Using crop genetic diversity to improve resilience: Agronomic potential of evolutionary breeding under differing management systems

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List of Abbreviations

CCP	Composite Cross Population
O	Organic
C	Conventional
CCQ	Composite Cross Quality
CCY	Composite Cross Yield
CCYQ	Composite Cross Yield x Quality
NGLA	Non Green Leaf Area
AUDPC	Area Under the Disease Progress Curve
RAUDPC	Relative Area Under the Disease Progress Curve
DI	Disease Index
EV_i	Environmental Variance
I_i	Yield Reliability Index
W^2	Wricke's Ecovalence
Pi	Superiority Index
b_i	Regression Coefficient
GEI	Genotype x Environment Interaction
AMMI	Additive Main Effect and Multiplicative Interaction
IPCA	Interaction Principal Component Axes
ASV	AMMI Stability Value
YSi	Yield Stability Index
NC	Non-Cycling
TKW	Thousand Kernel Weight
NUE	Nitrogen Use Efficiency
DUS	Distinctness, Uniformity and Stability

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Die Doktorarbeit

Smeik tauchte ein. Er tauchte in Dunkelheit, in Schwärze, wie in ein Faß voller Tinte. Er hörte Hunderte, Tausende von Stimmen durcheinander, er verstand kaum ein Wort, aber es hörte sich an, als würden wissenschaftliche Formeln und Lehrsätze heruntergeleiert. Dann konnte er plötzlich wieder sehen, die Stimmen waren schlagartig verstummt – und er fand sich innerhalb einer Kuppel wieder, schwebend in der Mitte eines großräumigen Domes, umgeben von diffusem Licht. Smeik sah sich um. Einen Boden konnte er aus der Höhe nicht ausmachen, nach unten verlor sich der Raum in immer dunkler werdendem Grau. Halbfertige Mauern ragten daraus auf wie aus Nebel, Wendeltreppen, die ins Nichts führten, Türme ohne Fenster. Es sah aus wie der Neubau eines Palastes, dessen Bauherrn das Geld ausgegangen war.

„Mir ist das peinlich“ sagte Kolibril betreten. „Ich kann es nicht haben, wenn Leute unfertige Sachen von mir sehen. Das sieht alles so unausgegoren aus.“

„Unfug!“ rief Smeik. „Das ist die interessanteste Ruine, die ich je gesehen habe.“

„Es ist ein Gedankengebäude“ seufzte Kolibril. „Meine ewige Baustelle. Halbgare Theorien, Ideenruinen. Ich bezweifle, daß ich mit dieser Doktorarbeit zu Lebzeiten jemals zu Rande kommen werde.“

Ein Schwarm von grauen Schlangen rauschte durch die Kuppel und flog wispernd an Smeik vorbei. Wirklich greifbar schienen die Würmer nicht zu sein, er hatte den Eindruck, daß sie aus einzelnen winzigen, schwarzen Partikeln bestanden. Staunend sah er ihnen hinterher.

„Fußnoten“, erläuterte Kolibril. „Sie sind lästig, aber für eine Doktorarbeit unverzichtbar. Man braucht Unmengen davon.“

Der Doktor pfiff, und der graue Schwarm stoppte seine wilde Jagd. Eine der Schlangen flog dicht an Smeik heran, und jetzt konnte er erkennen, daß die schwarzen Partikel Buchstaben und Zahlen waren.

Smeik las:

244 Siehe: Prof. Dr. Abdul Nachtigaller, " Die florinthische Kapitelornamentierung und ihr Einfluß auf den zamonischen Dudel-Barock während der Regierungszeit Reganam Salias des Dritten“ , Seiten 4567-48969. Gralsund, Nachtigaller-Verlag.

Smeik mußte lachen, worauf die Fußnote beleidigt zu ihren Artgenossen zurückhuschte. Sie wuselten wispernd durcheinander, und dann verschwand der ganze Schwarm kichernd im Dunkeln.

Es rumpelte, als würden Wagenladungen von Steinen ausgeschüttet, und ein schwarzer Turm wuchs aus dem Grau empor, wie aufschießender Spargel. Kaum war er errichtet, fuhr ein zweiter neben ihm hoch, nur halb so groß.

„Sehen Sie?“ rief der Doktor. „Selbst jetzt kann ich nicht aufhören, daran zu arbeiten. Das sind zwei neue Ideen zur Stützung der Hauptthese.“

„Was ist das Thema der Doktorarbeit?“ fragte Smeik.

„*Der Einfluß der Unvorhandenen Winzlinge auf die zamonische Mikromechanik*“, antwortete Kolibril zackig.

„Aha“, sagte Smeik. „Das klingt spannend.“

„Nein“, seufzte Kolibril. „Das tut es nicht. Das klingt völlig verschroben und hoffnungslos speziell. Trotzdem danke.“

„Jetzt sind Sie wieder zu bescheiden.“

„Da gebe ich Ihnen recht. Denn glauben Sie mir: Hinter diesem Thema verbergen sich vielleicht die Lösungen für unsere größten Probleme.“

„Welche Probleme meinen Sie?“

„Nun, das Sterben zum Beispiel. Den Tod.“

„Hoho!“ lachte Smeik. „Sie sind doch nicht etwa einer von diesen verkappten Alchimisten?“

„Ich bin Wissenschaftler, kein Quacksalber.“ Kolibrils Stimme klang sachlich und bestimmt. „Hier werden keine unappetitlichen Körpersäfte zusammengerührt oder tote Ochsenfrösche unter Strom gesetzt. Hier werden Messungen vorgenommen. Exakteste, winzigste Messungen.“

„Messungen? Wovon?“

„Ja, wovon eigentlich? Tatsächlich vermesse ich etwas, das es schon lange nicht mehr gibt. Ich vermesse die Unvorhandenen Winzlinge.“

Ein Rumoren kam aus einem der abgehenden Korridore. Smeik sah – er traute seinen Augen kaum -, er sah tatsächlich Professor Doktor Abdul Nachtigaller aus dem Dunkel auf sich zukommen. Nachtigaller brabbelte unverständlich vor sich hin, er war viermal so groß wie im richtigen Leben und – durchsichtig. Der Eydeet schenkte Smeik keine Beachtung, sondern marschierte über ihn hinweg und verschwand im Dunst der Kuppel. Smeik rieb sich die Augen.

„War das tatsächlich Nachtigaller?“ fragte er verunsichert.

„Nein. Ja. Nein. Also, gewissermaßen…das war die Verkörperung einer der Doktorarbeiten Nachtigallers: *Die Verwendung von bipolaren Linsen in multiplen Anordnungsformen*. Ich brauche sie dringend für den theoretischen Überbau.“

„Das war auch eine Doktorarbeit? Wieso sieht sie aus wie ein Lebewesen?“

„Doktorarbeiten können in vielen Gestalten erscheinen“, antwortete Kolibril. „Das hat mit ihrer Qualität zu tun. Alle Doktorarbeiten von Nachtigaller tragen seine Züge, das liegt an seiner starken Persönlichkeit, an seinem Stil. Unverwechselbar.“

„Wieso wirkte Nachtigaller so unfreundlich?“

„Die Doktorarbeit ist etwas ungehalten, weil sie sich mit der Grundtheorie meiner Arbeit noch nicht angefreundet hat. Sie ist noch auf der Suche nach einer Schnittstelle, wo sie andocken kann. Ich habe Ihnen ja gesagt, daß Sie damit rechnen müssen, Professor Nachtigaller zu begegnen.“

„Jetzt verstehe ich.“

„Wissen Sie, eine Doktorarbeit besteht zum großen Teil aus anderen Doktorarbeiten“, erläuterte Kolibril. „Eine neue Doktorarbeit ist immer auch eine Art Orgie von alten Doktorarbeiten, die sich untereinander, äh, befruchten, damit etwas Neues, etwas noch nie Dagewesenes aus ihnen hervorgeht.“ Der Doktor klang erregt.

Walter Moers, *Rumo und die Wunder im Dunkeln*.

Summary

Climate change will lead to the occurrence of unpredictable and increasingly uncertain climatic conditions including increased abiotic stresses such as extreme temperature events (heat or cold stress), increased risk of flooding through monsoons or rising sea levels, as well as flooding or drought due to changing precipitation patterns**.** Climate change is likely to not only increase abiotic pressures, but biotic pressures as well, such as an increase and more erratic occurrence of pathogens and pests. These increasing biotic and abiotic stresses cannot be wholly mitigated by external inputs and as such have led to a major rethink on current agricultural systems and their sustainability.

Mainly within organic and low-input cropping systems, evolutionary breeding based on the creation of heterogeneous evolving composite cross populations (CCPs) has been gaining attention. The advantages of these genetically diverse populations are multifold and include superior resilience to stress, the dynamic conservation of agricultural genetic resources, increased intra-specific diversity and the ability to evolve and adapt to specific environments and management systems. This adaptive capacity is particularly interesting for mixed cropping systems, as genetically diverse populations should be able to adapt to increased interspecific competition. Until recently, legislation impeded breeding for genetically diverse crops as it only allowed for the release of genetically uniform materials. Since 2014, in the frame of an EU wide initiative, experimental legislation allows for the marketing of heterogeneous crop populations for wheat, barley, maize and oats. Although legislation is in place, the potential of heterogeneous crop populations such as CCPs has not been fully realised, mainly because financing, marketing and processing of diverse populations remains challenging. Additional challenges include availability of genetically diverse populations that have been registered and tested in long-term trials and acceptance throughout the value chain from farmer to consumer. However, as the focus shifts towards more sustainable farming systems for the future in light of climate change and natural resource depletion, the breeding concept of CCPs and other heterogeneous populations is likely to play an increasingly important role within organic and low-input research and farming communities. The aim of this dissertation is to assess the agronomic potential and yield stability of wheat CCPs in comparison to pure line varieties under differing management systems and to evaluate whether evolutionary

breeding is an applicable and alternative breeding approach, comparable to current breeding practices, particularly relevant for organic and low-input systems.

Three winter wheat CCPs were created in the UK in 2001, based on parental varieties that were selected for either their high yield or baking quality. The baking Quality CCP (CCQ) was developed through the crossing of 12 high baking quality parental varieties, whilst the Yield CCP (CCY) was created through the crossing of 9 parental varieties selected for their yielding ability. The final CCP (CCYQ) was created through the crossing of eleven quality parents with eight high yielding parental varieties. Additionally, the nineteen parental varieties were crossed with the variety Bezostaya, which is considered to be both high yielding and have good quality, with these crosses also included into the CCYQ population. In the autumn of 2005, seed of all three CCPs (F_4) were given to the Department of Ecological Plant Protection, University of Kassel, to be grown at the research station in Neu-Eichenberg. Each CCP was divided into two and grown under both organic (O) and conventional (C) management in the 2005/06 experimental year (F_5) (6 CCPs in total). In 2006/07, each CCP was split into two parallel populations (I and II) within each management system (12 CCPs in total), in order to track and evaluate evolutionary changes of the CCPs within the same system and between systems. In addition, a number of modern pure line varieties have been grown alongside the populations in order to compare the agronomic potential of the CCPs to modern varieties commonly used in organic and conventional agricultural systems in Germany.

A number of agronomic and morphological parameters have been recorded over eleven generations (until the F_{15}), providing an historical dataset with which the agronomic potential and yield stability of the CCPs could be assessed and compared to pure line varieties under differing management systems. The yield stability assessment included stability indices to represent both the static and dynamic concept of stability and included mean grain yield, the regression coefficient (b_i), environmental variance (EV_i), a yield reliability index (I_i), yield superiority index (P_i) and Wricke's ecovalence (W^2). In addition, a two-year experiment looking at the adaptation of the YQCCPs to changing environments, based on the assessment of agronomic, morphological and baking quality parameters, is reported on for the experimental years of 2013/14 and 2014/15.

Yields under organic management over eight experimental years ranged from the highest of 5.3t/ha (Achat) to the lowest of 4.8 t/ha (OQI). All organically managed CCPs achieved comparable yields to the reference varieties Achat and Capo, except for the lowest yielding CCP OQI. In comparison, yields under conventional management ranged from 5.7t/ha in the variety Capo to 4.7t/ha in the CCP CQII. All conventionally managed CCPs yielded significantly lower than the pure line variety Capo, with the lowest yields found in the CQI, CQII and CYI populations. Results from these analyses indicate that the genetic background of the CCPs, provided through the parental variety selection, is still present for a number of agronomic and morphological parameters such as stem length, highlighting the importance of parental variety selection in order to achieve desired population characteristics. A significant interaction effect was found between CCPs and the experimental years for a number of agronomic parameters, indicating plasticity of the CCP response to differing environmental conditions and their ability to react and adapt to specific conditions.

CCPs with a wider genetic base (CCYQs) indicated both better yields and stability in comparison to the other CCPs, supporting the premise that increased genetic diversity may help to buffer environmental stresses, particularly under challenging conditions. Additionally, the CCYs, whose parental set included more modern varieties were able to make better use of the higher N inputs in the conventional system. However, the CCY CCPs, tended to be the most reactive populations indicating an apparent divergent evolution for both yield and yield stability between parallel populations under conventional conditions. Under organic management, the OYQII CCP achieved greater yield stability in comparison to the pure line varieties Achat and Capo for the majority of indices. In comparison, conventionally managed CCPs had lower yield stability for a number of parameters in comparison to the pure line variety Capo. These results, both in terms of yield and yield stability, are indicative of the parental variety selection for agronomic performance in low-input systems.

CCYQ populations that had been subjected to changing environmental conditions (cycling) for five years remained similar for a number of important agronomic parameters such as yield; however, some differentiation for morphological characteristics such as degree of awnedness and kernel colour was found, indicating differentiation of the CCPs within a short timeframe of five generations. Many of the CCYQ populations were comparable to pure line varieties for a number of baking quality parameters, as well as agronomic performance, particularly in the experimental year of 2014/15, which was characterised by drought. These results show the potential of CCPs, not only in terms of yield and yield stability, but also as an alternative option to pure line varieties for baking quality. However, evolutionary breeding should not be seen as a static tool with which to solve all problems. CCP adaptation to specific environments may be improved through the introduction of modern breeding progress through the mixing and crossing of newer varieties or elite lines into genetically diverse populations or through the selection of genotypes within populations better suited to a given environment. Additionally, dynamic management of genetic resources, achieved through the cultivation of genetically diverse populations subjected to differing environments and selective pressures, provides an excellent complementary tool with which to conserve the genetic diversity of agricultural crops.

