Wittwer *et al.*, 2021). These improved soil conditions due to, for example organic management and conservation tillage, are expected to better sustain crop growth and productivity under drought compared to conventional management and intensive tillage (Ding *et al.*, 2009; Knutson *et al.*, 2011). However, respective research on crop performance was often limited to yields (Pittelkow *et al.*, 2015; Lorenz & Lal, 2016), even fewer studies consider changes in plant ecophysiology and growth characteristics. In addition, studies assessing if benefits by changes in crop management can translate into higher crop drought resistance reported inconsistent results, depending on crop species and climate (e.g. Lotter *et al.*, 2003; Pimentel *et al.*, 2005; Kundel *et al.*, 2020; Wittwer *et al.*, 2023). Therefore, our current understanding of crop responses to cropping systems under different water availabilities is still insufficient.

Only a limited number of major arable crops, such as wheat, rice, maize, and barley, feed the world (Khoury *et al.*, 2014). Among these, wheat is the most important source of food calories globally, covering the largest share of global cropland (*c.* 14%; OECD/FAO, 2020). Yet, insight on the simultaneous response of multiple plant traits to drought, a key insight needed for improving agriculture for a future with more frequent and severe drought events, is still widely lacking. This is why we carried out a management × drought experiment with winter wheat (*Triticum aestivum* L.) grown under conventional vs organic management with intensive vs conservation tillage. We aimed to investigate plant water and vegetative traits along the soil–plant–atmosphere continuum and asked (1) how crop management affects plant traits, (2) how drought affects these traits under different cropping systems, and (3) if the trait space changes in response to cropping systems and drought.

Materials and Methods

Research site and drought simulation

This study used a long-term cropping systems experiment, operated by the Swiss Federal Agricultural research station Agroscope and located in Rümlang, near Zurich, Switzerland (47.44°N, 8.53°E). The long-term average annual precipitation for the site is 988 mm, and mean annual temperature is 9.8°C (1989 to 2018; Table 1), based on data obtained from a nearby weather station, Zürich/Kloten (KLO, 47.48°N, 8.54°E, 4.6 km to the north of the research site, MeteoSwiss, 2020). The soil at the field site is a calcareous Cambisol with 23% clay, 34% silt, and 43% sand, and a total soil carbon content of 1.6–1.8% (Loaiza Puerta *et al.*, 2018). The plant available soil depth is 50–70 cm, with solid rock below (Kanton Zürich, 2021).

The Farming Systems and Tillage experiment (FAST) began in 2009 with a typical Swiss crop rotation of 6 yr (for details on setup and crop rotation see Wittwer *et al.*, 2021). Winter wheat (*Triticum aestivum* L. cv 'CH Camedo') was sown on 25 October 2018 on all plots and harvested on 24 July 2019 Supporting Information (Table S1). The experiment includes conventional (C) and organic management (O) with intensive (IT) or soil conservation tillage practices, that is no tillage (NT) and reduced tillage (RT). The conventional systems were managed according to the 'Proof of Ecological Performance' guidelines of the Swiss Federal Office for Agriculture (Swiss Federal Council, 2021). The organic systems were managed under the BioSuisse guidelines, without any use of synthetic fertilisers or pesticides (BioSuisse, 2021). Hence, different fertilisation was applied in conventional and organic systems, while pesticides were only used in conventional systems. Intensive tillage (IT) was applied using a mouldboard plough to 20 cm depth and seedbed preparation was carried out with a rotary harrow to 5 cm depth in both conventional (C-IT) and organic systems (O-IT). Direct sowing and no other soil management was implemented in the conventional no tillage plots (C-NT), whereas superficial noninverting soil tillage to a maximum of 10 cm depth was used for reduced tillage in organically managed plots (O-RT) for weed control. These four cropping systems were repeated in four blocks with a 6 m × 30 m area per cropping system in each block following a Latin-square design. The drought subplots were set up using portable rain shelters made of metal frames (3 m × 5 m at base area and *c.* 2.1 m of height at the highest

Table 1 Precipitation and air temperature close (4.6 km north) to the research site (data from the weather station Zürich/Kloten KLO, 47.48°N, 8.54°E; MeteoSwiss, 2020), as well as dates for the growing season (from sowing to harvest) of winter wheat (*Triticum aestivum* L.) and the treatment periods.

Period	Date	Total precipitation (mm)	Mean air temperature (°C)
Long-term annual (1989–2018)	1 January to 31 December	988	9.8
Annual (2019)	1 January to 31 December	1072	10.5
Growing season	25 October 2018 to 24 July 2019	775	8.6
Before drought treatment	25 October 2018 to 24 April 2019	438	4.9
During drought treatment	25 April to 19 June 2019	229	13.1
After drought treatment	20 June to 24 July 2019	108	21.0

point of the roof) covered with transparent and ultraviolet light-transmissible plastic foil (Gewächshausfolie UV5, 200 µm; Folitec Agrarfolien-Vertriebs, Westerburg, Germany) to simulate an intensive drought period from 24 April to 19 June 2019. The shelters had an opening at both ends, to all sides, and at the top along the full length, which allowed extensive ventilation (for technical details, see Hofer *et al*., 2016). PVC half pipes were used to collect rain running down the foil and to direct it away from the plots. Control subplots received natural precipitation during the entire growing season. In total, 32 experimental subplots (four cropping systems × two water availability treatments × four replicates) were used in the study reported here.

Soil water content

Volumetric soil water content (SWC) at 10 and 40 cm depths was measured continuously with two replicates in all cropping systems (EC-5; Decagon Devices Inc., Pullman, WA, USA), from 15 April (a week before the drought treatment) to 24 July 2019 (the day of harvest). Ten-minute averages were recorded by data loggers (CR1000 and CR216; Campbell Scientific Ltd, Loughborough, UK), then averaged for daily values.

Stable water isotopes

Root water uptake depths were assessed using stable water isotopes in xylem water and soil water from different depths (Ehleringer & Osmond, 1989). Plant and soil samples were collected on 19 April and 14 June 2019, that is before the drought treatment (BT) and at the end of the drought treatment (ET). Root crowns, best representing the xylem water as the mixture of water sources from the soil in herbaceous plants, were collected for stable isotope analysis (Barnard *et al*., 2006; von Freyberg *et al*., 2020). Four to six root crowns were collected and pooled into one sample per subplot, cleaned quickly to remove remaining soil and then immediately sealed in air-tight glass tubes (12-ml exetainer; Labco Ltd, Ceredigion, UK). At the same time, soil cores were sampled close to the sampled plants with a soil auger (1 cm diameter) and separated into six depths, that is 0–5, 5–10, 10–20, 20–30, 30–40, and 40–60 cm, and sealed in air-tight glass tubes (18 ml; Schott AG, Mitterteich, Germany). All root crown and soil samples were kept in a cool box in the field and afterwards stored at −18°C. Extraction of xylem and soil water was carried out with cryogenic vacuum distillation (Ehleringer & Osmond, 1989). The extracted water samples were analysed for stable oxygen isotope ratios ($\delta^{18}O$) with an isotope ratio mass spectrometer (IRMS; DeltaplusXP, Finnigan MAT, Bremen, Germany; Werner *et al*., 1999; Gehre *et al*., 2004). All $\delta^{18}O$ values are expressed in delta notation relative to the Vienna Standard Mean Ocean Water (VSMOW-SLAP, Craig & Gordon, 1965; Gat, 2010) in parts-per-thousand (or 'per mil', ‰). The long-term precision of the lab's quality-control standard *IsoLab 1* over the last 4 yr was 0.22‰ for $\delta^{18}O$. Overall, 64 xylem samples and 378 soil samples were used for further analyses using Bayesian statistics (see below).

Root water uptake patterns

We modelled the proportional contributions of soil water from six different soil depths to total root water uptake using mixing models from the R package SIMMR (Parnell, 2020) within a Bayesian framework based on Parnell *et al.* (2013). The $\delta^{18}O$ signatures of xylem water were considered the mixture to be modelled, while the $\delta^{18}O$ values of soil water from the six soil depths (i.e. 0–5, 5–10, 10–20, 20–30, 30–40, and 40–60 cm) were used as model inputs for each subplot at both sampling times (BT and ET, see Fig. S1 for $\delta^{18}O$ of xylem water and soil profiles). Isotope values for six missing soil samples (due to sampling difficulties in the field) were estimated based on the mean values of the other replicates from the same cropping system and treatment to ensure balanced model inputs. The outputs were from four Markov chain Monte Carlo Bayesian models (with at least: iterations = 300 000, burns = 50 000, thinning = 100 times for each chain), summing up to 10 000 possible combinations of contributions from sampled soil depths. Due to the soil texture being dominated by silt and sand (see 'Research site and drought simulation' in the Materials and Methods section), we considered all soil water being available for root water uptake and therefore used the soil water signatures as inputs into the Bayesian framework without any further constraint. Since intensive tillage treatments disturbed the soil down to 20 cm and to make treatments more comparable, these proportional contributions from the six soil depths were then aggregated into three soil layers with 20 cm intervals each: namely shallow (0–20 cm) as the sum of 0–5, 5–10, and 10–20 cm depths; middle (20–40) as the sum of 20–30 and 30–40 cm depths; and deep (40–60 cm). Finally, the median of the model outputs on the proportional contribution (MPC) from each aggregated soil layer was calculated for each subplot and used for further statistical analyses on root water uptake depths. We did not weigh these root water uptake depths by (1) soil moisture or (2) root distributions, since we were not interested in water uptake rates and because this would have introduced unknown bias due to untested assumptions, namely (1) that with more soil water present in any given soil depth, more water is taken up from this depth, and (2) that the presence of roots in any given soil depth, those roots are actively participating in root water uptake. Many earlier studies have proven those assumptions wrong for different ecosystems as well as biodiversity and environmental settings (e.g. Dawson & Ehleringer, 1991; Bachmann *et al*., 2015; Prechsl *et al*., 2015; Jesch *et al*., 2018; for a review of different approaches, see Dubbert *et al*., 2023).

