**Front. Agr. Sci. Eng.** 2021, 8(3): 400–415 https://doi.org/10.15302/J-FASE-2021394

RESEARCH ARTICLE

# RESPONSE OF WHEAT COMPOSITE CROSS POPULATIONS TO DISEASE AND CLIMATE VARIATION OVER 13 GENERATIONS

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## KEYWORDS

evolutionary breeding, heterogeneous crop population, management system

## HIGHLIGHTS

- Agronomic performance of wheat populations comparable to modern cultivars.
- Performance of populations depends on parental cultivar selection.
- Agronomic advantage of populations under particular environmental stresses.
- Heterogeneous populations better suited to low-input conditions.

Received September 23, 2020;
Accepted March 22, 2021.

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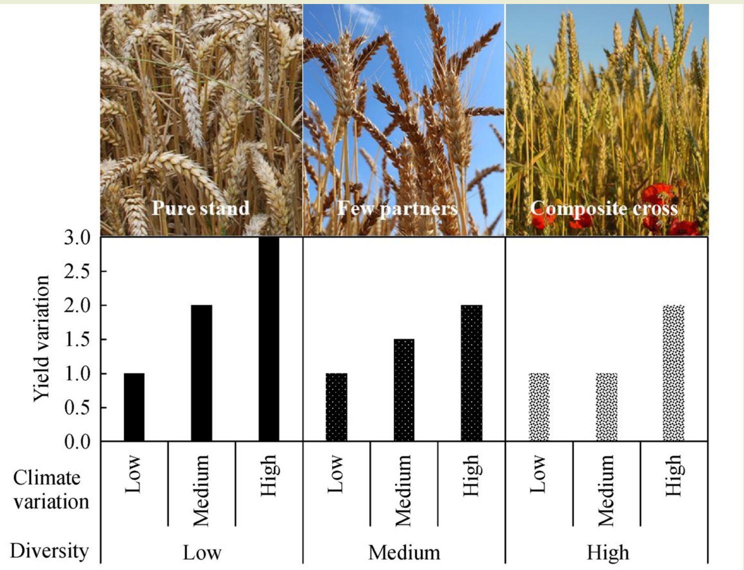
## GRAPHICAL ABSTRACT



## ABSTRACT

Since the $F_5$ (2005), three winter wheat composite cross populations (CCPs) based on germplasm specifically suitable for low-input conditions were subjected to natural selection under organic and conventional management. In the $F_6$, each CCP was divided into two parallel populations (12 CCPs in total) and maintained continuously until 2018. Commonly used modern cultivars with different disease susceptibilities were grown alongside to assess the agronomic performance of the CCPs. The organically managed CCPs were comparable in yield and foliar disease resistance to two continuously used reference cultivars, Achat and Capo. In contrast, under conventional management the cv. Capo outyielded the CCPs (Achat was not tested), highlighting the importance of parental cultivar choice for specific management systems. The CCPs were found to be moderately resistant to brown rust and even to the newly emerged stripe rust races prevalent in Europe since 2011. Differences between the CCPs were mainly due to parental genetic background and were significant in the first five generations, but were no longer so in the last five generations. In addition, these differences tended to vary depending on the experimental year and the environmental stresses present. In conclusion, the CCPs despite being derived from older cultivars are able to compete with more recently released reference cultivars under organic farming practices and represent a dynamic germplasm resource.

## 1 INTRODUCTION

The success of crop diversity can be attributed to “complementation, cooperation, compensation and capacity” particularly in uncertain environmental conditions[1]. Heterogeneous populations such as composite cross populations (CCPs) will likely make an important contribution in the future, especially as the merits of diversifying agricultural and food systems, but also diet become known[2]. CCPs can be used to produce locally-adapted genetically-diverse materials[3] while contributing to an overall diversification of the agricultural system and thus to dynamic development and conservation of genetic resources[4]. They also allow for adaptation to climatic changes and shifting pathogen populations[5].

For barley CCPs, Suneson[6] concluded that there was a need for at least 15 generations in order to ensure higher and stable yields. In dynamically managed wheat populations, Goldringer et al.[7] reported continuous evolution and significant changes in several yield traits from the $F_1$ to the $F_{10}$. In addition, a tendency for smaller yield variances in wheat populations in later generations was observed by Qualset[8], indicating a stabilizing effect within populations over time. However, there are still many open questions about the time frame of adaptation processes and the necessary strength of selective forces in order to ensure advantageous directional selection in heterogeneous populations. For example, Goldringer et al.[9,10] reported that extensively cultivated wheat populations tended to be more resistant to powdery mildew (*Blumeria graminis*) and brown rust (*Puccinia triticina*) and showed equal or superior agronomic potential in comparison to those populations that had been cultivated intensively.

We have been studying a set of three wheat CCPs that were created in 2001 by the John Innes Centre (Norwich, UK) in cooperation with the Elm Farm Research Centre (Newbury, UK) and these are described in detail by Döring et al.[11] and Brumlop et al.[12]. They are based on 20 European wheat cultivars (release dates from 1934 to 2000) chosen for their broad genetic background and good performance under low-input conditions in Europe and the UK[13]. The first population (Y_CCP, Y for yield) is made up of the half diallel crossing of nine high yielding parental cultivars, and the second (Q_CCP, Q for quality) is the half diallel crossing of 12 parental cultivars known for high baking quality. Both populations contain Bezostaya as a parent. The third population (YQ_CCP, YQ for yield by quality) is the product of crossing eight Y by 11 Q parents, plus the crosses of these 19 parents with Bezostaya. A number of male sterile lines were crossed with the parental cultivars and aliquots of the progenies added to the three populations in the $F_1$[11]. Since 2005/2006 ($F_5$), the populations have been evolving in our research field at the University of Kassel. Upon arrival, the three populations were divided and the $F_5$ was grown under both organic (O) and conventional (C) management (six populations in total). In the following generation ($F_6$), two subpopulations were created for each population (i.e., I and II), which were kept separately thereafter resulting in a total of 12 populations (six organic and six conventional). Examples of the population nomenclature used include OYQII (O, organically managed; YQ, yield by quality; and II, parallel population II) and CYI (C, conventionally managed; Y, yield; and I, parallel population I).

Apart from the removal of plants over 130 cm in height, no other direct selection was applied to the CCPs. Each population was maintained in plots > 150 $m^2$ ensuring an effective population size well over 10,000 individuals[12], a prerequisite to minimize the risk of genetic drift[7]. Overall, the 12 populations can thus be considered separate and distinct and the product of natural selection without drift since 2005. It is therefore possible to compare the parallel populations to each other and to see whether they have evolved and changed within the same growing system in parallel, while comparing populations grown under organic and conventional production practices will allow for system comparison.

First comparative studies of early seedling development showed that when maintained under conventional practices with soluble mineral nitrogen fertilizer for 5 and 10 years, the seedling root systems of wheat populations were more shallow and thinner than when maintained under organic management where plant nutrition depends on natural mineralization processes[14,15]. Yield stability was highest in the YQ_CCPs with the broadest genetic base[16].

For this paper, we analyzed the performance of the three winter wheat CCP types (Q, Y, YQ) as affected by their parental genetics and farming system from the $F_5$ to the $F_{17}$. We provide an historical analysis of agronomic traits in order to address the following questions: (1) How do the CCPs perform under varying environmental conditions and their stresses such as drought, high disease pressure, heat and cold? (2) How different are the CCPs from one another within their respective management system and are there changes or trends that have developed over time in terms of their agronomic characteristics? (3) Are there effects of organic or conventional management on agronomic traits measurable and how are these affected by parental genetics? Grain yield ($t \cdot ha^{-1}$), thousand grain weight (TGW, g), foliar and foot diseases were analyzed.

# 2 MATERIALS AND METHODS

## 2.1 Field site

The experimental research fields of the Department of Ecological Plant Protection are situated in Neu-Eichenberg (51°22′25″ N, 9°54′13″ E), 247 m above sea level. For 2005–2018, mean precipitation from September to August was 663 mm and mean temperature 9.6°C. From 2005/2006 until 2012/2013, the conventional CCPs were grown on the field Saurasen located about 500 m from the organic field Teilanger. Post 2012/2013, the conventionally managed CCPs were moved to a conventional field section set up on Teilanger. The soil of Saurasen is a sandy loam loess soil (Stagnic Luvisol) of low yield potential and Teilanger is a fine loamy loess (Haplic Luvisol) with much greater yield potential[17].

