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# Exploring the differences between organic and conventional breeding in early vigour traits of winter wheat

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ABSTRACT

Breeding for organic systems may be done as pure line or population breeding. Early vigour, critical to organic systems, was compared for different winter wheat breeding origins in a hydroponic system, as well as in the field. Entries were: the $F_{15}$ of composite cross populations (CCPs), based on high yielding (Y), high quality (Q) or Y*Q varietal intercrosses after 11 generations evolving under organic management; four organically bred; four conventionally bred baking quality varieties; a hybrid bread wheat and a high yielding variety. Hydroponic traits corresponded well with ground cover and plant height measured in the field. The organically evolved Q and YQ CCPs, organic varieties 'Poesie', 'Butaro' and 'Tobias' and the conventional 'Capo' were best suited for organic conditions. Compared to most modern varieties, CCPs had fewer seminal roots, their roots tended to be thicker and their root systems heavier, suggesting specific adaptation to penetration into deeper soil zones. Conventionally bred 'Capo' exhibits a diverse combination of root traits adaptive to a variable range of soil and environmental conditions, which may contribute to higher nutrient-use efficiency. Average root diameter of conventional E-varieties (0.28 mm) was significantly lower compared to organic varieties or the Q/YQ CCPs (both 0.30 mm). Specific root length of conventional E-varieties (17.5 cm $mg^{-1}$) was significantly higher than for organic varieties (15.9 cm $mg^{-1}$) and both differed from the Q and YQ CCPs (14.3 cm $mg^{-1}$). Seminal root length and shoot length were identified as reasonable non-destructive predictors for direct selection within segregating materials and populations.

## 1. Introduction

Conventional breeding aims to create crop varieties or hybrids that are suitable for a wide range of growing environments, rather than locally adaptable varieties or varieties suitable for specifically targeted environments (Lammerts van Bueren et al., 1999). Standard pedigree breeding has successfully produced high yielding or baking quality wheat varieties suitable for conventional farming systems under high inputs of mineral fertilizers and synthetic pesticides (Phillips and Wolfe, 2005). In organic farming, where a range of chemical inputs are prohibited, many pedigree varieties may not perform as expected due to lesser phenotypic plasticity, resulting in significant yield and quality shortfalls (Döring et al., 2011; Murphy et al., 2013). Overall, information about varietal performance in conventional systems cannot predict quantitative traits such as yield or quality accurately, e.g. under organic conditions, due to genotype by environment interactions (Lammerts van Bueren et al., 2011; Muellner et al., 2014).

Currently, organic cereal breeding is done in three main ways: (i) direct selection under organic growing conditions at all stages of the breeding process (Murphy et al., 2007; Lammerts van Bueren et al., 2011; Messmer et al., 2009); (ii) indirect selection through crosses and early selection ($F_1$ - $F_5$) in conventional, and advanced generations ($F_6$ - $F_7$) evaluated in organically managed sites (Löschenberger et al., 2008) and (iii) evolutionary breeding based on composite cross populations (CCPs), created through careful selection and intercrossing of pure line varieties. The ensuing populations are harvested in bulk and then resown for several years to improve adaptability, genetic variability and to limit human selection (Finckh and Wolfe, 2015; Murphy et al., 2005; Döring et al., 2011; Dawson and Goldringer, 2012). Well-designed CCPs offer greater flexibility under variable and stressful environments and provide for the dynamic conservation of gene pools (Brumlop et al., 2013; Finckh, 2007; Paillard et al., 2000). Diversified populations may evolve and adapt to local conditions, as well as to continuously changing climate, pests and diseases (Finckh, 2007; Paillard et al., 2000).

Unlike conventional breeding that mainly focuses on generative plant growth, breeding objectives for organic farming already focus on

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traits that improve early stages of seedling development (Wolfe et al., 2008). During this phase, the plant allocates more assimilates to roots, which in turn has a strong effect on the vegetative and early reproductive phase (Watt et al., 2013; Tekrony and Egli, 1991). Vigour may be described as rapid growth, with growth being an irreversible change to quantitative plant biomass (Atwell et al., 2003) and usually influenced by seed germination and initial root and shoot growth (Clarke et al., 1984). Greater seedling vigour and rooting depth in wheat improves nitrogen uptake (An et al., 2006; Ytting et al., 2014; Thorup-Kristensen et al., 2009; Rengel, 2005). In turn, root vigour positively affects shoot growth, leading to greater weed competitive ability (Bertholdsson, 2005; Barraclough et al., 1991). Despite the role of root systems in resource exploration and rhizodeposition, little work has been done to include root morphological traits in breeding for organic environments. Root phenotyping for a large number of genotypes in-field is resource demanding and technically challenging (Sanguineti et al., 2007; Richard et al., 2015). As an alternative, artificial techniques like hydroponics provide a sensitive way to characterise root morphology in seedlings under controlled conditions, and the results can be correlated with root development in the field (Frantz et al., 1998; Thorup-Kristensen, 1998; Grando and Ceccarelli, 1995; Kaspar et al., 1984).

The aim of this study is to assess the early seedling vigour of a set of 10 winter wheat varieties and the $F_{15}$ of three winter wheat composite cross populations (CCPs) that have been maintained under organic conditions for 11 years, in a hydroponic system. In addition, the 10 varieties and the most diverse CCP were compared for ground cover and height under organic field conditions with two nitrogen (N) input levels over two years. The varieties were selected based on quality properties, yield potential, breeding origin and farmer preference. The following questions were addressed: (a) Does seedling vigour tested in nutrient solution correspond to performance patterns in the field? (b) What are the differences in early root and shoot growth among modern organically- and conventionally- bred varieties in comparison to natural selection in a CCP maintained under organic conditions over eleven generations? (c) Which entries possess the adaptive traits of early vigour morphological characteristics needed for organic conditions?

## 2. Materials and methods

### 2.1. Plant material

Conventionally bred E-grade (highest quality) winter wheat varieties were ‘Genius’ (Saaten Union, Germany), ‘Kerubino’ (IG Pflanzenzucht, Germany) and ‘Capo’ and ‘Achat’ (Probstdorfer Saatzucht, Austria). Directly selected organic E-grade varieties were ‘Butaro’ (Dottenfelder Hof Getreidezüchtungsforschung, Germany) and ‘Wiwa’ and ‘Poesie’ (Getreidezüchtung, Peter Kunz, Switzerland), while ‘Tobias’ (Probstdorfer Saatzucht, Austria) has been indirectly selected. In addition, B-grade (bread-making) ‘Hybery’, a hybrid and C-grade (not for baking) ‘Elixer’ (both Saaten Union, Germany) were included.

The ten varieties were contrasted with three winter wheat CCPs. These were created in 2001 in the UK through half-diallel crossing of twenty parental wheat varieties (released between 1934 and 2000), chosen based on their agronomic performance under low-input or organic conditions in Europe and the UK, as well as to ensure a broad genetic base for the CCPs (Wolfe et al., 2006; Döring et al., 2015). The Y CCP was based on the intercross of 9 high yielding parents and the Q CCP on 12 high baking quality parents. The parental variety ‘Bezostaya’ is both high yielding and high baking quality and was included in both Y and Q CCPs. The YQ CCP is a product of crossing 8 Y x 11 Q parents, plus the addition of the crosses from these 19 parents with Bezostaya (Weedon, 2018). More information about individual parents and creation of CCPs has been previously reported (Jones et al., 2010; Döring et al., 2015; Weedon, 2018). Since the $F_5$ (2005/06), the three CCPs are maintained at the University of Kassel under organic (O) or conventional (C) growing conditions in at least 150 $m^2$ separate plots without conscious selection, apart from the removal of plants taller than 130 cm in the first few years (Brumlop et al., 2017). Each generation, 1 kg of seeds was stored frozen at −20 °C for future analyses. In autumn 2016, the stored seeds of the organic CCPs of the $F_{15}$ were multiplied in 6 $m^2$ plots, and the ensuing fresh seeds of OY, OQ and OYQ of the $F_{15.1}$ were used for the hydroponic tests.