Stem anatomy

One plant stem per subplot was sampled on 24 June 2019 and kept cool until further preparation. The growth stage of the plants was between 61 to 77 (AHDB) when the stem length stabilised. Cross sections (15–25 µm thick) of two stem positions were prepared per plant stem, one at the top of the stem close to the spike (cross section 1), and one in the middle of an internode (cross section 2; Fig. 1a) where the distance to the tip of the stem

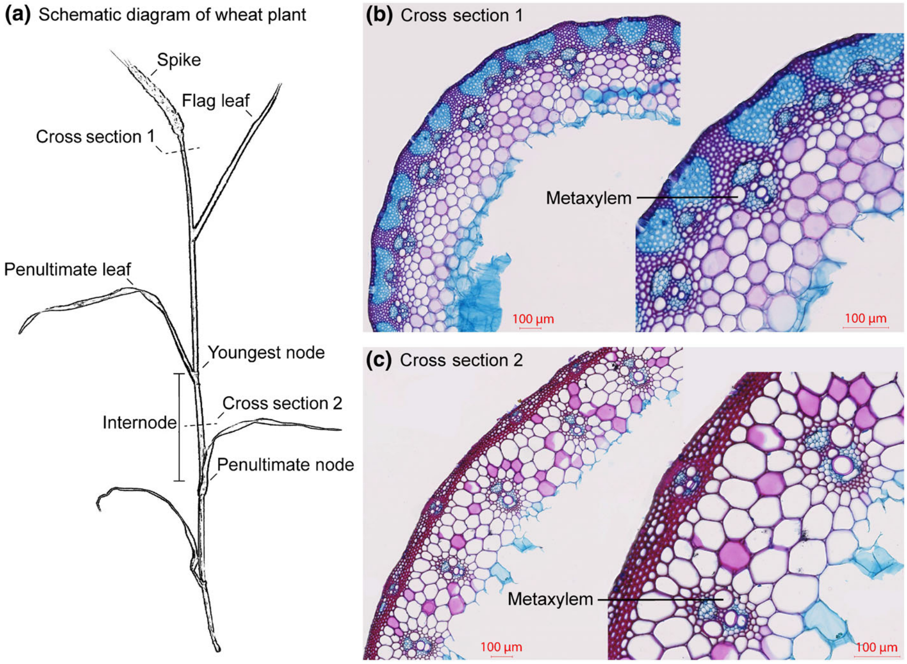

Fig. 1 Schematic diagram of (a) the aboveground parts of a winter wheat plant (*Triticum aestivum* L.) showing the position of cross section 1 (stem cross section close to the spike) and cross section 2 (stem cross section at the middle of internode) as well as cross section images at (b) cross section 1 and (c) cross section 2, with a zoom-in on the metaxylem to the right.

varied < 2 cm among individuals. Stems cross sections were cut using a WSL-Lab-Microtome (Gartner *et al*., 2015), stained with Safranin-Astra blue, and permanently mounted for microscopic observation according to Gartner & Schweingruber (2013). Digital images of each slide were taken using a high-resolution slide scanner (Axio Scan Z1, Zeiss, Germany). The metaxylem area of individual inner vascular bundles (MX; Fig. 1b,c) was measured and averaged for each cross section per subplot using FIJI v.1.51n (Schindelin *et al*., 2012). As the number of vascular bundles are determined genetically (Abbasi *et al*., 2017; Nakhforoosh *et al*., 2021), with the wheat cultivar being identical in all subplots, and the drought treatment starting 6 months after sowing (around stem elongation stage, well after crop establishment), no differences in the number of vascular bundles among cropping systems are expected.

Leaf water potentials and stomatal conductance

Leaf water potentials were measured on the youngest mature leaf (top fully unfolded leaf at the time of sampling) of one plant per subplot with a Scholander pressure chamber (SKPM, Skye Instruments Ltd, Powys, UK). Predawn measurements (ψ_{pd}) were taken between 03:00 h and 05:00 h on 19 April 2019 (before the drought treatment, BT), and on 18 June 2019 (at the end of treatment, ET). Midday water potentials (ψ_{md}) were measured on sunny days between 11:00 h and 13:00 h on 18 April (before the drought treatment, BT), on 7 and 17 May 2019 and 1 June (during the drought treatment, T) as well as on 13 June 2019 (at the end of treatment, ET).

Stomatal conductance (g_s) was measured with a handheld porometer (SC-1 Leaf Porometer; Decagon Inc., Pullman, WA, USA) on the youngest mature leaf of one plant per subplot, the same leaf which was also used for ψ_{md}. Both sides of the leaf, that is adaxial and abaxial, were measured, and the values were summed up as the g_s of the leaf. Measurements were carried out on leaves, fully exposed to the sun, during sunny days between 11:00 h and 13:00 h on 18 April (before the drought treatment, BT), on 7 and 17 May and 1 June 2019 (during the drought treatment, T) as well as on 13 June 2019 (at the end of treatment, ET). The porometer was calibrated in the field shortly before each measurement.

Leaf Chl content

Leaf Chl content was assessed using SPAD values measured with a SPAD-502 meter (Konica-Minolta, Tokyo, Japan; Markwell *et al*., 1995) using always the youngest mature leaves. Three leaves were measured in each subplot (10 SPAD measurements along each leaf) on 18 April (before the drought treatment, BT), 7 and 17 May and 1 June (during the treatment, T) as well as on 13 June 2019 (at the end of treatment, ET). The SPAD readings were then averaged per subplot for each measurement date.

Plant height and leaf area

Plant height was measured from the ground to the youngest leaf auricle using a folding rule on 10 plants in each subplot on 23 April (before the drought treatment, BT), 7 and 17 May and 1 June (during the treatment, T) as well as on 13 June 2019 (at the end of treatment, ET), and then averaged per subplot for each measurement date. Three to five youngest mature leaves were collected on 23 April (BT; penultimate leaf in Fig. 1a) and 14 June 2019 (T; flag leaf in Fig. 1a) in each subplot, then scanned and analysed using FIJI v.1.51n (Schindelin *et al*., 2012) to assess leaf area. Note that only the top two leaves (i.e. flag and penultimate leaves) were active and the bottom two were senesced during sampling on 14 June 2019. Both top leaves were collected and showed a significant linear regression in leaf area with the flag leaf

($R^2 = 0.97$, $P < 0.001$). Therefore, the flag leaf was considered representative for the leaf area of both still functional leaves.

Yield variables

To assess yields, plants were cut 1 cm above the ground within two 0.25 m^2 areas per subplot on 24 July 2019. In addition, the number of tillers was recorded for both areas. The grains were separated from the straw of harvested plants, then oven-dried at 60°C until constant weight. Grain yield per tiller and total grain yield per area were calculated accordingly. Total aboveground biomass per area was calculated as the sum of grain yield and straw.

Statistical analyses

Statistical analyses were done using R (v.4.0.4; R Core Team, 2020). Linear mixed models were used to test the effects of cropping systems and drought treatment on the investigated traits with the function *lmer()* from the R package LMERTEST (Kuznetsova *et al*., 2017). 'Cropping systems (CS)', 'drought treatment (D)', and 'blocks' were treated as three fixed factors (Dixon, 2016), with interactive effects between 'CS' and 'D' (CS × D). 'Plots' was included as a random factor in the models to account for the split-plot design. Changes between before drought treatment (BT) and end of drought treatment (ET) were tested for control and drought plots separately, where 'CS', 'date', and 'blocks' were three fixed factors, with interactive effects between 'CS' and 'date' (CS × date) and 'plots' as a random factor. Model assumptions were checked visually for normality and homoscedasticity of residuals with diagnostic plots. Differences among cropping systems and between treatments were tested by the Tukey HSD (honestly significant difference) test using the function *glht()* from the R package MULTCOMP (Hothorn *et al*., 2008). Principal components analysis (PCA) with the function *prcomp()* was used to assess the multivariate covariation among plant traits measured before (BT) and at the end (ET) of the drought treatment. Only those traits significantly affected by either cropping systems or the drought treatment or both were included in the PCA. Missing values due to sampling difficulties were filled with the mean values of other replicates from the same cropping system and treatment ($n = 1$ for metaxylem area, MX, at top of the stem; $n = 2$ for MX in the middle of internode). All traits were scaled to unit variance for the PCA. The important traits contributing to each principal component (PC) were assessed with the function *fviz_contrib()*, and factor loadings were extracted with the function *get_pca_var ()*, both as parts of R package FACTOEXTRA (Kassambara & Mundt, 2020). The correlation matrix was plotted using the *chart.Correlation()* from the R package PERFORMANCEANALYTICS (Peterson *et al*., 2020).

Results

Environmental conditions

Annual precipitation during the study year (2019) was relatively high with 1072 mm compared to the long-term mean (988 mm; Table 1). Similarly, mean annual temperature in 2019 was 10.5°C, 0.7°C higher than the years before. During the drought treatment period (25 April to 19 June 2019), *c*. 30% of the growing season precipitation was excluded by the rain shelters. The simulated drought fits well with the climate scenarios available for Switzerland, where precipitation is projected to decrease by 25% in 2060, and up to 40% by the end of the century (CH2018). During the treatment period, several heavy rain events with amounts of c. 30 mm occurred (Fig. S2). Consequently, average daily soil water contents (SWC) strongly fluctuated at both 10 and 40 cm depths in control subplots, ranging between 19% to 30% at 10 cm, and 28% to 36% at 40 cm depth (Fig. 2a,b). In the drought subplots, SWC at both 10 and 40 cm depths declined continuously during the drought treatment, ranging between 19% to 22% at 10 cm, and 23% to 28% at 40 cm depth (Fig. 2c,d). The differences in SWC among cropping systems were small in both control and drought subplots, except for C-NT which tended to have slightly lower SWC at 40 cm in both subplots compared to the other cropping systems.

Root water uptake depths

Winter wheat took up water mainly from the shallow layer (0–20 cm) of the soil profile when water was sufficient, that is in control subplots both before (BT) and at the end of (ET) the drought treatment, as well as in drought subplots before the treatment (BT; Fig. 3a–c). The median proportional contributions of soil water from different soil layers to total root water uptake (MPC) were between 41% and 64% for the shallow layer (0–20 cm depth; Table S2), between 25% and 39% for the middle layer (20–40 cm depth), and between 9% and 31% for the deep layer (40–60 cm depth) for all subplots under all cropping systems (CS: $P \geq 0.379$; D: $P \geq 0.139$; CS × D: $P \geq 0.233$; Table 2) before the treatment started (BT). At the end of the treatment (ET), drought significantly affected MPC ($P \leq 0.013$), with winter wheat taking up proportionally less water from shallow (0–20 cm depth) and more from middle (20–40 cm depth) as well as deep (40–60 cm depth) layers in drought compared to control subplots (Table 2; Table S2). However, cropping systems did not show any significant effects ($P \geq 0.362$); no interactions existed between cropping systems and the drought treatment for any of the soil layers ($P \geq 0.233$; Table 2).