Zusammenfassung

Der Klimawandel wird zum Auftreten unvorhersehbarer und zunehmend unsicherer klimatischer Bedingungen führen. Es ist von erhöhtem abiotischen Stress wie z.B. Extremtemperaturen (Hitze- oder Kältestress), erhöhtem Überschwemmungsrisiko durch Monsunregen oder den steigenden Meeresspiegel sowie von Überschwemmungen oder Dürreperioden aufgrund sich verändernder Niederschlagsmuster auszugehen. Der Klimawandel wird sehr wahrscheinlich nicht nur den abiotischen Druck erhöhen sondern auch biotische Stressfaktoren, etwa durch die Zunahme und das unberechenbare Auftreten von Pathogenen und Schädlingen. Diese zunehmenden biotischen und abiotischen Stressfaktoren werden nicht alleine durch externe Inputs entschärft werden können und haben daher ein Neudenken gegenwärtiger landwirtschaftlicher Systeme und ihrer Zukunftsfähigkeit bewirkt.

Vor allem innerhalb ökologischer low-input Anbausysteme hat die Züchtung von Evolutionsramschen (evolutionary breeding), die auf der Herstellung heterogener, evolvierender Composite Cross Populationen (CCPs) basiert, zunehmende Aufmerksamkeit geweckt. Die Vorteile dieser genetisch vielfältigen Populationen sind vielfältig und umfassen flexiblere Reaktionen auf Stressfaktoren, die Möglichkeit zum dynamischen Erhalten landwirtschaftlicher genetischer Ressourcen, erhöhte intra-spezifische Diversität und die Fähigkeit, sich an spezifische Umwelten und Anbausysteme anzupassen und sich darin zu entwickeln. Diese Anpassungskapazität ist besonders im Mischanbau von Interesse, da genetisch vielfältige Populationen fähig sein sollten, sich an interspezifische Konkurrenzsituationen anzupassen. Bis vor kurzem wurde die Züchtung genetisch vielfältiger Kulturpflanzen durch die Sortenschutz-Gesetzgebung sehr erschwert, da nur die Zulassung genetisch einheitlichen Materials vorgesehen war. Seit 2014 ist es im Rahmen eines EU-weiten Experiments in der Gesetzgebung aber möglich, heterogene Populationen von Weizen, Gerste, Mais und Hafer zu vermarkten. Trotzdem wird das Potenzial heterogener Pflanzenpopulationen wie z.B. das der CCPs nicht voll ausgeschöpft, da vor allem Finanzierung, Vermarktung und Verarbeitung solcher Populationen eine Herausforderung bleiben. Zusätzliche Herausforderungen stellen die Verfügbarkeit genetisch vielfältiger, angemeldeter und in Langzeitversuchen geprüfter Populationen sowie die Akzeptanz derartiger Populationen in der gesamten Erzeugerkette vom Anbauer bis zum Endverbraucher dar. Da sich im Lichte von Klimawandel und

Ressourcenknappheit der Fokus für die Zukunft aber immer stärker auf nachhaltige landwirtschaftliche Systeme richtet, ist davon auszugehen, dass Züchtungsansätze wie das Konzept der CCPs und anderer heterogener Populationen innerhalb ökologisch ausgerichteter Forschungs- und Anbauerkreise eine zunehmend wichtige Rolle spielen werden. Das Ziel dieser Dissertation ist eine Bewertung des agronomischen Potentials und der Ertragsstabilität von Winterweizen-CCPs im Vergleich mit Liniensorten unter unterschiedlichen Anbausystemne und eine Einschätzung, ob Evolutionsramsche einen geeigneten alternativen Züchtungsansatz darstellen, der mit der gegenwärtigen züchterischen Praxis - besonders für ökologische und low-input Anbausysteme - gleichwertig ist

Im Jahr 2001 wurden in England drei Winterweizen-CCPs erstellt, die auf Elternlinien zurückgehen, die entweder aufgrund hohen Ertrags oder aufgrund ihrer guten Backqualität ausgewählt worden waren. Die Backqualitäts-CCP (CCQ) wurde durch eine Kreuzung von 12 Elternsorten mit guter Backqualität erstellt, die Ertrags-CCP (CCY) durch eine Kreuzung von 9 Elternsorten mit hohem Ertragspotenzial. Die dritte Population (CCYQ) wurde durch die Kreuzung von elf Qualitätssorten mit acht Hochertragssorten erstellt. Zusätzlich wurden die 19 Sorten mit der Sorte Bezostaya gekreuzt, die sowohl hohes Ertragspotenzial als auch gute Backqualität hat, und diese Kreuzungen gingen ebenfalls in die CCYQ-Population ein. Im Herbst 2005 wurde Saatgut aller drei CCPs (F_4) an das Fachgebiet Ökologischer Pflanzenschutz der Universität Kassel abgegeben und im Versuchsbetrieb Neu-Eichenberg angebaut. Jede der drei Populationen wurde geteilt und im Versuchsjahr 2005/06 (F_5) sowohl unter ökologischen (O) als auch unter konventionellen (C) Anbaubedingungen angebaut (insgesamt 6 CCPs). Im Jahr 2006/07 wurde jede CCP innerhalb der beiden Anbausysteme in zwei parallele Populationen aufgeteilt (I und II) (insgesamt 12 CCPs), um evolutionäre Veränderungen der CCPs innerhalb eines Systems und zwischen beiden Systemen erfassen und evaluieren zu können. Zusätzlich wurden immer moderne Liniensorten neben den Populationen angebaut, um einen Vergleich des agronomischen Potentials der Populationen mit gängigen Sorten im ökologischen und konventionellen Weizenanbau in Deutschland zu ermöglichen.

Verschiedene agronomische und morphologischen Parameter wurden über elf Generationen (bis zur F_{15}) hinweg erfasst und stellen eine Datensammlung dar, anhand derer das agronomische Potential und die Ertragsstabilität der CCPs erfasst und mit dem von Liniensorten unter unterschiedlichen Anbaubedingungen verglichen werden konnte. Die Auswertung der Ertragsstabilität umfasst Stabilitätsindices, die sowohl das statische als auch das dynamische Konzept von Stabilität repräsentieren und umfasst den mittleren Kornertrag, den Regressionskoeffizienten (b_i), die Umweltvarianz (EV_i), einen Index der Ertragszuverlässigkeit (I_i), Ertragsüberlegenheitsindex (superiority index) (P_i) und Wrickes Ökovalenz (W^2). Zusätzlich werden Ergebnisse eines zweijährigen Versuchs dargestellt, der die Anpassung der YQCCPs an sich ändernde Umwelten untersuchte. Aus den Versuchsjahren 2013/14 und 2014/15 werden Ergebnisse der Prüfung agronomischer und morphologischer Parameter sowie Backqualitätsparameter dargestellt.

Unter ökologischen Anbaubedingungen reichten die Erträge über acht Versuchsjahre hinweg von maximal 5.3 t/ha (Achat) bis minimal 4.8 t/ha (OQI). Alle ökologisch angebauten CCPs erreichten Erträge, die mit denen der Referenzsorten Achat und Capo vergleichbar waren, mit Ausnahme der CCP OQI, die darunter lag. Die Erträge unter konventionellen Anbaubedingungen reichten im Vergleich dazu von maximal 5.7 t/ha bei der Sorte Capo bis minimal 4.7 t/ha bei der CCP CQII. Die Erträge aller konventionell angebauten CCPs lagen statistisch signifikant unter dem Ertrag der Liniensorte Capo, die niedrigsten Erträge zeigten die CCPs CQI, CQII und CYI. Ergebnisse dieser Untersuchungen zeigen, dass der genetische Hintergrund der CCPs, der durch die Auswahl der Elternsorten geben ist, für eine Anzahl von agronomischen und morphologischen Parametern, wie z.B. Halmlänge, nach wie vor von Bedeutung ist. Dies unterstreicht die Bedeutung der Auswahl von Elternsorten für das Erreichen gewünschter Populationseigenschaften. Für einige agronomische Eigenschaften konnten signifikante Interaktionseffekte zwischen den CCPs und dem Versuchsjahr festgestellt werden, was einen Hinweis auf die Plastizität der CCPs in Bezug auf sich ändernde Umweltbedingungen gibt und ihre Fähigkeit zur Reaktion auf und Anpassung an bestimmte Bedingungen unterstreicht.

CCPs mit einer breiten genetischen Basis (CCYQs) zeigten im Vergleich mit den anderen CCPs sowohl höhere Erträge als auch höhere Ertragsstabilität, was die Annahme stützt, dass hohe genetische Diversität dazu beitragen kann, Umweltstress - besonders unter schwierigen Bedingungen – abzupuffern. Die CCYs, deren Elternset mehr moderne Sorten enthielt, waren besser in der Lage, das im konventionellen Anbau höhere Stickstoffangebot zu nutzen. Insgesamt zeigten die CCY-CCPs die stärkste Tendenz zum Reagieren, was offensichtlich auf eine divergierende Evolution sowohl für Ertrag als auch für Ertragsstabilität zwischen den parallelen Populationen unter konventionellen Anbaubedingungen hindeutet. Unter ökologischen Anbaubedingungen erreichte die OYQII CCP für die meisten Indices höhere Ertragsstabilität als die Liniensorten Achat und Capo. Im Vergleich dazu hatten konventionell gemanagte CCPs für mehrere Parameter eine geringere Ertragsstabilität als die Liniensorte Capo. Diese Ergebnisse deuteten sowohl im Hinblick auf Ertrag als auch auf Ertragsstabilität darauf hin, dass die Wahl der Elternsorten für die agronomische Performance unter low-input Anbaubedingungen ausschlaggebend ist.

CCYQ Populationen, die für fünf Jahr wechselnden Umweltbedingungen ausgesetzt gewesen waren (cycling), blieben für mehrere wichtige, agronomische Merkmale wie Ertrag ähnlich; allerdings ließen sich Differenzierungen für morphologische Eigenschaften wie Stärke der Begrannung und Kornfarbe feststellen, was auf eine Differenzierung der CCPs innerhalb des relativ kurzen Zeitraums von fünf Generationen hindeutet. Viele der CCYQ Populationen waren hinsichtlich einiger Backqualitäts-Parameter und in ihrer agronomischen Performance mit Liniensorten vergleichbar, besonders im Versuchsjahr 2014/15, das durch große Trockenheit charakterisiert war. Diese Ergebnisse zeigen das Potential der CCPs nicht nur im Hinblick auf Ertrag und Ertragsstabilität, sondern auch als Alternative zu Liniensorten mit hoher Backqualität.

Dennoch sollte das Konzept der Evolutionsramsche nicht als ein statisches Werkzeug zur Lösung aller Probleme verstanden werden. Die Anpassung von CCPs an bestimmte Umwelten könnte verbessert werden, wenn neuere Sorten oder Elitelinien in die genetisch vielfältigen Populationen gemischt oder eingekreuzt werden um auf diese Weise mit dem Züchtungsfortschritt mitzuhalten. Auch die Selektion bestimmter Genotypen innerhalb einer Population mit besserer Eignung für eine bestimmte Umwelt könnte eine Möglichkeit sein. Darüber hinaus stellt das dynamische Management genetischer Ressourcen, das man erreicht, wenn genetisch vielfältige Populationen unterschiedlichen Umwelt- und Selektionsbedingungen unterworfen werden, eine gute zusätzliche Möglichkeit dar, die genetische Diversität landwirtschaftlicher Kulturarten zu erhalten.

1. General Introduction

Achieving higher yields under organic and low-input systems can only be achieved through the breeding and selection of suitable varieties within such systems (Murphy *et al*., 2007; Dawson *et al*., 2011a; Muellner *et al*., 2014). Murphy *et al*. (2005) and Østergård *et al.* (2009) discuss the importance of developing new and innovative strategies for crop breeding and management in order to deal with unpredictable and increasingly variable climatic conditions. As environmental and agronomic conditions are so unique and heterogeneous between and within locations, a diverse range of varieties and genetically diverse populations will need to be bred in order to be able to adapt to the changing and variable range of growing environments. It is essential that these varieties and populations also provide a diverse range of qualities in order to fit each unique location and meet the needs of farmers in these environments (Wolfe *et al*., 2006, 2008). The importance of understanding genotype x environment interactions (GEIs) cannot be underestimated and the selection of crops within and suitable for specific environments is gaining importance, particularly as environmental manipulation is limited and in light of climate change (Lammerts Van Bueren *et al*., 2008; Østergård *et al*., 2009). In order to do this, crop breeding will have to take full advantage of all available genetic resources, including landraces and exotic and wild relatives (Kern, 2002).

Many scientists have proposed an alternative discussion to the recommendation of genetically uniform “new and improved” crop varieties. These uniform crop varieties have limited adaptive capacity, which reduces their ability to cope with the environmental fluctuations caused by climate change (Finckh, 2008; Dawson & Goldringer, 2012). It is questionable whether these “new and improved” crop varieties, as proposed by Laidig *et al*. (2014), will be able to reduce yield gaps sufficiently when the rising costs of modern production techniques considerably reduces the importance of the agronomic component in yield progress, making it almost impossible to achieve yield improvements.

1.1 Improving food security through yield gap reduction and yield stability

Yield progress and yield gap analysis are two important criteria that need further exploration in order to ensure future food security (Lobell *et al*., 2009; Fischer *et al*., 2014; Laidig *et al*., 2014;). This is particularly the case as the unpredictability of climate change threatens the security and stability of agricultural systems (Østergård *et al*., 2009; Döring *et al*., 2011). Yield progress as described by Laidig *et al*. (2014), is dependent on genetic and non-genetic (agronomic) components. It is the separation of the genetic (e.g. new varieties) from the agronomic component (e.g. management strategies), which enables the estimation of yield progress through each component's individual contribution to yield success. Laidig *et al.* (2014) examined the yield gaps between on-farm and trial-station yields for a number of crops in Germany over the last 30 years, which highlighted the tendency for increasing gaps between on-farm and trial-station yields, with trial-station yields generally yielding more than those on-farm. The study indicated that agronomic traits (management strategies) contributed less to yield progress in comparison to genetic factors, but that particularly in cereal crops, ageing effects (genetic component) were responsible for significant yield losses. One of the main reasons given for the reduction in yield in older (ageing varieties) is the break-down of the variety's disease resistances (Fischer & Edmeades, 2010; Laidig *et al*., 2014). Yield gaps for winter wheat between trial-station and on-farm lie at around 23% in this German study, helping to emphasize the potential improvements that are possible on-farm in order to close this gap (Laidig *et al.*, 2014). Lobell *et al.* (2009) also report on yields in most irrigated rice, wheat and maize systems only reaching 80% of yield potential, while under rain-fed systems the average yields generally only tend to reach up to 50% of yield potential.