### 2.2. Hydroponics

Early vigour was assessed in spring 2018 using a hydroponic system based on Bertholdsson et al. (2016). Seeds were grown in containers (20 L) filled with a balanced complete nutrient solution with a phosphate buffer (pH 6.5) (Larsson, 1982) at 2 mM N concentration. The seeds were placed in strips of corrugated cardboard with 10 mm within row spacing with the embryo facing down towards the solution and suspended over special frames into the hydroponic containers and connected with filter paper strips as wicks with the solution. The lower part of the cardboard was ironed beforehand to prevent seeds from falling down. The plants were grown in a greenhouse with 18/12 °C (day/night) temperature regime for two weeks at a photoperiod of 16 h supplemented with artificial light to maintain a minimum light intensity of 250 μ mol quanta $m^{-2}$ $s^{-1}$. The 13 entries were randomized as rows of ten plants per entry in a single container and replicated eight times. The nutrient solution was renewed after seven and ten days and aerated by continuous bubbling of air through the solution. Every two days, two replicates were sown to allow sufficient time for handling and processing of the plant samples after each harvest.

After two weeks, the number of seminal root axes (NSR) on each plant were counted. The length of the longest seminal root (SRL) and the shoot length (SL) from the seed to the tip of the highest leaf was measured on each plant directly using a ruler. Subsequently, the roots per plant were scanned using an Epson photo scanner (Epson Perfection V700 with 6400 dpi resolution) (Epson, Long Beach, CA) and using WinRHIZO Pro image analysis system (Regent Instruments, Inc., Quebec City, QC), total root length (TRL) (sum of the lengths of all roots in the seminal root system), average root diameter (ARD), total root surface area (TRSA) and total root volume (TRV) were determined. Roots were stained in neutral red (0.16 mg/L) prior to imaging. Root (RDW) and shoot (SDW) dry weights were determined after drying at 105 °C overnight. Specific root length (SpecificRL) was calculated as TRL/RDW.

Prior to the hydroponic experiments, 1000 kernel weights (TGW) of each variety were determined based on three times 100 seeds. Germination rates were assessed with two times 25 seeds per entry at 20 °C for 8 days. Germinating seeds were counted after four and eight days.

### 2.3. Field trials

A two-year field experiment was conducted from October 2015 to August 2017 at the organic research field of University of Kassel in Neu Eichenberg, situated at 51°22″N latitude, 09°54″E longitude at 247 m above sea level. Fields are a fine loamy loess soil (deep Haplic Luvisol) with about 80 soil points according to the German soil grading scale. No pesticides were applied. Weeds were controlled mechanically through harrowing and/or hoeing at the tillering stage (Weedon, 2018).

The experiment was a split plot design with four replicates. Main plots were N input levels at 0 kg N/ha or 100 kg N/ha, respectively. Subplots were assigned to the 10 wheat varieties and the OYQ CCP of the $F_{15}$ (2015/16) and $F_{16}$ (2016/17) and were 12 m × 1.5 m (18 $m^2$). The 100 kg N/ha application of hairmeal pellets (Biofa) took place each year before sowing in early October. A total of 350 germinable seeds $m^{-2}$ were sown on 28 October 2015 and 17 October 2016 with a plot sowing machine at 30 cm row distance to allow for hoeing. Ground cover of wheat (%) was visually assessed six times per plot at BBCH

27–31 using a sampling frame of 0.1 $m^2$. Plant height (from base of stem to tip of ear) was measured three times on approximately 50 randomly chosen stems per plot at BBCH 75 - 85. Additional field data will not be reported as the focus here is early seedling vigour.

### 2.4. Statistical analyses

Prior to the analysis, percentage ground cover data were arcsine transformed. Normality and equal variance of data were tested using residual and graphing methods. A linear mixed-effects model was developed in R, version 3.2.2 (R Core Team, 2013) using the lme4 package (Pinheiro et al., 2019). Differences among entries were determined with Posthoc Duncan tests and group comparisons for different breeding types of the baking quality entries were done with linear contrasts.

To identify association between traits and trait profiles of the entries, Principal Component Analysis (PCA) was computed using the FactoMineR package (Husson et al., 2018), and functions from the Factoextra package were used for extracting and identifying top contributing variables to the principal components (PC) as well as visualising the results of the PCA using biplots (Kassambara and Mundt, 2017; Le et al., 2008). Traits are positively correlated if the angle between the vectors is acute, negatively correlated if the angle is obtuse and not correlated if vectors are perpendicular to one another (Krzanowski, 2004; Yan and Tinker, 2006). Trait relationships were separately analysed using the PerformanceAnalytics package ($P < 0.05$) (Petereson et al., 2018). In addition, the built-in Rank function of Microsoft Excel 2016 was used to estimate the rank of an entry within a set of entries for each trait, with the highest rank indicating the best performance for a particular trait.

## 3. Results

### 3.1. Seedling vigour traits in hydroponics

Germination rate exceeded 96% and there were no significant differences among entries ($P = 0.22$ and 0.19 for day 4 and day 8, respectively). Seed size (TGW) varied between entries. 'Butaro', 'Poesie' and 'Elixer' had the highest TGWs followed by 'Tobias', 'Poesie', 'Hybery', OYQ, OQ and all E-grade varieties, with the only exception of 'Achat', which had the lowest TGW similar to OY CCP (Fig. 1a). Covariate analysis with TGW indicated that TGWs had very weak associations or did not significantly affect the seedling traits ($P > 0.05$); hence, seedling mean values were not adjusted according to TGW-based regression analyses.

The number of seminal roots (NSR) varied from 5.6 in 'Poesie' to 4.7 in the OQ CCP (Fig. 1b). Among the CCPs, seminal root length (SRL) of the OQ CCP was longest followed by OYQ and OY (Fig. 1c). SRL of 'Elixer' and 'Wiwa' were shortest among all entries, while SRL of 'Capo' was greatest.

There were no significant differences for total root length (TRL) within or between the CCPs and organic entries (Fig. 1d). However, TRL was significantly higher in 'Capo' than in the other conventional entries or the CCPs. Only the organically bred varieties 'Tobias' and 'Poesie' had TRL similar to that of 'Capo'. Average root diameter (ARD) was relatively uniform and significantly lower for conventional E-entries (mean = 0.28 mm) than in the OQ and OYQ CCPs or the organically-bred E-varieties (both with mean ARD = 0.30 mm) ($P < 0.05$, linear contrast). Among the organically bred entries 'Butaro' had the smallest ARD, while the OY CCP showed similar low ARD values (Fig. 1e). Increased TRL in 'Capo' also significantly increased total root surface area (TRSA) and total root volume (TRV) above that of the other conventional entries, except for the hybrid 'Hybery' (Fig. 1f,g).

Root dry weight (RDW) followed the same pattern as SRL with few statistically significant differences (Fig. 1h). Specific root length (SpecificRL) did not differ significantly within or between the CCPs and organic entries, but was lowest in the OQ CCP (Fig. 1i). Here, the group comparisons between OQ and OYQ CCPs (mean = 14.3 cm $mg^{-1}$), organically-bred varieties (mean = 15.9 cm $mg^{-1}$) and conventional E-varieties (mean = 17.5 cm $mg^{-1}$) all differed significantly from each other ($P < 0.05$, linear contrast). Among all entries, conventional 'Capo' had the highest SpecificRL, significantly exceeding the B and C varieties, the CCPs and organic 'Tobias' and 'Butaro'.

'Poesie' and 'Tobias' had the highest shoot length (SL) (Fig. 1j). Apart from 'Genius', SL was similar for all other E-grade entries, the CCPs and the organically bred 'Butaro' and 'Wiwa'. 'Genius' and the hybrid variety 'Hybery' grouped together and the C-grade variety 'Elixer' was shortest. Shoot dry weights (SDW) followed largely the SL pattern, with 'Capo' exceeding all conventional entries (Fig. 1k).

### 3.2. Early vigour in the field

Compared to 2016, the main growing season 2017 was drier. The extremely wet weather during July and August was of no relevance to early vigour (Fig. 2).

N input of 100 kg/ha overall slightly increased ground cover and plant height with no interactions between entries and N input levels in either experimental year (Fig. 3, see Supplementary Table 1 for ANOVA calculations). Germination of 'Poesie' in 2016/17 was unusually low resulting in poor ground cover values in the second year. However, it recovered and grew to normal height. In both years, percentage ground cover of the OYQ CCP was comparable with 'Tobias', 'Capo', 'Achat' and 'Hybery'. Additionally in 2016, ground cover of the OYQ CCP was similar to 'Poesie' and in 2017 to 'Butaro' and 'Kerubino' (Fig. 3a, c). The C-grade 'Elixer' had very poor ground cover in both experimental years. Most organic varieties and the OYQ CCP produced taller plants in comparison to the conventional varieties, except for 'Capo' (Fig. 3b, d).