Metaxylem area

The metaxylem area (MX) of winter wheat stems was smaller at the top of stem, close to the spike (cross section 1; Fig. 4a) compared to the MX in the middle of the internode (cross section 2; Fig. 4b), with on average 665 μm^2 vs 1171 μm^2, respectively. The MX was not significantly affected by cropping systems at either position ($P = 0.644$ and 0.156 for cross sections 1 and 2, respectively; Table 2). However, after the treatment, MX in drought subplots (627 μm^2 at cross section 1, 1053 μm^2 at cross section 2) was significantly smaller at both positions compared to those in control subplots (704 μm^2 at cross section 1, 1299 μm^2 at cross section 2) under all cropping systems ($P = 0.035$ and

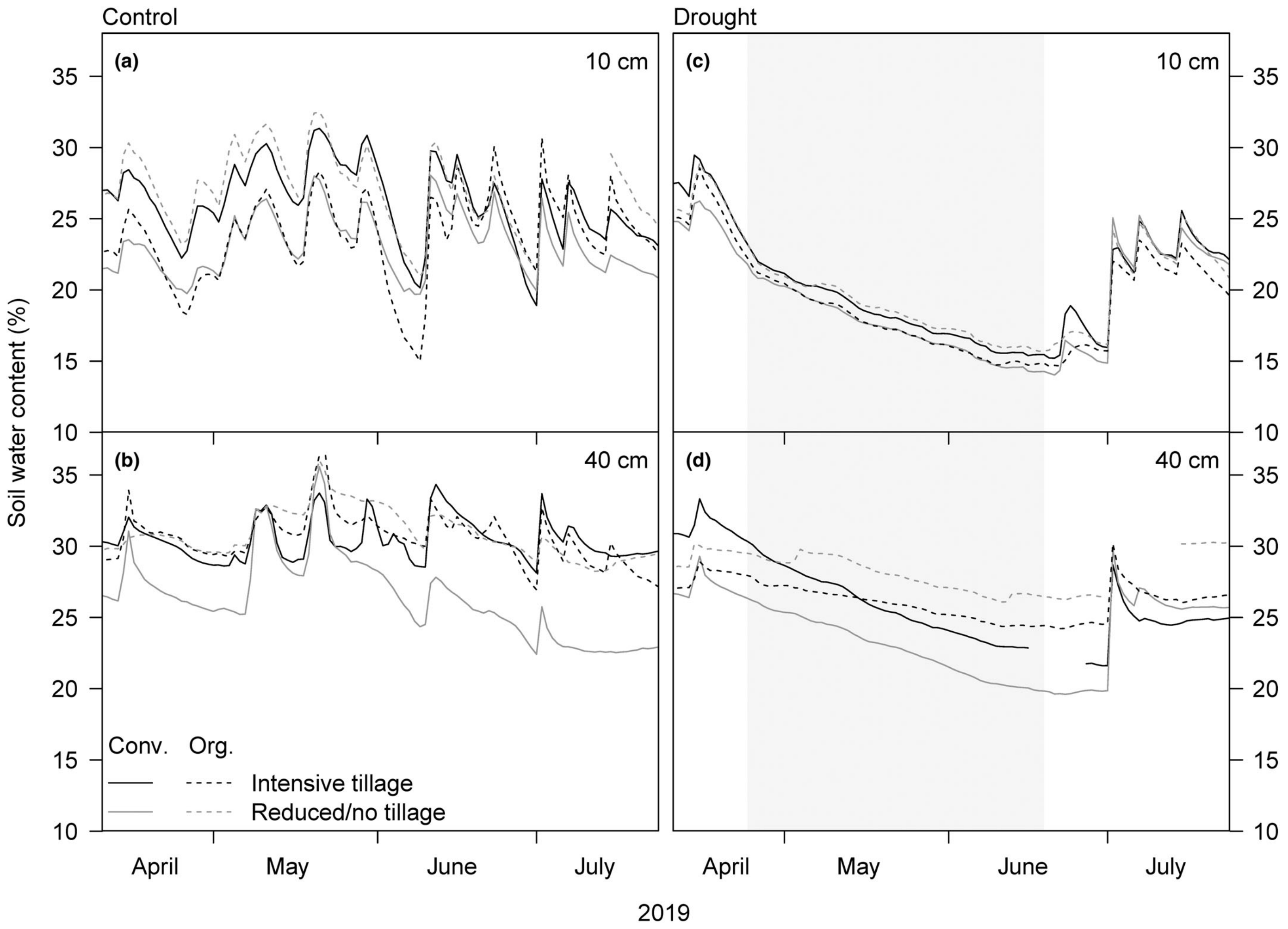

Fig. 2 Daily mean soil water contents at 10 and 40 cm depth (n = 2 each) in (a, b) control and (c, d) drought subplots under different cropping systems (Conv. for conventional, Org. for organic) in 2019. Breaks in continuous lines indicate sensor malfunction. Shaded areas in (c) and (d) represent the drought treatment period from 25 April to 19 June 2019.

0.001, respectively; Table 2). Significant differences among the cropping systems were only found in drought subplots, where the MX in the middle of the internode for winter wheat grown under O-IT was smaller than under C-IT, while intermediate MX under O-RT and C-NT (Fig. 4; Table S2). There were no significant interactions between cropping systems and drought treatment at either position (P = 0.536 and 0.145, respectively; Table 2).

Predawn and midday leaf water potentials

Predawn leaf water potential (ψ_{pd}) ranged between −0.3 and −0.5 MPa in all subplots before the drought treatment (BT; Fig. 5a), while the variation became larger at the end of drought treatment (ET), with values ranging between −0.2 and −0.6 MPa (Fig. 5b). This was due to significant drought effects at ET (P < 0.001), resulting in significantly lower ψ_{pd} values in drought (−0.6 MPa) than in control (−0.3 MPa) subplots. A small yet significant drought effect on ψ_{pd} was present before the drought treatment started (BT; P = 0.034; drought: −0.4 MPa, control: −0.5 MPa), but was completely overtaken by the experimental drought effects at ET (P < 0.001; drought: −0.3 MPa, control: −0.6 MPa; Table S2). For both control and drought subplots, date was a significant factor (P < 0.001). Cropping systems did not significantly affect ψ_{pd} on either date (P = 0.291 and 0.122 at BT and ET, respectively) nor interacted with drought (P = 0.334 and 0.855, respectively; Table 2).

Compared to the predawn water potentials (ψ_{pd}; Fig. 5), midday leaf water potentials of winter wheat (ψ_{md}; Fig. 6a) were much lower and decreased over the season from *c*. −1.3 MPa in April (before the drought treatment; BT) to −1.8 MPa in June (during and at the end of the drought treatment, T and ET, respectively). Cropping systems never significantly affected ψ_{md} (all dates: $P \geq$ 0.094; Table 2), while the drought treatment started to show significant effects in mid-May, 3 wk into the drought treatment period (Table 2). These effects persisted until the end of the drought treatment in June (ET; Fig. 6a). Similar to the effects on ψ_{pd}, drought resulted in consistently lower ψ_{md}

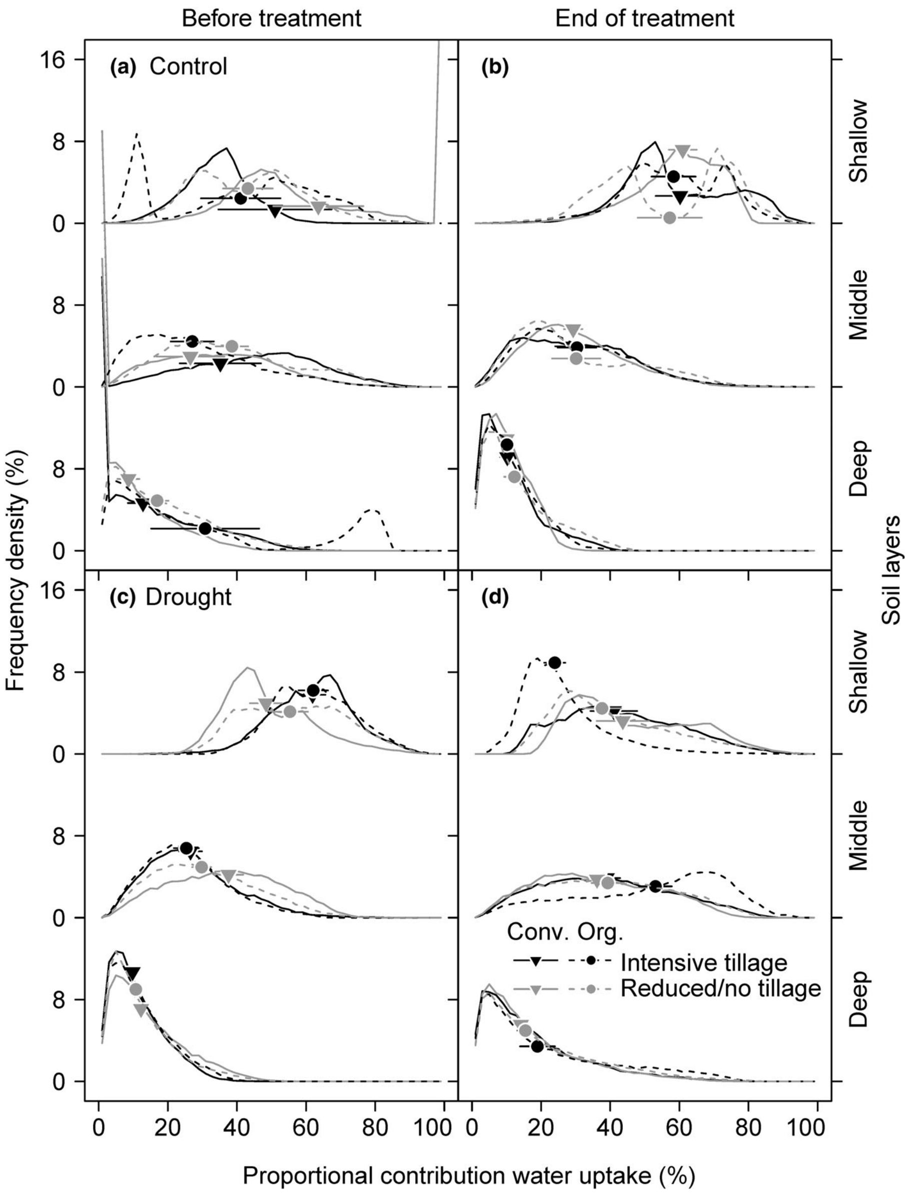

Fig. 3 Frequency density distribution of proportional soil water contribution to winter wheat (*Triticum aestivum* L.) water uptake from shallow (0–20 cm, sum of 0–5, 5–10, and 10–20 cm depths), middle (20–40 cm, sum of 20–30 and 30–40 cm depths), and deep (40–60 cm) soil layers under different cropping systems (a, c) before the drought treatment on 19 April and (b, d) at the end of treatment on 14 June 2019 in (a, b) control and (c, d) drought subplots. Frequency density was derived from 10 000 simulations at 2% increment of mixing models using $\delta^{18}O$ for each subplot. Data were pooled for all subplots in each cropping system (Conv. for conventional, Org. for organic); therefore, more than one peak can be present in the frequency distributions. Symbols (triangles for conventional, circles for organic) with horizontal lines on the curves (solid for conventional; dashed for organic) indicate the means ± 1 SE of the proportional contributions for each soil layer for different cropping system (n = 3–4). The 'spikes' in (a) for middle and deep layers represent frequency densities exceeding the axis range due to the respective proportional contribution water uptake being close to 0 (i.e. plants often did not take up water from these soil layers).

values for winter wheat under drought (−1.3 to −1.9 MPa) compared to control (−1.2 to −1.6 MPa) in May and June (Fig. 6a; Table S2). There was no significant interaction between cropping systems and drought (all $P \geq 0.070$).

Stomatal conductance

Similar to midday water potentials (ψ_{md}), leaf stomatal conductance (g_s) showed a gradual change over time (Fig. 6b; Table S2). The g_s values increased from April (BT; 366 mmol m^{-2} s^{-1}) to June (T; 1022 mmol m^{-2} s^{-1}), exhibiting a very large variation among cropping systems and treatments. Towards the end of the drought treatment (ET), g_s declined again to 729 mmol m^{-2} s^{-1} on average (Fig. 6b; Table S2).

Moreover, as for ψ_{md}, g_s was not significantly affected by cropping systems at any time (all $P \geq 0.168$; Table 2). By contrast, the drought treatment triggered significant differences in g_s in June, 5 wk into the drought treatment period (both $P \leq 0.001$; Table 2), 2 wk later than for ψ_{md} (Fig. 6b). For two out of the five measurement dates during the drought treatment, significant interactions occurred between cropping systems and drought treatment (both $P \leq 0.015$; Table 2). At both dates (early May and early June), g_s differed only among cropping systems in the control, but not the drought subplots, with plants growing under intensive tillage showing higher g_s than under reduced and no tillage (Table S2).