The growing conditions for the CCPs have been described in detail before[14,16]. In brief, row spacing was generally 30 cm to allow for easy mechanical weed control. The organic CCPs were grown after two years of grass-clover without additional fertilizers or pesticides and mechanical weed control. The conventional CCPs received no fungicides or insecticides, but herbicides were generally used once a year in early spring. Urea was applied in two split applications during the growing season (50 and 75 $kg \cdot ha^{-1}$ N, respectively). At stem elongation, growth regulators were applied in 2008, 2009, 2017, and 2018 (chlormequatchlorid).

## 2.2 CCPs and reference materials

The wheat CCPs were maintained in plots > 150 $m^2$, i.e., with 350 germinable seeds $m^{-2}$ (> 50,000 individuals) and bordered by 3 m of non-wheat or themselves in order to prevent outcrossing between the different populations. Alongside the CCPs, three to six popular modern wheat cultivars for either organic or conventional agriculture in Germany were also grown each year in smaller plots next to the populations in order to compare disease incidence and agronomic performance. The cvs Achat and Capo (Probstdorfer Saatzucht, Austria) were grown with the organically managed CCPs since 2007/2008 and Capo since 2008/2009 under conventional management. Both Achat and Capo (E class) were bred for conventional agriculture, but they are popular with organic farmers in Germany due to their good yielding and baking qualities. In 2008/2009 and 2014/2015, in addition to the populations, the parental cultivars were grown in unreplicated plots under organic practices to multiply seed.

## 2.3 Assessments

Grain yields ($t \cdot ha^{-1}$) and TGW (g) adjusted to 14% moisture content were recorded for each population and reference cultivar in most seasons. Some yield data from 2011, 2012, and 2013 were not available for the analyses (Table 1). Two to three yield measurements were taken from the population plots as replicate samplings in order to estimate variance and to allow for approximate statistical analysis within-year.

Foliar diseases caused by fungal pathogens were assessed from 2005/2006 onwards in most years unless disease pressure was quite low and the two main foliar leaf pathogens were recorded at each assessment date (Table 1). The proportion of non-green area (NGLA) was recorded for the flag leaf (F), the leaf below the flag leaf (F-1) and the F-2 leaf. Leaves where foliar disease or senescence could not be separated were excluded. From 2005/2006 to 2010/2011, 50–100 individual tillers per CCP were assessed for foliar diseases and 30 per reference cultivar. From 2013/2014, an average NGLA over the three leaf canopy levels (F, F-1 and F-2) was estimated from an area of neighboring plants of approximately 25 cm in length. Depending on the year, NGLA averages were recorded from between 3 and 12 times per population and reference cultivar (Table 1).

In addition to foliar pathogens, foot diseases were assessed at the beginning of July (BBCH growth stage 70–75) in each of the eight years (Table 1). At least 30 plants with roots were pulled from five to six points per plot and cleaned from soil residues and the outer stem sheath. The symptoms of foot rot pathogens (*Fusarium* spp., *Oculimacula yallundae*, and *Ceratobasidium*

Table 1 Data available for the wheat composite cross populations and foliar assessment methods (non-green leaf area, NGLA) used in the different years

| Experimental season | Yield $(t\cdot ha^{-1})$ | TGW (g) | DI (Foot) | Foliar disease assessments | | |
|---|---|---|---|---|---|---|
| | | | | Dates | | Method |
| 2005/2006 | x | – | – | 30.6 | – | % NGLA (F and F-1) on 100 tillers |
| 2006/2007 | x | x | – | – | – | – |
| 2007/2008 | x | x | – | 28.6 | – | % NGLA (F and F-1) on 50 tillers |
| 2008/2009[a] | x | x | x | 29.6 | 9.7 | % NGLA (F and F-1) on 30 tillers |
| 2009/2010 | x | x | x | 21.6 | 9.7 | % NGLA (F and F-1) on 50 tillers per CCP, 30 per ref |
| 2010/2011 | Conv. | x | x | 7.6 | 5.7 | % NGLA (F and F-1) on 50 tillers per CCP, 20 per ref |
| 2011/2012 | Conv. | x | – | – | – | – |
| 2012/2013 | Org. | x | – | – | – | – |
| 2013/2014 | x | x | x | 31.5 | 12.6 | % NGLA (F, F-1 and F-2), 25 cm row sections per plot (3 times) |
| 2014/2015[a] | x | x | x | 2.6 | 16.6 | % NGLA (F, F-1 and F-2), 25 cm row sections per plot (10 times) |
| 2015/2016 | x | x | x | 31.5 | 16.6 | % NGLA (F, F-1 and F-2), 25 cm row sections per plot (9 times) |
| 2016/2017 | x | x | x | 31.5 | 12.6 | % NGLA (F, F-1 and F-2), 25 cm row sections per plot (10 times) |
| 2017/2018 | x | x | x | 5.6 | 24.6 | % NGLA (F, F-1 and F-2), 25 cm row sections per plot (12 times) |

Note: Foot rot disease assessments (DI, disease index) were also conducted for eight generations. [a]Parents were grown for seed multiplication and assessed for foliar disease in 2008/2009 and 2014/2015 for disease and yield. Conv., yield data from the conventional populations missing; Org., yield data for the organic populations missing. x, the seasons in which data was collected. –, the seasons in which no data was available.

*cereale*) were identified on the lower stems based on a pictorial key[18]. Foot disease severity was assessed on a 0 to 3 scale according to Bockmann[19], where 0 is a healthy stem with no symptoms, 1 is given to plants with < 50% of the stem diameter showing symptoms, 2 is allocated to plants with > 50% of the stem diameter showing symptoms and 3 is assigned to rotten or broken stems (caused by *O. yallundae* only).

## 2.4 Data processing and statistical analysis

The mean NGLA% over the three leaf levels was calculated according to Brumlop et al.[17] through the weighting of the F leaf by a factor of 4, and the F-1 and F-2 leaves by a factor of 3. This accounts for the greater contribution of the flag leaf to total grain yield in comparison to lower leaves[20]. In seasons where more than one foliar disease assessment was made, the cumulative area under the disease progress curve (AUDPC) was calculated according to Shaner and Finney[21] and the relative AUDPC (RAUDPC) according to Fry[22].

A foot disease severity index (DI) was calculated according to Bockmann[19] for the three pathogens combined or for each foot rot pathogen separately as follows:

$$\mathrm{DI} = \frac{x_1 + 2x_2 + 4x_3}{n} \times 25$$

where $x_1$, $x_1$, $x_3$ are the numbers of plant stems with the disease scores 1 to 3, respectively, and $n$ is the total number of stems assessed.

Data analysis was conducted with the statistical software R Version 3.4.4, using the packages “nlme”, “lme4” and “emmeans”. Linear mixed effects models (*lmer* function) were conducted on untransformed data of yield, thousand grain weight, AUDPC and RAUDPC for foliar diseases and the DI.

Linear mixed models were used to analyze the CCPs and reference cultivars within separate growing systems (organic and conventional), with the CCP group (CCP type by system, CQ, CY, CYQ, OQ, OY, and OYQ), as well as the CCP entry with the inclusion of the parallel populations (QI and II, YI and II, and YQI and II) used as fixed factors. Random factors included year and replicate samplings within the organic system analyses and year, and replicate samplings and site within the conventional system analyses.

To determine site effect between the organically and conventionally managed CCPs for both yield and TGW, the data sets were divided into two time periods: (1) $F_5$–$F_{12}$ (organic CCPs maintained at Teilanger and conventional CCPs maintained at Saurasen) and (2) $F_{13}$–$F_{17}$ (all CCPs maintained at Teilanger). Type of CCP (Q_CCP, Y_CCP and YQ_CCP), growing system (organic and conventional) and year were used as fixed effects and replicate samplings as the random effect. Additionally, the site effects analyses on the CCP groups included CCP group (type by system), CCP entry and year as fixed effect and replicate samplings as the random effect.

The type of CCP as used above assumes that all populations of the same type, regardless of management history, are identical in their genetic composition, allowing for the testing of a management system's effect on the CCPs. This management system effect was also tested using foliar disease data including type of CCP and management system as fixed effects, with experimental year and replicate samplings used as random effects.