### 3.3. Seedling traits vs. field traits

Ground cover in the field correlated well with several root traits in hydroponics that were all also significantly correlated among themselves: SRL, RDW, TRL, and TRSA. Plant height in the field correlated best with hydroponic shoot traits, but also with RDW, TRV and TRSA (Table 1). Details per entry for the correlations (coefficient of determination [$R^2$]) between seedling and field traits are shown in Supplementary Fig. 1 The NSR, ARD and SpecificRL were not informative for the measured field traits, nor did they correlate with any of the hydroponic traits except for the strong negative correlation between ARD and SpecificRL, which is not surprising. The low germination of 'Poesie' seed in 2017 affected the overall relationships, resulting in a negative albeit non-significant correlation between NSR and ground cover values. Removing 'Poesie' from the calculations resulted in even more significant correlations between hydroponic root traits, especially TRV and TRSA and ground cover measured in the field (Supplementary Table 2). Correlations between shoot traits and ground cover and ground cover and plant height were also stronger.

Value in each cell represents Pearson correlation coefficient (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

NSR - number of seminal roots; SRL - seminal root length; RDW– root dry weight; TRL – total root length; ARD – average root diameter; TRV– total root volume; SpecificRL – specific root length; TRSA – total root surface area; SL – shoot length and SDW –shoot dry weight.

The biplot for the hydroponic traits alone accounts for 78% of the variations due to entries and entry by trait interactions. The strong negative association of ARD with SpecificRL is indicated by the opposite vectors in Fig. 4a. On the first axis, 'Capo', 'Tobias', OQ, OYQ, 'Poesie' and 'Butaro' are grouped to the right, however, 'Capo' is separated on the second axis due to its lower ARD in contrast to other four entries (see also Fig. 1e). 'Butaro' is placed in the middle due to its lower value for all the measured traits, compared to the other five entries. 'Elixer' stands out on the very left, due to its overall lower

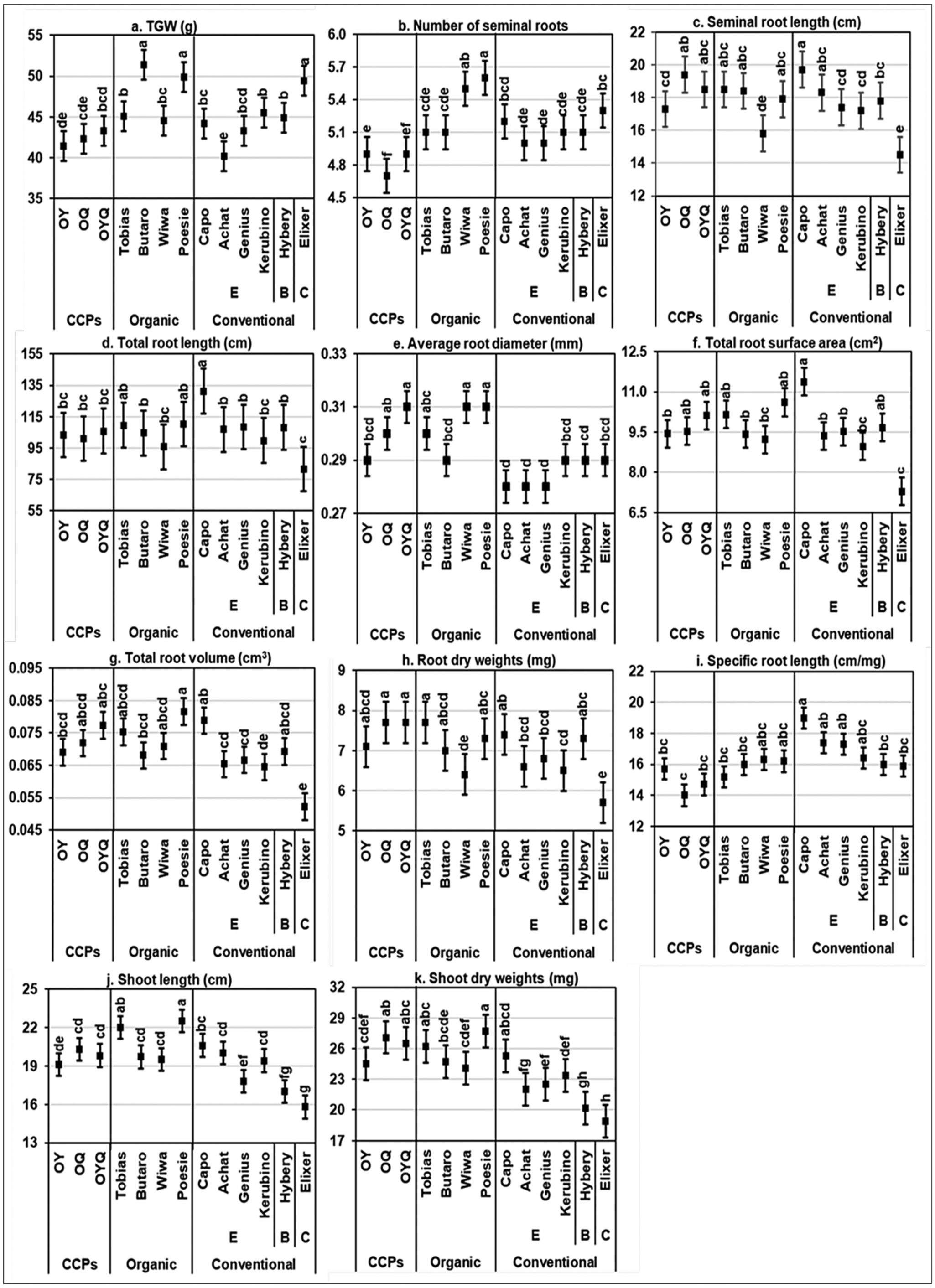


**Fig. 1.** Mean values of seed size (TGW) and early vigour traits from seeds of organically maintained winter wheat composite cross populations (CCPs), organically bred E-grade winter wheat varieties or conventionally bred E, B and C grade winter wheat varieties assessed hydroponically under greenhouse conditions. Bars within a panel marked with the same letters are not significantly different (Duncan, $P < 0.05$).

performance in all traits, except for NSR, ARD and SpecificRL. The organically bred 'Wiwa', as well as OY CCP group with other conventional entries (Fig. 4a).

Plant height and ground cover in the field were not very closely related, with the vectors almost perpendicular to each other (Fig. 4b). Using only these two parameters, the varieties grouped rather closely together with only 'Elixer' taking a separate position (Supplementary Fig. 2). Taking into account both seedling and field traits, for which the OY and OQ CCP were removed, Fig. 4b corresponds in some ways to Fig. 4a. Again, 'Capo' 'Elixer' and 'Poesie' take extreme positions. Additionally, 'Wiwa' is separated from the conventionally bred varieties, which tend to form a group, while 'Butaro' groups together with 'Tobias', 'Poesie' and OYQ (Fig. 4b).

Adding up the ranks for the various traits that were assessed hydroponically and in the field, the top five entries were 'Poesie', 'Tobias', OYQ, 'Capo' and 'Butaro'. 'Hybery' is in the middle followed by 'Wiwa' and the other three conventionally bred E-varieties. 'Elixer' ranks by far the lowest (Table 2). Regarding the hydroponics results, 'Butaro' is more similar to 'Hybery' and both ranked below the OQ and OYQ CCPs, which were similar. Again, 'Wiwa' is similar to the OY CCP and the conventionally bred varieties, while 'Elixer' remains the lowest ranking entry for the hydroponically assessed traits.

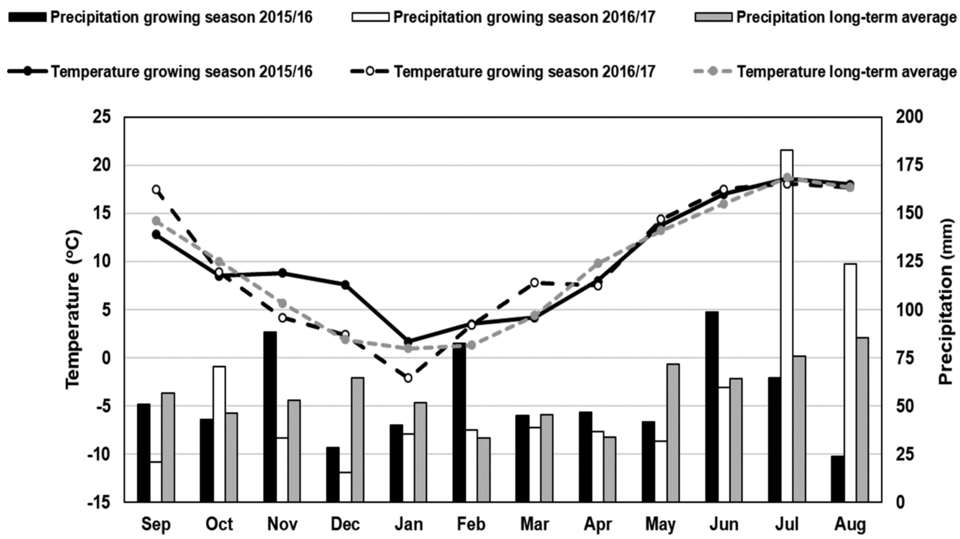


**Fig. 2.** Monthly mean temperatures (°C) and monthly total precipitation (mm) in the winter wheat growing season 2015/16 and 2016/17 in Neu Eichenberg, Germany, compared to the long-term average (2005–2014).