Leaf Chl content

Leaf Chl content did not show large variations over time, ranging from 39 to 52 SPAD units (Table S2; Fig. S3). Cropping systems significantly affected leaf Chl contents (all dates: $P \leq 0.013$; Table 2), with values being significantly higher in conventional than in organic systems (considering all dates and both control

Table 2 Effects of cropping systems (CS, df = 3), drought treatment (D, df = 1) and their interaction (CS × D, df = 3) on anatomical and ecophysiological traits as well as yield characteristics of winter wheat (*Triticum aestivum* L.) at different times during the study, that is before (BT), during (T), and at the end of the drought treatment (ET).

		Linear mixed model effects			
Variable	Date	CS	D	CS × D	Block
MPC (shallow)	19 April (BT)	0.819	0.262	0.233	0.154
MPC (middle)		0.652	0.660	0.389	0.263
MPC (deep)		0.379	0.139	0.256	0.326
MPC (shallow)	14 June (ET)	0.434	< **0.001*****	0.458	0.381
MPC (middle)		0.362	**0.003****	0.351	0.429
MPC (deep)		0.775	**0.013***	0.675	0.650
MX at stem top	24 June (ET)	0.644	**0.035***	0.537	0.907
MX at internode	24 June (ET)	0.156	**0.001****	0.145	0.907
Predawn leaf water potential	19 April (BT)	0.291	**0.034***	0.334	0.163
	18 June (ET)	0.122	< **0.001*****	0.855	< **0.001*****
Midday leaf water potential	18 April (BT)	0.572	0.352	0.258	0.701
	7 May (T)	0.620	0.162	0.070	0.299
	17 May (T)	0.570	< **0.001*****	0.359	0.123
	1 June (T)	0.094	< **0.001*****	0.452	**0.019***
	13 June (ET)	0.170	**0.001****	0.156	0.280
Stomatal conductance	18 April (BT)	0.168	0.606	0.430	**0.049***
	7 May (T)	0.367	0.396	**0.009****	0.832
	17 May (T)	0.782	0.555	0.657	0.985
	1 June (T)	0.391	**0.001****	**0.015***	0.899
	13 June (ET)	0.199	< **0.001*****	0.069	0.183
Leaf Chl content	18 April (BT)	**0.001****	0.879	**0.047***	0.504
	7 May (T)	**0.008****	0.976	0.765	0.348
	17 May (T)	**0.007****	**0.008****	0.623	0.491
	1 June (T)	< **0.001*****	**0.007****	0.274	0.079
	13 June (ET)	**0.013***	0.395	0.067	0.393
Plant height	23 April (BT)	< **0.001*****	**0.045***	0.218	0.442
	7 May (T)	**0.001****	0.490	0.789	0.257
	17 May (T)	**0.009****	0.499	0.448	0.211
	1 June (T)	0.112	**0.008****	0.219	0.134
	13 June (ET)	0.913	< **0.001*****	0.780	0.887
Leaf area	23 April (BT)	0.109	0.973	0.114	0.256
	14 June (ET)	**0.042***	**0.008****	0.934	0.526
Yield per tiller	24 July	**0.039***	0.102	0.723	0.128
Tiller density		**0.001****	< **0.001*****	0.115	0.224
Total yield		**0.011***	< **0.001*****	0.182	0.092
Aboveground biomass		**0.008****	< **0.001*****	0.346	0.149

P-values of linear mixed models are given for the medians of proportional contributions to root water uptake (MPC) from different soil layers (shallow: 0–20 cm, middle: 20–40 cm, deep: 40–60 cm), metaxylem areas (MX) at the top of the stem and the middle of the internode, predawn and midday leaf water potentials, leaf stomatal conductance, leaf Chl content, plant height, leaf area, as well as yield per tiller, tiller density, total yield, and aboveground biomass. Significant differences are shown in bold as well as marked with asterisks for different levels (*, $0.01 \leq P < 0.05$; **, $0.001 \leq P < 0.05$; ***, $P < 0.001$).

and drought subplots; Table S2; Fig. S3). Drought started to show significant positive effects on leaf Chl content in mid-May (Table 2), 3 wk into the drought treatment, although differences were small (Table S2; Fig. S3). At the end of the treatment in June (ET), the differences between drought and control subplots disappeared ($P = 0.395$; Tables 2, S2; Fig. S3). No significant interactions between cropping systems and drought were observed during the treatment period (all $P \geq 0.067$: Table 2).

Plant height and leaf area

The height of all winter wheat plants increased from on average 13 cm in April (BT) to on average 60 cm in June (T and ET; Table S2; Fig. S3). Cropping systems significantly affected height of winter wheat in April and May (BT and T, all $P \leq 0.009$; Table 2), with plants in conventional systems being significantly taller than those in organic systems (averaging over control and drought subplots; Table S2). These differences among cropping systems disappeared in June. Similar to g_s, plant height was only significantly affected by drought towards the end of the treatment (June; $P = 0.008$ and $P < 0.001$), with plants being significantly shorter in drought than in control subplots (Fig. S3; Table S2). Cropping systems and drought never showed significant interactions ($P \geq 0.218$; Table 2).

The average leaf area of the youngest mature leave was not affected by cropping systems nor drought in April (BT), although

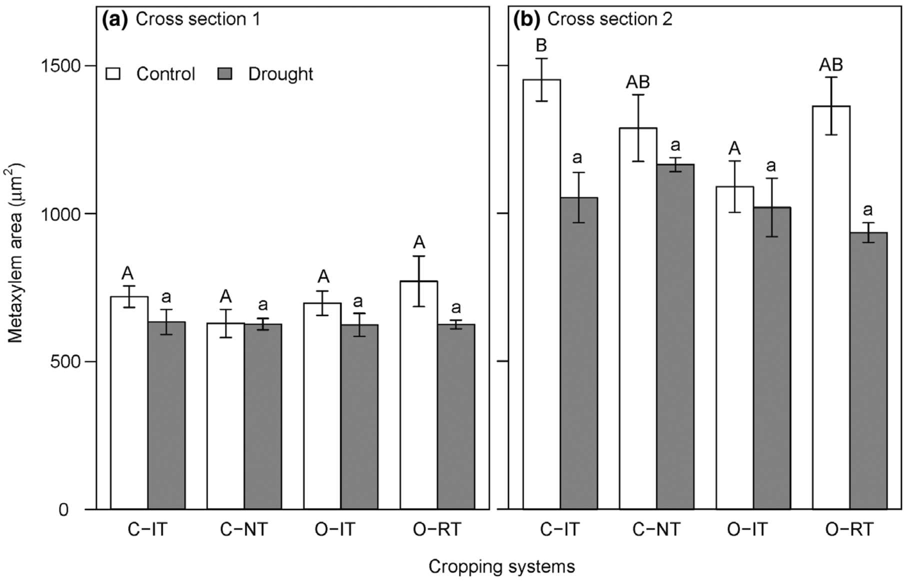

Fig. 4 Average metaxylem area of vascular bundles at (a) cross section 1 (at the top of the stem) and (b) cross section 2 (at middle of the internode) of winter wheat (*Triticum aestivum* L.) grown under different cropping systems (C-IT for Conventional intensive tillage, C-NT for Conventional no tillage, O-IT for Organic intensive tillage, O-RT for Organic reduced tillage) in control (white bars) and drought (grey bars) subplots. Means ± 1 SE are given (n = 3–4); samples were taken after the drought treatment on 24 June 2019 (AT). Different small and capital letters indicate significant differences among CS in drought and control subplots, respectively, tested with Tukey HSD (honestly significant difference, $P < 0.05$).

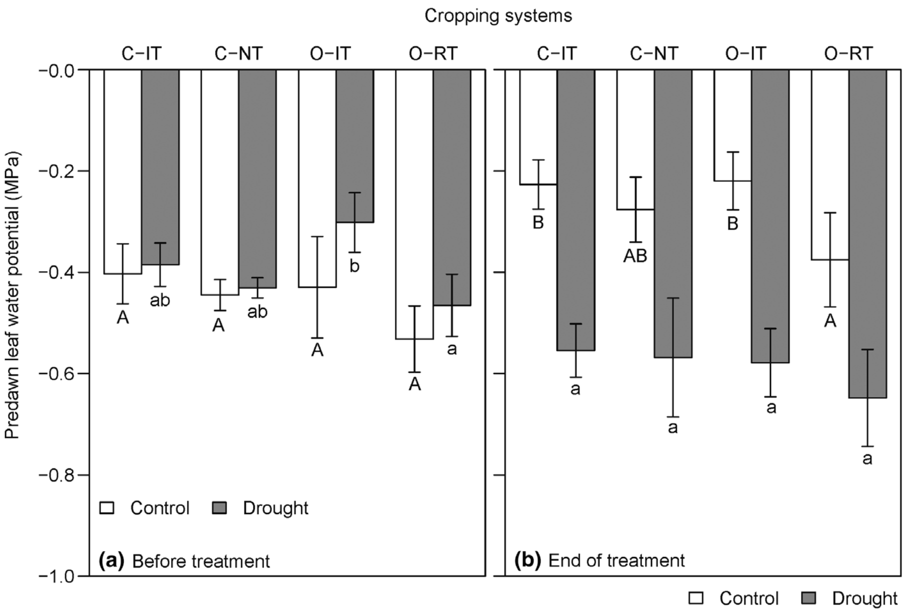

Fig. 5 Predawn leaf water potential of winter wheat (*Triticum aestivum* L.) grown under different cropping systems (C-IT for Conventional intensive tillage, C-NT for Conventional no tillage, O-IT for Organic intensive tillage, O-RT for Organic reduced tillage) in control (white bars) and drought (grey bars) subplots. Means ± 1 SE are given (n = 4); measurements were taken BT (a) and ET (b). Different small and capital letters indicate significant differences among CS in drought and control subplots, respectively, tested with Tukey HSD (honestly significant difference, $P < 0.05$).

leaf area was slightly lower in O-RT than in the three other CS (Table S2). In June (ET) this changed, and cropping systems as well as drought significantly affected leaf area ($P = 0.042$ and 0.008, respectively; Table 2). Both conventional systems had significantly larger leaves than the two organic systems (Table S2). Moreover, the youngest mature leaves were larger in control than in drought subplots (Table S2), but cropping systems and drought never showed significant interactions (both $P \geq 0.114$; Table 2).