Potential yield is a crop yield that could be achieved under "the best possible growing conditions" (Lobell *et al*., 2011), which is not dissimilar to the yields achievable under trial-station conditions. According to Lobell *et al.* (2009) and Laidig *et al.* (2014), closing yield gaps will depend on modern management techniques, which aim to limit the potential effects of climate change and enable a quick response to changes and variation in "soil, water and nutrient conditions". Although agronomic components play only a minor role in improving yield progress (in irrigated systems); these management and production strategies such as water availability and optimum nutrient application for crop growth cannot be taken for granted. This is especially the case when one considers the increasing costs involved in the "perfect management of crop and soil factors", which leaves these modern production techniques (agronomic components) often financially unviable and optimal yield potential no longer profitable for the majority of farmers (Lobell *et al.*, 2009). In conclusion, Laidig *et al.* (2014) recommend further investment in breeding to create “new and improved varieties”, particularly as it is this genetic component, which contributes the most to yield progress.

In addition to yield progress and yield gap analysis, perhaps the most important crop trait needed for less predictable environments is that of optimum yield stability (Lammerts van Bueren & Myers, 2011). As mentioned by Piepho & Lotito (1992), there are an increasing number of stability parameters available for genotype testing, however, as many of these parameters measure the same stability concept (Duarte & de O. Zimmermann, 1995) or may be mathematically similar (Becker, 1981), choosing a few relevant and reliable parameters should be sufficient (Piepho & Lotito, 1992). The environmental variance (EV_i) is considered a measure of the genotypic variance across environments (Roemer, 1917) and genotypes that show low yield variance across a range of environments are considered more stable in the static sense. However, high static stability does not necessarily correlate with high yields. Therefore I_i, a yield reliability index, as a combined analysis of both yield and EV_i stability, allows for the selection of higher yielding genotypes displaying lower yield variance across environments and including the risk aversion level of a farmer in a given environment as a fixed factor (Kataoka, 1963; Annicchiarico, 2002). Both EV_i and I_i were included in the yield stability analyses of winter wheat CCPs by Döring *et al*. (2015), making these stability parameters of great interest for comparison. The regression coefficient $b_{i,}$ introduced by Finlay & Wilkinson (1963), is based on joint regression analysis of the mean genotype performance in individual environments as a function of the environment mean performance. This stability parameter provides a measure of both static and dynamic stability and can be used as an indicator to identify genotypes best suited to particular environments (Figure 1.1).

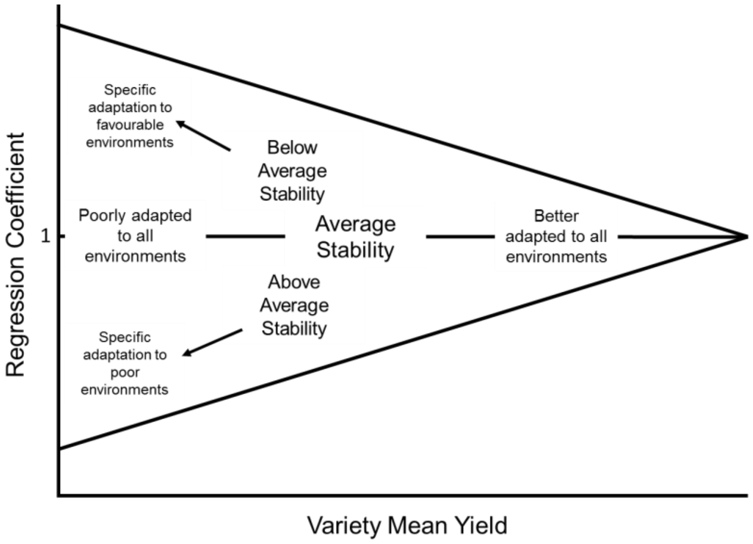


Figure 1.1: General interpretation of the yield stability concept according to Finlay and Wilkinson (1963) using the regression coefficient plotted against the mean entry yield.

Wricke's ecovalence W^2 (Wricke, 1962), is a measure of the dynamic stability concept and measures the GEI effect of a genotype in relation to individual environmental means and the grand environmental mean. Smaller W^2 values indicate greater dynamic stability with lower GEIs. The yield superiority measurement P_i, suggested by Lin & Binns (1988), measures the difference between a genotype's response in an environment to the maximum response achieved in that environment. Genotypes with low P_i values are considered to be superior to other genotypes, an indication that their yields were close to the maximum yields achieved over multiple environments. The AMMI (Additive Main Effects and Multiplicative Interaction) analysis, including both ASV (AMMI stability value) and YSi (Yield Stability index) values, is a multivariate approach that combines both ANOVA (Analysis of Variance) with principal component analysis (PCA) (Gollob, 1968). This analysis method allows for the visualization of the dataset through PCA analysis and allows for the selection of genotypes for specific environments with high GEIs or for broader adaptation (Onofri & Ciriciofolo, 2007; Stagnari *et al*., 2013;). The ASV value (Purchase *et al*., 2000) reports on the distance of genotypes from the centre of the axes using the AMMI Biplot, a visualization of the PCA analysis. Lower ASV values indicate greater stability and adaptability across all environments through a low GEI (Farshadfar *et al*., 2011; Stagnari *et al*., 2013). The YSi combines both the ASV ranking with mean yield ranking in order to provide a measure of stable genotypes with high yields (Farshadfar *et al*., 2011).

1.2 Traditional breeding approach based on the crop ideotype

Plant breeding relies heavily on the idea of a conceptual crop ideotype (Donald, 1968). An excellent example of a crop, which is particularly suited for monoculture, is wheat. The aim of wheat breeders is to create plants that will be poor competitors, so allowing them to flourish in high-density conventional monoculture systems, which can ensure high soil fertility, through synthetic fertilizers, and that all unfavourable conditions, such as pests and disease, can be controlled through external inputs. This wheat ideotype "has a short, strong stem; few small erect leaves; a large, erect ear; awns and a single culm" and is able to take absolute advantage of light supply in order to maximise grain production (Donald, 1968; Phillips & Wolfe, 2004). As all other inputs needed for growth are supplied through external sources, light becomes the only limiting factor to the success of this wheat ideotype, but one needs to question the sustainability of such a crop community so reliant on all other factors needed for growth, except light.

Breeders aim to create crop varieties, which are as homogeneous as possible, and this is particularly the case for inbreeding crops. This homogeneity ensures not only that the particular crop variety will react the same to all external inputs, but also that they will then be uniform in terms of growth phases, flowering and harvest times. The fact that the given variety also has the same physical features also means that technology can be planned and standardised around this uniformity. The breeder selects and isolates traits bred into the crop varieties that he/she and the industry find important and these crop varieties are also adapted to the conditions supplied and selected by the breeder (Phillips & Wolfe, 2004). This process of breeding crop varieties in high input environments and with high genetic uniformity leaves little adaptive capability for the crop subjected to changing environments or selective pressures.

The success of breeding strategies focussing on crop ideotypes that rely heavily on external inputs and that will cope well in a monocultural system has in turn spurred the spread of monocultures and their complimentary technologies and industries, which supply monoculture crop communities with all external inputs and have contributed tremendously to the loss of agricultural crop diversity worldwide (Fowler & Mooney, 1990; Phillips & Wolfe, 2004; Pascual & Perrings, 2007). It is through this mainstream breeding process that variability and adaptive capacities within single crop varieties have been reduced, leaving behind genetically uniform crops, which are more reliant on external inputs and less suitable to challenging and unpredictable environments. Crop homogeneity and the planting of monocultures on a large scale, as mentioned above, leave crops vulnerable to pests and pathogens (Finckh, 2008; Østergård *et al*., 2009). Although constant monitoring, cataloguing and germplasm improvement are of utmost importance and necessity, there will always be some degree of uncertainty with anticipatory breeding in the sense that the plant-pathogen relationship is so complex that it is impossible to predict pathogen population changes. Unpredictable climatic conditions, which are increasingly occurring, also compound the problem and this method of breeding will face more and more challenges in the future. One of these challenges is the constant threat of pathogen adaptation and the constant race against time in order to find effective and durable resistances.

Pathogens in agricultural systems are able to evolve and adapt to the selective pressures presented to them (i.e. specific resistances), but genetically uniform crops within the same system are not afforded the same ability and so co-evolution with the pathogen cannot happen (Finckh & Wolfe, 1997; Finckh, 2008; Döring *et al*., 2012). The limited genetic variability and adaptability in modern crop varieties reduces their ability to co-evolve with the pathogens that threaten them and puts them at a distinct disadvantage whereby they are wholly reliant on man for their resistance. This is related to “crop ageing effects”, as described by Fischer & Edmeades (2010) and Laidig *et al*. (2014), and refers to the breaking of a crop’s disease resistance, as they are unable to co-evolve with the pathogen, resulting in significant yield losses (Laidig *et al.*, 2014). The danger of not allowing co-evolution of hosts and pathogens has been recognised since the mid-20th century. As discussed by Stevens (1942): “…by the wide use of hybrid corn we are depriving this important crop of its power of taking care of itself to the equally variable parasites which attack it”. The instability of such agricultural systems, as mentioned by Finckh (2008) and Østergård *et al.* (2009), will never provide a lasting solution to pathogen control and the use of diversity within breeding programmes and agricultural systems may be the only real solution. Palumbi (2001) summarised it extremely well when he said, “each defence sows the evolutionary seeds of its own demise”.

1.3 Novel breeding approaches

Breeders for low-input and organic systems have looked at ways to re-invent the conceptual crop ideotype as described by Donald (1968). A reinvention of this conceptual crop ideotype is the “competition ideotype”, which is better suited to extensive systems and which has a better ability to adapt to changing environments and higher competitive pressure (Baresel, 2006). There are a number of traits characteristic of the competition ideotype, which gives it a number of advantages over its predecessor and enables a higher adaptive capacity to uncertain environmental conditions including high competitive ability, greater plant height, high tillering capacity, a higher degree of adventitious roots and greater responsiveness to mycorrhizal symbiosis (Baresel, 2006). This competition ideotype is most effective in coping in diversified systems, identified by an increase of the plant species grown. As described above, new insights into breeding strategies for low-input and extensive systems has led to a rethinking of crop traits, which give varieties greater adaptive and competitive capacity, affording increased resilience and stability in variable environments (Lammerts Van Bueren *et al*., 2002; Baresel, 2006; Lammerts van Bueren & Myers, 2011).

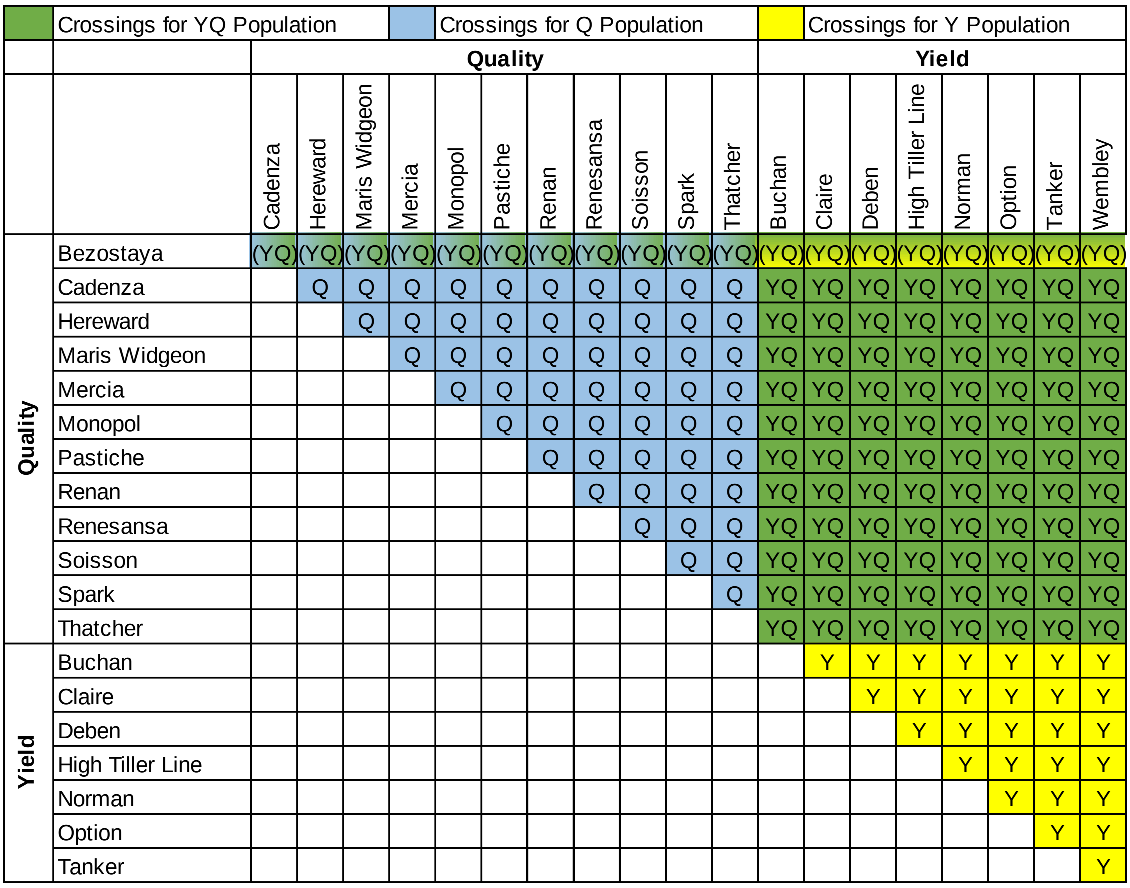
Heterogeneous crop populations are an additional novel breeding approach that has been supported and developed by breeders for low-input and organic systems (Döring *et al*., 2015; Raggi *et al*., 2017). Experimentation with heterogeneous cereal populations began in the early 1920s with barley (*Hordeum vulgare* L.) (Harlan & Martini, 1929). The hypotheses behind such mixed populations were that they would be genetically diverse, high yielding and able to adapt to different environments and selection pressures. An early composite cross population (CCP) was produced in 1929 through the paired crossing of 28 barley varieties in all possible combinations, which produced 378 different F_1 hybrids that were then bulked and increased without conscious selection (barley Composite Cross II) (Muona *et al*., 1982). The term “evolutionary plant breeding” was coined by Suneson in 1956 to describe the creation of genetically diverse populations undergoing both artificial and natural selection under different environmental conditions, through the careful selection of high-yielding and quality parents. Composite cross populations (CCPs) have been made for barley, wheat, oats and phaseolus beans, although composite cross breeding for barley has been the most successful (Phillips & Wolfe, 2005; Finckh, 2008). Composite cross populations are subjected to natural selection for many years, harvested in bulk and then resown, in order to improve adaptability, genetic variability and to limit human selection (Finckh & Wolfe, 1997; Döring *et al*., 2011; Dawson & Goldringer, 2012). The breeding of composite cross populations fulfils a number of goals. The first of these includes the breeding of genetically diverse composite cross populations in order to reduce the costs involved in "the isolation of superior individual lines". Secondly, CCPs should be comparable to pure line varieties in terms of yield, baking quality and pathogen resistance (Phillips & Wolfe, 2004).