For all analyses, fixed and random factor interactions were included or eliminated depending on the model with the lowest Akaike information (AIC) and Bayesian information (BIC) criteria fitted by the maximum log-likelihood. Factors of the final model were then tested for violation of variance homogeneity using Levene's Test in the R package "car". For models indicating heteroscedastic distribution of residuals, the constant variance function *varIdent* in the "emmeans" package was included in the linear mixed effects models for each treatment as described by Zuur et al.[23] and the model with the lowest AIC and BIC was chosen based on log-likelihood tests.

# 3 RESULTS

## 3.1 Weather data and epidemic years

There were a number of unusual weather events during the experimental seasons from 2005/2006 to 2017/2018. Mean temperatures for the experimental seasons (September to August) were slightly higher (9.6°C) than the long-term mean of 9.0°C from 1971 to 2000 (Table 2). The warmest season was 2006/2007 (11.2°C) and the coolest season was 2012/2013 (8.4°C). Total mean precipitation (663 mm) was comparable to the long-term mean (1971–2000) of 628 mm. However, precipitation patterns over the 13 experimental seasons appear to be shifting toward drier late winter-early spring periods and more uneven distribution of the precipitation. Since 2010, dry spells were often not compensated by higher than average rains in the previous or following months leading to more or less extended drought periods. The winters and springs of 2010/2011, 2013/2014, 2016/2017 and 2017/2018 had higher than normal temperatures, exacerbating stress and 2017/2018 was, in addition to being the second hottest year recorded, also the driest with seasonal precipitation of only 471 mm. A particularly stressful event occurred in winter/early spring of 2011/2012. After a frost-free wet winter, temperatures dropped by > 20°C within 24 h followed by a two-week black frost period in early February, resulting in 50 cm-deep frozen soils. This was followed by hot, dry weather in the second half of February and March which resulted in severe frost damage in the region[17] (Table 2).

In addition to the weather variation, in 2009 and 2018 brown rust (*Puccinia triticina*) epidemics occurred and stripe rust (*Puccinia striiformis*) has been prevalent since 2014. Otherwise, *Blumeria graminis*, *Septoria tritici* and *Drechslera tritici-repentis* and cereal leaf beetles (*Oulema* sp.) were among the dominant causal agents of non-green leaf area.

## 3.2 Agronomic performance of the parental cultivars

The CCP parental cultivars were grown in a neighboring field under organic management in the experimental seasons of 2008/2009 and 2014/2015 when brown and yellow rust epidemics occurred, respectively. Yields, however, were only assessed in 2014/2015. A brief descriptive summary is given for reference and details are given in supplementary materials (Table S1).

In 2008/2009, the maximum percentage NGLA was recorded in Mercia (Q group at first assessment, 78% NGLA) and the lowest on Spark (Y group at first assessment, 1% NGLA). During the stripe rust epidemic in 2014/2015, maximum NGLA was recorded in Thatcher (Q group at first assessment, 9% NGLA) and the lowest on Pastiche (Q group at first assessment, 0% NGLA) and the cultivar ranking did not correspond to the ranking during the brown rust season of 2008/2009 (Table S1). Renan, Spark, Pastiche and Wembley had low to moderate RAUDPC values for brown and stripe rust. Overall, mean values of the parental groups were similar in both 2008/2009 and 2014/2015 (Table S1). Cv. Deben (Y group) yielded the highest (5.0 $t \cdot ha^{-1}$) but within the same group cv. Wembley yielded lowest (2.1 $t \cdot ha^{-1}$) (Table S1). Mean yields of the parental cultivar groups grown in 2014/2015 were comparable. The Y group, however, tended toward the highest yield (4.2 $t \cdot ha^{-1}$), followed by the YQ group (4.0 $t \cdot ha^{-1}$) and the Q group (3.9 $t \cdot ha^{-1}$) (Table S1).

**Table 2** Mean monthly and overall mean temperature (°C) and total monthly and overall total precipitation (mm) per experimental season from 2005/2006 to 2017/2018

| Experimental season | Sep. | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May | Jun. | Jul. | Aug. | Mean temp. and total ppt. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2005/2006 | 14.9 | 11.3 | 5.2 | 1.8 | −2.4 | −0.5 | 1.5 | 8.1 | 12.7 | 16.3 | 21.2 | 15.6 | 8.8°C |
| | 28 | 20 | 38 | 56 | 21 | 40 | 56 | 38 | 84 | 28 | 59 | 73 | 540 mm |
| 2006/2007 | 16.8 | 12.7 | 7.8 | 5.2 | 5.3 | 4.4 | 6.5 | 10.7 | 13.8 | 17.2 | 17.2 | 16.4 | 11.2°C |
| | 18 | 49 | 41 | 48 | 99 | 57 | 59 | 5 | 103 | 117 | 77 | 78 | 750 mm |
| 2007/2008 | 12.8 | 8.5 | 4.0 | 1.7 | 4.5 | 4.0 | 4.4 | 7.7 | 14.5 | 17.1 | 18.3 | 17.9 | 9.6°C |
| | 128 | 23 | 106 | 69 | 70 | 25 | 82 | 73 | 16 | 91 | 56 | 46 | 785 mm |
| 2008/2009 | 12.7 | 9.2 | 5.2 | 0.3 | −2.4 | 1.1 | 4.5 | 12.3 | 13.9 | 14.7 | 18.6 | 18.6 | 9.1°C |
| | 48 | 66 | 54 | 61 | 11 | 33 | 75 | 33 | 78 | 51 | 81 | 69 | 659 mm |
| 2009/2010 | 14.6 | 8.3 | 8.0 | 0.3 | −3.8 | −0.3 | 4.6 | 9.2 | 10.6 | 16.4 | 20.7 | 16.7 | 8.8°C |
| | 77 | 67 | 81 | 96 | 10 | 42 | 71 | 19 | 89 | 46 | 48 | 147 | 791 mm |
| 2010/2011 | 12.5 | 8.3 | 4.8 | −4.1 | 1.3 | 0.4 | 3.5 | 12.7 | 15.6 | 17.3 | 16.5 | 18.4 | 8.9°C |
| | 86 | 29 | 87 | 43 | 49 | 29 | 9 | 37 | 18 | 90 | 43 | 105 | 627 mm |
| 2011/2012 | 15.4 | 9.8 | 4.8 | 4.1 | 2.4 | −2.3 | 7.5 | 8.4 | 14.6 | 14.9 | 17.3 | 18.9 | 9.6°C |
| | 41 | 42 | 2 | 111 | 121 | 24 | 15 | 35 | 61 | 127 | 140 | 59 | 779 mm |
| 2012/2013 | 13.8 | 8.8 | 5.2 | 2.1 | −0.1 | −0.6 | −0.6 | 8.4 | 11.6 | 15.2 | 19.0 | 18.4 | 8.4°C |
| | 44 | 42 | 33 | 90 | 53 | 51 | 25 | 33 | 146 | 26 | 36 | 37 | 615 mm |
| 2013/2014 | 13.8 | 11.2 | 4.8 | 4.8 | 2.8 | 5.3 | 7.3 | 11.5 | 12.4 | 15.2 | 19.0 | 16.0 | 10.3°C |
| | 62 | 81 | 72 | 37 | 38 | 16 | 11 | 29 | 96 | 37 | 125 | 79 | 681 mm |
| 2014/2015 | 15 | 12.3 | 7.0 | 2.7 | 2.7 | 1.3 | 5.1 | 8.6 | 12.3 | 15.5 | 19.0 | 19.6 | 10.1°C |
| | 37 | 45 | 15 | 36 | 44 | 18 | 50 | 36 | 25 | 28 | 95 | 160 | 588 mm |
| 2015/2016 | 12.8 | 8.5 | 8.8 | 7.6 | 1.7 | 3.5 | 4.2 | 8.0 | 13.8 | 17.0 | 18.6 | 18.0 | 10.2°C |
| | 51 | 43 | 89 | 29 | 40 | 83 | 45 | 47 | 42 | 99 | 65 | 24 | 654 mm |
| 2016/2017 | 17.5 | 8.9 | 4.2 | 2.4 | −2.1 | 3.4 | 7.8 | 7.5 | 14.4 | 17.5 | 18.1 | 17.7 | 9.8°C |
| | 21 | 71 | 33 | 16 | 36 | 37 | 39 | 37 | 32 | 60 | 183 | 124 | 686 mm |
| 2017/2018 | 13.0 | 11.9 | 5.8 | 3.6 | 4.2 | −1.8 | 2.7 | 12.8 | 15.6 | 17.6 | 20.6 | 20.2 | 11.0°C |
| | 35 | 61 | 73 | 47 | 80 | 9 | 43 | 29 | 33 | 15 | 15 | 31 | 471 mm |
| Mean temp. | 14.3 | 10.0 | 5.8 | 2.5 | 1.1 | 1.4 | 4.5 | 9.7 | 13.5 | 16.3 | 18.8 | 17.9 | 9.6°C |
| Mean ppt. | 52 | 49 | 56 | 57 | 52 | 36 | 45 | 35 | 63 | 63 | 79 | 80 | 663 mm |
| Long-term mean temp. (1971–2000) | 13.6 | 9.2 | 4.7 | 2.3 | 1.0 | 1.4 | 4.9 | 8.1 | 12.9 | 15.5 | 17.4 | 17.3 | 9.0°C |
| Long-term mean ppt. (1971–2000) | 52 | 44 | 51 | 58 | 49 | 36 | 49 | 43 | 58 | 74 | 59 | 55 | 628 mm |