For practical breeding when the aim is to improve populations, the possibility of direct selection for early vigour from segregating materials based on trait expression under hydroponic conditions is highly attractive. To enable such direct selection it has to be non-destructive. Seminal root length and shoot length can be assessed non-destructively by simple direct measurements and plants can then be grown to maturity. To determine, how well these two parameters reflect early vigour traits as a whole, the rank sums of these two traits alone were calculated in the last column of Table 2. This results in 'Elixer' with the lowest rank sum of 2, the OY CCP, 'Wiwa', 'Genius', 'Kerubino', and 'Hybery' with rank sums of 8 or 9 and all other entries with rank sums between 16 and 24. 'Achat' groups differently and is comparable to entries with higher rank sums (Table 2).

## 4. Discussion

Seedling vigour under hydroponic conditions corresponded well with ground cover and plant height measured in the field. Using both a combination of the seedling traits and the field measurements, it was possible to identify the organically evolved CCP populations OQ and OYQ, organically directly selected 'Poesie' and 'Butaro' and indirectly selected 'Tobias', as well as the conventionally bred 'Capo' as best suited for organic conditions. The C-grade high yielding variety 'Elixer' clearly differed from all other entries, while the organically evolved Y (yield) CCP took an intermediate position. Root traits of the hybrid were well adapted to low input, in contrast, its shoot behaviour followed the high yielding variety 'Elixer'. Of all the measured root traits, average root diameter (ARD) and specific root length clearly differentiated organically- or conventionally-bred E-varieties and the OQ and OYQ CCPs containing baking quality parents from each other. Despite the great variation in seedling traits, seminal root length (SRL) and shoot length (SL) could be identified as reasonable non-destructive predictors of seedling performance in the field. In our study, the aim was to compare the CCPs as a whole with pure line varieties. Therefore,

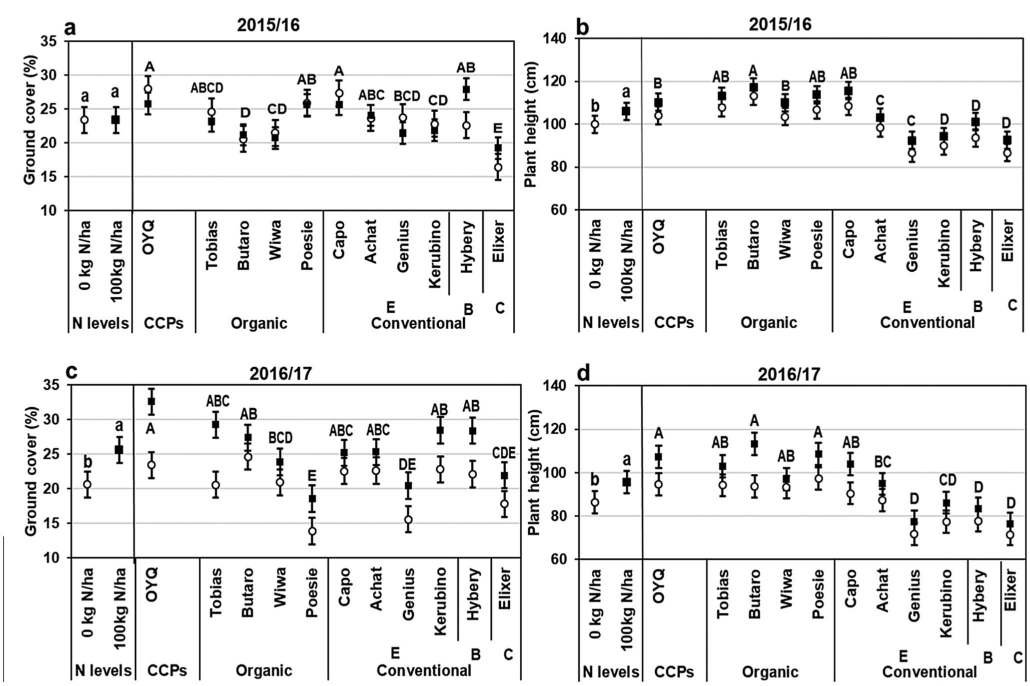


**Fig. 3.** Ground cover and plant height among winter wheat entries grown at differing N levels (open circles: 0 kg N/ha, black squares: 100 kg N/ha treatment) in 2016 (a, b) and 2017 (c, d) under organic field conditions in Neu Eichenberg. Entries included organically maintained YQ composite cross population (CCP), organically bred E varieties or conventionally bred E, B and C winter wheat varieties. Bars within a panel with different lower case letters indicate significant differences between N levels ($P < 0.05$) and different upper case letters shows the mean of entries for two N levels, as no N x entries interactions occurred.

**Table 1**
Correlations among early vigour traits assessed hydroponically under greenhouse conditions and ground cover and plant height assessed in 2016 and 2017 under organic field conditions in Neu Eichenberg in a set of 10 winter wheat entries (organically bred E varieties and conventionally bred E, B and C varieties) and the organically maintained most diverse YQ composite cross population (CCP).

| | SRL | RDW | TRL | ARD | TRV | Specific RL | TRSA | SL | SDW | Ground cover | Plant height |
|---|---|---|---|---|---|---|---|---|---|---|---|
| NSR | −0.40 | −0.28 | −0.17 | 0.50 | 0.16 | 0.07 | −0.01 | 0.23 | 0.17 | −0.56 | 0.19 |
| SRL | | **0.85***** | **0.90***** | −0.24 | **0.72*** | 0.26 | **0.87***** | **0.62*** | 0.59 | **0.72*** | 0.59 |
| RDW | | | **0.75**** | 0.16 | **0.86***** | −0.16 | **0.86***** | **0.63*** | **0.70*** | **0.73*** | **0.61*** |
| TRL | | | | −0.32 | **0.75**** | 0.54 | **0.93***** | 0.56 | 0.52 | 0.53 | 0.48 |
| ARD | | | | | 0.38 | **−0.69**** | 0.04 | 0.37 | 0.52 | 0.01 | 0.41 |
| TRV | | | | | | 0.02 | **0.94***** | **0.80**** | **0.87***** | 0.51 | **0.75**** |
| Specific RL | | | | | | | 0.29 | 0.01 | −0.14 | −0.14 | −0.08 |
| TRSA | | | | | | | | **0.73*** | **0.74**** | 0.55 | **0.66*** |
| SL | | | | | | | | | **0.90***** | 0.32 | **0.82**** |
| SDW | | | | | | | | | | 0.36 | **0.86***** |
| Ground cover | | | | | | | | | | | 0.37 |

variability within the CCPs was reduced by using the means of 10 plants for each replicate. Consequently, the possibility to select for these traits out of populations needs to be confirmed using single plants and their respective progenies.

We eliminated the influence of seed size differences on seedling growth by exposing seedlings to a common hydroponic solution, where nutrients were not a limiting factor. Seedling development in hydroponics is hardly affected by nutrient level (Bertholdsson et al., 2016). This and the good correlation between the hydroponic and field data under two input levels suggests that the rooting patterns reflect the genetically determined potential of the entries tested.

Specific root length (i.e. root length produced per unit of root biomass) and root diameter (ARD) are often considered important breeding traits connected to penetrating ability of roots in different soil zones (Paula and Pausas, 2011; Eissenstat, 1992; Clark et al., 2008). The OQ and OYQ CCPs had the lowest specific root length of the three baking quality groups. While this might be connected to the fact that they are based on older genetics, no trends for changes in specific root length between old and recent genotypes of spring wheat and barley have been found (Løes and Gahoonia, 2004). The group comparison clearly differentiated organic varieties from conventional E-varieties. ARD was overall significantly lower in the conventional E-entries, compared to the organic varieties and OQ and OYQ CCPs. Nevertheless, among the organic entries, variation was relatively high with 'Butaro' tending to show ARD values similar to the conventional varieties. Among the populations, due to its high yielding parental genetic background, the Y CCP, also had the lowest ARD compared to the other two populations. This may point to important differences in rooting strategies affected by selection within a growing system connected to nutrient availability and spatial distribution rather than effects of old versus new genetics (see below).

