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Running head: Cropping Systems Alter Crop Hydraulic Traits

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Abstract

Extreme events such as drought and heatwaves are among the biggest challenges to agricultural production and food security. However, effects of cropping systems on drought resistance of arable crops via their hydraulic behaviour remain unclear. We investigated how hydraulic traits of a field-grown pea-barley (*Pisum sativum* L. and *Hordeum vulgare* L.) mixture were affected by different cropping systems, i.e., organic and conventional farming with intensive or conservation tillage. Xylem vulnerability to cavitation of both species was estimated by measuring the pressure inducing 50% loss of hydraulic conductivity (P_{50}), while the water stress plants experienced in the field was assessed using native percentage loss of hydraulic conductivity (nPLC). Pea and barley showed contrasting hydraulic behaviours: pea was less vulnerable to xylem cavitation and less stressed than barley; cropping systems affected xylem vulnerability of barley, but not of pea. Barley grown under

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conventional farming with no tillage was more vulnerable and stressed than under organic farming with intensive tillage. nPLC proved to be a valuable indicator for plant water stress. Our results highlight the impact of cropping systems on crop xylem vulnerability and drought resistance, thus plant hydraulic traits, for protecting food security under future climate.

Keywords: cavitation, conservation tillage, organic farming, xylem vulnerability

Introduction

Under changing climate, agricultural production systems will be progressively subjected to more frequent and severe drought events as well as heatwaves (IPCC, 2012, 2019). The effect of these extreme events on agricultural production represents one of the biggest challenges to food security (Boyer, 1982; Dai, 2011; Farooq, Wahid, Kobayashi, Fujita, & Basra, 2009). Thus, adaptations of farming practices to climate change require assessing the responses of different crops and cropping systems to drought (FAO, IFAD, & WFP, 2013; Vermeulen et al., 2012). Besides crop breeding and cultivar selection to reduce transpiration or increase drought resistance, some of the most important and widely discussed measures in arable agriculture include organic farming and soil conservation tillage (Follett, 2001; Tiessen, Cuevas, & Chacon, 1994). Both measures affect physical soil properties relevant for the soil water regime. For example, increased soil organic matter and improved soil structure can increase soil moisture holding capacity and thereby soil water availability, in general but maybe also longer into a drought (Colombi et al., 2019; Fliessbach, Oberholzer, Gunst, & Mader, 2007; Hudson, 1994). In addition, organic matter increases the diversity and activity of soil organisms, which have been reported to improve drought resistance of crops (Auge, 2001; Bot & Benites, 2005; Gosling, Hodge, Goodlass, & Bending, 2006; Grover, Ali, Sandhya, Rasul, & Venkateswarlu, 2011). Moreover, soil conservation practices (i.e., reduced or no tillage) have been proposed to improve soil texture by forming soil aggregates (Loaiza Puerta, Pereira, Wittwer, Heijden, & Six, 2018), to increase carbon sequestration (Emmel et al., 2018; Lal, 1997), and to reduce energy consumption (Holland, 2004; Wittwer, Dorn, Jossi, & van der Heijden, 2017). On the other hand, intensive tillage can be helpful for improving infiltration and water harvesting (Falkenmark & Rockstrom, 2006) and for reducing weed pressure (O'Donovan & McAndrew, 2000). However, if these cropping systems can outweigh any benefits of breeding when a drought actually occurs, remains to be seen (Messina et al., 2015). Especially, how plant-water relations and crop productivity change under different cropping systems, and how drought resistance of crops can be increased by farming practices is currently unclear.

To better understand the drought resistance of crops, their hydraulic behaviour needs to be investigated. Droughts, i.e. conditions with low soil water availability, high atmospheric water demand or the combination thereof, can lead to xylem hydraulic failure (Anderegg, 2015). In other words, as soil water potentials decline and the tension of the water in the xylem increases due to continued transpiration, the water being transported in the xylem might undergo a phase-change from liquid to gas. As a result, air bubbles (emboli) will form within the xylem conduits, slowing and even stopping the conductance of liquid water. As emboli spread in the xylem under tension, the water conduits become "embolised", also called "cavitated" (Sperry & Tyree, 1988). Hydraulic failure and thereby drought vulnerability of plants can be assessed by studying the relationship between the percentage loss of hydraulic conductivity (PLC, Cochard et al., 2013; Tyree & Sperry, 1989) and xylem water potential, which is typically referred to as a vulnerability curve (VC; Sperry, Stiller, & Hacke, 2003). It is commonly an S-shaped curve fitted with sigmoidal functions (Pammenter & Vander Willigen, 1998). The P_{50} value, i.e., the xylem water potential when 50% of hydraulic conductivity is lost (Pammenter & Vander Willigen, 1998), is one of the most commonly used hydraulic thresholds for assessing xylem vulnerability to drought. The higher the P_{50} value (i.e., the less negative the xylem water potential), the higher the xylem vulnerability to cavitation. Combining these VCs, assessed in the laboratory by the Cavitron technique (Cochard, 2002), with xylem water potential measurements in the field, the range of native PLC (nPLC) can then be estimated (Lens et al., 2016; Stiller & Sperry, 2002), i.e., the water stress that plants experience in the field. As xylem hydraulic conductivity is influential for plant physiological processes and consequently biomass production, maintaining a low nPLC which allows high water transport is beneficial for overall plant performance (Gleason et al., 2019; Wang, Du, Huang, Peng, & Xiong, 2018; Zhu et al., 2021). Therefore, farming practices and crop improvement programs which aim at maintaining plant water uptake and transport, thus avoiding water stress and yield reductions, might be effective means to adapt to climate change (Timothy J. Brodribb, Holloway-Phillips, & Bramley, 2015; Holloway-Phillips & Brodribb, 2011; Vitra et al., 2019). However, how exactly xylem vulnerability and nPLC might further be associated with specific plant growth traits and biomass production, will need further investigation.

While the majority of research on xylem vulnerability has focused on trees and other woody species (see Jansen, Baas, Gasson, Lens, & Smets, 2004; McCulloh, Domec, Johnson, Smith, & Meinzer, 2019; Olson et al., 2018), studies on herbs or grasses are generally scarce. On the one hand, this is probably due to the technical difficulties in conducting measurements on non-woody tissues, e.g., their fragility and relatively lower hydraulic conductivities. On the other hand, crop hydraulics might not have gained similar attention as tree hydraulics since crops are more heavily bred for certain traits or even irrigated. Moreover, most studies on non-woody plant species took place under controlled conditions in pots, and only a few studies were conducted under field conditions (Gleason et al., 2017; Neufeld et al., 1992; Stiller, Lafitte, & Sperry, 2003). Hence, the knowledge on hydraulic failure of crops and the consequences for agricultural systems is still considerably limited (Lamarque et al., 2020; McDowell, Brodribb, & Nardini, 2019), strongly restricting our ability to identify solutions for improving crop drought resistance and safeguarding food security.