Color key

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Temp. deviations from mean | 🟧 | > +3°C | 🟨 | > +1.5°C | 🟩 | < +1.5°C and > −1.5°C | ⬜ | < −1.5°C | 🟦 | < −3°C |
| Ppt. deviations from mean | 🟦 | > +50% | ⬜ | > +25% | 🟩 | < +25% and > −25% | 🟨 | > −25% | 🟧 | > −50% |

Note: The color-coding keys indicate divergences from mean monthly temperatures and precipitation over all experimental seasons. Extreme temperature divergences and dry seasonal spells are boxed with black lines. The long-term means (1971–2000) are given for overall comparison. (Color key is included as a table footnote). Temp., temperature; ppt., precipitation.

## 3.3 Agronomic performance of the CCPs and references

### 3.3.1 Disease

The mean foot disease indices for the organic and conventional CCPs were 31 and 32, respectively, with no significant differences between any of the entries or systems over the experimental seasons (Table S2). Under organic management the two dominant pathogens were *O. yallundae* and *Fusarium* spp., with *O. yallundae* the most relevant pathogen under conventional management. *C. cereale* was rarely found, regardless of system. Disease indices ranged from 8 to 54 except for the CQI population in 2013/2014 with a value of 71. This was due to the fact that after the relocation of the conventional CCPs to Teilanger, part of the wheat was grown directly after wheat due to space constraints.

Depending on the experimental season and reference cultivar included, the CCPs displayed both significantly higher and lower AUDPC in comparison to the reference cultivars under organic practices (Fig. 1). Reactions to stripe rust since 2014 varied greatly. In the organic field, Naturastar was strongly affected in 2014 and 2015 while Scaro, Akteur and Achat were more susceptible in 2015. In the conventional field, Akteur was the most susceptible in 2014 but less so in 2015.

Some statistically significant differences occurred between parallel populations depending on year and pathogen occurrence. However, except in 2009, overall differences in disease levels among the CCPs were low (Fig. 1). No significant differences for AUDPC were found between the entries and the reference cultivars in the respective management systems (Table 3), indicating general similarities in foliar disease resistances between the CCP types under differing management systems. Analysis of mean RAUDPC values of CCP types over the eight experimental years and between systems indicate no significant differences between the organically managed CCPs (0.19) and the conventionally managed CCPs (0.18) ($F_{1,82.99}$ = 0.67, $P$ = 0.41).

### 3.3.2 Yield and thousand grain weight

Depending on the comparisons conducted, the number of years for which yield data were available varied (Table 1, Table 4, and Table 5). The respective degrees of freedom, F, and p values are summarized in Table 6. Under organic practices the highest mean annual yield of the CCPs was achieved in 2010/2011 (7.4 $t\cdot ha^{-1}$) and the lowest in 2013/2014 (3.1 $t\cdot ha^{-1}$) (Table 4). Mean yield of the OQ group was lowest (4.8 $t\cdot ha^{-1}$), whereas the OYQ and OY groups had significantly higher yields (both 5.1 $t\cdot ha^{-1}$) (Table 4 and Table 6). In the 10 years when Achat and Capo were grown with the organic CCPs, the OQ group still tended toward the lowest yields per season (4.84 $t\cdot ha^{-1}$) (Table 4), but these yield differences were no longer statistically significant (Table 6). Similar results were found in the comparison of the CCP entries and reference cultivars (Table 3 and Table 6). After the winterkill of 2012, in contrast to the other seasons, the OY group yielded the lowest (3.7 $t\cdot ha^{-1}$) (Table 4), the OYQ and OQ groups both yielded 4.1 $t\cdot ha^{-1}$, and Achat and Capo gave the highest yields in that year (5.2 and 4.8 $t\cdot ha^{-1}$, respectively). Yields of the OY group (4.8 $t\cdot ha^{-1}$) were significantly greater than both reference cultivars, as well as the OQ and OYQ groups in the extremely dry season of 2018, where mean yield of the experimental season was 4.4 $t\cdot ha^{-1}$.

Under conventional practices the highest mean annual yield was achieved in 2016/2017 (6.3 $t\cdot ha^{-1}$) and the lowest yield in 2006/2007 (2.2 $t\cdot ha^{-1}$) (Table 4). Over the eight experimental seasons in which Capo was grown alongside the conventional CCPs, it yielded significantly higher than the conventional CCPs (Table 6). The conventional CCP group yield ranking mirrored the organic CCP group ranking. The CQ group had the lowest mean group yield over the experimental seasons of 4.6 $t\cdot ha^{-1}$, followed by the CY group with 4.8 $t\cdot ha^{-1}$ and the CYQ group yielding highest (5.0 $t\cdot ha^{-1}$) (Table 4 and Table 6). Also, no significant differences in yield were found in the comparison of CCP entries and Capo under conventional management ($F_{3,43.5}$ = 0.8, $P$ = 0.50) (Table 6), with Capo and CYII achieving the highest yields of 5.8 and 5.5 $t\cdot ha^{-1}$, respectively, and the two CQ parallel populations the lowest (5.0 and 5.1 $t\cdot ha^{-1}$, respectively) (Table 3). Unfortunately, no data are available for the conventional CCPs in 2012 to compare the frost effects to the organic CCPs. However, in the extreme year of 2018, both the CY and CYQ groups significantly outyielded the reference cv. Capo.

The highest mean annual TGW was found in 2010/2011 under organic practices (54.1 g) and the lowest in 2009/2010 under conventional practices (35.1 g) (Table 5) with no significant differences between the CCP groups or entries under either management system (Table 5 and Table 6). Overall, within system the Y_CCP groups tended toward slightly lower TGWs than the other CCP groups (Table 5).

### 3.3.3 Effect of site and/or generation and system on CCP yields and TGW

Until 2012/2013, the conventional mean yields on Saurasen were 4.1 $t\cdot ha^{-1}$, considerably lower than the mean yields achieved on the conventional field at Teilanger with higher soil quality since 2013/2014 (5.2 $t\cdot ha^{-1}$) (Table 4). Yield performance on Saurasen