The rooting strategies of the OQ and OYQ CCPs evolving under organic conditions differed from most varieties. The increased root diameter and higher root weights led to low specific root length. This resulted in thicker, heavier and deeper main root systems reflecting enhanced soil penetrating ability to access deeper soil layers with heterogeneous conditions of low nutrient supply (Barraclough et al., 1989; Thorup-Kristensen et al., 2009). This extensive root systems strategy with the Q and YQ CCPs is likely due to the better adaptation of the quality parents to organic conditions compared to the yield parents (Jones et al., 2010). Comparing organically evolved and conventionally evolved CCPs over 10 generations, we found that the two farming systems led to similar differences in specific root length over time as observed here between the high and low ranked entries (Vijaya Bhaskar et al., Unpublished results). Under low nutrient supply, plant roots become thicker improving mycorrhization capacity (Brundrett, 1991; Smith and Read, 2010) and angles become steeper to absorb nitrogen efficiently in deep soil layers (Trachsel et al., 2013; Lynch, 2013). Only the organically bred 'Tobias' and 'Poesie' had overall trait profiles similar to the OQ and OYQ CCPs. Organically bred 'Butaro' and 'Wiwa' were comparable to 'Tobias' and 'Poesie' and to OQ and OYQ CCPs for specific root length; however, they achieved this through different strategies, in 'Butaro' through higher root weights combined with lower root diameter, while the reverse occurred in 'Wiwa'.

The low root diameter of the conventionally bred entries indicates that they invest more in finer roots that may exert a less penetrative

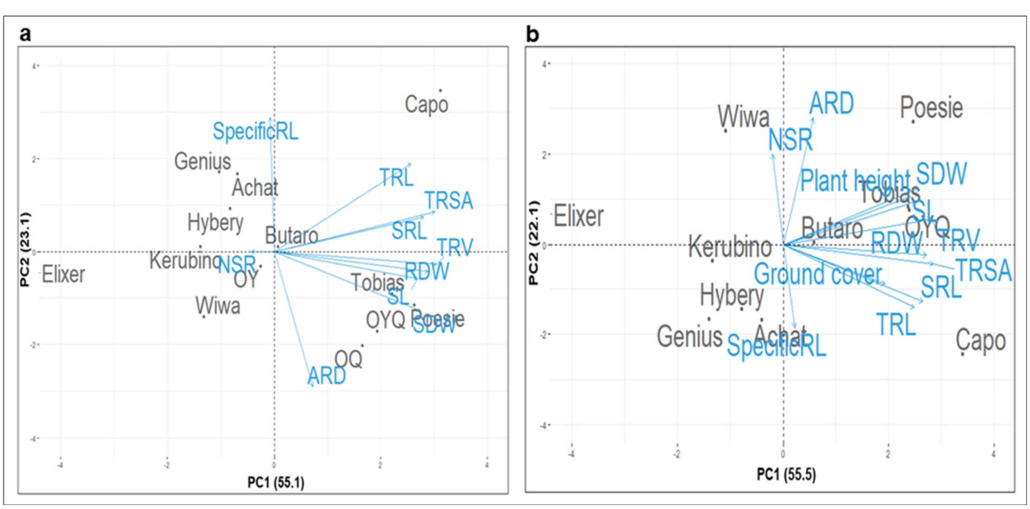


**Fig. 4.** Biplots of the principal component analysis (PCA) showing the interrelationship among different traits for the mean values of ten winter wheat varieties and three composite crosses OY, OQ, and OYQ evaluated in hydroponics (a) and the same ten winter wheat varieties and the OYQ composite cross only tested both in hydroponics and in organic field experiments in 2016 and 2017 in Neu Eichenberg (b). Traits are marked as, NSR – number of seminal roots, SRL – seminal root length, TRL – total root length, ARD – average root diameter, TRV – Total root volume, TRSA – Total root surface area, RDW – root dry weight, SpecificRL – Specific root length (i.e. TRL/RDW) SL – shoot length, SDW – shoot dry weight and mean values of ground cover and plant height for both years.

**Table 2**
Genotype ranking based on seedling and field traits of winter wheat entries assessed in hydroponics and in organic field experiments in Neu Eichenberg in 2016 and 2017, respectively. Higher ranking indicates better performance with respect to early vigour traits. Top 5 ranked entries are highlighted in bold.

| Entry | Seedling traits | | | | | | | | | | | Field traits | | | | Overall ranking | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NSR | SRL | RDW | TRL | ARD | TRV | TRSA | SpecificRL | SL | SDW | Total | Ground cover | | Plant height | | | |
| | | | | | | | | | | | | 2016 | 2017 | 2016 | 2017 | | SRL + SL |
| OY | 3 | 4 | 7 | 5 | 8 | 2 | 6 | 10 | 4 | 7 | 56 | – | – | – | – | – | 8 |
| OQ | 1 | 12 | 13 | 4 | 10 | 9 | 8 | 13 | 10 | 12 | **92** | – | – | – | – | – | **22** |
| **OYQ** | 3 | 11 | 13 | 7 | 13 | 11 | 10 | 12 | 8 | 11 | **99** | 11 | 11 | 7 | 9 | **137** | **19** |
| **Tobias** | 9 | 11 | 13 | 11 | 10 | 10 | 11 | 11 | 12 | 10 | **108** | 7 | 7 | 9 | 8 | **139** | **23** |
| **Butaro** | 9 | 9 | 6 | 6 | 8 | 6 | 6 | 7 | 7 | 8 | 72 | 2 | 10 | 11 | 11 | **106** | **16** |
| Wiwa | 12 | 2 | 2 | 2 | 13 | 8 | 3 | 5 | 6 | 6 | 59 | 3 | 4 | 6 | 6 | 78 | 8 |
| **Poesie** | 13 | 7 | 9 | 12 | 13 | 13 | 12 | 6 | 13 | 13 | **111** | 9 | 1 | 8 | 10 | **139** | **20** |
| **Capo** | 10 | 13 | 10 | 13 | 3 | 12 | 13 | 1 | 11 | 9 | **95** | 10 | 5 | 10 | 7 | **127** | **24** |
| Achat | 7 | 8 | 4 | 8 | 3 | 4 | 6 | 2 | 9 | 3 | 54 | 6 | 6 | 5 | 5 | 76 | **17** |
| Genius | 7 | 5 | 5 | 10 | 3 | 5 | 8 | 3 | 3 | 4 | 53 | 5 | 2 | 1 | 2 | 63 | 8 |
| Kerubino | 9 | 4 | 3 | 3 | 8 | 4 | 2 | 4 | 5 | 5 | 47 | 4 | 9 | 3 | 4 | 67 | 9 |
| Hybery | 9 | 6 | 9 | 9 | 8 | 7 | 9 | 7 | 2 | 2 | 68 | 8 | 8 | 4 | 3 | 91 | 8 |
| Elixer | 11 | 1 | 1 | 1 | 8 | 1 | 1 | 9 | 1 | 1 | 35 | 1 | 3 | 2 | 1 | 42 | 2 |

NSR - number of seminal roots; SRL - seminal root length; RDW– root dry weight; TRL – total root length; ARD – average root diameter; TRV– total root volume; TRSA – total root surface area; SpecificRL – specific root length; SL – shoot length and SDW –shoot dry weight.

force on the soil. Roucou et al. (2017) also showed that modern genotypes tend to increase the proportion of finer roots with diameter < 0.2 mm, resulting in lower root weights (Siddique et al., 1990).

The conventionally bred 'Capo' possessed unique root characteristics owing to its increased spreading behaviour, i.e. greater total root length, surface area and thus exceptionally high specific root length among all entries. Thus, 'Capo' exhibits a diverse combination of root traits adaptive to a variable range of soil and environmental conditions, apparently facilitating better belowground investment that may improve nutrient-use efficiency. Furthermore, with the exception of ARD and specific root length, 'Capo' tended to be more similar to organic 'Tobias' and 'Poesie'. This could explain why 'Capo' is highly popular among organic growers in Germany and covers one-third of the organic acreage in Austria (Löschenberger et al., 2008). Under organic field conditions, 'Capo' and OYQ CCP yielded similarly with similar stability of yield over eight years. In contrast, under conventional conditions, 'Capo' yielded significantly higher than the conventional YQ CCP and had higher yield stability (Weedon, 2018).