1.4 Dynamic Management

Dynamic management of genetic resources, achieved through the cultivation of genetically diverse populations 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 & Wolfe, 2005). Dynamic management ensures that genetic conservation is not "static" and that the crop species will be able to maintain genetic variability within the populations, as well as between them (Brumlop *et al*., 2013). Low input and organic agricultural systems are characterised by their minimal external inputs, as well as increased biotic and abiotic stresses mainly due to the reduced external inputs (Annicchiarico & Filippi, 2007; Lammerts van Bueren & Myers, 2011; Messmer *et al*., 2012). The creation of composite cross populations using carefully chosen parental varieties, coupled with the ability of the populations to adapt to local environments means that these populations can be well suited for low-input and organic agricultural systems (Phillips and Wolfe, 2005). Murphy *et al*. (2005) and Dawson *et al*. (2008) stress the importance of developing modern landraces; populations created from carefully selected parental varieties and further subjected to selection by farmers. These modern landraces can be particularly successful when grown on farm with the farmer directly participating in selecting and guiding populations in order to produce a sustainable modern landrace that contributes profitably to their farm (Murphy *et al.*, 2005). Collaborating with farmers through participatory breeding programmes can be very advantageous, particularly in developing countries or where farmers routinely produce their own seed. Not only is this approach cost effective and eases the process of variety adoption by farmers, but it also provides superior germplasm suited to the particular needs of farmers (Ceccarelli, 2000; Gyawali *et al*., 2007; Dawson *et al*., 2011b). The breeding of composite cross populations and the inclusion of farmers in breeding and selection of crop varieties allows for the decentralisation of the breeding process and gives farmers better control and increased responsibility for the crops that they plant (Ceccarelli, 2000; Desclaux *et al*., 2008; Dawson *et al*., 2008).

1.6 Winter wheat composite cross populations at Neu-Eichenberg

In 2001, three composite cross wheat (*Triticum aestivum* L.) populations (CCPs) were created at the John Innes Centre (Norwich, UK), in co-operation with the Elm Farm Research Centre (Newbury, UK). The CCPs were created through the half-diallel crossing of twenty European wheat varieties, in order to create three separate populations (see Jones *et al*. 2010 for review). The first population (CCYQ, YQ = Yield x Quality) is the product of crossing the eleven high baking quality parents with eight high yielding parents (88 crosses) (Figure 1.2). The variety “Bezostaya”, which is regarded as both high yielding and high quality, was inter-crossed with all other parental varieties and these additional 19 crosses were also included in the CCYQ population (total of 107 crosses). The second population (CCY, Y = Yield) is made up of crossing nine high yielding parental varieties with each other (36 crosses) and the third population (CCQ, Q = Quality) is a crossing of twelve parental varieties known for high baking quality (66 crosses) (Figure 1.2). Four naturally male sterile lines were also included in the original crosses for the three populations to enhance further outcrossing in later generations.



🟩 Crossings for YQ Population 🟦 Crossings for Q Population 🟨 Crossings for Y Population

		Quality											Yield							
		Cadenza	Hereward	Maris Widgeon	Mercia	Monopol	Pastiche	Renan	Renesansa	Soisson	Spark	Thatcher	Buchan	Claire	Deben	High Tiller Line	Norman	Option	Tanker	Wembley
Quality	Bezostaya	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)	(YQ)
	Cadenza		Q	Q	Q	Q	Q	Q	Q	Q	Q	Q	YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
	Hereward			Q	Q	Q	Q	Q	Q	Q	Q	Q	YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
	Maris Widgeon				Q	Q	Q	Q	Q	Q	Q	Q	YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
	Mercia					Q	Q	Q	Q	Q	Q	Q	YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
	Monopol						Q	Q	Q	Q	Q	Q	YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
	Pastiche							Q	Q	Q	Q	Q	YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
	Renan								Q	Q	Q	Q	YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
	Renesansa									Q	Q	Q	YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
	Soisson										Q	Q	YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
	Spark											Q	YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
	Thatcher												YQ	YQ	YQ	YQ	YQ	YQ	YQ	YQ
Yield	Buchan													Y	Y	Y	Y	Y	Y	Y
	Claire														Y	Y	Y	Y	Y	Y
	Deben															Y	Y	Y	Y	Y
	High Tiller Line																Y	Y	Y	Y
	Norman																	Y	Y	Y
	Option																		Y	Y
	Tanker																			Y

Figure 1.2: Parental varieties and half-diallel crosses made in order to create the three populations (YQ, Q and Y). (The Organic Research Centre, Wolfe et al., 2006).

In 2005 (F_5), seed of the three populations composed of an equal mixture from three UK locations, was given to a number of scientists in France, Hungary and Germany who agreed to maintain the populations either under conventional and/or organic conditions without conscious selection. The composite cross wheat populations have since been growing at the research fields of the University of Kassel in Neu Eichenberg (51°22” N and 9°54” E, average annual precipitation: 619mm, average annual temperature: 7.9°C, altitude: 247m above sea level). In 2005 (F_5), the three populations (Table 1.1) were divided and grown under two agricultural systems, i.e. organic (O) and conventional (C) and additionally in the following generation (F_6), two sub-populations were created for each population (i.e. I and II). The parallel populations were kept separately thereafter so that the total number of populations equals twelve (six organic and six conventional 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 in parallel, while comparing populations grown under organic and conventional conditions will allow to compare between systems.

Table 1.1: Description of the development of the composite cross wheat populations growing in Neu-Eichenberg (C=Conventional, O=Organic, YQ=Yield x Quality, Q = Quality and Y = Yield).

Generation	**Year**	**Composite cross wheat population development in Witzenhausen**											
F_5*	2005/06	CYQ		OYQ		CQ		OQ		CY		OY	
F_6**	2006/07	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_7	2007/08	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_8	2008/09	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_9	2009/10	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{10}	2010/11	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{11}	2011/12	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{12}	2012/13	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{13}	2013/14	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{14}	2014/15	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{15}	2015/16	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII

*YQ, Q and Y populations were split into organic (O) and conventional (C).
** CYQ, OYQ, CQ, OQ, CY, and OY were split into two parallel populations (I and II).

1.7 Objectives and thesis outline

The main objective of this thesis was to assess the agronomic potential of CCPs as an alternative breeding approach as affected by management system. A number of agronomic parameters such as yield, foliar and foot rot disease incidence, thousand kernel weight, harvest index and kernel per ear, as well as morphological characteristics such as plant height and ear length, were analysed for the CCPs in each management system. Additionally, a stability analysis of the CCPs in comparison to two pure line varieties was performed. Chapter 2 is a historical analysis on data available for the twelve CCPs grown at the University of Kassel under both organic and conventional conditions between 2005/06 (F_5) and 2015/16 (F_{15}) and includes analyses on agronomic performance, as well as morphological characteristics between the CCPs, as well as a number of pure line varieties. Chapter 3 extends these analyses by looking at yield stability of the CCPs and pure line varieties included in the majority of experimental years, using the same historical data as found in Chapter 2. A number of yield stability parameters have been calculated in order to describe not only static, but also the dynamic concept of stability. Chapter 4 presents the results of a two-year experiment within the framework of a CORE Organic project. This experiment explored the adaptive capacity of CCPs to changing environments in comparison to static CCPs and pure line varieties and deals with possible selective pressures and timeframes that may be needed before CCPs are able to adapt to differing environments. Additionally, in this chapter, a number of baking quality parameters were also analysed and discussed in order to assess the potential of CCPs for baking quality. The final chapter (Chapter 5) provides a general discussion of the results and gives some closing remarks and an outlook on the application and challenges facing CCPs in terms of acceptance and application.

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2. Effects of management system on the performance of three wheat composite cross populations over 11 generations

Abstract

Evolutionary breeding of heterogeneous crop populations is a novel breeding concept that has been promoted mainly for organic and low-input agriculture. Three composite cross winter wheat populations (CCPs) have been grown at the University of Kassel research station in Neu-Eichenberg since the experimental season of 2005/06 (F_5). The CCPs were divided into four populations each, with two parallel populations managed in both an organic and conventional system for 10 years (twelve CCPs in total). A selection criterion for the CCP parental varieties was agronomic performance particularly for low-input agriculture in Europe. The CCPs were grown under organic and conventional management alongside commonly used modern pure line varieties in order to compare the agronomic performance and suitability of CCPs as an alternative germplasm source, particularly for organic and low-input agriculture. There were strong interaction effects between CCPs and experimental seasons, under both management systems, for most agronomic and morphological parameters, indicating that the CCPs show high plasticity in their response to differing environments. The organically managed CCPs were comparable to the commonly grown reference varieties Capo and Achat in terms of agronomic performance, but under conventional management, the CCPs were outyielded by the variety Capo and these results further support the importance of parental variety choice for specific management systems. Differences between the CCPs were mainly due to the parental genetic background, but divergent evolutions between parallel populations at the same multiplication site indicate that different biotic and physical environmental pressures may have led to separate evolutions even between genetically similar populations. The significant differences in morphological and agronomic traits demonstrate the genetic variability still present in the CCPs, even after 11 generations, further supporting the premise that heterogeneous crop populations have the capacity to change and adapt to their environments, and as such are an important alternative germplasm resource, particularly in light of climate change.

2.1 Introduction

Agricultural research has started looking for alternatives to high external input agriculture by focusing on ecological intensification, which supports the optimal use of ecosystem services and management of all resources such as soil, biodiversity, water and nutrients in order to improve agronomic performance, whilst reducing external inputs (Cassman, 1999). Increased inter-and intraspecific diversity are main building blocks for ecologically intensified systems. Both intra- and interspecific diversity within agriculture can have positive effects not only for plant protection, but in terms of yield stability, and soil conservation in general (Østergård *et al*., 2009; Tooker & Frank, 2012; Finckh & Wolfe, 2015; Vidal *et al*., 2017). The success of crop diversity can be attributed to a number of advantageous strategies such as "complementation, cooperation, compensation and capacity", particularly in uncertain environmental conditions (see Döring *et al*., 2011 for review). In addition, under natural selection, heterogeneous populations are also subject to changes over time, as they adapt to their environments. There has been a growing interest in breeding approaches such as "evolutionary breeding" (Suneson, 1956) based on heterogeneous crop populations that are subjected to natural selection as these may provide the needed diversity and, in addition, may help generate and conserve plant genetic diversity within agricultural systems.

Populations for evolutionary breeding are commonly based on composite cross populations (CCPs) that are created through the careful selection and intercrossing of parental varieties. The ensuing populations are harvested in bulk and then resown for many years, in order to improve adaptability, genetic variability and to limit human selection (Harlan and Martini, 1929; Finckh & Wolfe, 1997; Murphy *et al*., 2005; Döring *et al*., 2011; Dawson & Goldringer, 2012). Plants that do well in a specific environment exhibit better fitness over others, and as such produce more seeds, resulting in an ever-changing and adapting population, which is able to evolve with "stressful, variable and unpredictable environments" (Döring *et al*. 2011).

Composite cross populations of barley and wheat often outyield their parental varieties and/or their mixtures (Soliman & Allard, 1991; Goldringer *et al*., 2001a; Phillips & Wolfe, 2005; Wolfe *et al*., 2006a; Döring *et al*., 2015; Brumlop *et al*., 2017). For barley, Suneson (1956) concluded that there was a need for at least 15 generations in order to ensure higher and stable yields. Later Allard and Adams (1969) reported on improved yields and yield stability of these same barley CCPs over 18 years. In wheat, Goldringer *et al*. (2001b) reported a significant generation effect in plant height, kernel number per plant and per tiller and kernel weight per plant in a number of dynamically managed wheat populations from the F_1 to the F_{10}. There was also the tendency for smaller variances in the populations in later generations (Goldringer *et al*., 2001b) indicating a stabilizing effect within the populations over time. This is in line with results by Qualset (1968), who had reported on two selection phases in wheat composite cross populations. Genetic changes within CC populations due to selective pressures tended to be dramatic in early generations, but later generations (post F_{10} to F_{15} depending on the measured trait) generally experienced a loss of overall diversity and an increased selection for improved genotypes. The second phase in CC population evolution results in slower and less dramatic changes, hence the tendency towards smaller variance in terms of agronomic performance and in phenotypical traits in later generations.

The working of the abovementioned mechanisms of complementation, cooperation, compensation and capacity were impressively documented for wheat CCPs that survived a severe black frost despite the fact that most of the parental varieties failed to survive (Brumlop *et al*., 2017). A similar result for a barley CCP was reported by Hensleigh *et al*. (1992). In addition to stabilizing effects on yields and variability, selection for disease resistance in response to local disease pressure has been reported in barley for *Rhynchosporium secalis* (Jackson *et al.* 1978; Webster *et al.* 1986), *Pyrenophora teres* (Soliman and Allard 1991), and *Blumeria graminis* f. sp. *hordei* (Reinhold *et al*., 1990; Ibrahim & Barrett, 1991; Danquah & Barrett, 2002a) and in wheat for *B. graminis* f.sp. *tritici* (Le Boulc'h *et al.* 1994).