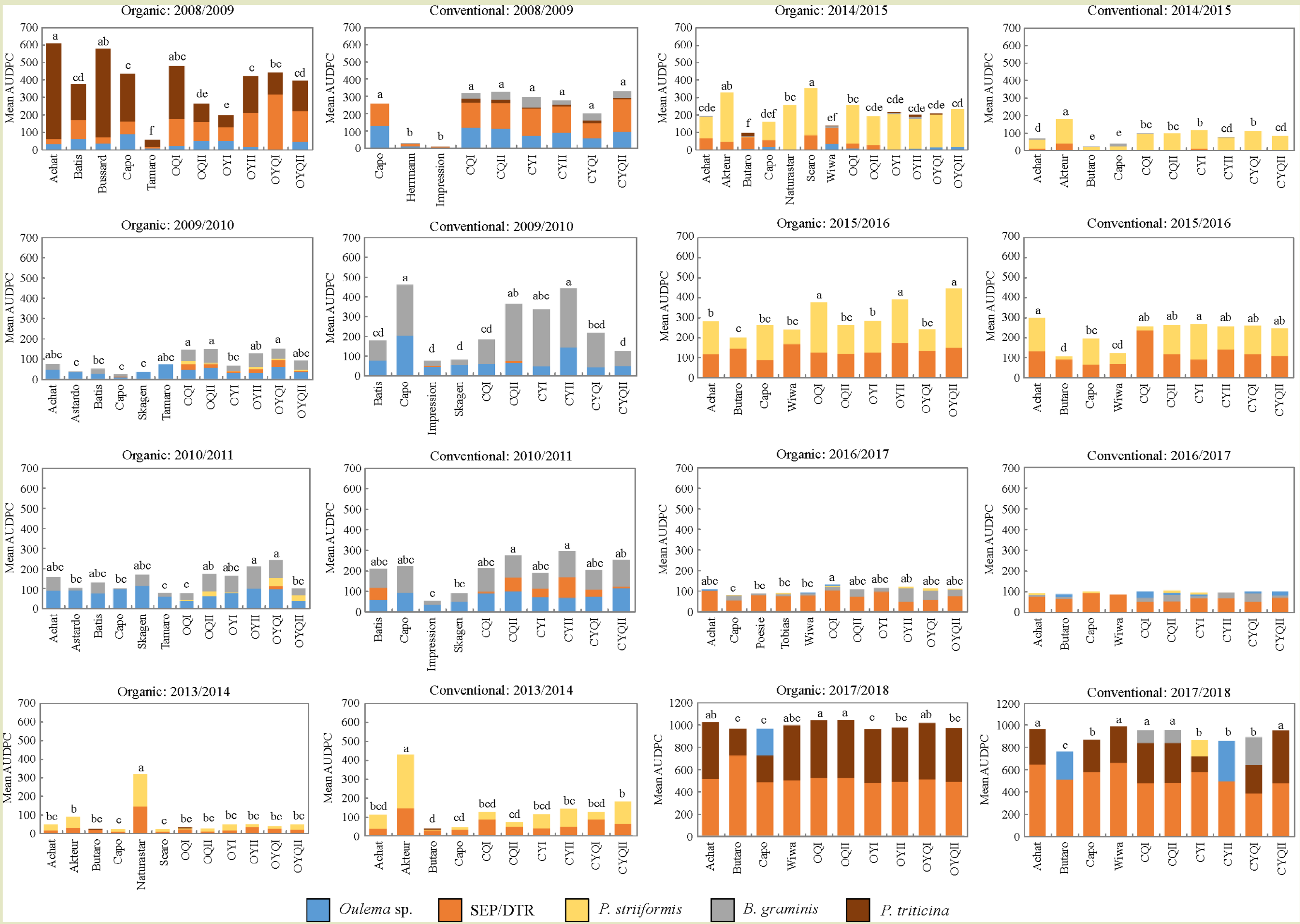


**Fig. 1** Estimated mean area under the disease progress curve (AUDPC) and dominance of foliar and insect pathogens in the organically and conventionally managed wheat composite cross populations and reference cultivars from 2008/2009 to 2017/2018 (SEP/DTR, *Septoria tritici*/*Drechslera tritici-repentis*). Differing small letters indicate significant differences at $P < 0.05$ between entries within an experimental season.

**Table 3 Estimated mean area under the disease progress curve (AUDPC) and yields (t·ha$^{-1}$) for the organic and conventional wheat composite cross entries and reference cultivars**

| Entry | AUDPC | | Yield | |
|---|---|---|---|---|
| | Organic | Conventional | Organic | Conventional |
| Achat | 311 | | 5.29 | |
| Capo | 255 | 273 | 5.17 | 5.75 |
| QI | 317 | 281 | 4.77 | 4.97 |
| QII | 277 | 308 | 4.91 | 5.10 |
| YI | 256 | 285 | 5.00 | 5.21 |
| YII | 311 | 305 | 5.21 | 5.45 |
| YQI | 306 | 263 | 5.11 | 5.43 |
| YQII | 298 | 283 | 5.20 | 5.35 |

(conventional) versus Teilanger (organic) was analyzed for the type of CCPs (Q_CCP, Y_CCP and YQ_CCP) for five experimental seasons (2005/2006–2009/2010, i.e., $F_5$–$F_9$) (Table S3) and for the CCP type by system groups (CQ, CY, CYQ, OQ, OY and OYQ) and CCP entries for four experimental seasons ($F_6$–$F_9$) versus five experimental seasons (2013/2014 to 2017/2018) at Teilanger (Table 7). TGWs were compared for seven generations (2006/2007–2012/2013, i.e., $F_6$–$F_{12}$) (see Table 1 for missing values) at Saurasen and Teilanger, with the $F_{13}$–$F_{17}$, i.e., 2013/2014–2017/2018 included in the systems comparison at Teilanger (Table 7; Table S3).

In the $F_6$–$F_{9,}$ when grown conventionally at Saurasen and organically at Teilanger, yields of the CCP groups followed the same patterns at both sites (Fig. 2(a)). On average, the Q_CCP (4.3 t·ha$^{-1}$) yielded significantly lower than the Y_CCP (4.6 t·ha$^{-1}$) and YQ_CCP (4.9 t·ha$^{-1}$) groups (Fig. 2(a)). These differences between CCP types were no longer present in the $F_{13}$–$F_{17}$ when all CCPs, both organically and conventionally managed, were grown at Teilanger (Fig. 2(b)). However, once grown at the same site the conventionally grown CCP groups yielded significantly more than the organically grown CCP groups.

The YQ_CCP and Q_CCP types had significantly greater mean TGW compared to the Y_CCP type (44.2, 44.2 and 43.3 g, respectively) from the $F_6$ to the $F_{12}$ when the CCPs had been grown at both Saurasen and Teilanger. However, these differences between CCP groups were only significant at Saurasen and not at Teilanger (Fig. 2(c) and Table S3). Once all populations were grown at Teilanger from the $F_{13}$ to the $F_{17,}$ there were no differences in TGW within growing system. However, in contrast to yields, TGW was consistently and significantly higher under organic management than under conventional management, independent of site (Fig. 2(c,d)). There was no significant interaction between type of CCP and year when the conventional CCPs were grown at Saurasen ($F_{12,85.3}$ = 1.1, $P$ = 0.37) but this interaction became significant when all CCPs were grown at Teilanger from 2013/14 to 2017/18 ($F_{8,114}$ = 3.8, $P < 0.001$) (Table S3). Similarly, a significant interaction between CCP group and year was found only when all CCPs were grown at Teilanger ($F_{13}$–$F_{17}$) ($F_{20,63.7}$ = 12.7, $P < 0.001$) (Table 7).

## 4 DISCUSSION

Averaged across all years and under both management systems, the YQ_CCPs achieved the significantly highest yields and the Q_CCPs the lowest, confirming a consistent influence of parental genetics over time. Depending on year, the Y_CCPs yielded higher or lower than the YQ_CCPs. The exceptionally low yield of the OY_CCP in 2011/2012 was due to its genetic background that was particularly affected by extreme black frost[17]. In 2011/2012, the OYQ populations yielded similarly to the OQ populations highlighting the compensatory capacity of the Q genetics to buffer poor winter hardiness of the Y genetics in the YQ_CCP under extreme frost conditions. In the particularly dry seasons of both 2014/2015 and 2017/2018, yields were reduced in both systems, especially under organic management. With respect to diseases, the CCPs generally performed similarly to modern cultivars despite their rather “old” genetics (release dates of the parents: 1934–2000)[13]. In 2017/2018, the driest of all reported experimental seasons, the OY populations also yielded significantly higher than both the OYQ and OQ populations. However, under conventional