In this study, we aimed to determine whether organic farming and soil conservation tillage affect crop vulnerability to cavitation, and hence crop drought resistance in the field. We focused on a pea-barley (*Pisum sativum* L. and *Hordeum vulgare* L.) mixture, an important intercrop that provides animal feed and can be used as cover crop (Gilliland & Johnston, 1992). Specifically, this research aimed to (1) identify hydraulic traits of pea and barley grown under field conditions; (2) determine their vulnerability when grown under different cropping systems; and (3) assess the potential implications of plant hydraulic vulnerability on yields.

Materials and Methods

Research site and experimental setup

The study was conducted at the Swiss Federal Agricultural research station Agroscope in Zurich-Reckenholz, Switzerland (47.44° N, 8.53° E, 4.6 km from the research site) within the Farming Systems and Tillage experiment (FAST; for details see Wittwer et al., 2017). The soil at the field site is a calcareous Cambisol with 23% clay, 34% silt, and 43% sand, and an organic carbon content of 1.6 to 1.8% (Loaiza Puerta et al., 2018). The long-term average annual precipitation is 994 mm, and the mean annual temperature is 9.7 °C (1988 to 2017; MeteoSwiss).

The FAST experiment began in 2009 with a six-year crop rotation typical for Swiss cropping systems, including conventional and organic farming as well as intensive and soil conservation tillage systems. The conventional systems are managed according to the "Proof of Ecological Performance" (PEP) guidelines of the Swiss Federal Office for Agriculture, which allow synthetic fertilisers and pesticide applications. Intensive tillage (IT) with a plough to 20 cm depth and a rotary harrow to 5 cm depth for seedbed preparation was applied in both conventional (C-IT) and organic systems (O-IT). Direct sowing and no soil management (but herbicide spraying) were implemented in the no tillage conventional plots (C-NT). A disc or rotary harrow (5 cm depth), which superficially disturbed the soil for weed control, was used for reduced tillage in organically managed plots (O-RT). A total of 16 experimental plots (four cropping systems × four replicates) were investigated. In 2018, a pea (*Pisum sativum* L. cv. 'Alvesta') and barley (*Hordeum vulgare* L. cv. 'Eunova') mixture was sown in all plots on 26 March 2018 and harvested on 12 July 2018. No fertilisation was applied to the pea-barley mixture because pea plants were expected to provide sufficient nitrogen supply through rhizobium symbiosis.

Precipitation and soil water content

Precipitation data were obtained from a nearby MeteoSwiss station, Zürich/Kloten (KLO, 47.48° N, 8.54° E, 4.6 km from the research site). The study year (2018) was extremely warm with a mean annual temperature of 11.2 °C and an annual precipitation of 854 mm considerably below the long-term average (Fig. S1). Particularly, June 2018 had the lowest precipitation recorded in the last 30 years (MeteoSwiss). Therefore, this natural drought in 2018 (Gharun et al., 2020) provided an ideal opportunity to study the effect of different cropping systems on plant hydraulic traits. Soil water content (SWC) was continuously recorded at 10 and 40 cm depths with two replicates per cropping system (EC-5, Decagon Devices Inc., Pullman, WA, USA). Data were averaged at 10 min intervals by data loggers (CR1000 and CR216, Campbell Scientific Ltd., Loughborough, UK).

Vulnerability to cavitation and hydraulic traits

To assess vulnerability to cavitation, plants were cut 1 cm above the ground between 07:00 h and 11:00 h on a cloudy day (7 June 2018). Eight to ten individuals per species were collected from each plot. The stems were promptly defoliated to reduce water loss by transpiration, then cut to 40 cm length, wrapped in wet paper tissue, and sealed in a plastic bag to minimise dehydration during transport to the laboratory within two days. Upon arrival in the laboratory, the samples were kept in a fridge before finishing all measurements within three days. A flow-centrifuge method, i.e., Cavitron technique, housed at University of Bordeaux (France), was used to generate vulnerability curves (VCs; Cochard, 2002; Cochard et al., 2005). Stems were completely rehydrated in water before the measurements to ensure that no functional vessels would be even partially embolised and bias the results. Prior to the measurements, stems were cut again underwater to 27 cm length. To increase the water flow, four to six stems were grouped to a bundle with a diameter between 1 and 2.5 cm for each VC measurement. The stem segments were then fixed to water reservoirs at both ends. Three to five bundles were measured for pea and four to six for barley per cropping system. The Cavitron technique generates negative pressure at the central part of the measured stem segments, and at the same time measures the mass flow of water transported through the stems from the reservoirs to calculate xylem hydraulic conductance (after Alder, Pockman, Sperry, & Nuismer, 1997). The negative pressure is gradually decreased by 0.3 to 0.6 MPa, by spinning the stems with a 27 cm diameter rotor, until the measured conductance reaches 0. PLC was calculated according to Equation (1):

$$PLC = \left(1 - \frac{K}{K_{max}}\right) \times 100, \qquad (1)$$

where K (m^2 MPa^{-1} s^{-1}) is the conductance measured as water flowed through the stem segment under a given pressure (i.e., water potential), and K_{max} is the maximum conductance of the stem segment measured at a xylem water potential of 0 MPa.

VCs were obtained for each measurement by fitting the relationship of PLC and xylem water potential (ψ_x) according to Equation (2):

$$PLC_{fit} = \frac{100}{1 + exp\left(\frac{slope}{25} \times (\psi_x - P50)\right)}, \tag{2}$$

where P_{50} (MPa) is the ψ_x when 50% of xylem hydraulic conductivity is lost, and *slope* (% MPa^{-1}) is the slope of the VC at the inflection point (Pammenter & Vander Willigen, 1998). A non-linear fitting with the optimisation function, *optim()*, from base R (v3.6.2; R Core Team, 2020) was used to obtain the parameters of Equation (2), i.e., P_{50} and *slope*. The native PLC (nPLC) can then be determined using Equation (2) and the midday plant water potential measured in the field, based on the assumption that the VC does not change during the experimental period. P_{12} and P_{88} are additional commonly used hydraulic thresholds of ψ_x when 12 and 88% of hydraulic conductivity is lost, respectively. The slope at the inflection point indicates how fast cavitation and embolism developed in the xylem (Domec & Gartner, 2001). The highest nPLC recorded for each plot was noted as $nPLC_{max}$.