Yield variables

At the harvest on 24 July 2019, grain yield per tiller ranged between 2.2 and 2.6 g for all subplots (Fig. 7a). While the drought had no effect ($P = 0.102$), cropping systems significantly affected grain yield per tiller ($P = 0.039$; no interaction CS × D; Table 2), with lowest yield in C-NT compared to all other cropping systems (Table S2). By contrast, tiller density was significantly affected by cropping systems ($P = 0.001$) and drought ($P < 0.001$; no interaction CS × D; Table 2). Conventional systems had significantly higher tiller density than organic systems, independent of the drought treatment (Table S2). Yet, drought subplots exhibited significantly lower tiller density than control subplots (Table S2). As a result, total yield per area ranged from 4.2 to 6.6 t ha^{-1} and biomass per area from 9 to 14.5 t ha^{-1} for all subplots and was significantly affected by cropping systems ($P = 0.011$ and 0.008, respectively) and drought (both $P < 0.001$, no interaction CS × D; Fig. 7b; Table 2). Thus, total yield and biomass were significantly higher

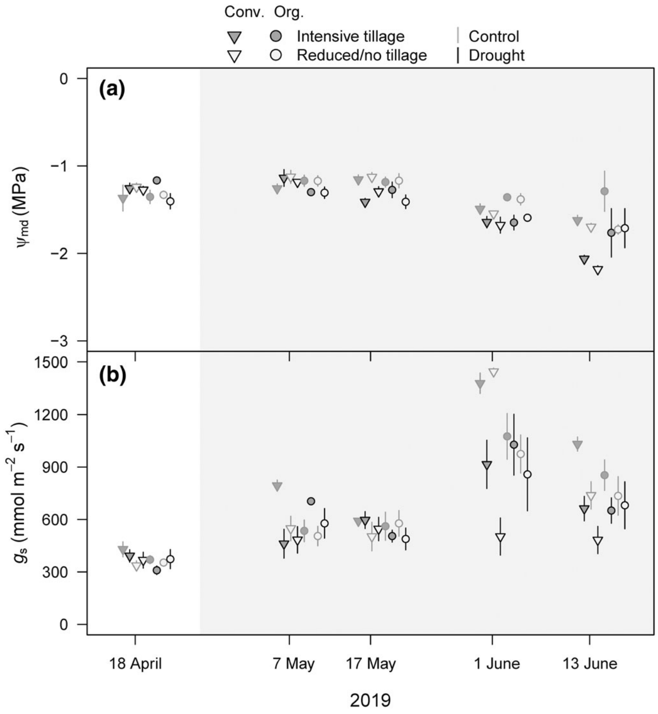

Fig. 6 Midday leaf water potential (ψ_{md}; a) and stomatal conductance (g_s; b) of winter wheat (*Triticum aestivum* L.) grown under different cropping systems (C-IT for Conventional intensive tillage, C-NT for Conventional no tillage, O-IT for Organic intensive tillage, O-RT for Organic reduced tillage) in control (grey symbol outline) and drought (black symbol outline) subplots measured on different dates. Means ± 1 SE are given (n = 4). Shaded areas reflect the drought treatment period from 25 April to 19 June 2019.

in conventional than in organic systems (Table S2), while yield and biomass were significantly lower in drought than in control subplots, without any interactions (Fig. 7b; Table S2). Since winter wheat is a cereal crop used for its grains, and total aboveground biomass showed a very similar response as the grain yield, further analysis and discussion focus grain yield.

Trait space

To integrate the information from the many traits described above into a trait space, a principal component analysis (PCA) was performed (Fig. 8). A total of 56.1% of the overall variation in the dataset was captured by the first two principal components. The first principal component (PC; 34.6% explained variance) was most strongly related to root water uptake (MPC from all three soil layers) at the end of treatment (ET), plant height (ET), metaxylem area at internode (cross section 2), leaf area (ET) and predawn leaf water potential (ψ_{pd}, ET; Table S3). This means that high scores on the first PC axis indicated high MPC from the shallow soil layer (0–20 cm) and low MPC from the middle (20–40 cm) and deep (40–60 cm) layers, large plant height (ET), large metaxylem area at the middle of the internode, large leaf area (ET), and high ψ_{pd} (ET). The second PC (21.5%) was negatively associated with leaf Chl content before (BT) and at the end (ET) of treatment, and with plant height (BT), but positively correlated with midday leaf water potential ψ_{md} (ET; Fig. 8a). This means that high scores on the second PC were associated with low leaf Chl content (BT and ET), low plant height (BT), and high ψ_{md}. Overlays of the PCA with yield variables revealed that yield per tiller and total yield per area had nearly perpendicular loadings. Yield per tiller was positively related to the second PC (R^2 = 0.21), while tiller density was largely explained by both PCs, being positively related to the first PC (R^2 = 0.38) and negatively to the second PC (R^2 = 0.43). This resulted in the total yield also being associated with the first PC (R^2 = 0.43) and the second PC (R^2 = 0.22; Fig. 7a; Table S3). Moreover, total yield was closely aligned with leaf area (ET), indicating a strong correlation between these two variables (Fig. 8a; for correlation see Fig. S4). For the correlation matrix of the variables used for principal component (PC) analysis and yield variables, see Fig. 9.

The PC scores of individual subplots along the first and second axes showed clear groupings of conventional (C-IT and C-NT) vs organic (O-IT and O-RT) systems, with conventional systems on the lower right relative to organic systems (Fig. 8b). This separation reflected the generally higher Chl content both before (BT) and at the end of (ET) treatment, higher plant height (BT), and leaf area (ET) of winter wheat in subplots under conventional compared to organic systems (Tables 2, S2). Therefore, the differentiation between conventional and organic systems was mainly based on growth and biomass related traits. Subplots with intensive tillage and conservation tillage in all systems largely mixed and showed no such separation (Fig. 8b).

Drought and control treatments also showed a clear separation along the two axes with only little overlap, with drought subplots being located more to the left relative to control subplots (Fig. 8c). This showed that winter wheat in drought subplots was mainly characterised by lower MPC from shallow (0–20 cm) and higher MPC from middle (20–40 cm) and deep (40–60 cm) layers at the end of treatment (ET), lower plant height (ET), smaller metaxylem area at internode (cross section 2), smaller leaf area (ET), and lower ψ_{pd} (ET) as well as g_s (ET) than winter wheat in control subplots (Tables 2, S2). Traits such as plant height before the treatment (BT), and leaf Chl content before (BT) or end of (ET) treatment were quite irrelevant for the separation of control and drought plots. Thus, contrary to the cropping system separation, drought and control subplots mostly differed in traits related to water relations at the end of treatment (ET). Furthermore, the relative positioning of conventional and organic systems vs drought and control subplots were nearly perpendicular to each other (Fig. 8b,c), illustrating the lack of interactions between the effects of cropping systems and drought on the trait space.

Discussion

Insight into what drives crop water relations along the soil–plant–atmosphere continuum (SPAC) are of utmost relevance for rainfed arable agriculture in the face of climate change. This study is the first to simultaneously assess water and vegetative traits of winter wheat along the SPAC and relate these

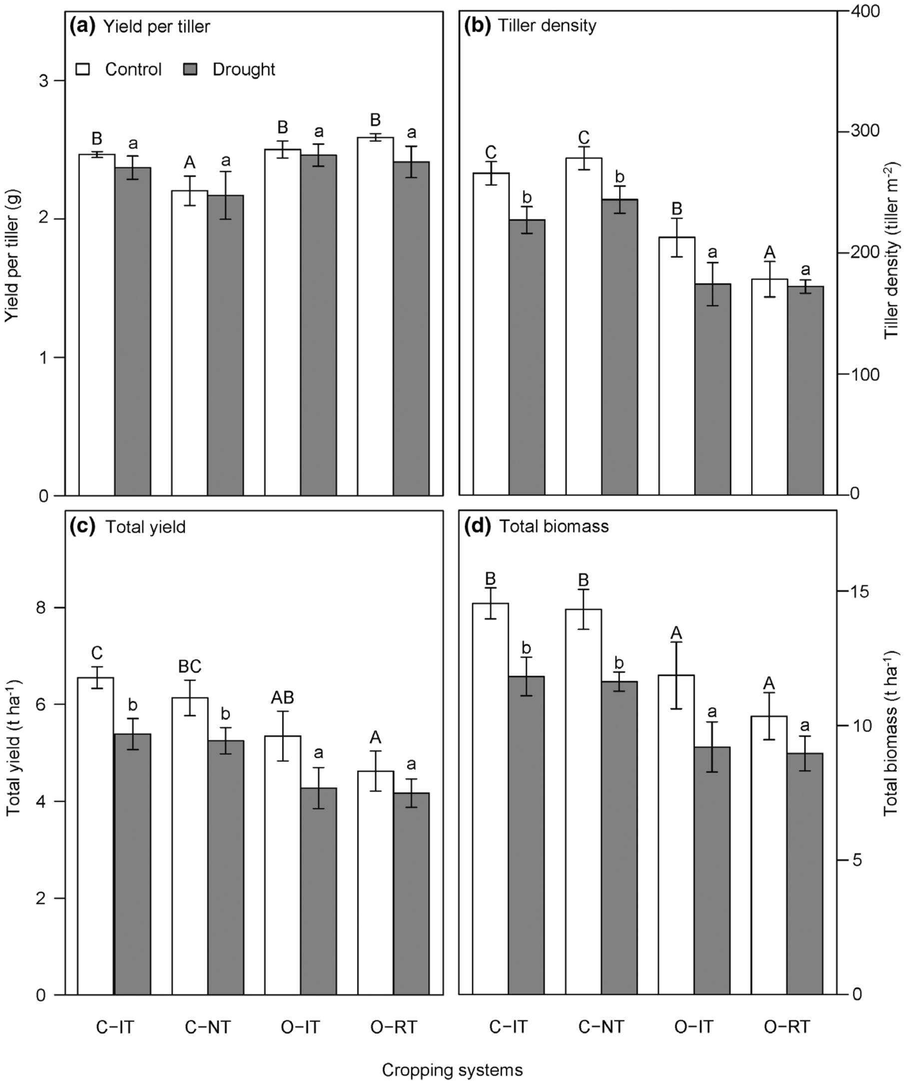

Fig. 7 Grain yield per tiller (a), tiller density (b), total grain yield (c), and total aboveground biomass (d) of winter wheat (*Triticum aestivum* L.) grown under different cropping systems (C-IT for Conventional intensive tillage, C-NT for Conventional no tillage, O-IT for Organic intensive tillage, O-RT for Organic reduced tillage) in control (white bars) and drought (grey bars) subplots. Means ± 1 SE are given ($n = 4$); samples were taken on 24 July 2019. Different small and capital letters indicate significant differences among CS in drought and control subplots, respectively, tested with Tukey HSD (honestly significant difference, $P < 0.05$).