**Table 4** Estimated means of yields ($t \cdot ha^{-1}$) in experimental season for wheat composite cross population (CCP) and the reference cvs Achat and Capo (organic), and Capo (conventional)

| Entry | 2005/2006 | 2006/2007 | 2007/2008 | 2008/2009 | 2009/2010 | 2010/2011 | 2011/2012 | 2012/2013 | 2013/2014 | 2014/2015 | 2015/2016 | 2016/2017 | 2017/2018 | Mean | SE | Mean CCPs |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Organic | | | | | | | | | | | | | | | | |
| Achat | | | 6.61 a | 5.32 | 6.46 a | 7.34 | 5.20 a | | 2.85 ab | 4.11 b | 4.33 | 6.37 a | 4.30 b | 5.29 | 0.41 | |
| Capo | | | 5.66 ab | 5.52 | 6.56 a | 7.31 | 4.80 a | | 3.48 a | 4.16 b | 3.84 | 5.92 ab | 4.27 b | 5.17 | 0.41 | |
| OQ | 5.85 | 2.73 b | 5.37 b | 4.99 | 5.61 b | 7.30 | 4.06 b | | 2.64 b | 4.64 ab | 4.12 | 5.50 b | 4.19 b | 4.84 | 0.41 | 4.76 B** |
| OY | 6.29 | 3.43 a | 6.32 a | 4.97 | 6.00 ab | 7.34 | 3.70 b | | 3.26 a | 5.12 a | 4.23 | 5.46 b | 4.78 a | 5.11 | 0.41 | 5.07 A** |
| OYQ | 5.62 | 3.69 a | 6.31 a | 4.96 | 6.28 a | 7.64 | 4.11 b | | 3.34 a | 4.64 ab | 4.29 | 5.81 ab | 4.25 b | 5.16 | 0.41 | 5.09 A** |
| **Mean** | **5.92** | **3.28** | **6.03** | **5.08** | **6.10** | **7.40** | **4.22** | | **3.10** | **4.63** | **4.18** | **5.73** | **4.38** | | | |
| Conventional | | | | | | | | | | | | | | | | |
| Capo | | | | 5.92 a | 5.10 a | | | 6.18 | 5.54 a | 6.59 | 5.42 a | 6.89 a | 4.44 b | 5.75 A* | 0.29 | |
| CQ | 4.98 | 2.27 | 3.48 ab | 4.96 b | 4.12 b | | | 5.46 | 4.54 b | 6.02 | 4.46 b | 5.92 b | 4.81 ab | 5.04 B* | 0.27 | 4.64 B** |
| CY | 5.30 | 2.00 | 3.37 b | 5.62 a | 4.36 b | | | 6.06 | 4.79 ab | 6.38 | 4.01 b | 6.42 ab | 5.04 a | 5.33 AB* | 0.27 | 4.84 AB** |
| CYQ | 5.16 | 2.23 | 4.20 a | 5.44 ab | 4.96 a | | | 5.93 | 4.78 ab | 5.99 | 4.52 b | 6.41 ab | 5.05 a | 5.39 AB* | 0.27 | 4.97 A** |
| **Mean** | **5.14** | **2.17** | **3.68** | **5.42** | **4.57** | | | **5.87** | **4.82** | **6.20** | **4.49** | **6.34** | **4.89** | | | |

Note: Estimated means over all experimental seasons CCP group and reference cultivar are also given. Differing letters indicate significant differences at $P < 0.05$. Different small letters indicate significant differences of the entries within the experimental year. *Different capital letters indicate significant differences between the CCP groups and reference varieties. **Different capital letters indicate significant differences between the CCP groups only. Mean values of yield per experimental year are marked in bold.

**Table 5** Estimated means of thousand grain weight (TGW) (g) in experimental season for wheat composite cross population (CCP) and the reference cvs Achat and Capo (organic), and Capo (conventional)

| Entry | 2006/2007 | 2007/2008 | 2008/2009 | 2009/2010 | 2010/2011 | 2011/2012 | 2012/2013 | 2013/2014 | 2014/2015 | 2015/2016 | 2016/2017 | 2017/2018 | Mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Organic | | | | | | | | | | | | | |
| OQ | 44.0 a | 52.3 | 40.7 | 42.3 | 53.4 | 49.7 | 45.5 | 48.7 a | 45.8 b | 44.6 | 44.3 b | 42.8 | 46.1 |
| OY | 41.5 b | 54.5 | 37.5 | 40.7 | 53.5 | 48.3 | 46.6 | 48.4 a | 47.9 a | 43.5 | 45.4 a | 43.3 | 45.9 |
| OYQ | 43.2 ab | 53.4 | 39.6 | 40.7 | 55.3 | 49.8 | 44.9 | 46.8 b | 46.5 b | 46.0 | 45.8 a | 42.3 | 46.1 |
| **Mean** | **43.0** | **53.3** | **39.4** | **41.2** | **54.1** | **49.3** | **45.5** | **47.9** | **46.6** | **44.8** | **45.2** | **42.8** | |
| Conventional | | | | | | | | | | | | | |
| CQ | 37.9 | 50.9 | 36.7 | 36.4 | 51.5 b | 49.6 | 42.5 | 41.2 | 45.4 | 41.9 a | 49.1 | 39.8 b | 43.5 |
| CY | 38.0 | 46.9 | 35.5 | 33.0 | 53.6 ab | 46.3 | 41.3 | 43.0 | 46.4 | 39.4 b | 46.9 | 43.1 a | 42.9 |
| CYQ | 38.9 | 48.4 | 35.8 | 35.9 | 54.1 a | 48.7 | 43.5 | 42.4 | 45.4 | 41.2 ab | 47.3 | 40.8 b | 43.6 |
| **Mean** | **38.3** | **48.8** | **36.0** | **35.1** | **53.1** | **48.2** | **42.4** | **42.2** | **45.7** | **40.8** | **47.8** | **41.3** | |

Note: Estimated means over all experimental seasons CCP group and reference cultivar are also given. Differing letters indicate significant differences at $P < 0.05$. Mean values of TGW per experimental year are marked in bold.

**Table 6** Numerical degrees of freedom (DF), denominator degrees of freedom (DenDF), mean squares (MS), and F and P values from the analysis of variance for yield ($t \cdot ha^{-1}$) and TGW (g) for the wheat composite cross population (CCP) groups and entries, and CCPs and entries including reference cultivars under organic and conventional management

| Item | CCP group and entry (yield) | | | | | CCP group and reference (yield) | | | | | CCP group and entry (TGW) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DF | DenDF | MS | F value | *P* value | DF | DenDF | MS | F value | *P* value | Df | DenDF | MS | F value | *P* value |
| Organic | | | | | | | | | | | | | | | |
| CCP Group | 2 | 41.2 | 0.5 | 7.5 | < 0.01 | 4 | 50.2 | 0.1 | 1.5 | 0.23 | 2 | 49.1 | 1.2 | 0.9 | 0.42 |
| CCP Entry | 3 | 27.5 | 0.1 | 1.2 | 0.33 | 3 | 22.6 | 0.1 | 1.3 | 0.31 | 3 | 34.3 | 2.6 | 1.8 | 0.16 |
| Conventional | | | | | | | | | | | | | | | |
| CCP Group | 2 | 42.4 | 0.1 | 3.4 | 0.04 | 3 | 43.5 | 0.2 | 4.2 | 0.01 | 2 | 46.4 | 0.4 | 0.2 | 0.81 |
| CCP Entry | 3 | 27.1 | 0.02 | 0.8 | 0.48 | 3 | 43.5 | 0.03 | 0.8 | 0.50 | 3 | 28.3 | 3.2 | 1.8 | 0.18 |

Note: Year was included as a random factor.

management the CY and CYQ populations yielded similarly. Preliminary molecular analysis of the YQ populations over time suggests that this singular event did not change the overall genetic makeup of the populations[24], supporting the conclusions of Brumlop et al.[12] that genetic drift may be avoided by using a large plot size>150 $m^2$.

Occasionally, differences between parallel CCPs in a given year for yield and TGW were statistically significant[16]. Yield stability analysis based on the eight years since 2009 indicates that the CYI population (mean yield 4.8 $t \cdot ha^{-1}$) reacted much more strongly to environmental conditions in comparison to all other conventional CCPs and it emerged as considerably less stable than CYII (mean yield 5.2 $t \cdot ha^{-1}$)[16]. In our analysis when including experimental year as a random effect, the differences in yield were still evident but no longer statistically significant (Table 3). Early root development of these two populations from the $F_6$ to the $F_{15}$ diverges considerably, however[15]. These differences in yielding ability and stability between the two CY parallel populations may indicate differing selection pressures over the experimental years in which they were grown. Differentiation among populations and between generations can be attributed mainly to environmental pressures, plant-plant competition and plant-pathogen coevolution, which makes specific selective forces difficult to pinpoint[25]. Weather conditions were the same for each population in each generation, but localized differing environmental conditions in soil quality (particularly challenging for the conventional CCPs prior to 2013/2014), disease pressure and nutrient availability might have occurred. Yield comparisons in replicated trials under