Plant water potentials were measured on one plant per species per plot in the field with a Scholander pressure chamber (SKPM, Skye Instruments Ltd., Powys, UK). We used stems cut below the top leaves for pea and youngest mature leaves for barley, which was also used as proxy for plant water potentials to calculate nPLC. Predawn measurements (ψ_{pd}) took place between 03:00 h and 05:00 h on 2 and 28 June 2018; midday measurements (ψ_{md}) were taken on sunny days between 11:00 h and 13:00 h during the driest period of the growing season, on 15, 20, and 26 June 2018.

Plant height and aboveground biomass

Plant height was measured from the ground to the growing point for pea plants and from the ground to the youngest leaf auricle for barley. This was done with a ruler with 10 replicates per species in each plot on 22 May, 6 and 20 June 2018 and then averaged per species per plot for each measurement date. Aboveground biomass was collected within two 0.25 m^2 areas per plot by cutting the plants 1 cm above the ground before harvest. Grain yield and straw biomass for pea and barley were separated and weighed for fresh weight before and dry weight after oven drying at 60 °C until dry weight was constant. Pea plant number and barley stem number were counted at harvest time to calculate biomass per plant and per stem, respectively. Total aboveground biomass was the sum of grain yield and straw biomass. Grain dry matter content (DM) and harvest index (HI) were calculated according to Equations (3) and (4), respectively:

$$DM = \frac{dry\ grain\ weight}{fresh\ grain\ weight} \tag{3}$$

$$HI = \frac{grain\ yield}{total\ aboveground\ biomass} \tag{4}$$

Statistical analyses

All statistical analyses were carried out using R (v3.6.2; R Core Team, 2020). The effects of cropping systems were tested with linear effect mixing models using the function *lmer()* from the R package 'lmerTest' (Kuznetsova, Brockhoff, & Christensen, 2017). Differences among cropping systems were tested by the Tukey HSD (honestly significant difference) test with "BH method" (Benjamini & Hochberg, 1995) using the function *glht()* from the R package 'multcomp' (Hothorn, Bretz, & Westfall, 2008). Differences between pea and barley were assessed using Student's t-tests.

Results

Xylem vulnerability to cavitation of pea and barley

The VCs for pea showed a steep S-shape, with very low PLC values for xylem water potentials (ψ_x) between 0 and -2 MPa for all cropping systems, and a quick development of PLC between -2.5 and

-3.5 MPa, until reaching very high PLC values below -4 MPa (Fig. 1). The P_{12} threshold for pea was reached between -1.98 and -2.47 MPa, while P_{50} ranged from -2.84 to -3.03 MPa, and P_{88} was finally reached between -3.70 and -4.04 MPa (Table 1). In contrast, barley showed flatter curves compared to pea. VCs of barley developed gradually and reached P_{12} at relatively high ψ_x, between -0.87 and -1.07 MPa. The P_{50} of barley was already reached from -2.04 to -2.92 MPa, and P_{88} from -3.21 to -4.77 MPa (Table 1). Thus, the xylem of pea was less vulnerable at high ψ_x, with significantly lower P_{12} and P_{50} values, compared to barley ($P < 0.001$). However, once pea ψ_x reached P_{12}, cavitation progressed significantly faster in pea than in barley as indicated by steeper VCs ($P = 0.004$). The P_{88} thresholds of pea and barley were not significantly different from each other (Table 1), indicating that a ψ_x below c. -3.45 MPa would be highly dangerous if not fatal for both pea and barley.

Besides the general shape, also the VCs of the different cropping systems for pea and barley were different. For pea, the four VCs were very similar and the xylem vulnerability to cavitation was not affected by the different cropping systems (Fig. 1). Although not significantly different among cropping systems, pea under C-NT tended to be the most vulnerable, while the least vulnerable under C-IT. On the other hand, the VCs of the four cropping systems for barley were more distinct (Fig. 1). Cropping systems significantly affected P_{50} and P_{88} of barley ($P = 0.045$ and 0.024, respectively; Table 1). Barley plants grown under C-NT were more vulnerable to cavitation as indicated by higher P_{50} and P_{88} values (-2.04 and -3.21 MPa, respectively), followed by those under O-RT and C-IT. Barley under O-IT were least vulnerable, with lower P_{50} and P_{88} values (-2.92 and -4.77 MPa, respectively).

Plant water potentials in situ and native percentage loss of conductivity

Precipitations in 2018, and particularly between end of June and beginning of July, were exceptionally low (Fig. 2a). Thus, soil moisture at 10 cm and 40 cm depths dropped to relatively low values, which were slightly higher in organic compared to conventional cropping systems (Fig. 2b, c). Consequently, ψ_{pd} was significantly reduced by the end of June compared to early June for both species. On average, pea exhibited ψ_{pd} values from -0.15 to -0.73 MPa, and barley from -0.14 to -0.69 MPa (Fig. 3, Table S1).

Nevertheless, in none of the cropping systems pea ψ_{md} values exceeded P_{12}, which represents the threshold for embolism development (Fig. 4a). While pea under O-IT had the highest $nPLC_{max}$ of 11% (P = 0.009) due to the lowest ψ_{md} (albeit not significant), plants grown under all other cropping systems showed values only between 2 and 6% (Fig. 4b, Table 2), clearly indicating that negligible cavitation occurred in pea during the dry summer 2018. Much in contrast, barley ψ_{md} values (-1.87 to -2.31 MPa) were very close to the P_{50} values (-2.04 to -2.92 MPa) during this dry period (late June 2018; Fig. 4c). Although cropping systems did not have a significant effect on barley ψ_{md} (Fig. 4c), barley nPLC was significantly affected by cropping systems (Fig. 4d). Barley plants grown under C-NT were the most stressed, showing nPLC values of 54% on average, while the least stressed under O-IT, with nPLC values of 27% on average (Table 2). Moreover, drought stress as indicated by $nPLC_{max}$ was also significantly affected by cropping systems for barley (P < 0.001; Table 2). Similarly to P_{50} and P_{88} values, barley plants were the most stressed under C-NT with the highest $nPLC_{max}$ (68%), followed by O-RT and C-IT (52 and 49%, respectively), while the least stressed under O-IT with the lowest $nPLC_{max}$ (32%; Fig. 4d, Table 2). In addition, barley plants with higher xylem vulnerability, indicated by high P_{50} and P_{88} values, were also more stressed, shown by field-derived $nPLC_{max}$ being positively related with P_{50} and P_{88} (Fig. 5). No such relationship was found for pea (data not shown).