Generally, water and nutrient uptake are related to total root length rather than root mass, as genotypes with higher specific root length may invest their root biomass more efficiently (Eissenstat, 1992). Finer roots with smaller diameter allow for a greater share of carbohydrates to be available for the grains without affecting nutrient- and water- use efficiency (Bertholdsson and Brantestam, 2009; Richards and Passioura, 1989). For example, when grown under minimum fertilizer inputs, specific root lengths of modern Danish barley cultivars were increased without affecting yields (Bertholdsson and Brantestam, 2009). On the other hand, wheat yield was increased if energy and carbon translocation to the roots was prevented through root pruning (Shou-Chen et al., 2008). Overall, the multi-correlated root traits suggest that the plasticity in root development is high and there may be a trade-off between fast-resource acquisitions through finer rooting patterns and conservation of acquired resources through thicker rooting patterns. It is possible, that adaptive changes towards evolutionary and environmental drivers have occurred. Thus, it has been hypothesized that while genotypes with higher specific root length have a higher capacity for water and nutrient uptake per given root mass (fast growth rate), they have lower mycorrhizal dependency due to thinner roots (Eissenstat, 1992; Brundrett, 1991; Smith and Read, 2010). However, this view was recently challenged by Maherali, (2014) through meta-analysis. For example, Donn et al. (2017) found that specific root length or root diameter of *Brachypodium distachyon* do not necessarily relate with dependence or responsiveness to mycorrhiza. Soil factors or location may be as or more critical than plant-related factors to the structure of rhizosphere microbial communities (Edwards et al., 2015; Peiffer et al., 2013).

In comparison to OY, OQ displayed greater early vigour confirming genetic differences among the CCPs as reported before (Bertholdsson et al., 2016; Vijaya Bhaskar et al., Unpublished results; Weedon, 2018). The similarities of OQ and OYQ CCPs indicate that in the OYQ with mixed genetics, the expression of the Q genetics may have been favoured through evolutionary changes under organic conditions. When evolving under conventional conditions, the conventional CQ CCPs did not differ from the organically evolved OQ CCPs. In contrast, the CYQ CCPs tended more towards the CY populations (Vijaya Bhaskar et al., Unpublished results). The high yielding variety 'Elixer' invested considerably less into early development. No direct comparison is available under hydroponic conditions with the conventional CY CCP. However, the greater changes of the Y CCP under conventional condition over time compared to organic conditions (Vijaya Bhaskar et al., Unpublished results) suggest that the CY CCP has become more similar to 'Elixer' than the OY CCP.

The seminal roots germinating directly from the wheat seed are considered most critical for accessing deeper soil resources (Watt et al., 2008). They remain functionally active through to the reproductive stage (Manschadi et al., 2013) and are mostly involved in adaptive responses to the growing environments (Richard et al., 2015). Most wheat genotypes develop between three to six seminal roots (Araki and Iijima, 2001). Across entries, we usually observed four well-developed seminal roots; the fifth seminal root was partially developed, while additional seminal roots were usually at the juvenile stage. The modern organic or conventional varieties selected by breeders had a tendency to develop several, often more than five short seminal roots. In contrast, the CCPs created from parental varieties dated between 1934 and 2000 (Jones et al., 2010) and exposed to natural selection under organic conditions over time seem to develop usually less than five seminal roots. The Q CCPs had fewer seminal roots followed by YQ and Y CCPs and this was unaffected over time by farming system (Vijaya Bhaskar et al., Unpublished results). The fact that the number of seminal roots was not correlated with other root traits and that there was no consistent trend among the entries with different breeding histories, fits into this picture. Longer seminal roots with increased branching in deeper zones are considered advantageous in supporting steeper and compact seminal root systems that may access deeper soil resources in conditions where nutrients and water are scarce and heterogeneously distributed within the soil zones (Richard et al., 2015; Lilley and

Kirkegaard, 2011). The genotypic differences for seedling root length therefore have implications for nitrogen-use efficiency, allowing for the utilization of available nitrogen supplied by soil or fertilizers more effectively (Moll et al., 1982; Bingham et al., 2012). The seminal roots of OQ, OYQ, 'Tobias', 'Butaro', 'Poesie', 'Capo', 'Achat' and 'Hybery' point to greater root plasticity and adjustment capacity to organic or other nutrient limited conditions.

Total root length affects distribution and prolificacy of root system in the soil profile (Manschadi et al., 2006). Across baking quality entries, only little variation was observed, with the only exception of 'Capo' having total root length greater than 130 cm. Overall, seminal- and total- root length results indicate that the OQ and OYQ CCPs do not differ from most modern varieties selected by breeders despite their older genetic background and maintenance without conscious selection. Variation in total root length between recent barley genotypes and historical materials was also low, although maximum rooting depth was reduced in modern types (Bertholdsson and Brantestam, 2009). In the comparison of the CCPs having evolved for ten years in two growing systems, we found longer seminal roots, but a decrease in total root length in the organically grown CCPs in comparison to the conventionally grown ones (Vijaya Bhaskar et al., Unpublished results). Total root surface area and total root volume are both connected to seminal root length and total root length. They correlated positively with both ground cover and plant height, indicating that nutrient uptake from soil increases with increasing volume or contact area between root surface and soil, which in turn allows the plants to establish rapidly, grow taller and increase biomass. Similar positive correlations were reported by Narayanan et al. (2014) for root traits in spring wheat germplasm.

Early shoot growth improves light interception by increasing leaf size and/or stem growth and biomass, which in turn provides greater weed competitive ability under conditions where no herbicides are applied (Bertholdsson, 2005). The organically bred varieties, especially 'Tobias' and 'Poesie', had more vigorous shoot growth and were taller than most conventional varieties or the CCPs. Nevertheless, their shoot weights were similar to that of OQ and OYQ CCPs and conventionally bred 'Capo'. Thus, early differences in leaf production or net photosynthetic rate between these modern wheats and the CCPs were low. These observations also suggest that the changes in early shoot vigour are related to early root vigour, supporting Liao et al. (2004). The hybrid 'Hybery' is an exception in this case, whereby improved early vigour root growth or ground cover was not related to shoot length. This may be explained by parental uniformity for the dwarf growth type ensuring lodging resistance, improved harvest index and good response to mineral fertilizers combined with hybrid vigour in the rooting system where parents likely were not genetically uniform. Thus, 'Hybery' may respond well to organic or other nutrient limited conditions, provided weeds are controlled adequately. In contrast, organic 'Wiwa' had better early shoot growth and was taller; however, reduced rooting depth and ground cover make it apparently more dependent on good soil nutrient status in comparison to the other organically bred varieties. These distinguishable features highlight that artificial selection has altered the functional coordination of above- and below- ground components and has created a type of network of trait covariations (Roucou et al., 2017).

## 5. Conclusions

Nutrient-use efficiency and weed competitive ability are the two most important traits for successful organic cereal production. For organic systems, genotypes are needed with rapid establishment and root resource foraging capacity/capability, as well as increased crop height and aerial biomass to outcompete weeds. Vigorous root and shoot growth may also improve the ability of a plant to buffer environmental stresses, especially during critical stages of seedling development. In this regard, specific breeding methods developed for organic farming such as the heterogeneous crop populations and/or organically bred varieties seem to be an attractive option.

The large differences in root thickness among entries indicate that the breeding process may result in differences in root quality and soil penetrating ability among wheat genotypes. While the general differences in root diameter and specific root length apparently differentiate organically- and conventionally- bred varieties and also the CCPs from each other, the fact that 'Capo' in most cases has root morphological traits more similar to the organic 'Tobias' and 'Poesie', makes it suitable for both organic and conventional farming systems. The organically maintained CCPs with high quality parental genetics combined high root diameter with low specific root length. This can be considered a conservative strategy of growing thicker, heavier and steeper main root systems, as a result of adaptation to organic conditions.

The strong positive relationship between hydroponic seedling and field traits and the possibility to use seminal root length and shoot length as non-destructive selection parameters should make it possible to apply this method to improve heterogeneous populations such as CCPs. Overall, selection for early vigour under hydroponic conditions could be an effective indirect selection tool. The focus should be less on average root diameter and specific root length, but rather on total root surface area and volume, where seminal root length and shoot length are good non-destructive proxies that should allow for direct selection.