Breeding and selecting for heterogeneous crop populations in the long term can help to produce locally adapted materials (i.e. modern landraces) (Murphy *et al*., 2005; Dawson *et al*., 2008), contributing to an overall diversification of the agricultural system and thus to dynamic development and conservation of genetic resources (Brumlop *et al*., 2013). Heterogeneous populations such as CCPs will likely play an important role in the future, especially as the merits of diversifying agricultural and food systems, but also diet become known (Dwivedi *et al*., 2017). Natural selection within genetically diverse populations will ensure adaptation to climatic changes and shifting pathogen populations (Kole, 2013). However, there are still many open questions with regards to the timeframe 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*. (1998, 2001a) reported that extensively cultivated wheat populations tended to be more resistant to powdery mildew and brown rust, and showed equal or superior agronomic potential in comparison to those populations that had been cultivated intensively. This suggests that farming system effects should be taken into consideration when working with CCPs.

The purpose of this paper is to present data on the performance of three wheat CCPs as affected by their parental genetics and farming system from the F_5 to the F_{15}. The three CCPs were multiplied at four different locations in the UK (2 organic and 2 conventional sites) without conscious selection until the F_4. In 2005, F_4 seed of the three populations composed of an equal mixture from the four UK locations was divided and one part was given to the Department of Ecological Plant Protection at the University of Kassel. Upon arrival, the three populations (see Table A 2.9) were divided and the F_5 was grown under organic (O) and conventional (C) management. In the following generation (F_6), two sub-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 organic and six conventional populations).

Apart from the removal of plants over 130cm in height, the composite cross populations, organic and conventional, have been maintained at the research fields of the University of Kassel in Neu Eichenberg since 2005 without conscious selection. Each population was grown in plots >150m^2 and bordered by 3m non-wheat or themselves in order to prevent outcrossing between the different populations. Even without outcrossing, based on variation in family size, the effective population size (N_e) of the 12 CCPs were at all times considerably greater than 5000 plants (Brumlop, 2017; Weedon *et al*., 2010), a prerequisite to minimise the risks of drift (Goldringer *et al*., 2001a,b). Overall, the twelve 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 if they have evolved and changed within the same growing system in parallel, while comparing populations grown under organic and conventional conditions will allow to compare between systems.

Data on the CCPs (F_5-F_{15}) and pure line reference varieties have been recorded for most seasons for a range of agronomic and phenotypical parameters. For this paper, the available data were analysed to provide an historical analysis of agronomic and phenotypical traits in the twelve winter wheat CCPs under organic and conventional management 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 and cold?
2) How different are the CCP groups (CY, CQ and CYQ) from one another and are there changes or trends that have developed over time in terms of their agronomic and phenotypical characteristics?
3) Are there management system effects on agronomic or phenotypical traits visible between the organic and conventional CCPs and can these be attributed to parental variety genetics?

In order to answer the above questions, morphological and agronomic assessments over the seasons including grain yield, thousand kernel weight (TKW), foliar and foot diseases were analysed. In addition, ear length and plant height data from an early and a late generation are available. The results give insight into the performance and evolution of twelve CCPs managed separately under organic and conventional conditions.

2.2 Materials and Methods

2.2.1 Field site

The experimental research fields of the Department of Ecological Plant Protection are situated in Neu Eichenberg (51°22’24.7”N and 9°54’12.5”E), 247m above sea level. For 2000-2013, mean annual precipitation: 684mm, mean annual temperature: 9.3°C. From 2005/06 until 2012/13, the conventional CCPs were grown on a field (Saurasen) located at about 500m distance from the organic field (Teilanger). The soil of Saurasen is a sandy loam loess soil (Stagnic Luvisol) with 52 soil points according to the German soil grading system (0-100) (Wildhagen, 1998). The organic field (Teilanger) is classified as fine loamy loess (Haplic Luvisol) with 76 soil points (Wildhagen, 1998). Since the experimental year of 2013/14, the conventional populations have been grown in a conventionally managed field on Teilanger with the same soil quality as the organic populations.

The pre-crop for the organic wheat populations was a two year grass-clover mixture and the populations were grown under organic conditions without the addition of fertilizers or pesticides. Weeds were controlled through mechanical harrowing and/or hoeing before winter and/or at tillering, dependent on seasonal and field weed pressure. The conventional populations on Saurasen were rotated yearly with grass-clover. On Teilanger, conventional wheat mostly follows maize or a green manure. No fungicides or insecticides were applied, but herbicides were generally used once a year in early spring. Mineral nitrogen fertilizer at a rate of 125kg/ha was applied in two split applications during the growing season (50kg and 75kg/ha at each application, respectively). At stem elongation, growth regulators were applied in 2008 and 2009, but not thereafter. Row spacing was generally 30cm to allow for weed control through harrowing at tillering and/or hoeing at later stages if needed (see Bertholdsson *et al*., 2016 for further details).

2.2.2 The CCPs and reference materials

In 2001, the John Innes Centre (Norwich, UK) in co-operation with the Elm Farm Research Centre (Newbury, UK), performed a complete half-diallel crossing of twenty European wheat varieties (varietal release dates from 1934-2000), chosen for their broad genetic background and performance under low-input conditions in Europe and the UK. The productivity and stability of the parental varieties varied according to varietal release date. In addition, the parental varieties provided ample variation for ability to cope with diseases and for nutrient uptake under organic conditions (Jones *et al*., 2010) and for winter hardiness (Brumlop *et al*., 2017). The progeny of the crossings were multiplied for one season in a glasshouse before being bulked into three separate CCPs. The first population (CCY, Y = Yield) is made up of the diallel crossing of nine high yielding parental varieties (36 crosses), the second, (CCQ, Q = Quality) is the diallel crossing of twelve parental varieties known for high baking quality (66 crosses). Both populations contain Bezostaya as a parent as this variety had high yield and high baking quality at the time of release. The third population (CCYQ, YQ =

Yield x Quality) is the product of eight x eleven Y x Q parents (88 crosses) plus all these 19 parents with Bezostaya (total=107 crosses). In addition, all parents except Bezostaya were crossed with a naturally male sterile parent and aliquots of the progenies added to the three populations in the F_1 (Döring *et al*., 2015; Brumlop, 2017). After the bulking of the three populations they multiplied at three sites in the UK until 2005, where after each population from each site was bulked in equal measure before being sent to Hungary, France and Germany in 2005 (F_5). In 2005, each population was split equally in two and managed in both an organic and conventional system (six populations in total). In 2006 (F_6), the six populations were again split in two in order to create two parallel populations, bringing the total number of populations to twelve (six under organic and six under conventional management).

Besides the CCPs that were grown in plots >150m^2 as described above, three to six currently popular modern wheat varieties were also grown every year in smaller plots next to the populations in order to determine disease pressure and general growing conditions. In 2008/09 and in 2014/15, in addition to the populations, the parental varieties were grown in unreplicated plots under organic conditions to increase seed.

2.2.3 Assessments

Growth stages according to the BBCH scale were recorded at the time of each field assessment based on the BBCH stage most frequently observed (Witzenberger *et al*., 1989; Lancashire *et al*., 1991). Grain yields and thousand kernel weight (TKW) adjusted to 14% moisture content were recorded for each population and pure line variety every season. Some yield data from 2011, 2012 and 2013 was not available for the analyses (Table 2.1). Usually, two to three yield measurements were taken from the population plots, in order to estimate variance and to allow for approximate statistical analysis within year.

Foliar diseases caused by fungal pathogens were assessed from 2005/6 onwards in most years unless disease pressure was very low. Non green area (NGLA) was recorded in % (1-100%) on the flag leaf (F), the leaf below the flag leaf (F-1) and the F-2 leaf. The first assessment was usually done with all three leaf levels. If foliar disease progressed considerably, the second assessments were usually done with only two leaf levels as foliar disease or senescence could not be separated. From

2005/06 to 2010/11, individual plants were assessed for foliar diseases. From 2013/14, individual plants were no longer assessed, but rather an average per leaf level estimated from an area of neighboring plants of approximately 25cm in length. Foliar diseases of CCPs and reference varieties were assessed and the two main foliar leaf pathogens were recorded at each assessment date (Table 2.1*)*.

Table 2.1: Assessments available for the CCPs and foliar assessment methods used in the different years.

Season	**Yield**	**TKW**	**Foot Dis**	**Foliar assessments**			**Height, ear length**
				Dates		**Foliar assessment methods**	
2005/06	x[2]			30.6	-	% non-green leaf area F and F-1 leaves on 100 tillers	x
2006/07	x	x					x
2007/08	x	x		28.6	-	% non-green leaf area F and F-1 leaves on 50 tillers	
2008/09[1]	x	x	x	29.6	9.7	% non-green leaf area F and F-1 leaves on 30 tillers	
2009/10	x	x	x	21.6	9.7	% non-green leaf area F and F-1 leaves on 50 tillers per CCP, 30 per ref.	
2010/11	Conv.[3]	x	x	7.6	5.7	% non-green leaf area F and F-1 leaves on 50 tillers per CCP, 20 per ref.	
2011/12	Conv.[3]	x					
2012/13	Org.[3]	x					
2013/14	x	x	x	31.5	12.6	% non-green leaf area on F, F-1 and F-2 leaves, 3 25cm row sections per plot	
2014/15[1]	x	x	x	2.6	16.6	% non-green leaf area on F, F-1 and F-2 leaves, 10 25cm row sections per plot	x
2015/16	x	x	x	31.5	16.6	% non-green leaf area on F, F-1 and F-2 leaves, 9 25cm row sections per plot	

[1] Parents were grown for seed increase and assessed for foliar disease in 2008/09 and in 2014/15 for disease and yield

[2] Yield data for 2005/06 not included in general ANOVA as parallel populations were only created in 2006/07

[3] Org.: yield data from organic populations missing, Conv: Yield data from conventional populations missing.

In addition to foliar pathogens, foot diseases were assessed at the beginning of July (BBCH 70-75) for 6 experimental seasons (Table 2.1). 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 lower stems were assessed for foot disease severity on a 0 to 3 scale according to Bockmann (1963), 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 *Pseudocercosporella herpotrichoides* only). The foot rot pathogens (*Fusarium* spp., *P. herpotrichoides* and *Rhizoctonia cerealis*) symptoms were assessed based on a pictorial key by Bayer CropScience (2013).

Plant height and ear length were recorded over three experimental seasons. In 2005/06, the plant height of 200 tillers was measured in the field at maturity (BBCH 80) (from stem base to ear tip); additionally ear length was recorded from the beginning of the ear to the tip for the three original populations in each management system. In 2006/07, the original populations in each management system were split into parallel populations and plant height and ear length of 50 individual tillers were measured in the field using the same assessment procedure. In 2014/15, biomass cuts were made by cutting 3 x 0.5m rows (0.450m^2) of mature plants (BBCH 80) from each population. The plants were removed as close to the ground as possible and plant height and ear length were recorded for 45 tillers.

2.2.4 Data processing and statistical analysis

The calculation of a mean NGLA% over all three leaf levels was done according to Brumlop *et al*. (2017) through the weighting of the F leaf by the factor of 4, and the F-1 and F-2 leaves by the factor of 3. This accounts for the greater contribution of the flag leaf to total grain yield in comparison to lower leaves (Lupton, 1969). 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 & Finney (1977) and the Relative Area under the Disease Progress Curve (RAUDPC) based on Fry (1978) as follows:

$$RAUDPC = \frac{AUDPC_i}{AUDPC_{max}}$$

in which AUDPC_i= AUDPC of the *i*th genotype is divided by $\mathrm{AUDPC}_{\max}$ = the maximum potential AUDPC value of all genotypes in one trial (total no. of days in assessment period multiplied by maximum NGLA% of 100).

A foot disease severity index (DI) was calculated as described by Bockmann (1963), for all three pathogens combined or for each foot rot pathogen separately as follows:

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

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

Data analysis was performed with the statistical software R (Version 3.3.3, 2017.03.06). Percentage data were transformed using the arcsine transformation and data were thereafter tested for normal distribution of the residuals through QQ plots and the Shapiro-Wilk Test. Data were then tested for homogeneity of variance using the Levene Test for parametric and the Fligner-Killeen Test for non-parametric data sets. As ANOVA is considered a robust test against minor violations to data normality, data sets that were normally distributed or had minor deviations from normality, but that indicated homogeneity of variance, were tested using a univariate ANOVA and subsequent Post-hoc Tukey HSD Test. For data that was found to be normally distributed, but that indicated heterogeneity of variance, a Welch’s ANOVA and Post-hoc Games-Howell Test was calculated. In data sets that displayed neither normality, nor homogeneity of variance, a non-parametric Kruskal Wallis H Test and pairwise comparison with Holm correction were used.

For comparisons between CCP attribute groups (organically and conventionally managed population groups of CCQ, CCY and CCYQ) and CCP entries (organically and conventionally managed parallel populations of CCQ, CCY and CCYQ), CCP groups or CCP entries and experimental seasons were used as factors in the ANOVAs. The additional factor of site was used when comparing the conventionally managed CCP groups and entries. In the comparison of differences between CCP attribute groups (CCQ, CCY and CCYQ) for yield and TKW, environmental seasons and management system were used as factors. In the comparison of mean parameters such as yield, TKW, AUDPC values, plant height and ear length for parental variety groups, between CCP entries and reference varieties and between growing sites when sample sizes were unequal and variances heterogeneous, a Dunnett’s Modified Tukey-Kramer Test for unequal variance and sample size, was used.