Plant height

Cropping systems significantly affected plant height of pea and barley (P < 0.05 except for pea at the end of June; Table S1). Under intensive tillage (C-IT and O-IT), pea plants were generally taller and barley plants had longer stems than those under soil conservation tillage (C-NT and O-RT). However, despite those height differences, no relationships of plant height with P_{50} or $nPLC_{max}$ were observed for pea (data not shown), supported by similar P_{50} values and low $nPLC_{max}$ values for pea in all four cropping systems. In contrast, taller barley plants were less vulnerable (lower P_{50}

value) and less stressed (lower $nPLC_{max}$ value) than shorter ones, as shown by the significant negative correlations of barley plant height with P_{50} and $nPLC_{max}$ (Fig. S2). Moreover, relationships of barley plant theight with $nPLC_{max}$ were consistently stronger than with P_{50}.

Aboveground biomass and grain yield

For pea, cropping systems showed no impact on total aboveground biomass and grain yield per plant or on harvest index (HI), but on grain dry matter content (DM; $P = 0.016$). Nevertheless, pea tended to have higher grain yield per plant under C-NT than under O-RT (Table S1). In comparison, cropping systems affected barley grain yield per stem ($P = 0.021$), grain DM ($P < 0.001$), and HI ($P = 0.002$), but not total aboveground biomass per stem ($P = 0.239$; Table S1). Barley under C-IT and O-IT had significantly higher grain yield per stem, grain DM and HI, followed by O-RT, whereas C-NT had the lowest yield. In addition, the more stressed barley plants were (i.e., higher $nPLC_{max}$ value), the lower their grain yield per stem, grain DM, and HI, as shown by the negative relationships with $nPLC_{max}$ (Fig. 6). No significant relationships were found between aboveground biomass or grain yield with ψ_{pd} or ψ_{md} for pea nor barley.

Discussion

Research on the xylem vulnerability of crop species is still rare, especially under field conditions (Table 3), as most of the studies on crops (c. 80%) took place in pots under controlled conditions. The majority of studies focussed on grass species (both C_3 and C_4), while only two legume species were studied, common bean (Holste, Jerke, & Matzner, 2006) and pea (this study). Moreover, different methods were employed, most likely contributing to some variability in the reported P_{50} values (but see Venturas et al., 2019; Yin et al., 2019). Our P_{50} values for barley and pea were within the ranges of other field studies. Pea had a significantly lower stem xylem vulnerability (e.g., lower P_{12} and P_{50} values) than barley, in agreement with a recent review which showed field pea having a lower yield reduction under water limitation than barley (Daryanto, Wang, & Jacinthe, 2017), but in contrast to Lens et al. (2016) who did not find a significant general difference in stem P_{50} values between grasses and herbaceous dicots using a global dataset. Thus, understandings on the vulnerability to hydraulic failure for a wide variety of crops remain insufficient, increasing the uncertainty for food security under future climate conditions.

Selection of crop species as well as cropping systems can help to ensure agricultural production. Here, we demonstrated that cropping systems affected xylem vulnerability (reflected in P_{50}) and water stress (shown by $nPLC_{max}$) of barley, but not of pea, although the same seed mixture was sown in all plots. This excluded genetic diversity as an explanation for the observed differences, but rather indicated phenotypic acclimation to the respective cropping systems. P_{50} values for barley showed a wide range of 0.88 MPa , with plants being more vulnerable under C-NT (P_{50} of -2.04 MPa) than under O-IT (P_{50} of -2.92 MPa; Table 1). Since $nPLC_{max}$ was positively correlated with P_{50} (Fig. 5), this translated to an identical ranking for water stress (Table 2). Barley plants were most water-stressed under C-NT ($nPLC_{max}$ of 68%) and least under O-IT ($nPLC_{max}$ of 32%), with O-RT and C-IT being intermediate ($nPLC_{max}$ of c. 50%). Thus, particularly for C-NT, water potentials in barley were close to or below P_{50} during June/July 2018, while barley grown under O-IT suffered much less, typically losing < 30% of their hydraulic conductivity. Lower soil water contents at 40 cm in C-NT compared to O-IT during the dry period (Fig. 2) supported this ranking. This situation was most likely further intensified by differences in soil hydraulic conductivity among cropping systems, driven by the type of tillage. It is well known that soils under conservation tillage have lower total porosity and less macropores in the top soil compared to intensive tillage (e.g., Colombi et al., 2019; Kay & VandenBygaart, 2002), leading to lower saturated soil hydraulic conductivity (see Strudley, Green, & Ascough, 2008). Indeed, estimating saturated soil hydraulic conductivity for our plots, based on soil texture and bulk density at 10 cm depth using the Rosetta database (Schaap, Leij, & van Genuchten, 2001), resulted in significantly lower values for C-NT (22 cm d^{-1}) and O-RT (25 cm d^{-1}) than O-IT (59 cm d^{-1}), with C-IT being intermediate (40 cm d^{-1}). The low soil water supply to plant roots in C-NT compared to O-IT triggered phenotypic changes in xylem hydraulic traits as observed for barley in this study. Similar acclimation with higher stem xylem vulnerability in soils with lower saturated soil hydraulic conductivity was also reported by Holste, Jerke, and Matzner (2006), while Hacke et al. (2000) reported the opposite pattern for *Pinus taeda*. However, annual herbaceous species are known to have different strategies than long-lived perennial trees and to show different responses to environmental factors, including soil conditions (e.g., McCulloh et al., 2019). Nonetheless, the trade-off between xylem hydraulic conductivity and xylem vulnerability (see Brodersen, 2016; Liu, Kang, Davies, & Ding, 2020; Sperry et al., 2003) can be highly relevant when selecting different cropping systems as well, since the physical conditions created by the respective soil management (tillage) can have unwanted consequences on plant hydraulic traits and thus their drought resistance. However, these pronounced consequences on plant hydraulic traits were not observed in pea. While the P_{50} values of pea tended to be lower for C-NT than for the others, the differences were very small (0.27 MPa) and insignificant (Table 1). Although the $nPLC_{max}$ values of pea differed among cropping systems, they never exceeded 11% (Table 2), clearly showing that pea was never severly stressed. This might be due to their N_2 fixing capability. Field studies, both experimental (Signarbieux & Feller, 2011) and based on observations (Adams, Buchmann, Sprent, Buckley, & Turnbull, 2018), showed that N_2-fixing plants can maintain low stomatal conductance when water is limited without compromising photosynthesis due to high foliar N concentrations. Therefore, unfavourable soil hydraulic conditions might not affect pea to the same extent as barley. Whether soil depths for root water uptake also generally differ between legumes and grasses is not fully clear and might be species-specific (Bachmann et al., 2015; Hoekstra, Finn, Hofer, & Lüscher, 2014). Nevertheless, since N_2-fixing legume crops also spare soil mineral N (Temperton, Mwangi, Scherer-Lorenzen, Schmid, & Buchmann, 2007), they can be considered highly beneficial crop species for climate mitigation, withstanding frequent drought events in the future.