**Table 7 Numerical degrees of freedom (DF), denominator degrees of freedom (DenDF), mean squares (MS), and F values and p values from the analysis of variance for yield (t·ha$^{-1}$) and TGW (g) of the wheat composite cross populations (CCPs) across management system and depending on the site**

| Site | Item | CCP group and entry (yield) | | | | | CCP group and entry (TGW) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | DF | DenDF | MS | F value | *P* value | DF | DenDF | MS | F value | *P* value |
| Saurasen and Teilanger ($F_6$–$F_9$/$F_{12}$) | CCP Group | 5 | 28.9 | 3.1 | 65.2 | < 0.001 | 5 | 33.0 | 37.9 | 16.8 | < 0.001 |
| | CCP Entry | 6 | 16.0 | 0.1 | 1.4 | 0.26 | 6 | 5.5 | 3.0 | 1.3 | 0.37 |
| | Year | 3 | 6.0 | 18.5 | 389.9 | < 0.001 | 6 | 31.6 | 531.4 | 235.9 | < 0.001 |
| | CCP Group × Year | 15 | 28.9 | 1.0 | 20.1 | < 0.001 | 30 | 43.7 | 3.7 | 1.6 | 0.06 |
| | CCP Entry × Year | 18 | 16.0 | 0.2 | 3.8 | < 0.001 | 36 | 35.4 | 2.6 | 1.2 | 0.33 |
| Teilanger ($F_{13}$–$F_{17}$) | CCP Group | 5 | 21.4 | 1.6 | 33.8 | < 0.001 | 5 | 63.6 | 10.5 | 11.4 | < 0.001 |
| | CCP Entry | 6 | 8.6 | 1.0 | 3.5 | 0.04 | 6 | 38.9 | 3.5 | 3.8 | < 0.01 |
| | Year | 4 | 6.4 | 5.0 | 107.1 | < 0.001 | 4 | 8.9 | 31.2 | 34.1 | < 0.001 |
| | CCP Group × Year | 20 | 32.8 | 0.3 | 5.8 | < 0.001 | 20 | 63.7 | 11.5 | 12.7 | < 0.001 |
| | CCP Entry × Year | 24 | 19.0 | 0.2 | 3.3 | < 0.01 | 24 | 42.3 | 5.2 | 5.7 | < 0.001 |

Note: Year represents the experimental seasons, the CCP represents CCP type by system groups (CQ, CY, CYQ, OQ, OY and OYQ) and CCP entries represents the 12 CCP parallel populations (organic and conventional).

conventional and organic practices are under way to test all 12 CCPs for potential differences due to growing system. Molecular studies will be necessary to confirm divergent evolutionary trajectories.

As expected, once grown in the same soil conditions from 2013/2014 onwards the conventionally grown CCPs achieved higher overall yields than the organically managed populations. Under organic management the organic CCPs all yielded similarly to the reference cultivars Achat and Capo, with the OYII and OYQII populations outyielding Capo. Similar results were reported by Danquah and Barrett[26] in which three composite cross barley generations outyielded the well-known reference cv. Atem in 1992, a particularly dry year. However, under conventional management the reference cv. Capo had significantly greater yields than the CQ populations. This reflects both the parental selection for cultivars with better baking quality in the Q_CCPs and cultivars best suited to low-input conditions in Europe.

The significant interactions between CCP group, CCP entries and experimental seasons under both organic and conventional management indicate, however, that CCP yield ranking was not fixed and that depending on the experimental year differing CCP groups and entries yielded more or less. Clear examples of these interactions can be seen particularly in experimental seasons with strong environmental stresses. As pointed out above, the extreme winterkill in 2011/2012 resulted in the OQ_CCPs outyielding the OY_CCPs due to their parental heritage. Also, Achat and Capo outyielded the CCPs due to their good winter hardiness[17]. These results are in contrast to the extreme drought seasons 2014/2015 and 2017/2018 when the CCPs mostly outyielded Capo and Achat. Also, the organic and the conventional Y_CCPs outyielded both the YQ_CCP and Q_CCP CCPs, likely due to the more modern parental cultivar genetics used for the Y_CCPs[13]. Yields of the parental cultivars in 2014/2015 showed a similar yield ranking pattern confirming the effects of parental genetic background in yield performance under these particular environmental conditions.

TGW varied according to cultivation system and year, but little due to parental genetics in line with earlier observations that heritability of seed size is generally low[27]. An explanation for the higher TGW under organic practices could be the fact that the potential number of seeds per spike is determined early during wheat development[28]. At that time, organic wheat is normally much more nutrient limited than conventionally grown wheat as nutrient availability under organic management depends on microbial processes that are slow early in the season due to low temperatures[29], leading to lower grain numbers per ear under organic practices and a respectively higher TGW. Alternatively, slow mineralization in spring under organic practices may have reduced tillering capacity, resulting in greater resource availability for grain filling and a higher TGW. In addition, the organically managed populations have evolved root systems more adapted to variation in nutrient availability compared to the conventionally managed populations[15]. This may have resulted in greater nutrient provision during the critical phase of grain filling.