2.3 Results

2.3.1 Weather data and epidemic years

There have been a number of extreme climatic events during the experimental seasons from 2005/06 to 2015/16. Mean temperatures for the experimental seasons (September to August) were slightly warmer (9.6°C) than the long-term annual average temperature of 9.0°C from 1971-2000 (Table 2.2). The warmest season was 2006/07 (11.2°C) and the coolest season was 2012/13 (8.4°C). Total precipitation over the experimental seasons ranged from 540mm in 2005/06 to 791mm in 2009/10 with a mean seasonal precipitation over the experimental years (2005-2016) of 679mm. This compares to the long-term average annual precipitation (1971-2000) of 628mm. However, precipitation patterns over the 11 experimental seasons appear to be shifting towards drier late winter-early spring periods since 2010/11 (Table 2.2). 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 droughts. The winter/springs of 2010/11, 2013/14 and 2014/15 were accompanied by higher than normal temperatures, exacerbating stress. A particularly stressful event occurred in winter/early spring of 2011/12. After a frost-free wet winter, within 24 hours a sudden two-week black frost period in early February resulted in 50 cm deep frozen soils. This period was followed by very warm weather in the second half of February and March with almost no rainfall, which resulted in severe frost damage in the region (Table 2.2, see Brumlop *et al*. 2017 for more details).

In addition to the weather variation, 2009 was characterized by a brown rust (*Puccinia recondita*) epidemic and stripe rust (*Puccinia striiformis*) has been prevalent since 2014. Otherwise, *Blumeria graminis*, *Septoria tritici* and *Drechslera tritici-repentis* were the main foliar pathogens observed. Cereal leaf beetles (*Oulema* sp.) were among the dominant causal agents for non-green leaf area in some years, but the damage caused by the beetle is considered to be negligible in respect to wheat yields and as such is not mentioned further when discussing foliar diseases.

Table 2.2: Mean monthly and overall mean temperature (°C) and total monthly and overall total precipitation (mm) per experimental season from 2005/06 to 2015/16. Please see colour-coding key for divergences from mean monthly temperatures and precipitation over all experimental seasons. Extreme temperature divergences and dry seasonal spells are blocked in black. The long-term means (1971-2000) are given for overall comparison.

Experimental seasons	**Sept**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Mean temp. and total ppt**
2005/06	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
2006/07	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
2007/08	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
2008/09	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
2009/10	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
2010/11	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
2011/12	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
2012/13	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
2013/14	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
2014/15	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
2015/16	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
Mean temperature	14,1	9,9	6,0	2,4	1,1	1,5	4,4	9,6	13,3	16,1	18,7	17,7	9,6 °C
Mean precipitation	56,3	46,0	56,1	61,4	50,5	37,8	45,2	35,2	68,9	67,2	74,9	79,6	679 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

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%

2.3.2 Agronomic and morphological characteristics of the parental varieties

The CCP parental varieties were grown in a neighbouring field under organic management in the experimental seasons of 2008/09 and 2014/15 when brown and yellow rust epidemics occurred. Yields and morphological characteristics were, however, only assessed in 2014/15. A brief descriptive summary is given for reference.

In 2008/09, the maximum percentage non green leaf area (NGLA) was recorded in Mercia (Q group, 1st assessment: 78% NGLA) and the lowest on Spark (Y group, 1st assessment: 1% NGLA). RAUDPC values of the parental varieties ranged from the highest of 0,76 (Mercia) to the lowest of 0,06 (Spark) (Table 2.3). In 2014/15, maximum NGLA was recorded in Thatcher (Q group, 1st assessment: 9% NGLA) and the lowest on Pastiche (Q group, 1st assessment: 0% NGLA). Mean RAUDPC values for each parental variety were lower during the stripe rust epidemic of 2014/15 and their ranking did not correspond to the ranking during the brown rust season of 2008/09 (Table 2.3). In 2014/15, the parents mean RAUDPC values ranged from the highest for Thatcher (Q group, 0.21) to the lowest in Pastiche (Q group 0.02). A number of parental varieties such as Renan, Spark, Pastiche and Wembley had low to moderate RAUDPC values for brown and stripe rust. Again, parental groups did not differ significantly in 2014/15 (Table 2.3).

The variety Deben (Y group) yielded the highest (5.0 t/ha), but within the same group the variety Wembley yielded the least (2.1 t/ha) (Table 2.4). In the comparison of the parental variety groups, there were no significant differences between them for yield (t/ha). The Y group, however, tended towards the highest yield (4.2 t/ha), followed by the YQ group (4.0 t/ha) and the Q group (3.9 t/ha).

There were significant differences between the parental varieties for mean plant height. The Q group was the tallest (70.4cm), followed by the YQ group (66cm) and the Y group, the shortest (59.5cm) (Table 2.3). Ear lengths and TKW were quite similar with no significant differences among parental groups.

Table 2.3: Mean area under the disease progress curve (AUDPC) and relative AUDPC (RAUDPC) in 2009 and 2015, as well as yield (t/ha), plant height (cm), ear length (cm), and TKW (g) in 2015 for all parental varieties and their respective grouping under organic conditions. Data are from unreplicated plots with multiple samplings per plot.

		2008/09				**2014/15**											
Group	**Entry**	**AUDPC**	**RAUDPC**	**Rank**	***SD***	**AUDPC**	**RAUDPC**	**Rank**	***SD***	**Yield (t/ha)**	**SD**	**Plant height (cm)**	***SD***	**Ear length (cm)**	***SD***	**TKW (g)**	***SD***
YQ	Bezostaya	739	0,67 ab**	19	*0,08*	283	0,14 a	18	*0,05*	4,03		67,2 cdef	*17,6*	7,00 ab	*1,5*	51,0 ab	*1,6*
Q	Cadenza	276	0,25 cdef	8	*0,05*	154	0,08 abcd	13	*0,02*	4,19		72,4 bcd	*8,6*	7,20 ab	*0,7*	44,8 efg	*0,5*
Q	Hereward	278	0,25 cdef	9	*0,07*	154	0,08 abcd	14	*0,03*	4,34		55,7 hi	*4,2*	7,53 ab	*0,9*	48,1 abcd	*0,3*
Q	Maris Widgeon	338	0,31 cdef	12	*0,15*	75	0,04 efgh	5	*0,00*	3,65		97,4 a	*5,2*	7,37 ab	*0,6*	51,2 ab	*0,6*
Q	Mercia	831	0,76 a	20	*0,13*	46	0,02 gh	2	*0,00*	4,79		59,4 efghi	*3,3*	7,73 ab	*0,8*	43,2 fg	*0,8*
Q	Monopol	545	0,50 abcd	17	*0,17*	100	0,05 bcdefg	9	*0,01*	3,52		75,5 abc	*7,8*	7,37 ab	*0,8*	47,7 bcde	*0,1*
Q	Pastiche	232	0,21 cdef	7	*0,08*	32	0,02 h	1	*0,00*	3,91		61,3 efgh	*4,1*	7,80 ab	*1,6*	45,8 efg	*1,1*
Q	Renan	131	0,12 ef	2	*0,06*	89	0,04 defgh	7	*0,00*	2,39		63,6 defg	*4,8*	7,50 ab	*0,7*	56,2 a	*0,2*
Q	Renesansa	406	0,37 bcdef	14	*0,10*	135	0,07 abcde	12	*0,02*	3,60		65,2 cdef	*8,2*	7,67 ab	*1,2*	46,7 def	*0,9*
Q	Soissons	382	0,35 bcdef	13	*0,05*	109	0,05 bcdefg	10	*0,01*	4,22		64,9 cde	*3,5*	6,57 b	*0,8*	46,1 efg	*0,1*
Q	Spark	71	0,06 f	1	*0,05*	53	0,03 fgh	3	*0,00*	4,26		72,0 abcd	*5,7*	7,13 ab	*1,1*	40,8 g	*2,0*
Q	Thatcher	226	0,21 cdef	6	*0,03*	428	0,21 a	19	*0,10*	3,36		89,8 ab	*17,9*	7,63 ab	*1,2*	43,3 fg	*0,0*
Y	Buchan	294	0,27 cdef	11	*0,13*	181	0,09 abc	16	*0,02*	4,29		51,7 i	*4,5*	8,13 a	*0,8*	47,4 cde	*1,1*
Y	Claire	189	0,17 def	4	*0,11*	109	0,05 bcdef	11	*0,00*	4,73		56,9 fghi	*7,3*	7,60 ab	*1,3*	46,9 def	*0,4*
Y	Deben	440	0,40 bcde	16	*0,18*	98	0,05 cdefg	8	*0,01*	5,00		58,7 efghi	*7,2*	7,63 ab	*1,1*	49,4 abc	*0,1*
Y	High Tiller Line	416	0,38 bcdef	15	*0,06*	54	0,03 fgh	4	*0,01*	4,22		74,5 bcd	*15,8*	7,00 ab	*0,8*	47,0 cdef	*0,1*
Y	Norman	283	0,26 cdef	10	*0,13*	-	- -	-	-	-	-	- -	-	- -	-	- -	-
Y	Option	577	0,52 abc	18	*0,14*	237	0,12 ab	17	*0,03*	4,65		56,8 ghi	*3,6*	7,10 ab	*0,9*	41,5 g	*0,5*
Y	Tanker	213	0,19 cdef	5	*0,13*	180	0,09 abc	15	*0,02*	4,41		51,5 i	*6,7*	7,73 ab	*1,7*	48,6 abcd	*1,1*
Y	Wembley	164	0,15 ef	3	*0,06*	87	0,04 defgh	6	*0,00*	2,12		58,9 efghi	*6,5*	7,23 ab	*1,0*	48,5 abcd	*1,1*
Mean Q		371	0,34	3	*0,22*	138	0,07	2	*0,04*	3,86	0,6	70,4 A	*14,7*	7,38	*1,1*	47,1	*4,1*
Mean Y*		368	0,33	2	*0,20*	154	0,08	3	*0,05*	4,18	0,9	59,5 C	*12,1*	7,43	*1,2*	47,5	*2,8*
Mean YQ*		352	0,32	1	*0,20*	137	0,07	1	*0,06*	3,98	0,8	66,0 B***	*14,7*	7,40	*1,1*	47,2	*3,6*

* High yielding parental variety Norman not included in 2014/15

** Differing letters indicate significant differences between the parental varieties at p<0,05 (ANOVA and Post-hoc Test in 200/09 and Kruskal H Test in 2014/15)

*** Differing letters indicate significant differences between the parental variety groups at <0,05 (Dunnett's Modified Tukey-Kramer Test)

2.3.3 Agronomic performance of the CCPs and references

2.3.3.1 Foliar diseases

Overall, foliar disease pressure was low at the experimental sites with a tendency to higher pathogen pressure in the organic field (Figure 2.1). The maximum percentage of non-green leaf area (NGLA) was observed on July 9 2009 in the variety Achat with 93% (data not shown). This resulted in the overall highest AUDPC of 609 on Achat in the organic field in that year (Figure 2.1).

Depending on the experimental season and reference variety, the organic CCPs displayed both significantly higher and lower AUDPC values. Thus, resistant varieties such as Butaro, Tamaro and Wiwa generally tended towards significantly lower AUDPC values in comparison to the CCPs (Figure 2.1). 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 much more affected in 2015 than in 2014. In the conventional field, Akteur was strongly affected in 2014 but less in 2015. Under organic conditions, the overall mean AUDPC of the two reference varieties Achat and Capo were 257 and 179, respectively. These were the only two references to be included in the six experimental years shown in Figure 2.1, while the minimum and maximum overall mean AUDPC of the organic CCPs were 147 for CCP OYI and 244 for CCP OYQI (Table 2.4). The differences between Capo and any of the CCPs were not significant, whilst Achat had a significantly higher AUDPC value in comparison to the CCP OYI (Figure 2.1).

Under conventional management, CYII had the highest overall mean AUDPC value of 321 and CYQI and CYQII had the lowest mean overall AUDPC values of 203 and 214, respectively (Table 2.4). As observed in the organic field, AUDPC of the reference variety Capo (254) was not significantly different to any of the conventional CCPs (data not shown) (see Table A 2.11 for more details). Analysis of mean RAUDPC values over all experimental years and between systems indicated a small, but statistically significant difference between the organically managed CCPs (0.14) and the conventionally managed CCPs (0.16) (Table 2.4).

Depending on year, the AUDPC values of the parallel CCPs varied considerably especially under organic conditions (Figure 2.1). In 2009 and 2016, AUDPC values for the OYII population were statistically significantly higher than those of OYI. Significant differences in the same two years were also found in the OQ CCPs and for the OYQ CCPs in 2010, 2011, and 2016 (Figure 2.1). For the OY CCPs and OYQ CCPs this resulted in overall statistically significant differences in RAUDPC between the parallel CCPs (Table 2.4). The overall mean AUDPC values of the CCP groups were, however, not significantly different from one another (Table 2.4).

Under conventional conditions in 2009/10, CQI was significantly less diseased than CQII and CYII (AUDPC 186, 366, and 443, respectively). Significant differences between parallel CCPs were also found in 2014/15 between both the CY and CYQ parallel populations, albeit at low overall disease levels (Figure 2.1). Overall, the CY CCPs had a significantly higher overall AUDPC (289) than the CYQ CCPs (209) (Table 2.4) (see Appendix Table A 2.10 for more details).

Table 2.4: Mean AUDPC and RAUDPC and standard deviation (SD) for the CCP entries and groups under organic and conventional management over eight (organic) and seven (conventional) experimental seasons (see Table 2.1 for details).

