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Evolutionary changes of weed competitive traits in winter wheat composite cross populations in organic and conventional farming systems

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ABSTRACT

Seedling root and shoot growth in hydroponics and allelopathic activity using a bioassay have been studied in very diverse populations of winter wheat grown under either organic or conventional conditions for a number of generations and subjected only to natural selection. The study was conducted on seeds from generation 6 (F_6) and 11 (F_{11}) from three composite cross populations (CCPs) produced by the Organic Research Centre in the UK. Since the F_5 the populations were maintained under organic and conventional conditions in Germany. Two parallel populations were created from each CC, resulting in a total of six organic and six conventional CCPs. The sets of parallel populations showed similar evolutionary trends indicating that the observed changes are related to differences in management rather than chance. Seedling root length and seedling root and shoot weight in the F_{11} of the organically-managed CCPs were significantly greater than in the organic F_6 CCPs. In the conventionally-managed CCPs no such differences were observed. Both organic and conventional CCPs produced for quality showed higher early root and shoot growth than those produced for yield pointing to genetic differences among population types and highlighting the importance of early vigour for NUE. There were no significant differences in the allelopathic activity of the populations and between generations. The Shannon-Weaver diversity indices were similar for the studied traits in organic and conventional CCPs and hence no major changes in diversity had occurred between F_6 to F_{11}. As changes in plant height were small and weed pressure in the fields low it is concluded that the observed differences are more related to NUE, rather than intra-specific competition for light or the direct effect of increased weed pressure in the organic system.
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1. Introduction

Increasingly uncertain environmental conditions require crops with high adaptability to unpredictable biotic and abiotic stresses. Genetically uniform crops often cannot adequately fulfil this requirement (Finckh, 2008; Döring et al., 2011). Biotic stresses such as pest and disease pressure can often be better managed through the use of genetic diversity. Cropping systems that are able to achieve this diversity include mixed cropping systems, multilines, variety mixtures, agroforestry systems, polycultures and genetically diverse populations produced under dynamic management such as composite cross populations (CCP) (Finckh and Wolfe, 2015; Altieri, 1999; Finckh, 2008; Döring et al., 2012; Dawson and Goldringer, 2012).

The term "evolutionary breeding", first used by Suneson (1956), describes the creation of genetically diverse populations of single crops undergoing both artificial and natural selection under different environmental conditions, but that have the added advantage of carefully selected parents for traits such as high yield and quality combined in a composite cross scheme. A well-known CCP was produced as early as the 1920's through the paired crossing of 28 barley varieties in all possible combinations (barley composite cross II) (Harlan and Martini, 1929; Muona et al., 1982). Since then, CCPs, as mentioned by Phillips and Wolfe (2005), have been made for barley (*Hordeum vulgare* (L.)), wheat (*Triticum aestivum* (L.)), oats (*Avena sativa* (L.)) and *Phaseolus* beans, although composite cross breeding for barley has been the most successful (Finckh, 2008).

Evolutionary breeding is an important tool that can be used in order to produce genetically diverse crop populations that are bet-

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ter able to adapt to changing biotic and abiotic conditions. This breeding strategy fulfils a number of goals that in light of the negative consequences of agriculture based on genetically uniform crops should be promoted and encouraged. Dynamic management of genetic resources, achieved through the cultivation of genetically diverse populations such as CCPs, subjected to different environments and selective pressures, provides an excellent complementary tool with which to conserve the genetic diversity of agricultural crops (Paillard et al., 2000; Goldringer et al., 2001, 2006; Porcher et al., 2004; Phillips and Wolfe, 2005; Döring et al., 2011). In addition, CCPs are widely used as a resource for selection (Clark et al., 2006; Jackson, 2011; Enjalbert et al., 2011; Goldringer et al., 2001, 2006; Döring et al., 2015).

Dynamic management ensures that genetic conservation is not "static" and that the crop species are able to maintain genetic variability within and between them (Brumlop et al., 2013). It ensures also that the populations are able to adapt and evolve to changing selective pressures in different environments and provides enough genetic diversity so that advantageous genetic combinations can arise, including novel and beneficial alleles through mutation and migration (Paillard et al., 2000; Goldringer et al., 2001, 2006; Porcher et al., 2004; Phillips and Wolfe, 2005; Stange et al., 2006; Döring et al., 2011). However, the need to improve baking quality characteristics and protein content in genetically diverse populations is essential in order to promote the wider use of CC populations in agriculture. Also, challenges to the adoption of diverse populations lie not only in farmer and consumer acceptance, but also in legislative and commercial uncertainties.