In addition to management, xylem vulnerability was also expected to relate to plant height and crop yields. No effect of cropping systems was found on total aboveground biomass production of barley nor pea (Table S1), probably since they are bred for grain (or pod) yield. Yet, we found strong effects of cropping systems on plant height and grain yield for both species (Table S1). This was mirrored by strong negative relationships between plant height and grain yield with P_{50} and $nPLC_{max}$ for barley (Fig. S2, Fig. 6). When functioning at lower nPLC (e.g., $nPLC_{max}$ 32.1% under O-IT and 49.4% under C-IT), plants can potentially maintain a relatively high transpiration rate compared to plants with higher nPLC (e.g., $nPLC_{max}$ of 51.6% under O-RT and 67.6% under C-NT). Then this behaviour might lead to roots taking up more water from the soil and consequently higher soil water redistribution to the root zone (Couvreur, Vanderborght, Beff, & Javaux, 2014; Logsdon, 2019; Sprenger, Leistert, Gimbel, & Weiler, 2016), thereby extracting soil water that would otherwise be unavailable to the plant. The higher grain yield of barley under C-IT and O-IT compared to plants under C-NT and O-RT may have resulted from higher soil water extraction. This relationship was not observed for pea, most probably because even the lowest ψ_{md} values recorded for pea were still higher than the P_{12} values for all cropping systems (Table S1).

Lastly, the nPLC values proved to be highly sensitive to soil conditions created by the cropping systems, reflecting differences better than the classical plant ψ_{md} (Fig. 4). Moreover, $nPLC_{max}$ values, but not ψ_{md}, were significantly correlated with barley grain yield and harvest index, suggesting that $nPLC_{max}$ might be a better indicator than ψ_{md} for water stress of certain crops.

Conclusion

The emphasis of this study was to understand the impact of cropping systems on crop hydraulic traits and their vulnerability, which, to the best of our knowledge, is the first study to report such work. Barley, but not pea, clearly responded to the different cropping systems with altered xylem vulnerability, thus with phenotypic acclimation. These results highlight the potential of cropping systems, in particular the organic intensive tillage system, as well as of legume crops for climate change adaptation in arable agriculture. Moreover, we suggest using $nPLC_{max}$ as a more sensitive and therefore better indicator for plant water stress since it proved to be more responsive to environmental conditions compared to the classical plant water potentials. Thus, the outcomes of this study provide important implications of plant hydraulics for future crop breeding and management as well as food security in the face of climate change.

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Author Contribution

QS, CS, and NB designed the study; QS, AKG, VHK, and CS carried out fieldwork including sensor installation, samplings, and measurements; QS analysed the data; QS, AKG, and NB wrote the first drafts of the manuscript; all authors discussed the results, revised and agreed on the final version of the manuscript.

Conflict of Interest

None declared.

Supporting Information

Additional supporting information can be found in the online version of this article.

Table S1 Water potentials for pea (*Pisum sativum* L.) and barley (*Hordeum vulgare* L.), plant height, aboveground biomass and grain yield per plant for pea and per stem for barley, grain dry matter content and harvest index for pea and barley under different cropping systems in 2018.

Fig. S1 Long-term annual and June air temperatures and precipitation from a nearby weather station.

Fig. S2 Relationships between barley (*Hordeum vulgare* L.) plant height measured on different dates and xylem water potential at 50% loss of hydraulic conductivity (P_{50}), as well as the highest native percentage loss of hydraulic conductivity ($nPLC_{max}$) of barley during soil drying period.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Table 1 Hydraulic thresholds (the xylem water potentials at 12, 50, and 88% loss of hydraulic conductivity: P_{12}, P_{50}, and P_{88}, in MPa) and the slope of vulnerability curves (in % MPa^{-1}) for pea (*Pisum sativum* L.) and barley (*Hordeum vulgare* L.) under different cropping systems (n = 3 to 5 for pea and 4 to 6 for barley) measured on 7 June 2018.

Species	Threshold	Mean ± 1 SE				Cropping systems			Pea vs barley
		C-IT	C-NT	O-IT	O-RT	df	*F*	*P*	*P*
Pea	P_{12}	-2.47 ± 0.30	-1.98 ± 0.53	-2.00 ± 0.37	-2.19 ± 0.37	3	0.34	0.796	< 0.001 ***
	P_{50}	-3.11 ± 0.11	-2.84 ± 0.30	-3.02 ± 0.15	-3.03 ± 0.16	3	0.31	0.815	< 0.001 ***
	P_{88}	-3.75 ± 0.08	-3.70 ± 0.16	-4.04 ± 0.32	-3.87 ± 0.07	3	0.43	0.734	0.983
	slope	101.4 ± 40.9	72.4 ± 26.1	69.5 ± 17.5	74.0 ± 20.2	3	0.32	0.814	0.004 **
Barley	P_{12}	-0.98 ± 0.17	-0.87 ± 0.08	-1.07 ± 0.29	-0.88 ± 0.21	3	0.27	0.848	
	P_{50}	-2.53 ± 0.17 ab	-2.04 ± 0.19 b	-2.92 ± 0.25 a	-2.27 ± 0.17 ab	3	3.41	0.045 *	
	P_{88}	-4.08 ± 0.23 ab	-3.21 ± 0.40 b	-4.77 ± 0.23 a	-3.67 ± 0.30 ab	3	4.04	0.024 *	
	slope	33.2 ± 2.7	49.6 ± 7.7	27.0 ± 0.9	38.9 ± 5.8	3	2.90	0.07	

C-IT, Conventional intensive tillage; C-NT, Conventional no tillage; O-IT, Organic intensive tillage; O-RT, Organic reduced tillage; df, degrees of freedom.

Effects of cropping systems were tested with linear mixed models (lmm). Different letters indicate significant differences among cropping systems tested with Tukey HSD ($P < 0.05$). Differences in the thresholds and slope between pea and barley were tested with a t-test (n = 15 for pea and n = 21 for barley). Asterisks indicate significant effects of cropping systems or differences between pea and barley.

Table 2 Native percentage loss of hydraulic conductivity (nPLC, in %) on different dates as well as the highest nPLC ($nPLC_{max}$, in %) of pea (*Pisum sativum* L.) and barley (*Hordeum vulgare* L.) under different cropping systems (n = 4) during 15 to 26 June 2018.