Group	**Mean Group AUDPC**	**Mean Group RAUDPC**	**Entry**	**Mean CCP AUDPC**	***SD***	**Mean CCP RAUDPC**	***SD***
OQ	196	0,14	OQI	207 ab	*218*	0,16 bc	*0,20*
			OQII	185 ab	*150*	0,12 abc	*0,13*
OY	189	0,12	OYI	147 b	*139*	0,09 c	*0,10*
			OYII	231 a	*184*	0,15 ab	*0,17*
OYQ	213	0,15	OYQI	244 a	*178*	0,16 a	*0,17*
			OYQII	183 ab	*177*	0,13 bc	*0,17*
Mean organic RAUDPC				199		0,14 B*	*0,16*
CQ	258 ab	0,16 a	CQI	217	*207*	0,14 ab	*0,15*
			CQII	299	*263*	0,18 a	*0,17*
CY	289 a	0,17 a	CYI	258	*227*	0,16 ab	*0,16*
			CYII	321	*272*	0,19 a	*0,17*
CYQ	209 b	0,13 b	CYQI	203	*188*	0,12 b	*0,12*
			CYQII	214	*194*	0,13 ab	*0,15*
Mean conventional RAUDPC				252		0,16 A	*0,16*

Differing small letters indicate significant differences at p<0,05 for mean AUDPC and RAUDPC values between CCP entries and groups over all experimental seasons within a management system (Kruskal H test)

*Differing capital letters indicate significant differences at p<0,05 between the organic and conventional mean CCP RAUDPC values over all experimental seasons (Kruskal H Test)

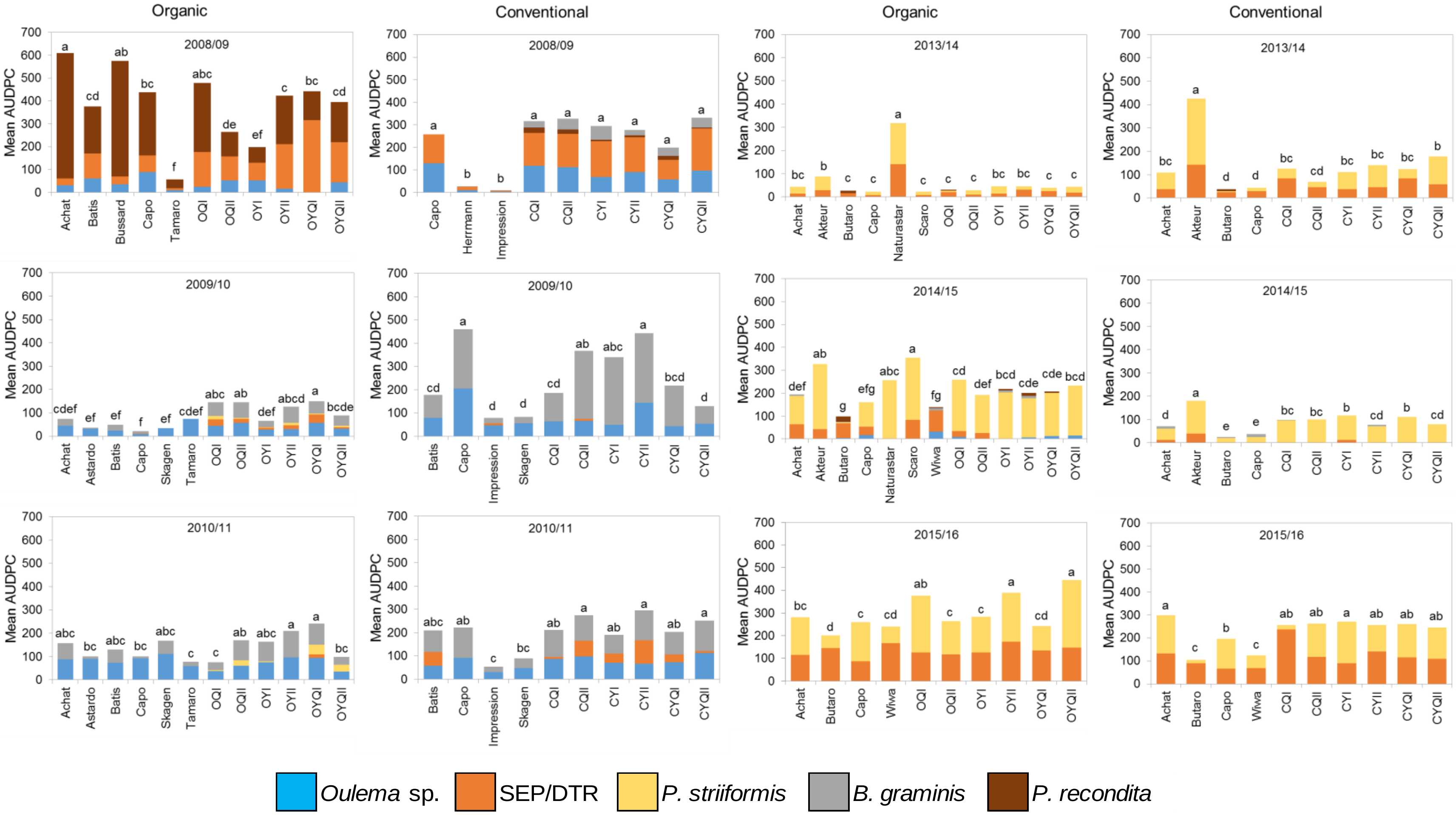

Figure 2.1: Mean AUDPC values and dominance of foliar and insect pathogens in the organically and conventionally managed CCPs and reference varieties from 2008/09 to 2015/16. Pathogens are abbreviated as follows: SEP/DTR = *Septoria tritici/Dreschlera tritici-repentis*. The foliar pathogens *S. tritici* and *D. tritici-repentis* were grouped together. Differing small letters indicate significant differences at p<0.05 between entries within an experimental season.

In 2009, during the brown rust epidemic the RAUDPC values of the parents were 0.32 to 0.34 (Table 2.3). RAUDPC of the CCPs under organic management ranged from 0.20 (OYI) to 0.48 (OQI) (data not shown). In the conventional CCPs where brown rust was much less prominent, maximum RAUDPC was 0.33 (CYQII and CQII) and the minimum 0.20 (CYQI). The mean RAUDPC value over all conventional CCPs was lower than for the organic CCPs (0.29 versus 0.37, respectively) (see Table A 2.10 and Table A 2.11 for details). In 2014, during the stripe rust epidemic, mean RAUDPC values for the organic CCP groups ranged between 0.14 to 0.17 (see Table A 2.10 for details), which were higher than that of their respective parental variety groups that ranged from 0.07 to 0.08 (Table 2.3). Conventional CCP RAUDPC values were similar to the parental variety RAUDPC, with values ranging from 0.05 to 0.08 (see Table A 2.11 for details), most likely indicating field variance for disease pressure.

2.3.3.2 Foot diseases

Foot rot pathogen pressure in the CCPs and reference varieties under both organic and conventional conditions was low. Disease indices ranged from 8 to 54 except for the CQI population in 2013/14 with a disease index of 71. The reason for the high values in this experimental year and field was the relocation of the conventional field to a field next to the organic fields (see 2.2) where part of the wheat was grown directly after wheat due to space constraints. The mean combined foot disease indices for the organic and conventional CCPs were 26 and 31, respectively. There were no significant differences for the mean combined foot disease index between any of the entries under organic or conventional conditions over all experimental seasons with little differences among system (Table A 2.12).

Under organic management, the two dominating pathogens were *Pseudocercosporella herpotrichoides* and *Fusarium* spp., whilst *P. herpotrichoides* was the most relevant pathogen under conventional management. *Rhizoctonia cerealis* was present in all experimental years, under both management systems, but infection was low and seen as unimportant.

2.3.3.3 Yields and Thousand Kernel Weights (TKW)

Under organic conditions, yield data for the CCPs were available for 9 years and with the references Achat and Capo for 8 years. Under conventional conditions, 7 years of CCP yield data and 5 years with Capo as reference were available for ANOVA (Table 2.5 A, Table A 2.13). For TKW, 10 and 9 years data were available (Table 2.5 B, Table A 2.13). Year effects on yields were strongest as expected. Although significant interactions occurred for all entry x year and group x year effects (Table A 2.13), under organic management the F-values for these interactions were about two or more orders of magnitude lower than the year effects, indicating the overwhelming influence of the experimental season on yield. Under conventional management, the year effect (7 years, F = 401) was also the greatest influence on yield variance, although significant site effects (F=198) were also found. Significant, but small interaction effects for CCP entry x site were found (F=5), but not for CCP group x site (F=2) (Table A 2.13). In contrast, when testing for site effects including the reference variety Capo (5 years only) overall site effects were considerably reduced (F=16) compared to year effects (F=126). The CCP group x site effects including Capo were significant, albeit no strongly (F=3, p=0.04) (Table A 2.13).

Under organic conditions, the highest mean annual yield of the CCPs was achieved in 2010/11 (7.4 t/ha) and the lowest in 2013/14 (3.1 t/ha) (Table 2.5 A). The OQ group had the lowest mean yield of 4.6 t/ha, whereas the OYQ and OY groups had significantly higher yields (5.02 and 4.9 t/ha, respectively). Across eight years, Achat and Capo were grown (5.3 and 5.2 t/ha, respectively) and they yielded similarly to the OY and OYQ groups (both 5.0 and 5.2 t/ha, respectively), but significantly higher than the OQ group (4.8 t/ha). The mean yields per season followed the same pattern as for the CCPs alone (Table 2.5 A). Additionally, across these years, the yield variance of Achat was highest (1.95) and of Capo lowest (1.58). The variances of the CCP groups ranged between (OYQ=1.78, OQ=1.62) (Table 2.5 A).

Despite the extreme frost event of 2011/12 and the ensuing winterkill, the mean annual yield of 4.0 t/ha was significantly better than in 2006/07 (3.3 t/ha) and 2013/14 (3.1 t/ha). After the winterkill 2012, in contrast to all other seasons the OY group yielded lowest (3.7 t/ha) (Table 2.5 A), the OYQ and OQ groups both 4.1 t/ha, whilst Achat and Capo achieved the highest yields in that year (5.2 and 4.8 t/ha, respectively).

Under conventional conditions, the highest mean annual yield was achieved in the extremely dry experimental season of 2014/15 (6.1 t/ha) and the lowest yield in the season of 2006/07 (2.2 t/ha) (Table 2.5 A). Over the six experimental seasons in which Capo was grown alongside the conventional CCPs, it yielded significantly higher than the conventional CCPs (mean yield 5.7 t/ha). The CQ group had the lowest mean group yield over all experimental seasons of 4.3 t/ha, followed by the CY group with 4.5 t/ha and the CYQ group achieving the highest mean group yield of 4.7 t/ha (Table 2.5 A). Variances across these six years were lowest for Capo (0.29) and highest for CY (1.01). Unfortunately, no data are available for the conventional CCPs in 2012 to compare the frost effects to the organic CCPs.

Table 2.5: (A) Mean yields (t/ha) and (B) Mean Thousand Kernel Weights (g) in each experimental season for each organically and conventionally managed CCP group and the reference varieties Achat and Capo (organic) and Capo (Conventional). Means across all seasons in which the references were also grown are shown together with the variances. Mean CCP group and reference variety yields (t/ha) over all experimental seasons are also given. See Table A 2.13 for details of ANOVA analysis and interaction effects.

A						**Mean yield (t/ha)**							
Entry	**2005/6**	**2006/7**	**2007/8**	**2008/9**	**2009/10**	**2010/11**	**2011/12**	**2012/13**	**2013/14**	**2014/15**	**2015/16**	**Mean**	***Var***	**Mean CCPs**
Organic														
Achat			6,66	5,32	6,46	7,35	5,20		2,85	4,16	4,33	5,27 A*	*1,95*	
Capo			5,71	5,52	6,56	7,31	4,80		3,48	4,21	3,85	5,21 A	*1,58*	
OQ	5,85	2,73	5,42	4,99	5,61	7,30	4,06		2,64	4,70	4,15	4,83 B	*1,62*	4,64 B** (OQ)
OY	6,29	3,43	6,37	4,97	6,00	7,35	3,70		3,26	5,17	4,20	5,04 AB	*1,71*	4,92 A (OY)
OYQ	5,62	3,69	6,37	4,97	6,28	7,64	4,11		3,34	4,69	4,29	5,17 A	*1,78*	5,02 A (OYQ)
Mean CCPs* **	5,92 B	3,28 E	6,05 B	4,97 C	5,96 B	7,43 A	3,96 D		3,08 E	4,85 C	4,22 D			
Mean CCP and refs******			6,09 B	5,09 C	6,10 B	7,40 A	4,22 DE		3,10 F	4,69 CD	4,19 E			
Conventional														
Capo				5,92	5,10			6,18	5,54	6,6	5,42	5,67 A*	*0,29*	
CQ	4,98	2,27	3,48	4,96	4,12			5,46	4,54	6,02	4,46	4,28 C	*0,55*	4,33 B** (CQ)
CY	5,30	2,00	3,37	5,62	4,36			6,06	4,79	6,38	4,01	4,42 BC	*1,01*	4,48 AB (CY)
CYQ	5,16	2,23	4,20	5,44	4,96			5,93	4,78	5,99	4,52	4,62 B	*0,41*	4,65 A (CYQ)
Mean CCPs* **	5,14 CD	2,17 G	3,68 F	5,34 BC	4,48 E			5,82 AB	4,70 DE	6,13 A	4,33 E			
Mean CCP and refs******				5,42 B	4,57 C			5,87 AB	4,8 C	6,19 A	4,49 C			

B **Mean TKW (g)**

Entry	2005/6	2006/7	2007/8	2008/9	2009/10	2010/11	2011/12	2012/13	2013/14	2014/15	2015/16	Mean
Organic												
OQ		43,9	52,6	40,8	41,8	53,2	49,5	45,4	48,7	45,6	44,6	45,9
OY		41,5	54,4	37,7	40,8	53,4	48,3	46,6	48,4	47,9	43,5	45,5
OYQ		43,3	53,4	39,7	40,7	55,2	49,5	44,8	46,6	46,6	45,4	45,8
Mean		42,9 F	53,4 A	39,4 G	41,1 FG	53,9 A	49,1 B	45,6 DE	47,9 BC	46,7 CD	44,5 E	
Conventional												
CQ		37,9	50,9	36,7	36,4	51,5	49,6	42,5	41,2	45,5	41,9	43,5 AB**
CY		38,0	46,9	35,5	33,0	53,6	46,3	41,3	43,0	46,5	39,4	42,9 B
CYQ		38,9	48,4	35,8	36,0	54,1	48,7	43,5	42,4	45,4	41,2	44,0 A
Mean		38,3 E	48,8 B	36,0 EF	35,1 F	53,1 A	48,2 BC	42,4 D	42,2 D	45,8 C	40,8 D	

*Differing capital letters indicate significant differences at p<0,05 between CCP groups and reference varieties excl. 2005/06 and 2006/07 (ANOVA and HSD Posthoc Test)

**Differing capital letters indicate significant differences at p<0,05 between CCP groups over all available experimental seasons (ANOVA and HSD Posthoc Test)

***Differing capital letters indicate significant differences at p<0,05 between all experimental seasons (ANOVA and HSD Posthoc Test)

**** Differing capital letters indicate significant differences at p<0,05 between all experimental seasons in which the respective reference varieties were grown (ANOVA and HSD Posthoc Test)

Within year, populations were grown in single plots and only two or three samples were taken per plot making statistical comparisons contentious and the very conservative Kruskal-H Test yielded only rarely significant differences among CCP entries (Table A 2.14). However, there were large differences in yearly variance in CCP yields with especially large variances in earlier years (Figure 2.2).