## Author contributions

MF, AV and OW conceived the project. AV conducted the hydroponic experiments, analysed the results and drafted the manuscript. OW conducted the field experiments. AV and MF prepared the data presentation. MF supervised the research study. All authors discussed the results, revised and improved the manuscript.

## Competing interests

The authors declare no competing interests.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.eja.2019.01.008.

## References

An, D., Su, J., Liu, Q., et al., 2006. Mapping QTLs for nitrogen uptake in relation to early growth of wheat (*Triticum aestivum L.*). Plant Soil 284, 73–84.
Araki, H., Iijima, M., 2001. Deep rooting in winter wheat: rooting nodes of deep roots in two cultivars with deep and shallow root systems. Plant Prod. Sci. 4 (3), 215–219.
Atwell, B.J., Kriedemann, P.E., Turnbull, C.G.N., 2003. Plants in Action: Adaptation in Nature, Performance in Cultivation South Yarra. Macmillan Education Australia.
Barraclough, P.B., Kuhlmann, H., Weir, A.H., 1989. The effects of prolonged drought and nitrogen-fertilizer on root and shoot growth and water-uptake by winter-wheat. J. Agron. Crop Sci. -Zeitschrift fur Acker und Pflanzenbau 163, 352–360.
Barraclough, P.B., Weir, A.H., Khulmann, H., 1991. Factors affecting the growth and distribution of winter wheat roots under UK field conditions. In: McMichael, B.L., Persson, H. (Eds.), Development in Agricultural and Managed-Forest Ecology—Plant Roots and Their Environment. Elsevier, Amsterdam, pp. 410–417.
Bertholdsson, N.O., 2005. Early vigour and allelopathy—two useful traits for enhanced barley and wheat competitiveness with weeds. Weed Res. 45, 94–102.
Bertholdsson, N.O., Brantestam, A.K., 2009. A century of Nordic barley breeding- Effects on early vigour root and shoot growth, straw length, harvest index and grain weight. Eur. J. Agron. 30, 266–274.