Nitrogen use efficiency (NUE), i.e. the grain dry matter yield divided by the supply of available nitrogen from the soil and fertilizer (Moll et al., 1982; Bingham et al. 2012) and weed competitive ability (WCA) are two characteristics that are of great importance for organic cereal production (Eisele and Köpke, 1997; Hoad et al., 2012; Arterburn et al., 2012; Costanzo and Bàrberi, 2014). In addition, early vigour of roots and shoots, as well as allelopathic activity, are important for WCA (Huel and Huel, 1996; Bertholdsson, 2005, 2011). Increasing evidence has shown that allelochemicals exuded from roots or volatiles from leaves may reduce weed growth and weed competition accordingly (Worthington and Reberg-Horton, 2013).

In diverse populations like CCPs, genotypes with early root and shoot vigour should have an advantage over non-vigorous types, as do taller genotypes. In the CCPs grown in the UK dwarfing alleles for height were reduced after 11 generations of natural selection and there were no differences found between the CCPs grown either organically or conventionally suggesting that the main reason for the natural selection of taller genotypes is competition for light (Knapp et al., 2013). Other alleles and genes introduced through breeding such as 1R from rye were also reduced over time, as were mutant alleles in favour of a selection for wild-type alleles. It is more difficult to hypothesize how allelopathic properties are affected by natural selection. In barley, most of the studied Nordic landraces showed higher allelopathic activity towards perennial ryegrass (*Lolium perenne* (L.)) than more recent cultivars (Bertholdsson, 2004); while spring wheat landraces showed low allelopathic activity (Bertholdsson, 2007).

In 2001, three wheat CCPs were created by the John Innes Centre (Norwich, UK) in co-operation with the Elm Farm Research Centre (Newbury, UK) (Wolfe et al., 2006). In 2005, progenies of the F_5 of these original three populations were received by the University of Kassel. In Germany, these populations have been maintained in two independent conventional and two independent organic sets. The two differing agricultural systems allow for the comparison of the populations for specific adaptation characteristics/traits that have developed due to differing agricultural management. The aim is to determine if specific adaptation characteristics of special interest in organic production systems will emerge and as such may be identified as useful breeding traits for organic production.

The present study focusses on the question of changes for traits of early vigour and allelopathy occurring in CCPs subjected to natural selection in organic and conventional systems at Kassel University from generation F_6 to F_{11}, and whether these changes can be related to the agricultural system the populations were subjected to. Seeds of the three CCPs created for high yield, high quality or a mixture of both, were assessed in a hydroponic system for seedling growth and with a bioassay for allelopathic activity. Changes in plant height and ear length and their diversity in the field were also analysed.

2. Materials and methods

2.1. Plant material

The three wheat (*Triticum aestivum* L.) composite cross populations used originated at the John Innes Centre (Norwich, UK), through the half-diallel crossing of twenty European wheat varieties, in order to create three separate populations that have been described in detail elsewhere (Wolfe et al., 2006; Döring et al., 2015). Briefly, the parental varieties chosen for the CC populations were varieties with either good baking quality or high yield that had performed well over the last few decades in the UK and were well known. Bezostaya is a well-known winter wheat variety bred in the former Soviet Union with excellent cold tolerance and has the characteristics of both high yield and high baking quality. The first population (YQ) is the product of crossing eleven high baking quality parents and Bezostaya with eight high yielding parents. The second population (Y) is made up of crossing eight high yielding parental varieties and Bezostaya with each other and the third population (Q) is a crossing of the eleven parental varieties known for high baking quality and Bezostaya with each other (Wolfe et al., 2006; Döring et al., 2015).

The F_2–F_4 were grown at various sites in the UK under organic and conventional management and grains from all sites were bulked before sending them to Germany. Since the F_5, the three populations were maintained at the University of Kassel as well under organic (O) as conventional (C) management. In the F_6, two parallel populations were created for each population (i.e. I and II), which were kept separately thereafter so that the total number of populations equals twelve (six organically- and six conventionally-managed populations). These parallel populations are therefore separate and distinct. In this way, it is possible to compare the I and II populations to each other and to see if they have evolved and changed within the same system, while comparing populations grown under organic and conventional conditions will allow to compare between systems. The CCPs used in this study were the F_6 (harvested 2007) and the F_{11} (harvested 2012). To allow for testing of lines instead of single plants in the bioassay for allelopathic activity, 50 random seeds of both the F_6 and F_{11} populations of CYQ and OYQ were multiplied in 2013/2014, resulting in 50 F_7 and 50 F_{12} breeding lines.

2.2. Field trials

The composite cross wheat populations were maintained at the research fields of the University of Kassel in Neu Eichenberg (51°22″N and 9°54″E, average annual precipitation: 619 mm, average annual temperature: 7.9 °C, altitude: 247 m above sea level) since 2005. The average precipitation for the growing seasons of F_6 and F_{11} was 512 mm and 737 mm and mean temperatures were 8.3 °C and 9.1 °C, respectively. The organic and conventional field were located about 500 m apart. The soil of the conventional field

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