Species	Variable	Date	Mean ± 1 SE				Cropping systems		
			C-IT	C-NT	O-IT	O-RT	df	*F*	*P*
Pea	nPLC	15 Jun	1.5 ± 0.2 a	2.7 ± 0.6 ab	5.5 ± 1.7 b	0.9 ± 0.3 a	3	4.68	0.022 *
		20 Jun	1.4 ± 0.1	3.9 ± 1.1	7.1 ± 3.4	3.0 ± 1.4	3	1.63	0.25
		26 Jun	2.4 ± 0.4 a	5.1 ± 1.1 b	5.7 ± 1.2 b	1.5 ± 0.2 a	3	8.21	0.006 **
		15 to 26 Jun (average)	1.7 ± 0.2 a	3.9 ± 0.8 b	6.1 ± 0.7 c	1.8 ± 0.6 a	3	11.80	0.002 **
	$nPLC_{max}$	15 to 26 Jun	2.4 ± 0.4 a	5.6 ± 1.1 a	10.8 ± 2.4 b	3.1 ± 1.4 a	3	7.36	0.009 **
Barley	nPLC	15 Jun	47.1 ± 2.0 b	62.9 ± 6.8 c	32.1 ± 2.5 a	44.4 ± 4.5 b	3	9.35	0.004 **
		20 Jun	36.6 ± 1.6 b	46.8 ± 4.3 c	23.0 ± 1.0 a	34.1 ± 3.5 b	3	11.02	0.001 **
		26 Jun	42.8 ± 5.4 b	51.0 ± 6.4 b	27.4 ± 1.8 a	46.4 ± 4.9 b	3	5.59	0.019 *
		15 to 26 Jun (average)	42.2 ± 2.1 b	53.6 ± 2.3 c	27.5 ± 1.0 a	41.6 ± 2.3 b	3	40.63	< 0.001 ***
	$nPLC_{max}$	15 to 26 Jun	49.4 ± 3.5 b	67.6 ± 2.2 c	32.1 ± 2.5 a	51.6 ± 2.2 b	3	29.98	< 0.001 ***

C-IT, Conventional intensive tillage; C-NT, Conventional no tillage; O-IT, Organic intensive tillage; O-RT, Organic reduced tillage; df, degrees of freedom.

Effects of cropping systems were tested with linear mixed models (lmm). Asterisks indicate significant effects of cropping systems, while different letters indicate significant differences among cropping systems tested with Tukey HSD ($P < 0.05$).

Table 3 Studies on xylem vulnerability to cavitation of herbaceous crops.

Plant species	Experimental setup	Method(s)[a]	Organ	P_{50} value (MPa)	Reference(s)
Common bean (*Phaseolus vulgaris* L.)	P, CE	Centrifuge with CA	Stem	Control: -0.43 Drought: -0.45 Low light: -0.59 Porous soil: -0.66 Low P: -0.38	Holste et al. (2006), Alder et al. (1997)
	P, CE, two cultivars	Centrifuge with CA	Stem	High light: ca. -0.47 to -0.80 Medium light: ca. -0.46 to -0.80 low light: ca. -0.40 to -0.43 Low water: ca. -0.75 to -1.0 High water: ca. -0.6 to -1.0	Matzner, Rettedal, Harmon, and Beukelman (2014), 2019)
Corn (*Zea mays* L.)	P, CE, two hybrids	Centrifuge with CA	Stem	-1.56 and -1.78	Li, Sperry, and Shao (2009)
	P, CE	Dehydration with conductivity calculated by transpiration	Whole plant	-1.29	Gleason et al. (2017), Sperry, Donnelly, and Tyree (1988)
	F	Dehydration with CA	Stem	-1.15	
	P, CE, different CO_2 concentration	Centrifuge with CA	Stem	Control: -0.78 to -1.83 Drought: -0.77 to -2.56	Liu et al. (2020)
Perennial ryegrass (*Lolium perenne* L.)	P, CE	Dehydration with rehydration kinetics	Leaf	-1	Holloway-Phillips and Brodribb (2011)
Rice (*Oryza sativa* L.)	F; P, CE, different varieties	Centrifuge with CA	Stem	Greenhouse: -1.6	Stiller et al. (2003)
			Leaf	Greenhouse: -1.9	
		Dehydration with CA	Leaf	Field: -1.6	
Sugarcane (*Saccharum sp.* L.)	F, different clones	Dehydration with CA	Leaf	-0.83 to -1.36	Neufeld et al. (1992)
Sunflower (*Helianthus annuus* L.)	P, GH	Centrifuge with CA	Stem	Control: -3.0 Drought: -0.8 Re-watering: -3.3	Stiller and Sperry (2002)
	P, GH	Dehydration with CA Dehydration with X-ray	Stem	-1.74 -0.87	Savi et al. (2017)
	P, CE, different varieties	Centrifuge with CA (Cavitron)	Stem	-2.67 to -3.22	Ahmad et al. (2018)
Tomato (*Solanum lycopersicum* L.)	P, CE	Dehydration with X-ray	Root	P_{40}[b]: -1.38	Skelton, Brodribb, and Choat (2017), Brodribb, Bienaime, and Marmottant (2016)
			Stem	P_{40}: -1.58	
		Dehydration with visual inspection	Leaf	P_{40}: -1.49 to -1.59 -1.68	
		Dehydration with rehydration kinetics		-1.54	
	P, CE, a wild type and a transgenic line	Centrifuge with CA (Cavitron) Dehydration with X-ray Centrifuge with CA (Cavitron)	Stem	90-day-old: -1.99 to -2.55 120-day-old: -1.52 to -2.69 170-day-old: -2.79 to -3.10	Lamarque et al. (2020)
Wheat (*Triticum aestivum* L.)	P, CE	Dehydration with visual inspection	Leaf	-2.87	Johnson, Jordan, and Brodribb (2018)
	P, CE	Dehydration with X-ray	Stem	-2.44	Corso et al. (2020)
		Dehydration with X-ray and visual inspection	Leaf	-2.22	
Pea (*Pisum sativum* L.)	F, different cropping systems	Centrifuge with CA (Cavitron)	Stem	-2.84 to -3.11	This study
Barley (*Hordeum vulgare* L.)				-2.04 to -2.92	

[a] How cavitation is induced and assessed.

[b] Values for root and stem reported by Skelton et al. (2017) were P_{40} instead of P_{50}.

P, pot experiment; F, field experiment; CE, controlled environment; GH, greenhouse; CA, conductivity apparatus.