Bertholdsson, N.O., Weedon, O., Brumlop, S., Finckh, M.R., 2016. Evolutionary changes of weed competitive traits in winter wheat composite cross populations in organic and conventional farming systems. Eur. J. Agron. 79, 23–30.
Bingham, I.J., Karley, A.J., White, P.J., Thomas, W.T.B., Russel, J.R., 2012. Analysis of improvements in nitrogen use efficiency associated with 75 years of spring barley breeding. Eur. J. Agron. 42, 49–58.
Brumlop, S., Reichenbecher, W., Tappeser, B., Finckh, M.R., 2013. What is the SMARTest way to breed plants and increase agrobiodiversity? Euphytica 194, 53–66.
Brumlop, S., Pfeiffer, T., Finckh, M.R., 2017. Evolutionary effects on morphology and agronomic performance of three winter wheat composite cross populations maintained for six years under organic and conventional conditions. Org. Farm. 3, 34–50.
Brundrett, M., 1991. Mycorrhizas in natural ecosystems. In: Macfayden Beong, A., Fitter, M. (Eds.), Advances in Ecological Research. Academic Press, London, pp. 171–313.
Clark, L.J., Price, A.H., Steele, K.A., Whalley, W.R., 2008. Evidence from near-isogenic lines that root penetration increases with root diameter and bending stiffness in rice. Funct. Plant Biol. 35, 1163–1171.
Clarke, J.M., Townley-Smith, F., McCaig, T.N., Green, D.G., 1984. Growth analysis of spring wheat cultivars of varying drought resistance. Crop Sci. 24 (3), 537–541.
Dawson, J.C., Goldringer, I., 2012. Breeding for genetically diverse populations: variety mixtures and evolutionary populations. In: Lammerts van Bueren, E.T., Myer, J.R. (Eds.), Organic Crop Breeding. Wiley-Blackwell, Oxford, UK, pp. 77–98.
Donn, S., Kawasaki, A., Delroy, B., Chochois, V., Watt, M., Powell, J.R., 2017. Root type is not an important driver of mycorrhizal colonization in Brachypodium distachyon. Pedobiologia J. Soil Ecol. 65, 5–15.
Döring, T.F., Knapp, S., Kovacs, G., Murphy, K., Wolfe, M.S., 2011. Evolutionary plant breeding in cereals-into a new era. Sustainability 3, 1944–1971.
Döring, T., Annicchiarico, P., Clarke, S., Haigh, Z., Jones, H.E., Pearce, H., Snape, J., Zhan, J., Wolfe, M.S., 2015. Comparative analysis of performance and stability among composite cross populations, variety mixtures and pure lines of winter wheat in organic and conventional cropping systems. Field Crops Res. 183, 235–245.
Edwards, J., Johnson, C., Santos-Medellín, C., Lurie, E., Podishetty, N.K., Bhatnagar, S., Eisen, J.A., Sundaresan, V., 2015. Structure, variation, and assembly of the root-associated microbiomes of rice. Proc. Natl. Acad. Sci. U. S. A. 112 (8), E911–E920.
Eissenstat, D.M., 1992. Costs and benefits of constructing roots of small diameter. J. Plant Nutr. 15 (6&7), 763–782.
Finckh, M.R., 2007. Conservation and generation of genetic resources through development of modern landraces of field crops: why we need Co-evolution in the field. In: Zikeli, S., Claupein, W., Dabbert, S., Kaufmann, B., Muller, T., Valle Zarate, A. (Eds.), Zwischen Tradition Und Globalisierung – 9, Wissenschaftstagung Ökologischer Landbau. Universität Hohenheim, Deutschland, pp. 20–23. http://orgprints.org/10742/.
Finckh, M.R., Wolfe, M.S., 2015. Biodiversity enhancement. In: Finckh, M.R., van Bruggen, A.H.C., Tamm, L. (Eds.), Plant Diseases and Their Management in Organic Agriculture. APS Press, St. Paul, MN, USA, pp. 153–174.
Frantz, J.M., Welbaum, G.E., Shen, Z.X., Morse, R., 1998. Comparison of cabbage seedling growth in four transplant production systems. HortScience 33, 976–979.
Grando, S., Ceccarelli, S., 1995. Seminal root morphology and coleoptile length in wild (*Hordeum vulgare ssp. spontaneum*) and cultivated (*Hordeum vulgare ssp. vulgare*) barley. Euphytica 86, 73–80.
Husson, F., Josse, J., Le, S., Mazet, J., 2018. R-core Package “FactomineR”: Multivariate Exploratory Data Analysis and Data Mining. URL:. https://cran.r-project.org/web/packages/FactoMineR/FactoMineR.pdf.
Jones, H., Clarke, S., Haigh, Z., Pearce, H., Wolfe, M., 2010. The effect of the year of wheat variety release on productivity and stability of performance on two organic and two non-organic farms. J. Agric. Sci. 148, 303–317.
Kaspar, T.C., Taylor, H.M., Shibles, R.M., 1984. Taproot-elongation rates of soybean cultivars in the glasshouse and their relation to field rooting depth[1]. Crop Sci. 24 (5), 916–933.
Kassambara, A., Mundt, F., 2017. R-core Package “factoextra”: Extract and Visualize the Results of Multivariate Data Analyses. pp. URL. https://cran.r-project.org/web/packages/factoextra/factoextra.pdf.
Krzanowski, W.J., 2004. Biplots for multifactorial analysis of distance. Biometrics 60, 517–524.
Lammerts van Bueren, E., Hulscher, M., Haring, M., Jongerden, J., van Mansvelt, J.D., den Nijs, A.P.M., Ruivenkamp, G.T.P., 1999. Sustainable Organic Plant Breeding; Final Report: a Vision, Choices, Consequences and Steps. Louis Bolk Institute.
Lammerts van Bueren, E.T., Jones, S.S., Tamm, L., Murphy, K.M., Myers, J.R., Leifert, C., Messmer, M.M., 2011. The need to breed crop varieties suitable for organic farming, using wheat, tomato and broccoli as examples: a review. Njas Wageningen J. Life Sci. 58, 193–205.
Larsson, S., 1982. A simple: rapid and non-destructive screening method useful for drought resistance breeding in oats (*Avena sativa L.*). Z. Pflanzenzüchtg 89, 206–221.
Le, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. J. Stat. Softw. 25 (1), 1–18.
Liao, M., Fillery, I.R.P., Palta, J.A., 2004. Early vigorous growth is a major factor influencing nitrogen uptake in wheat. Funct. Plant Biol. 31, 121–129.
Lilley, J.M., Kirkegaard, J.A., 2011. Benefits of increased soil exploration by wheat roots. Field Crops Res. 122, 118–130.
Løes, A.K., Gahoonia, G., 2004. Genetic variation in specific root length in Scandinavian wheat and barley accessions. Euphytica 137, 243–249.
Löschenberger, F., Fleck, A., Grausgruber, G., Hetzendorfer, H., Hof, G., Lafferty, J., Marn, M., Neumayer, A., Pfaffinger, G., Birschitzky, J., 2008. Breeding for organic agriculture –the example of winter wheat in Austria. Euphytica 163, 469–480.
Lynch, J.P., 2013. Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. Ann. Bot. 112, 347–357.
Maherali, H., 2014. Is there an association between root architecture and mycorrhizal growth response? New Phytol. 204 (1), 192–200.
Manschadi, A.M., Christopher, J., deVoil, P., Hammer, G.L., 2006. The role of root architectural traits in adaptation of wheat to water-limited environments. Funct. Plant Biol. 33, 823–837.
Manschadi, A.M., Manske, G., Vlek, P.L.G., 2013. Root architecture and resource acquisition wheat as a model plant. In: Eshel, A., Beeckman, T. (Eds.), Plant Roots: The Hidden Half. CRC Press, Taylor & Francis Group, pp. 1–22.
Messmer, M., Burger, H., Schmidt, W., Geiger, H., 2009. Importance of appropriate selection environments for breeding maize adapted to organic farming systems. Tagungsband der 60. Jahrestagung der Vereinigung der Pflanzenzüchter und Saatgutkaufleute Österreichs, November 24–26, 2009. Raumberg-Gumpenstein, Austria, pp. 49–52.
Moll, R.H., Kamprath, E.J., Jackson, W.A., 1982. Analysis and interpretation of factors which contribute to efficiency to nitrogen utilization. Agron. J. 75, 562–564.
Muellner, AlmuthElise, et al., 2014. Refining breeding methods for organic and low-input agriculture: analysis of an international winter wheat ring test. Euphytica 199 (1-2), 81–95.
Murphy, K., Lammer, D., Lyon, S., Carter, B., Jones, S.S., 2005. Breeding for organic and low-input farming systems: An evolutionary–participatory breeding method for inbred cereal grains. Renew. Agric. Food Syst. 20, 48–55.
Murphy, K.M., Campbell, K.G., Lyon, S.R., Jones, S.S., 2007. Evidence of varietal adaptation to organic farming systems. Field Crops Res. 102, 172–177.
Murphy, K.M., Carter, A.H., Jones, S.S., 2013. Evolutionary breeding and climate change. In: Kole, C. (Ed.), Genomics and Breeding for Climate-Resilient Crops. Springer, Netherlands, pp. 377–389.
Narayanan, S., Mohan, A., Gill, K.S., Prasad, P.V.V., 2014. Variability of root traits in spring wheat germplasm. PLoS One 9 (6), e100317. https://doi.org/10.1371/journal.pone.0100317.
Paillard, S., Goldringer, I., Enjalbert, J., Doussinault, G., de Vallavieille-Pope, C., Brabant, P., 2000. Evolution of resistance against powdery mildew in winter wheat populations conducted under dynamic management. I – is specific seedling resistance selected? Theor. Appl. Gent. 101, 449–456.
Paula, S., Pausas, J.G., 2011. Root traits explain different foraging strategies between resprouting life histories. Oecologia 165, 321–331.
Peiffer, J.A., Spor, A., Koren, O., Jin, Z., Tringe, S.G., Dangl, J.L., Buckler, E.S., Ley, R.E., 2013. Diversity and heritability of the maize rhizosphere microbiome under field conditions. Proc. Natl. Acad. Sci. U. S. A. 110 (16), 6548–6553.
Petereson, B.G., Carl, P., Boudt, K., Bennett, R., Ulrich, J., Zivot, E., Cornilly, D., Hung, E., Lestel, M., Balkissoon, K., Wuertz, D., 2018. R-core Package “PerformanceAnalytics”: Econometric Tools for Performance and Risk Analysis. URL. https://cran.r-project.org/web/packages/PerformanceAnalytics/PerformanceAnalytics.pdf.
Phillips, S., Wolfe, M., 2005. Evolutionary breeding for low input systems. J. Agric. Sci. 143, 245–254.
Pinheiro, J.Bates, D.DebRoy, S.Sarkar, D.Heisterkamp, S. EISPACK authors, 2016. R-core Package “nlme”: Linear and Nonlinear Mixed Effects Models. URL. https://cran.r-project.org/web/packages/nlme/index.html.
R Core Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Rengel, Z., 2005. Breeding crops for adaptation to environments with low nutrient availability. In: Ashraf, M., Harris, P.J.C. (Eds.), Abiotic Stresses: Plant Resistance Through Breeding and Molecular Approaches. The Haworth Press, New York.
Richard, C.A., Hickey, L.T., Fletcher, S., Jennings, R., Chenu, K., Christopher, J.T., 2015. High-throughput phenotyping of seminal root traits in wheat. Plant Methods 11 (1), 13.
Richards, R.A., Passioura, J.B., 1989. A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rainfed environments. Aust. J. Agric. Res. 40, 943–950.
Roucou, A., Violle, C., Fort, F., Roumet, P., Ecarnot, M., Vile, D., 2017. Shifts in plant functional strategies over the course of wheat domestication. J. Appl. Ecol. 55, 25–37.
Sanguineti, M.C., Li, S., Maccaferri, M., Corneti, S., Rotondo, F., Chiari, T., Tuberosa, R., 2007. Genetic dissection of seminal root architecture in elite durum wheat germplasm. Ann. Appl. Biol. 151, 291–305.
Shou-Chen, M., Bing-Cheng, X., Feng-Min, L., Wen-Zhao, L., Zhan-Bin, H., 2008. Effects of root pruning on competitive ability and water use efficiency in winter wheat. Field Crops Res. 105, 56–63.
Siddique, K.H.M., Belford, R.K., Tennant, D., 1990. Root: shoot ratios of old and modern, tall and semi-dwarf wheats in a Mediterranean environment. Plant Soil 121, 89–98.
Smith, S.E., Read, D., 2010. Mycorrhizal Symbiosis. Elsevier Science.
Tekrony, D.M., Egli, D.B., 1991. Relationship of seed vigour to crop yield: a review. Crop Sci. 31, 816–822.
Thorup-Kristensen, K., 1998. Root growth of green pea (*Pisum sativa L.*) genotypes. Crop Sci. 38, 1445–1451.
Thorup-Kristensen, K., Salmerón Cortasa, M., Loges, R., 2009. Winter wheat roots grow twice as deep as spring wheat roots, is this important for N uptake and N leaching losses? Plant Soil 322, 101–114.
Trachsel, S., Kaeppler, S.M., Brown, K.M., Lynch, J.P., 2013. Maize root growth angles become steeper under low N conditions. Field Crops Res. 140, 18–31.
Watt, M., Magee, L.J., McCully, M.E., 2008. Types, structure and potential for axial water flow in the deepest roots of field-grown cereals. New Phytol. 178, 135–146.
Watt, M., Moosavi, S., Cunningham, S.C., Kirkegaard, J.A., Rebetzke, G.J., Richards, R.A., 2013. A rapid, controlled-environment seedling root screen for wheat correlates well with rooting depths at vegetative, but not reproductive, stages at two field sites. Ann. Bot. 112, 447–455.
Weedon, O., 2018. Using Crop Genetic Diversity to Improve Resilience: Agronomic Potential of Evolutionary Breeding under Differing Management Systems PhD Thesis. University of Kassel. https://kobra.uni-kassel.de.

Wolfe, M., Hinchsliffe, K., Clarke, S., Jones, H., Haigh, Z., 2006. Evolutionary breeding of healthy wheat: from plot to farm. Aspects Appl. Biol. 79, 47–50.

Wolfe, M.S., Baresel, J.P., Desclaux, D., Goldringer, I., Hoad, S., Kovacs, G., Löschenberger, F., Miedaner, T., Østergård, H., Lammerts van Bueren, E.T., 2008. Developments in breeding cereals for organic agriculture. Euphytica 163 (3), 323–346.

Yan, W., Tinker, N.A., 2006. Biplot analysis of multienvironment trial data: principles and applications. Can. J. Plant Sci. 86, 623–645.

Ytting, N.K., Andersen, S.B., Thorup-Kristensen, K., 2014. Using tube rhizotrons to measure variation in depth penetration rate among modern North-European winter wheat (*Triticum aestivum L.*) cultivars. Euphytica 199, 233–245.