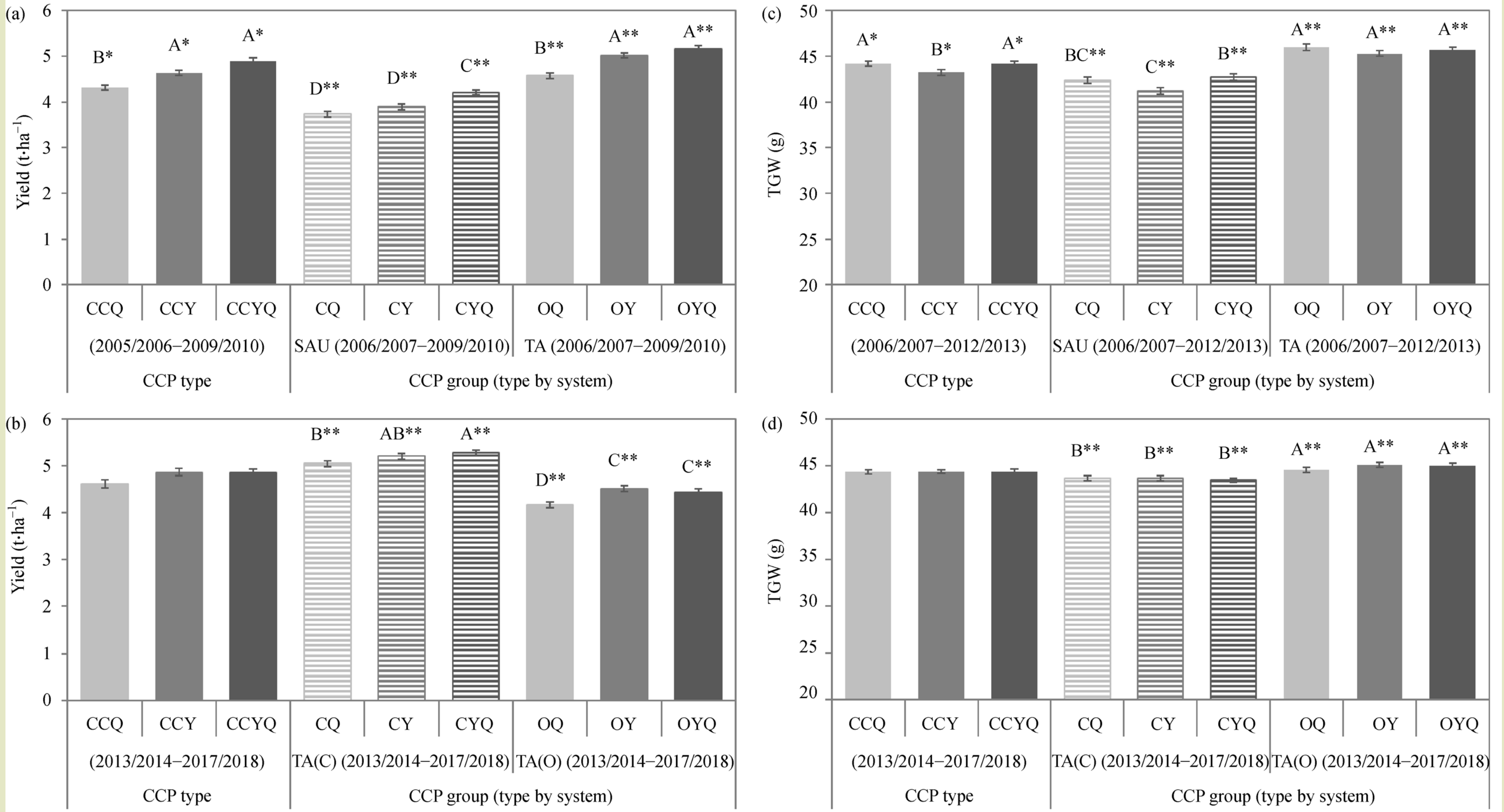


**Fig. 2** (a) Estimated mean yields ($t \cdot ha^{-1}$) of types of wheat composite cross populations (CCP) and CCP groups under organic (TA, Teilanger) and conventional (SAU, Saurasen) management for the five and four experimental seasons from 2005/2006 to 2009/2010 and from 2006/2007 to 2009/2010. (b) Estimated mean yields ($t \cdot ha^{-1}$) of types of CCPs and CCP groups under organic (O) and conventional (C) management at Teilanger (TA) for the five experimental seasons from 2013/2014 to 2017/2018. (c) Estimated mean TGW (g) of types of CCP and CCP groups under organic (TA) and conventional (SAU) management for seven experimental seasons from 2006/2007 to 2012/2013. (d) Estimated mean TGW (g) of types of CCP and CCP groups under organic (O) and conventional (C) management at TA for the five experimental seasons from 2013/2014 to 2017/2018. Different capital letters indicate significant differences at $P < 0.05$ within types of CCP and within the CCP groups. Error bars indicate standard error. Conventional CCPs are indicated by bars with horizontal lines. *Different capital letters indicate significant differences of the CCP types over the mentioned experimental years. **Different capital letters indicate significant differences between the CCP groups over the mentioned experimental years.

Genetic differences between the CCP types in terms of yield and TGW in earlier generations ($F_5$–$F_9$/$F_6$–$F_{12}$) were no longer present in later generations ($F_{13}$–$F_{17}$), although significant differences between CCP groups under both organic and conventional management for mean yield averaged over all experimental seasons were still present. As the organic CCPs were always grown at Teilanger, a site effect for the organic CCPs may be excluded. The greater genetic diversity present in the YQ populations (crossing of all 20 parents) may have resulted in greater pathogen resistance variation and diversity, increasing the adaptive capacity and resilience of the YQ CCPs. Although significant management system effects were found for yield and TGW, no significant interactions between management systems effect × CCP types were present. Thus, there were no differential responses of CCP types to management system, but the YQ_CCPs tended toward higher yields and TGW values under both management systems. Similarly, no significant management system × CCP type interactions occurred for foliar diseases and all CCPs reacted similarly under both management systems with no advantage to the YQ_CCPs.

Brown rust in 2009 and 2018 and stripe rust since 2014 varied considerably between fields, including large differences in disease severity on the reference cultivars. In 2009, the distance between the organic and conventional fields, soil and microclimatic conditions were large. Since 2013, the CCPs have been growing in adjacent fields with similar soil quality and within a 20-ha area with the same overall exposition and thus presumably quite similar microclimatic conditions. Nevertheless, Achat and especially Akteur suffered more from stripe rust in the conventional field than in the organic field in 2014. In contrast, in 2015 and 2018, disease was stronger in the organic field, but in 2016, AUDPC was similar across fields (Fig. 1). Higher disease severities in conventional systems are often reported due to high mineral fertilizer applications[30]. The mineral fertilizer applications at the experimental site at Neu-Eichenberg, however, are considered moderate to low (120 $\mathrm{kg \cdot ha^{-1}}$ N). Variation in foliar disease pressure was more likely due to spatial variation between Saurasen and Teilanger until 2013 and within Teilanger thereafter.

Of the three non-European stripe rust races present in Europe post-2011[31], it is likely that at least two were present, namely Warrior and Triticale Aggressive, as stripe rust was found in the triticale crops grown in Neu-Eichenberg in 2014 and 2015 (Weedon, unpublished data). The parental cultivars of the CCPs were chosen mainly for their high yielding and baking qualities and performance under low-input conditions in Europe. It is not known whether foliar pathogen resistance was of great importance in parental cultivar choice, although genetic distance between the parental cultivars was carefully considered[11]. Some parental cultivars with apparent resistance to the local brown rust had little to no resistance to the new stripe rust races present in 2014/2015 and vice versa. Others like Pastiche (Q), Renan (Q), Spark (Q), Wembley (Y) and to a degree Claire (Y), however, had low AUDPC even with the change in the dominant foliar pathogen. The reference cv. Capo possesses three quantitative trait loci (QTL) associated with both stripe and brown rust resistances all at the same chromosome position indicating “closely linked genes or pleiotropic gene action”[32]. This may provide possible resistance to both brown and stripe rust and helps to explain the long term resistance that cv. Capo (released in 1989) has retained. It is not known whether any of the CCP parental cultivars have these same QTLs, providing the CCPs with resistance sources to both stripe and brown rust. Rust severities among plants in the CCPs typically varied strongly (data not presented). Overall, the fact that all CCPs under both organic and conventional management had similar mean AUDPC and RAUDPC over the eight experimental seasons in comparison to cv. Capo demonstrates the ability of these heterogeneous wheat populations to compete with many commonly grown reference cultivars.

Managing CCPs under different environmental conditions and under natural selection means that unique alleles and genotypes may arise through mutation, recombination and gene flow[7,10], while allowing evolution in CCPs gives them the chance to evolve and compete against pathogen populations[33]. Depending on whether epidemics are single or recurrent events they may or may not affect population genetic composition over time. Stange et al.[34] reported divergence in pathogen resistance already in the $F_4$ of the three wheat CCPs used in this study and this initial variance in pathogen resistance frequency between CCPs and the subsequent multiplication of healthier genotypes through successive generations[1] may result in different evolutionary trajectories. Evidence for poorer adaptation to stripe rust was observed in a YQ_CCP that had been cultivated in Hungary from 2005 to 2013 under climatic conditions not conducive to stripe rust development (Weedon, Brumlop and Finckh, unpublished data).

The foot disease indices in the CCPs were similar to the modern reference cultivars. The overall lower foot disease incidences under organic practices were mainly due to greater overall crop diversity and the longer crop rotations under organic practice that may break pathogen cycles while increasing soil organic matter and, thus, microbial biomass and activity and achieving a more balanced fertility[35]. No selective effects were expected as foot disease indices were low over the experimental years.

## 5 CONCLUSIONS

Overall, genetic effects of the parental cultivars are still visible in terms of mean yield over all experimental seasons and management systems. However, it appears that over time the differences with respect to yield and TGW have decreased, a process that deserves close observation using molecular tools. The multiplication of the CCPs in large enough plots to limit genetic drift ensures that the CCPs continue to evolve and adapt to differing selection pressures. The CCPs, despite their older genetic background, perform as well as many commonly grown modern cultivars in terms of foliar pathogen resistance and agronomic performance, particularly under organic practices and under particularly stressful environmental conditions with respect to heat and drought in general. However, the reference cultivars were better able to withstand extreme cold events, which is not surprising as the parents of the CCPs were selected from germplasm suited to environmental conditions in the UK while the reference cultivars were selected for German conditions. Thus, the CCPs overall represent a dynamic germplasm pool capable of adaptation to changing environmental conditions that could be improved for central European conditions by integrating greater cold resistance. As future cropping systems will need to maintain or increase on current yield levels while further reducing external inputs, increasing both intra- and interspecific diversity could make a valuable contribution to increasing crop production in light of climate change, as well as partly replacing inputs through the provision of ecosystem services. Although comparatively little effort and resources have been allocated to the breeding of heterogeneous crop populations, their reported performance potential for various crops such as barley, wheat and maize, particularly within low-input systems, highlights the necessity of greater investment in population breeding for various farming systems.

### Supplementary materials

The online version of this article at https://doi.org/10.15302/J-FASE-2021394 contains supplementary materials (Tables S1–S3).

### Acknowledgements

We thank Drs Andreas Butz and Sarah Brumlop and numerous students and technicians for their work on the heterogeneous wheat populations in Neu-Eichenberg. This work was financed partly through the “Zentrale Forschungsförderung” University of Kassel, “Bundesprogramm Ökologischer Landbau und andere Formen nachhaltiger Landwirtschaft” Project No. 2812OE021 in the framework of CORE Organic II and through the INSUSFAR (INnovative approaches to optimize genetic diversity for SUStainable FARming systems of the future) Project (FKZ 031A350C), financed by the “Bundesministerium für Bildung und Forschung” in the framework of the IPAS (Innovative Pflanzenzüchtung im Anbausystem) Initiative and the EU-project ReMIX (Horizon 2020 Project No. 727217).

### Compliance with ethics guidelines

Odette Denise Weedon and Maria Renate Finckh declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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