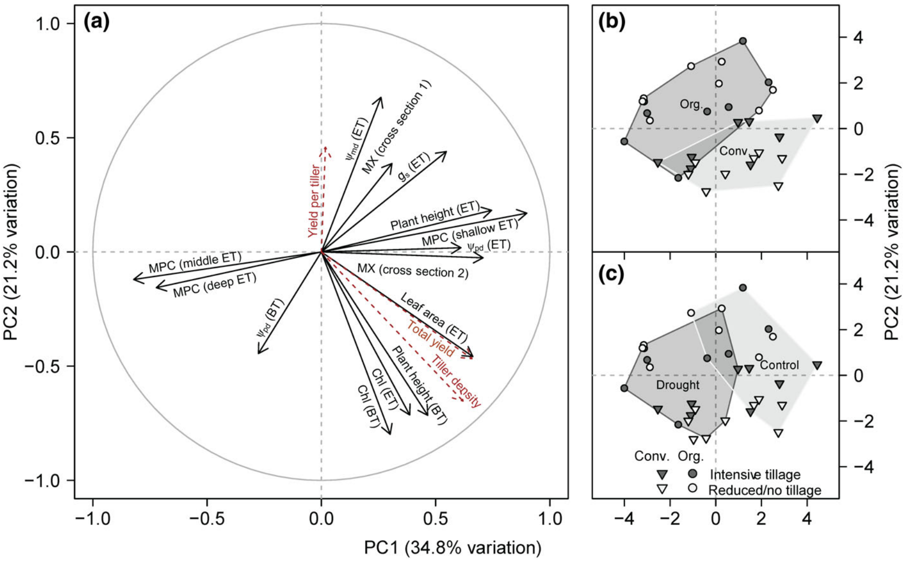

Fig. 8 Principal component plots of selected traits of winter wheat (*Triticum aestivum* L.) on subplot level. (a) Vector loading map of traits with yield per tiller, tiller density, and total yield as overlays (red dashed lines); (b) same analysis showing organic vs conventional and (c) drought vs control groupings. Principal components were derived from traits significantly affected by cropping systems or drought: medians of proportional contributions to root water uptake (MPC) from three soil layers (shallow: 0–20 cm, middle: 20–40 cm, deep: 40–60 cm) at the end of the drought treatment (ET), stem metaxylem areas (MX) at the top of the stem (cross section 1) and at the internode (cross section 2), predawn leaf water potentials (ψ_{pd}) before (BT) and the end (ET) of the drought treatment, midday leaf water potential (ψ_{md}; ET), leaf stomatal conductance (g_s; ET), leaf Chl contents (Chl; BT and ET), plant heights (BT and ET), and leaf area (ET).

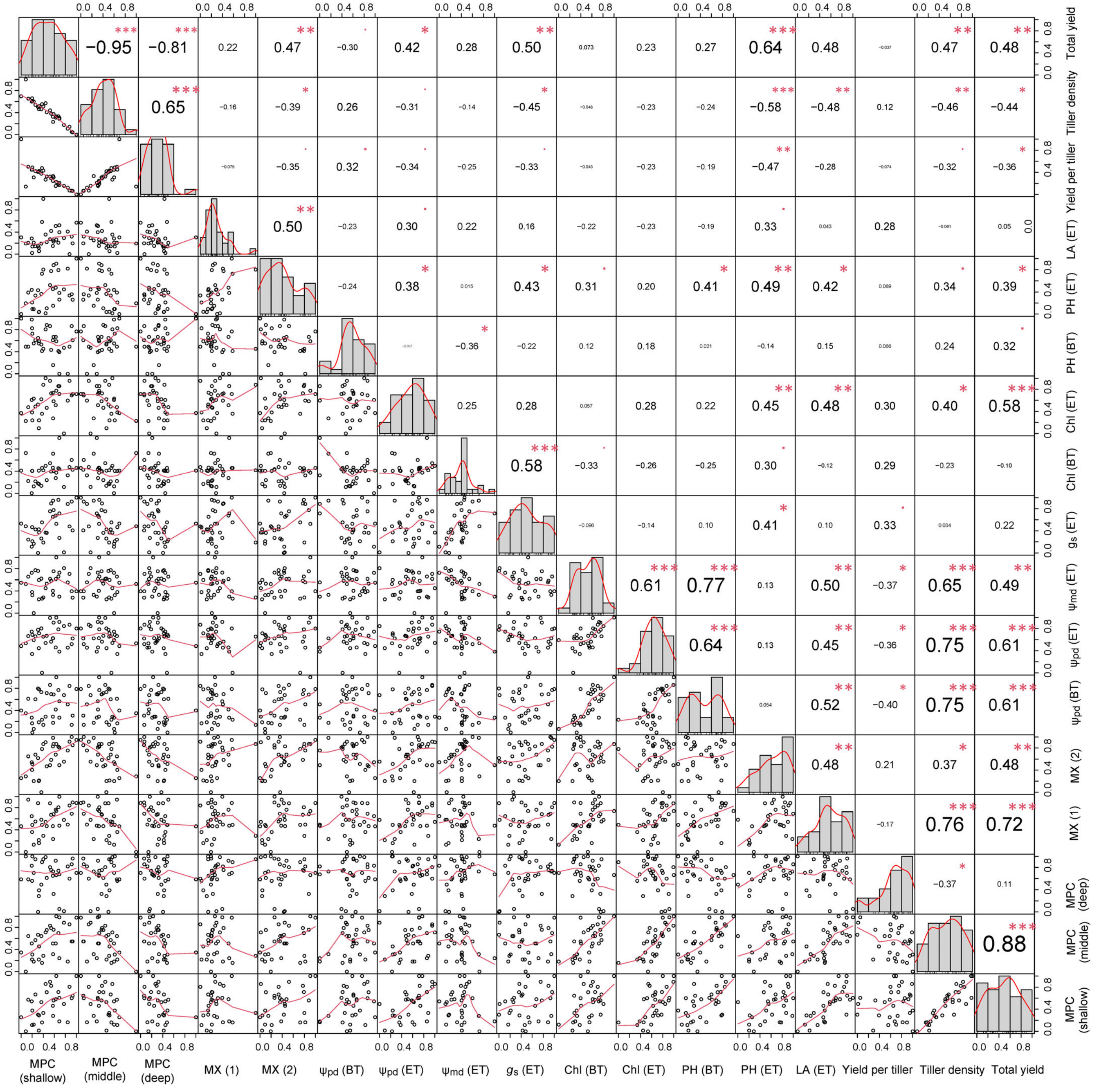

Fig. 9 Correlation matrix and correlation coefficients among winter wheat (*Triticum aestivum* L.) traits. The median of proportional contribution to root water uptake (MPC) from different soil layers (shallow: 0–20 cm, middle: 20–40 cm, deep: 40–60 cm) at the end of treatment (ET), metaxylem area (MX) at the top of the stem (cross section 1) and the middle of internode (cross section 2), predawn leaf water potential (ψ_{pd}) before (BT) and at the end (ET) of treatment, midday leaf water potential (ψ_{md}; ET), stomatal conductance (g_s; ET), leaf Chl content (Chl; BT and ET), plant height (PH; BT and ET) and leaf area (LA; ET), yield per tiller, tiller density, and total yield are included. The size of coefficients corresponds to the value. Asterisks indicate the significance of linear correlation: ***, $P < 0.001$; **, $0.001 \leq P < 0.01$; *, $0.01 \leq P < 0.05$.

traits to crop yield as affected by environment and management, that is drought and cropping systems. Results show that drought and cropping systems affected independent sets of traits, indicating that an alteration of cropping system is not a reliable strategy for climate change adaptation based on this field trial.

Cropping system effects on individual traits

We found significant cropping system effects on vegetative traits, such as leaf Chl content, plant height, leaf area, as well as yield. These traits are strongly related to the nutrition of the plants, especially to leaf N concentrations (Marschner, 2011) which are susceptible to soil N availability (Blackmer & Schepers, 1995). This finding is in line with previous research reporting cropping system effects on physiological processes, growth, and thus yield of winter wheat due to changed soil chemical, physical, and microbial properties (organic vs conventional: e.g. Ramesh *et al*., 2008; Mayer *et al*., 2015; different tillage practices: e.g. Khan *et al*., 2020; Li *et al*., 2020a,b; Ding *et al*., 2021). Thus, cropping system effects on vegetative traits observed in our study were most likely due to different soil chemical as well as structural properties (as shown by Gattinger *et al*., 2012; Colombi *et al*., 2019) resulted from different management, for example N fertilisation rates. In our experiment, conventional winter wheat was fertilised with readily available synthetic N fertiliser and thus performed better than the organic winter wheat, which were fertilised with cattle slurry. Meanwhile, effects of organic management or conservation tillage on soil properties are widely discussed to sustain crop growth and yield even under water-limited conditions, for example via increased water holding capacity of the soil (e.g. Lotter *et al*., 2003; van Eerd *et al*., 2014; Das *et al*., 2018). However, no cropping system effects were observed on water traits of winter wheat in this study, especially under drought conditions. Therefore, crop management was shown to have limited impacts on plant water relations of winter wheat, which questions the potential of using different cropping systems to alleviate drought stress for crops.

Drought effects on individual traits

Drought, however, affected winter wheat and its yield in other ways, not interacting with cropping systems. Winter wheat subjected to drought shifted its water uptake to deeper soil layers, that is increased the proportional contribution from the middle layer (20–40 cm) while the contribution from the shallow layer (0–20 cm) decreased. This is in line with increased proportional water uptake from deeper soil layers as a response to drying topsoil in a pot experiment with wheat (Zegada-Lizarazu & Iijima, 2004). The metaxylem area at both studied positions of the winter wheat stem decreased in response to drought stress. The upper metaxylem area was close to the stem tip therefore was not subjected to the potential bias introduced by tip-to-base conduit widening, which describes the scaling of stem vessel diameter with the distance from the stem tip (with a 0.2 exponent; Olson *et al*., 2021). Although the plants were significantly shorter after the drought treatment, the difference was only 3 cm on average (Table S2). As the lower metaxylem was sampled below the middle of the plant (Fig. 1a), the relatively small variability in sampling positions would lead to an *c*. 2% expected reduction under drought compared to the control according to Olson *et al*. (2021). Therefore, the conduit widening cannot explain the averaged 24% reduction in metaxylem area under the drought treatment. Reduced metaxylem area might increase cavitation resistance but reduces water transport efficiency, as reviewed by Hacke *et al*. (2017), who compared vessel diameter and xylem vulnerability among tree species. In an earlier study at our site, barley was shown to exhibit high cavitation vulnerability (Sun *et al*., 2021). Thus, reducing metaxylem area at both measured positions when subjected to drought clearly indicated acclimation of winter wheat, also a cereal crop, to reduce xylem vulnerability to drought stress. Supporting this hypothesis, smaller xylem areas accompanied by lower xylem vulnerability have recently been observed in different cereals when comparing different cultivars, including spring wheat (Degraeve *et al*., 2021). However, in our study, the plant water status of winter wheat due to the strong drought treatment was clearly impaired. Midday leaf water potentials as well as stomatal conductance became significantly lower three to five weeks into the drought treatment, finally reaching lower predawn leaf water potential at the end of the treatment (ET) under drought compared to control conditions. Therefore, the consequences of the lower metaxylem area in winter wheat could be twofold: It could have led to (1) reduced water transport efficiency and consequently worsened plant water status when soil water contents declined under drought, or (2) reduced xylem vulnerability to cavitation and thus less drought stress since conductivity for water from deeper soil layers was maintained.

Other than water traits along the SPAC, the drought effects expanded to winter wheat vegetative traits as well. Leaf Chl content was slightly higher during the drought treatment (T) in winter wheat undergoing water limitation compared to control conditions, which could be related to the likely lower leaf water content (see Martínez & Guiamet, 2004), as indicated by the relatively low midday leaf water potentials. At the end of the drought treatment (ET), leaf Chl content dropped and was close to values measured under control condition. This could be attributed to earlier senescence caused by drought (Yang *et al*., 2003). Meanwhile, plant height and leaf area of winter wheat were reduced by drought, and further resulted in a significant loss in yield as a common outcome of water stress (Nawaz *et al*., 2013; Farooq *et al*., 2014). Therefore, drought affected all individual water traits along the entire SPAC, and those effects and trade-offs translated to vegetative traits ultimately reducing yield in all cropping systems.