Fig. 1 Vulnerability of stem hydraulic conductivity to cavitation for pea (*Pisum sativum* L.) and barley (*Hordeum vulgare* L.) under different cropping systems (Conv. for conventional, Org. for organic) measured on 7 June 2018. Mean vulnerability curves are fitted with Equation (1) for pea and barley (n = 3 to 5 for pea and n = 4 to 6 for barley under each cropping system). The symbols on the curves correspond to the mean xylem water potential at 50% loss of hydraulic conductivity (P_{50}) of pea and barley. The shaded areas indicate 1 SE of P_{50}. The horizontal dashed lines indicate the thresholds when 12, 50, or 88% loss of hydraulic conductivity as labelled. Asterisks at the three levels of threshold indicate significant effects of cropping systems according to linear mixed models: * $0.01 \leq P < 0.05$. Different letters indicate significant differences among cropping systems tested with Tukey HSD ($P < 0.05$).

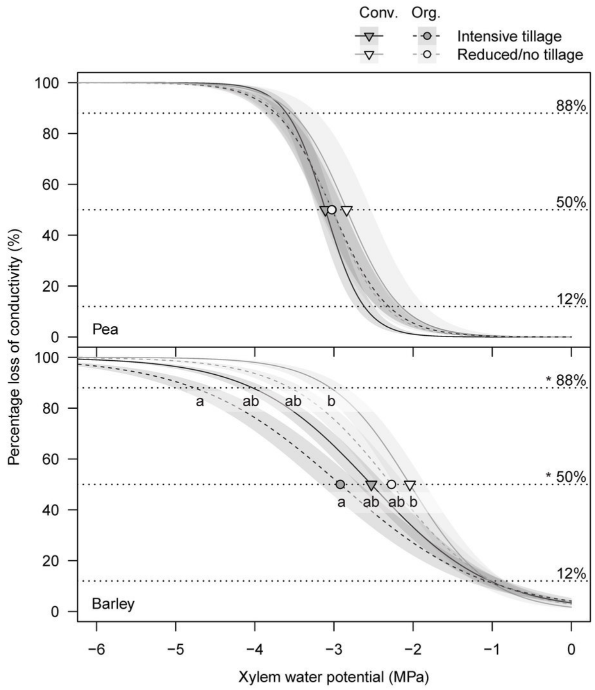
Fig. 2 (**a**) Precipitation recorded at a nearby weather station (Zürich/Kloten, KLO, 47.48° N, 8.54° E, 4.6 km from the research site; data from 1988 to 2017, MeteoSwiss, 2020), and (**b**) daily soil water content at 10 cm and (**c**) 40 cm depths under different cropping systems (Conv. for conventional, Org. for organic, n = 2 each). Vertical bars indicate dates when vulnerability curves (VC) and water potentials for the crops were measured: the black bar shows the sampling date for VC on 6 June 2018; dark grey bars show predawn water potential (ψ_{pd}) measurements on 2 and 28 June 2018; light grey bars show midday water potential (ψ_{md}) measurements on 15, 20, and 26 June 2018. Note that there was no precipitation between 14 June to 2 July 2018.

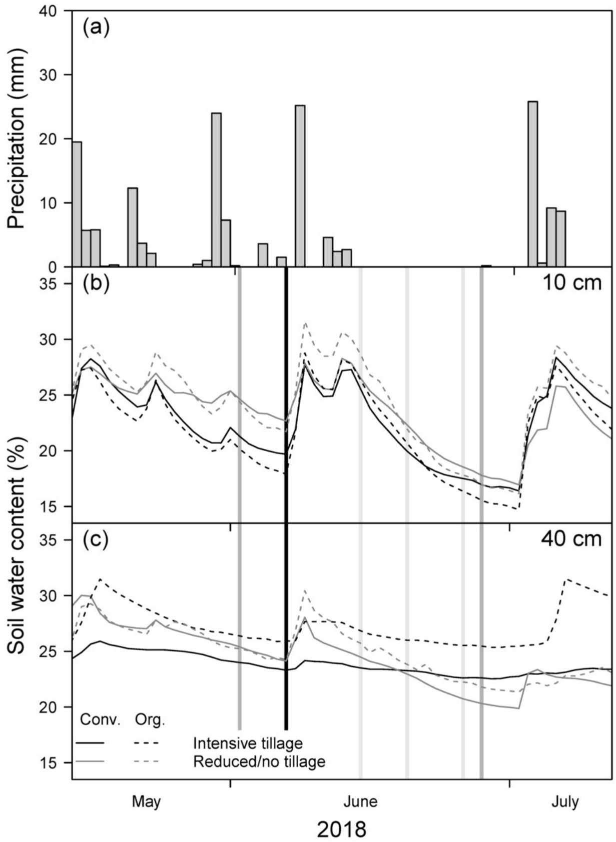
Fig. 3 Predawn water potentials (ψ_{pd}) of (**a**) pea (*Pisum sativum* L.) and (**b**) barley (*Hordeum vulgare* L.) under different cropping systems (Conv. for conventional, Org. for organic) measured on 2 and 28 June 2018. Means and 1 SE are shown (n = 4). Different letters indicate significant differences among cropping systems tested with Tukey HSD ($P < 0.05$).

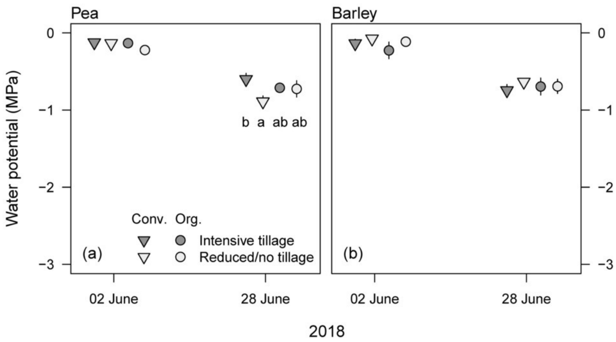
Fig. 4 (**a, c**) Midday water potentials (ψ_{md}) of pea (*Pisum sativum* L.) and barley (*Hordeum vulgare* L.) under different cropping systems (Conv. for conventional, Org. for organic) measured on 15, 20, and 26 June 2018 with the lowest value measured for each plot to the right (ψ_{min}), and (**b, d**) native percentage loss of conductivity (PLC) of pea and barley with the highest value ($nPLC_{max}$) to the right. Means and 1 SE are shown (n = 4). Asterisks indicate significant effects of cropping systems according to lineal mixed models: *** $P < 0.001$, ** $0.001 \leq P < 0.01$, * $0.01 \leq P < 0.05$, while different letters indicate significant differences among cropping systems tested with Tukey HSD ($P < 0.05$).