Changes in trait space of winter wheat

This study, for the first time, assessed a trait space of winter wheat, following the entire SPAC from root water uptake, xylem water transport (metaxylem area), and leaf water status (leaf water potential) to water use (stomatal conductance), as well as including vegetative traits such as leaf Chl content, plant height, and leaf area. The trait space was clearly altered by the experimental drought and reflected differences between organic vs conventional systems on individual water and vegetative traits as well as on yield. Interestingly, no differences between intensive vs conservation tillage were observed. In addition, the separation of conventional vs organic systems as opposed to drought vs control subplots within the PCA were nearly perpendicular to each other, illustrating the lack of interactions between cropping systems and drought effects. This underlines that changes in water relations due to the drought were independent of cropping systems, supporting the findings above from individual traits. These results raise strong concerns about the expectation to alleviate drought stress of winter wheat by the selection of different, widely common management practices, that is organic farming and conservation tillage.

Conclusions

Our findings demonstrated that drought and crop management impacts on traits of winter wheat were independent of each other. These results thus question the widespread expectations that management can alleviate drought impacts on crops. The shifts of the plant trait space in response to environmental and management conditions clearly showed the usefulness of the trait space concept and supports its application to assess the effectiveness of future strategies to adapt crop management to a changing climate. Such a comprehensive assessment of plant water and vegetative traits is also needed for other important crop plants and climates than studied here, using traits along the entire soil–plant–atmosphere continuum. Moreover, our study clearly showed that the trait space concept, a tool of trait-based ecology, works adequately well even in managed monoculture systems. Thus, trait space analyses could also be used to explore the resilience of innovative crop management systems such as intercropping and agroforestry to environmental change.

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Competing interests

None declared.

Author contributions

NB, AKG and MGAH initiated the experiment and the experimental design. RW managed the FAST experiment; QS and RW collected the data; GA coordinated the imaging of xylem anatomy; QS and VHK analysed the data; QS, AKG and NB wrote the first drafts of the manuscript; all authors discussed the results and revised and agreed on the final version of the manuscript.

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Data availability

The data that support the findings of this study are openly available in the ETH Zurich Repository at doi: 10.5905/ethz-1002-11290.

References

Abbasi M, Faghani E, Khani AH, Razzaghi MH. 2017. Evaluating drought resistant wheat cultivars based on stem anatomical characteristics. *Journal of Experimental Biology and Agricultural Sciences* **5**: 332–340.

AHDB. *Wheat growth guide.* [WWW document] URL https://ahdb.org.uk/knowledge-library/wheat-growth-guide [accessed 30 January 2024].

Ajal J, Jäck O, Vico G, Weih M. 2021. Functional trait space in cereals and legumes grown in pure and mixed cultures is influenced more by cultivar identity than crop mixing. *Perspectives in Plant Ecology, Evolution and Systematics* **50**: 125612.

Bachmann D, Gockele A, Ravenek JM, Roscher C, Strecker T, Weigelt A, Buchmann N. 2015. No evidence of complementary water use along a plant species richness gradient in temperate experimental grasslands. *PLoS ONE* **10**: e0116367.

Barnard RL, de Bello F, Gilgen AK, Buchmann N. 2006. The δ^{18}O of root crown water best reflects source water δ^{18}O in different types of herbaceous species. *Rapid Communications in Mass Spectrometry* **20**: 3799–3802.

BioSuisse. 2021. *Das Bioregelwerk.* [WWW document] URL https://www.bioaktuell.ch/aktuell/bioregelwerk.html [accessed 25 May 2021].

Blackmer TM, Schepers JS. 1995. Use of a chlorophyll meter to monitor nitrogen status and schedule fertigation for corn. *Journal of Production Agriculture* **8**: 56–60.

Boyer JS. 1985. Water transport. *Annual Review of Plant Physiology* **36**: 473–516.

CH2018. 2018. *CH2018 – climate scenarios for Switzerland, technical report.* Zurich, Switzerland: National Centre for Climate Services, 271.

Chen RQ, Kang SZ, Hao XM, Li FS, Du TS, Qiu RJ, Chen JL. 2015. Variations in tomato yield and quality in relation to soil properties and evapotranspiration under greenhouse condition. *Scientia Horticulturae* **197**: 318–328.

Colombi T, Walder F, Buchi L, Sommer M, Liu KX, Six J, van der Heijden MGA, Charles R, Keller T. 2019. On-farm study reveals positive relationship between gas transport capacity and organic carbon content in arable soil. *The Soil* **5**: 91–105.

Craig H, Gordon LI. 1965. Deuterium and oxygen 18 variation in the ocean and the marine atmosphere. In: Tongiorgi E, ed. *Stable isotopes in oceanographic studies and Paleotemperatures.* Pisa, Italy: Consiglio Nazionale delle Ricerche, Laboratorio di Geologia Nucleare, 9–130.

Das A, Lyngdoh D, Ghosh PK, Lal R, Layek J, Idapuganti RG. 2018. Tillage and cropping sequence effect on physico-chemical and biological properties of soil in Eastern Himalayas, India. *Soil and Tillage Research* **180**: 182–193.

Dawson TE, Ehleringer JR. 1991. Streamside trees that do not use stream water. *Nature* **350**: 335–337.

Degraeve S, De Baerdemaeker NJF, Ameye M, Leroux O, Haesaert GJW, Steppe K. 2021. Acoustic vulnerability, hydraulic capacitance, and xylem anatomy determine drought response of small grain cereals. *Frontiers in Plant Science* **12**: 599824.

Ding JF, Li FJ, Xu DY, Wu P, Zhu M, Li CY, Zhu XK, Chen YL, Guo WS. 2021. Tillage and nitrogen managements increased wheat yield through promoting vigor growth and production of tillers. *Agronomy Journal* **113**: 1640–1652.

Ding Y, Schoengold K, Tadesse T. 2009. The impact of weather extremes on agricultural production methods: does drought increase adoption of conservation tillage practices? *Journal of Agricultural and Resource Economics* **34**: 395–411.

Dixon PM. 2016. Should blocks be fixed or random? *Statistics conference proceedings, presentations and posters* 6.

Donovan LA, Sperry J. 2000. Scaling the soil–plant–atmosphere continuum: from physics to ecosystems. *Trends in Plant Science* **5**: 510–512.

Dubbert M, Couvreur V, Kübert A, Werner C. 2023. Plant water uptake modelling: added value of cross-disciplinary approaches. *Plant Biology* **25**: 32–42.

van Eerd LL, Congreves KA, Hayes A, Verhallen A, Hooker DC. 2014. Long-term tillage and crop rotation effects on soil quality, organic carbon, and total nitrogen. *Canadian Journal of Soil Science* **94**: 303–315.

Ehleringer JR, Osmond CB. 1989. *Stable isotopes*. Heidelberg, Germany: Chapman & Hall, 281–300.

Farooq M, Hussain M, Siddique KHM. 2014. Drought stress in wheat during flowering and grain-filling periods. *Critical Reviews in Plant Sciences* **33**: 331–349.

Fliessbach A, Oberholzer HR, Gunst L, Mader P. 2007. Soil organic matter and biological soil quality indicators after 21 years of organic and conventional farming. *Agriculture Ecosystems & Environment* **118**: 273–284.

von Freyberg J, Allen ST, Grossiord C, Dawson TE, Royles J. 2020. Plant and root-zone water isotopes are difficult to measure, explain, and predict: Some practical recommendations for determining plant water sources. *Methods in Ecology and Evolution* **11**: 1352–1367.

Gartner H, Lucchinetti S, Schweingruber FH. 2015. A new sledge microtome to combine wood anatomy and tree-ring ecology. *IAWA Journal* **36**: 452–459.

Gartner H, Schweingruber FH. 2013. *Microscopic preparation techniques for plant stem analysis*. Remagen, Germany: Kessel, Norbert, 18–70.

Gat JR. 2010. The isotopes of hydrogen and oxygen. In: Kwang wei T, ed. *Isotope hydrology: a study of the water cycle*. London, UK: Imperial College Press, 9–21.

Gattinger A, Muller A, Haeni M, Skinner C, Fliessbach A, Buchmann N, Mader P, Stolze M, Smith P, Scialabba NEH *et al.* 2012. Enhanced top soil carbon stocks under organic farming. *Proceedings of the National Academy of Sciences, USA* **109**: 18226–18231.

Gehre M, Geilmann H, Richter J, Werner RA, Brand WA. 2004. Continuous flow ^{2}H/^{1}H and and ^{18}O/^{16}O analysis of water samples with dual inlet precision. *Rapid Communications in Mass Spectrometry* **18**: 2650–2660.

Gleason SM, Cooper M, Wiggans DR, Bliss CA, Romay MC, Gore MA, Mickelbart MV, Topp CN, Zhang HH, DeJonge KC *et al.* 2019. Stomatal conductance, xylem water transport, and root traits underpin improved performance under drought and well-watered conditions across a diverse panel of maize inbred lines. *Field Crops Research* **234**: 119–128.

Hacke UG, Spicer R, Schreiber SG, Plavcova L. 2017. An ecophysiological and developmental perspective on variation in vessel diameter. *Plant, Cell & Environment* **40**: 831–845.

Hofer D, Suter M, Haughey E, Finn JA, Hoekstra NJ, Buchmann N, Luscher A. 2016. Yield of temperate forage grassland species is either largely resistant or resilient to experimental summer drought. *Journal of Applied Ecology* **53**: 1023–1034.

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* **50**: 346–363.

IPCC. 2018. Global warming of 1.5°C. In: Masson-Delmotte VPZ, Pörtner H-O, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, Waterfield T, eds. *An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. Cambridge, UK; New York, NY, USA: Cambridge University Press.

IPCC. 2019. *Climate change and land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems* [Shukla PR, Skea J, Calvo Buendia E, Masson-Delmotte V, Pörtner H-O, Roberts DC, Zhai P, Slade R, Connors S, van Diemen R, Ferrat M, Haughey E, Luz S, Neogi S, Pathak M, Petzold J, Portugal Pereira J, Vyas P, Huntley E, Kissick K, Belkacemi M, Malley J, eds]. in press.

Jesch A, Barry KE, Ravenek JM, Bachmann D, Strecker T, Weigelt A, Buchmann N, de Kroon H, Gessler A, Mommer L *et al.* 2018. Below-ground resource partitioning alone cannot explain the biodiversity–ecosystem function relationship: a field test using multiple tracers. *Journal of Ecology* **106**: 2002–2018.

Kanton Zürich. 2021. *Soil map of the agricultural areas*. Kanton Zürich. [WWW document] URL http://maps.zh.ch/?topic=BoKaZH [accessed 25 November 2020].

Kassambara A, Mundt F. 2020. *FACTOEXTRA: extract and visualize the results of multivariate data analyses*. [WWW document] URL https://CRAN.R-project.org/package=factoextra [accessed 18 June 2021].

Khan S, Anwar S, Shaobo Y, Gao ZQ, Sun M, Ashraf MY, Ren AX, Yang ZP. 2020. Soil water consumption, water use efficiency and winter wheat production in response to nitrogen fertilizer and tillage. *PeerJ* **8**: e8892.