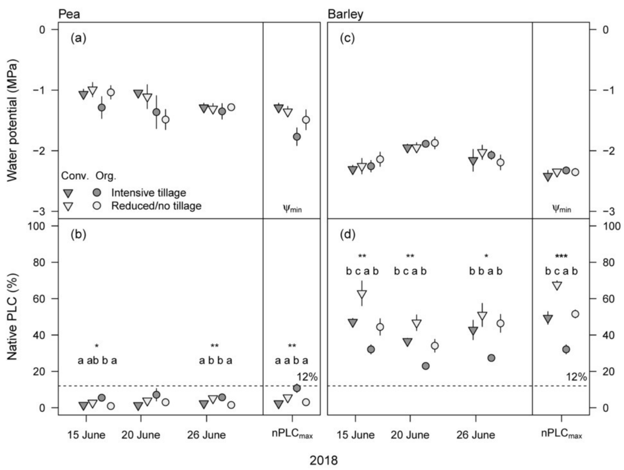
Fig. 5 (**a**) Relationships between the xylem water potential at 50% loss of hydraulic conductivity (P_{50}) and the highest native PLC during the growing season recorded for barley (*Hordeum vulgare* L.) in 2018 ($nPLC_{max}$), and (**b**) between the xylem water potential at 88% loss of hydraulic conductivity (P_{88}) and $nPLC_{max}$ (Conv. for conventional, Org. for organic). Small symbols show individual replicates (n = 14). Means and 1 SE are given with big symbols for all cropping systems. The dashed lines indicate linear regression based on 14 individual values across the four cropping systems. The shaded band lines correspond to the 95% confidence interval; asterisks indicate the significance of linear correlation: ** $0.001 \leq P < 0.01$, * $0.01 \leq P < 0.05$.

Fig. 6 Relationships of barley (*Hordeum vulgare* L.) (**a**) aboveground biomass per stem and the highest native PLC during the growing season ($nPLC_{max}$) in 2018, (**b**) $nPLC_{max}$ and grain yield per stem, (**c**) grain dry matter content (DM) and $nPLC_{max}$, and (**d**) harvest index (HI) and $nPLC_{max}$ (Conv. for conventional, Org. for organic). Small symbols show individual replicates (n = 16). Means and 1 SE are given with big symbols for all cropping systems. The dashed lines indicate linear regression based on 16 individual values across the four cropping systems (if significant). The shaded band lines correspond to the 95% confidence interval. Asterisk indicates the significance of linear correlation: *** $P < 0.001$, ** $0.001 \leq P < 0.01$, * $0.01 \leq P < 0.05$.

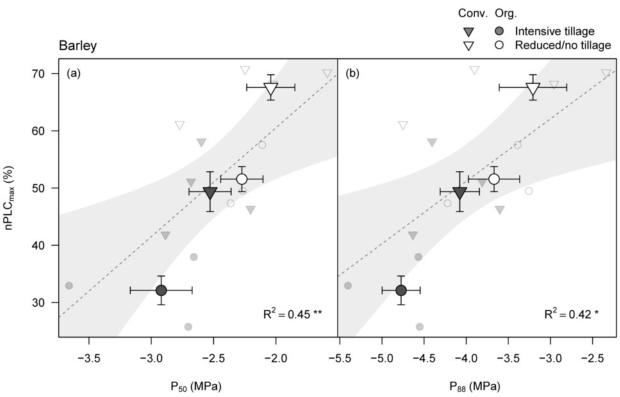

Conv.
Org.
Intensive tillage
Reduced/no tillage
88%
50%
12%
Pea
* 88%
* 50%
a
ab
ab
b
a
ab
ab
b
Barley
Percentage loss of conductivity (%)
Xylem water potential (MPa)

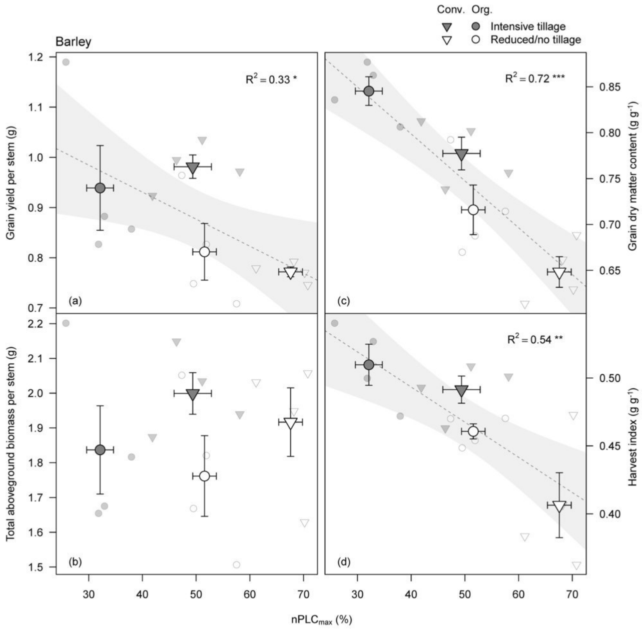

(a)
Precipitation (mm)
40
30
20
10
0
(b)
10 cm
35
30
25
20
15
(c)
40 cm
Soil water content (%)
Conv.
Org.
Intensive tillage
Reduced/no tillage
May
June
July
2018


Pea
Barley
Water potential (MPa)
0
−1
−2
−3
b a ab ab
Conv. Org.
Intensive tillage
Reduced/no tillage
(a)
(b)
02 June
28 June
2018



Pea
Barley
(a)
(b)
(c)
(d)
Water potential (MPa)
Native PLC (%)
Conv. Org.
Intensive tillage
Reduced/no tillage
Ψmin
nPLCmax
12%
15 June
20 June
26 June
2018


Conv. Org.
Intensive tillage
Reduced/no tillage
Barley
(a)
(b)
nPLCmax (%)
R2 = 0.45 **
R2 = 0.42 *
P50 (MPa)
P88 (MPa)


Conv. Org.
Intensive tillage
Reduced/no tillage
Barley
$R^2 = 0.33$ *
$R^2 = 0.72$ ***
$R^2 = 0.54$ **
(a)
(b)
(c)
(d)
Grain yield per stem (g)
Total aboveground biomass per stem (g)
Grain dry matter content (g g^{-1})
Harvest index (g g^{-1})
$nPLC_{max}$ (%)

Summary statement

Effects of cropping systems on drought resistance of arable crops were investigated for a field-grown *Pisum sativum* / *Hordeum vulgare* mixture. Pea was less vulnerable to xylem cavitation and less stressed than barley. Cropping systems only affected xylem vulnerability of barley, but not of pea.