Khoury CK, Bjorkman AD, Dempewolf H, Ramirez-Villegas J, Guarino L, Jarvis A, Rieseberg LH, Struik PC. 2014. Increasing homogeneity in global food supplies and the implications for food security. *Proceedings of the National Academy of Sciences, USA* **111**: 4001–4006.

Knutson CL, Haigh T, Hayes MJ, Widhalm M, Nothwehr J, Kleinschmidt M, Graf L. 2011. Farmer perceptions of sustainable agriculture practices and drought risk reduction in Nebraska, USA. *Renewable Agriculture and Food Systems* **26**: 255–266.

Kundel D, Bodenhausen N, Jorgensen HB, Truu J, Birkhofer K, Hedlund K, Mader P, Fliessbach A. 2020. Effects of simulated drought on biological soil quality, microbial diversity and yields under long-term conventional and organic agriculture. *FEMS Microbiology Ecology* **96**: fiaa205.

Kuznetsova A, Brockhoff PB, Christensen RHB. 2017. LMERTEST package: tests in linear mixed effects models. *Journal of Statistical Software* **82**: 26.

Lamanna C, Blonder B, Violle C, Kraft NJB, Sandel B, Simova I, Donoghue JC, Svenning JC, McGill BJ, Boyle B *et al.* 2014. Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences, USA* **111**: 13745–13750.

Lambers H, Oliveira RS. 2019. Plant water relations. In: *Plant physiological ecology*. Cham, Switzerland: Springer International, 187–263.

Lamy JB, Delzon S, Bouche PS, Alia R, Vendramin GG, Cochard H, Plomion C. 2014. Limited genetic variability and phenotypic plasticity detected for cavitation resistance in a Mediterranean pine. *New Phytologist* **201**: 874–886.

Li YB, Hou RX, Tao FL. 2020a. Wheat morpho-physiological traits and radiation use efficiency under interactive effects of warming and tillage management. *Plant, Cell & Environment* **44**: 2386–2401.

Li YB, Hou RX, Tao FL. 2020b. Interactive effects of different warming levels and tillage managements on winter wheat growth, physiological processes, grain yield and quality in the North China Plain. *Agriculture Ecosystems & Environment* **295**: 106923.

Loaiza Puerta V, Pereira EIP, Wittwer R, Heijden MVD, Six J. 2018. Improvement of soil structure through organic crop management, conservation tillage and grass-clover ley. *Soil & Tillage Research* **180**: 1–9.

Lorenz K, Lal R. 2016. Environmental impact of organic agriculture. *Advances in Agronomy* **139**: 99–152.

Lotter DW, Seidel R, Liebhardt W. 2003. The performance of organic and conventional cropping systems in an extreme climate year. *American Journal of Alternative Agriculture* **18**: 146–154.

Mader P, Fliessbach A, Dubois D, Gunst L, Fried P, Niggli U. 2002. Soil fertility and biodiversity in organic farming. *Science* **296**: 1694–1697.

Markwell J, Osterman JC, Mitchell JL. 1995. Calibration of the Minolta SPAD-502 leaf chlorophyll meter. *Photosynthesis Research* **46**: 467–472.

Marschner H. 2011. *Marschner's mineral nutrition of higher plants*. London, UK; Waltham, MA, USA; San Diego, CA, USA: Academic Press, 273.

Martínez DE, Guiamet JJ. 2004. Distortion of the SPAD 502 chlorophyll meter readings by changes in irradiance and leaf water status. *Agronomie* **24**: 41–46.

Mayer J, Gunst L, Mader P, Samson MF, Carcea M, Narducci V, Thomsen IK, Dubois D. 2015. Productivity, quality and sustainability of winter wheat under long-term conventional and organic management in Switzerland. *European Journal of Agronomy* **65**: 27–39.

MeteoSwiss. 2020. *Swiss Federal Office for meteorology and climatology*. [WWW document] URL https://www.meteoswiss.admin.ch/home.html?tab=overview [accessed 15 March 2020].

Nakhforoosh A, Nagel KA, Fiorani F, Bodner G. 2021. Deep soil exploration vs. topsoil exploitation: distinctive rooting strategies between wheat landraces and wild relatives. *Plant and Soil* **459**: 397–421.

Nawaz A, Farooq M, Cheema SA, Yasmeen A, Wahid A. 2013. Stay green character at grain filling ensures resistance against terminal drought in wheat. *International Journal of Agriculture and Biology* 15: 1272–1276.

Nouri A, Etminan A, da Silva JAT, Mohammadi R. 2011. Assessment of yield, yield-related traits and drought tolerance of durum wheat genotypes (*Triticum turjidum* var. *durum* Desf.). *Australian Journal of Crop Science* 5: 8–16.

OECD/FAO. 2020. *OECD-FAO agricultural outlook 2020–2029.* Rome, Italy; Paris, France: OECD; FAO.

Olson ME, Anfodillo T, Gleason SM, McCulloh KA. 2021. Tip-to-base xylem conduit widening as an adaptation: causes, consequences, and empirical priorities. *New Phytologist* 229: 1877–1893.

Parnell AC. 2020. *SIMMR: a stable isotope mixing model.* [WWW document] URL https://CRAN.R-project.org/package=simmr [accessed 11 March 2021].

Parnell AC, Phillips DL, Bearhop S, Semmens BX, Ward EJ, Moore JW, Jackson AL, Grey J, Kelly DJ, Inger R. 2013. Bayesian stable isotope mixing models. *Environmetrics* 24: 387–399.

Peltonen-Sainio P, Muurinen S, Rajala A, Jauhiainen L. 2008. Variation in harvest index of modern spring barley, oat and wheat cultivars adapted to northern growing conditions. *Journal of Agricultural Science* 146: 35–47.

Penna D, Geris J, Hopp L, Scandellari F. 2020. Water sources for root water uptake: Using stable isotopes of hydrogen and oxygen as a research tool in agricultural and agroforestry systems. *Agriculture Ecosystems & Environment* 291: ARTN 106790.

Peterson BG, Carl P, Boudt K, Bennett R, Ulrich J, Zivot E, Cornilly D, Hung E, Lestel M, Balkissoon K *et al.* 2020. *PERFORMANCEANALYTICS: econometric tools for performance and risk analysis.*

Pimentel D, Hepperly P, Hanson J, Douds D, Seidel R. 2005. Environmental, energetic, and economic comparisons of organic and conventional farming systems. *Bioscience* 55: 573–582.

Pittelkow CM, Liang X, Linquist BA, van Groenigen KJ, Lee J, Lundy ME, van Gestel N, Six J, Venterea RT, van Kessel C. 2015. Productivity limits and potentials of the principles of conservation agriculture. *Nature* 517: 365–368.

Prechsl UE, Burri S, Gilgen AK, Kahmen A, Buchmann N. 2015. No shift to a deeper water uptake depth in response to summer drought of two lowland and sub-alpine C-grasslands in Switzerland. *Oecologia* 177: 97–111.

R Core Team. 2020. *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Ramesh P, Panwar NR, Singh AB, Ramana S. 2008. Effect of organic manures on productivity, soil fertility and economics of soybean (*Glycine max*) – durum wheat (*Triticum durum*) cropping system under organic farming in Vertisols. *Indian Journal of Agricultural Sciences* 78: 1033–1037.

Roscher C, Schumacher J, Gubsch M, Lipowsky A, Weigelt A, Buchmann N, Schulze ED, Schmid B. 2018. Interspecific trait differences rather than intraspecific trait variation increase the extent and filling of community trait space with increasing plant diversity in experimental grasslands. *Perspectives in Plant Ecology Evolution and Systematics* 33: 42–50.

Santiago LS, De Guzman ME, Baraloto C, Vogenberg JE, Brodie M, Herault B, Fortunel C, Bonal D. 2018. Coordination and trade-offs among hydraulic safety, efficiency and drought avoidance traits in Amazonian rainforest canopy tree species. *New Phytologist* 218: 1015–1024.

Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, Schmid B *et al.* 2012. FIJI: an open-source platform for biological-image analysis. *Nature Methods* 9: 676–682.

Schuldt B, Knutzen F, Delzon S, Jansen S, Muller-Haubold H, Burlett R, Clough Y, Leuschner C. 2016. How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction? *New Phytologist* 210: 443–458.

Schulze ED, Beck E, Buchmann N, Clemens S, Müller-Hohenstein K, Scherer-Lorenzen M. 2019. Water relations. In: *Plant ecology, 2nd edn.* Berlin, Germany: Springer.

Sourour A, Afef O, Mounir R, Mongi BY. 2017. A review: morphological, physiological, biochemical and molecular plant responses to water deficit stress. *The International Journal of Engineering and Science* 6: 1–4.

Sun Q, Gilgen AK, Signarbieux C, Klaus VH, Buchmann N. 2021. Cropping systems alter hydraulic traits of barley but not pea grown in mixture. *Plant, Cell & Environment* 44: 2912–2924.

Swiss Federal Council. 2021. *Verordnung über die Direktzahlungen an die Landwirtschaft (Direktzahlungsverordnung, DZV) vom 23. Oktober 2013 (Stand am 1 Januar 2021) Swiss council regulation no. 910.13: Ordinance on Direct Payments of 23 October 2013 (as of 1 January 2021).*

Turner NC. 1997. Further progress in crop water relations. *Advances in Agronomy* 58: 293–338.

Werner RA, Bruch BA, Brand WA. 1999. ConFlo III – an interface for high precision δ^{13}C and δ^{15}N analysis with an extended dynamic range. *Rapid Communications in Mass Spectrometry* 13: 1237–1241.

Wittwer RA, Bender SF, Hartman K, Hydbom S, Lima RAA, Loaiza V, Nemecek T, Oehl F, Olsson PA, Petchey O *et al.* 2021. Organic and conservation agriculture promote ecosystem multifunctionality. *Science Advances* 7: eabg6995.

Wittwer RA, Klaus VH, Oliveira EM, Sun Q, Liu Y, Gilgen AK, Buchmann N, van der Heijden MGA. 2023. Limited capability of organic farming and conservation tillage to enhance agroecosystem resilience to severe drought. *Agricultural Systems* 211: 103721.

Yang JC, Zhang JH, Wang ZQ, Zhu QS, Liu LJ. 2003. Involvement of abscisic acid and cytokinins in the senescence and remobilization of carbon reserves in wheat subjected to water stress during grain filling. *Plant, Cell & Environment* 26: 1621–1631.

Zegada-Lizarazu W, Iijima M. 2004. Hydrogen stable isotope analysis of water acquisition ability of deep roots and hydraulic lift in sixteen food crop species. *Plant Production Science* 7: 427–434.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 δ^{18}O values of soil water and plant xylem water.

Fig. S2 Daily air temperature and precipitation during the growing season.

Fig. S3 Winter wheat leaf Chl content and plant height in different cropping systems.

Fig. S4 Correlation between leaf area at the end of treatment and total yield of winter wheat.

Table S1 Management operations during the growing season.

Table S2 Mean ± 1 SE of winter wheat traits.

Table S3 Characterisation of the first six principal components (PC) derived from winter wheat traits.