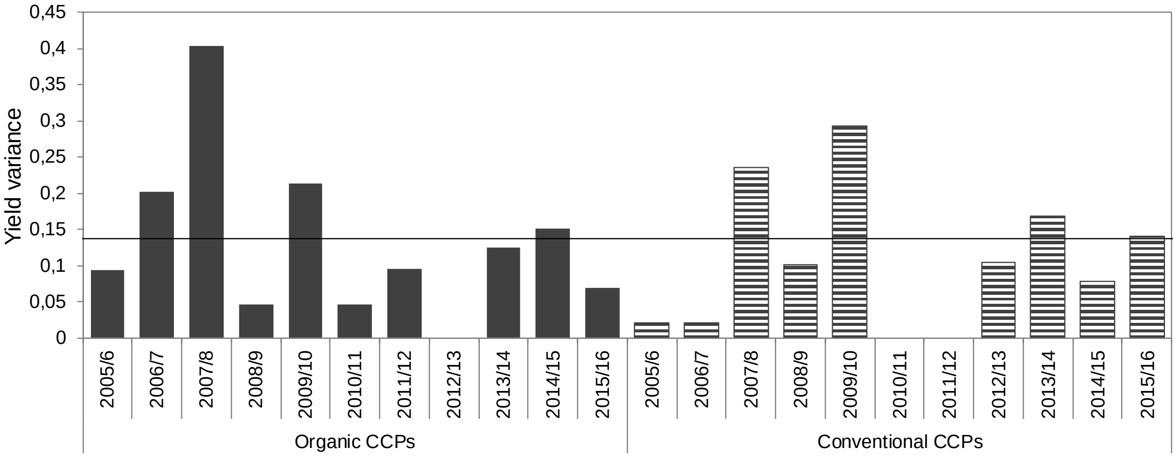

Figure 2.2: Yield variance of all organic and conventional CCPs per experimental season (solid line indicates the mean variance across management systems and over experimental seasons).

Comparing the mean performance of the CCP entries across the years resulted in some differences, especially among the YCCP entries, in both growing systems (Table A 2.14). Under organic management, OYQI achieved the highest yield of 7.8 t/ha in 2010/11, whilst OQI the lowest of 2.6 t/ha in 2013/14. Under conventional management, both the highest and lowest yield was observed in CYI with 6.4 t/ha in 2014/15 and 2.0 t/ha in 2006/07 (Table A 2.14). Under both management systems and over all experimental seasons, the QCCP entries tended towards the lowest yields, whilst the YQCCP entries generally achieved the highest yields. Under organic management, mean CCP entry yields ranged from 4.5 t/ha (OQI) to 5.0 t/ha in OYQII (Table 2.6, Table A 2.14). Yields under conventional management ranged from 4.3 t/ha (CQII) to 4.6 t/ha for CYQI, additionally a significant yield difference was found between the two parallel CY CCPs (Table 2.6, Table A 2.14).

Table 2.6: Mean yields across all available seasons except 2005/2006 for the CCP entries under organic and conventional conditions.

Entry	Organic	Conventional
QI	4,47 C*	4,30 B*
QII	4,66 BC	4,26 B
YI	4,75 ABC	4,27 B
YII	4,93 AB	4,56 A
YQI	4,95 AB	4,64 A
YQII	5,01 A	4,59 A

*Differing capital letters indicate significant differences at p<0,05 between CCP entries excl. 2005/06 (ANOVA and HSD Posthoc Test)

Year was also the single most important factor affecting TKW. The highest mean annual TKW was found in 2010/11 under organic conditions (53.9 g) and the lowest in 2009/10 under conventional conditions (35.1 g) (Table 2.5 B). While there were significant differences among entries and these interacted with year in both systems, the interaction F-values were 40 to 80 times smaller than for the year effects. In addition, under conventional management, a significant site effect on TKW was found for both the CCP entries and group; however, the F-values for the site effect (F=13) were more than 10 times lower than the year effect (F=186) on TKW and the interaction effects between CCP group and entry x site were not significant. A small significant effect of CCP group was found for TKW in the conventional system, but not in the organic. Under both management systems, significant interaction effects were found for CCP entry x year only, but not for CCP group x year (Table 2.5 B, Table A 2.13). There were significant differences among entries in both systems (Table A 2.13). The significance of the differences among mean TKW values of the organic CCP entries over all experimental seasons were due a difference between OYQI (46.5g) and OYQII (45.1g) with all other populations in between. Differences among the conventional entries were significant between CYII (42.5g) and CYQI (44.5g) with all other entries in between (data not shown).

2.3.3.4 Plant height and ear length

Over the three seasons that plant height and ear length were recorded yearly effects dominated for the CCP groups. As the CCPs were split into parallel populations only in 2006, data for these parameters were only available for all 12 CCP entries in the two experimental years of 2006/07 and 2014/15. Therefore, only CCP group data are presented (3 experimental years). For height, group differences were similar in both systems with YCCPs being shortest. Under organic management, the QCCPs and

YQCCPs did not differ significantly from one another, but under conventional management, the QCCPs were the tallest. These differences were evident in both the F_5 (2005/06) and F_{15} (2014/15), however, not in the F_6, under organic conditions (Table 2.7). Under organic management, both a significant year effect on stem length and a significant interaction effect between the CCP groups and year was found (Table A 2.16). Under conventional management, the site had the largest effect on plant height with F values more than three orders of magnitude greater than the year effect, however, no significant interaction effects were found between CCP groups x site or CCP groups x year (Table A 2.16). The insignificant interaction effect between both CCP group x year and CCP group x site supports the results that the stem length ranking of the conventional CCPs remained the same over all three experimental seasons (Table 2.7).

For ear length, in the F_5 (2005/06) the YQ CCPs had the significantly longest ears in both systems (8.7 and 8.0 cm organic versus conventional, respectively) (Table 2.7). The OY CCP was similar to the OQ CCP (both 8.2 cm), whilst the CY CCP was similar to the CYQ CCP (both 8.0 cm). In the F_6 (2006/07), under organic conditions the OY CCP was similar to the OYQ CCP (both 8.4 cm), whilst the OQ CCPs had the shortest ears (5.8 cm). Under conventional management, the CYQ and CQ had similar mean ear length (both 5.3 cm) and the CY CCP the longest ears with 5.9 cm. In the F_{15} (2014/15), no differences in ear length were evident amongst groups (Table 2.7). Over both management systems, the QCCPs tended towards the shortest ears, whilst the YCCPs and YQCCPs tended towards similarly longer ear length over all experimental seasons (Table 2.7).

Table 2.7: Mean plant height (cm) and standard deviation (SD) for organic and conventional CCP groups within each experimental season and over all experimental seasons.

	Mean plant height (cm)								**Mean ear length (cm)**							
Organic	**2005/06**	***SD***	**2006/07**	***SD***	**2014/15**	***SD***	**Mean**	***SD***	**2005/06**	***SD***	**2006/07**	***SD***	**2014/15**	***SD***	**Mean**	***SD***
OQ	98,7 a*	*13*	97,9	*15*	100,8 A*	*9*	98,9 A**	*12*	8,19 B*	*1,5*	5,77 B*	*1,3*	7,64	*1,0*	7,44 b**	*1,3*
OY	87,5 c	*11*	96,6	*19*	97,2 AB	*9*	92,1 B	*13*	8,17 B	*1,3*	6,84 A	*1,2*	7,52	*1,0*	7,67 ab	*1,2*
OYQ	95,8 b	*14*	101,7	*18*	95,8 B	*13*	97,3 A	*15*	8,69 A	*1,5*	6,78 A	*1,6*	7,43	*1,1*	7,90 a	*1,4*
Mean	94,0 B**	*14*	98,9 A	*17*	97,9 A	*11*			8,35 a**	*1,5*	6,46 c	*1,4*	7,53 b	*1,0*		
Conventional																
CQ	70,6 A*	*11*	72,5 A*	*15*	108,1 A*	*11*	79,8 A**	*12*	7,40 B*	*1,4*	5,34 B*	*1,2*	8,33	*1,2*	7,08 b**	*1,3*
CY	64,4 B	*9*	66,1 B	*13*	98,3 B	*13*	72,6 C	*12*	7,98 A	*1,2*	5,85 A	*1,6*	8,10	*1,0*	7,45 a	*1,3*
CYQ	68,8 A	*10*	68,6 AB	*15*	104,1 A	*16*	76,9 B	*13*	8,03 A	*1,4*	5,25 B	*1,4*	8,17	*1,3*	7,35 a	*1,3*
Mean	67,9 B**	*10*	69,0 B	*15*	103,5 A	*14*			7,80 b**	*1,4*	5,48 c	*1,4*	8,20 a	*1,2*		

*Differing small letters indicate significant differences at p<0,05 between between CCP groups within an experimental season (Kruskal H Test)

*Differing capital letters indicate significant differences at p<0,05 between CCP groups within an experimental season (ANOVA and Post-hoc HSD Test)

**Differing small letters indicate significant significant differences at p<0,05 between CCP groups over experimental seasons and between experimental seasons (Kruskal H Test)

**Differing capital letters indicate significant differences at p<0,05 between CCP groups over all experimental seasons and between experimental seasons (ANOVA and Post-hoc HSD Test)

2.3.4 Effect of site and/or generation and system on CCP yields and TKW

Prior to the experimental season of 2013/14, the conventional CCPs were grown at the field Saurasen, which is located about 500 m away from Teilanger and is characterized by lower soil quality (see 2.2 for details). Conventional overall mean yields on Saurasen were 4.3 t/ha and significantly lower in comparison to the mean yields achieved on the conventional field at Teilanger (4.8 t/ha, $P<0.001$) (Table A 2.13). These field differences make a direct comparison to the organically grown CCPs difficult. Significant interaction effects between the site and the conventional CCP entries were also found, indicating the differential yield response of conventional CPP entries depending on growing site and supporting the premise that direct comparison between the CCPs under differing management systems is challenging (Table A 2.13). Therefore, the two periods prior and post 2012/13 were compared in order to better elucidate the yield response of the CCPs under differing management.

At Saurasen, yields of the conventional CCP groups were analysed for five experimental seasons (2005/06-2009/10, i.e. F_5 – F_9), whilst for yields of the conventional CCP entries, four experimental seasons (2006/07-2009/10, i.e. F_6 – F_9) were used. Yield data included three experimental years at Teilanger (2013/14-2015/16, i.e. F_{13} – F_{15}) for both the conventional CCP groups and entries, which was compared to the yields of the organic CCPs during the same periods (Table 2.8). Mean yields of CCP attribute groups (Q, Y and YQ) were significantly different from one another in the F_5 – F_9 when the conventional CCPs were grown at Saurasen. The CCP Q group (4.3 t/ha) yielded significantly lower than the CCP Y (4.6 t/ha) and CCP YQ (4.8 t/ha) groups (Figure 2.3 A). These differences between CCP attribute groups were no longer present in the F_{13} – F_{15} when all CCPs, both organically and conventionally managed, were grown at Teilanger (Figure 2.3 B).

From 2006 to 2010 (F_5 – F_9,), a significant interaction effect was found between the experimental seasons (Year) and the CCP attribute groups (Group) ($F=2.3$; $p=0.03$). This interaction was, however, no longer significant when all CCPs were grown at Teilanger ($F=2.5$; $p=0.06$), indicating stability of CCP attribute group yield ranking over the three experimental seasons at the site (Table 2.8). There were no significant interactions between the CCP attribute groups and the management systems whether the conventional CCPs had been grown at Saurasen or at Teilanger. However, the significant three-way interaction effect between the CCP attribute group (Group), the environmental seasons (Year) and the management system (F=2.9; p=0.01) was no longer significant when all CCPs were grown at Teilanger in the F_{13} – F_{15} (Table 2.8).

Table 2.8: Mean squares (MS), F values and p values from analysis of variance for yield in the CCP attribute groups, CCP groups within system and CCP entries under organic and conventional management depending on the site. The analyses for the sites Saurasen (conv. CCPs) versus Teilanger (org. CCPs) were based on data from 2005/06 to 2009/10 (Figure 2.3 A). The analyses for the site Teilanger were based on data from 2013/14 to 2015/16 (Figure 2.3 B). System represents the management system (organic or conventional), Year represents the experimental seasons, CCP Attribute Group represents CCQ, CCY and CCYQ, excluding management history, the CCP Group represents CCP groups (CQ, CY, CYQ, OQ, OY and OYQ) and CCP entries represents the 12 CCP parallel populations (org. and conv.).

	CCP Attribute Group yield analysis					**CCP entry and group yield analysis**				
Site		**Df**	**MS**	**F value**	**p value**		**Df**	**MS**	**F value**	**p value**
Saurasen and Teilanger, F_5-F_9	Attribute Group	2	1,8	17,6	<0,001	CCP Entry	11	2,3	42,7	<0,001
	Year	4	28,1	278,6	<0,001	Year	3	33,3	619,7	<0,001
	System	1	21,8	216,0	<0,001	CCP Entry*Year	33	0,8	14,2	<0,001
	Group*Year	8	0,2	2,3	0,03	Residuals	36	0,1		
	Group*System	2	0,1	1,5	0,24					
	Year*System	4	4,6	45,7	<0,001	CCP Group	5	5,1	50.80	<0,001
	Group*Year*System	8	0,3	2,9	0,01	Year	4	28,1	278,6	<0,001
	Residuals	66	0,1			CCP Group*Year	20	1,1	11,2	<0,001
						Residuals	66	0,1		
		Df	**MS**	**F value**	**p value**		**Df**	**MS**	**F value**	**p value**
Teilanger, F_{13}-F_{15}	Attribute Group	2	0,3	2,3	0,11	CCP Entry	11	1,4	18,9	<0,001
	Year	2	10,4	80,2	<0,001	Year	2	10,4	139,3	<0,001
	System	1	13,5	104,3	<0,001	CCP Entry*Year	22	0,5	7,0	<0,001
	Group*Year	4	0,3	2,5	0,06	Residuals	24	0,1		
	Group*System	2	0,2	1,5	0,22					
	Year*System	2	3,6	27,9	<0,001	CCP Group	5	2,9	22,4	<0,001
	Group*Year*System	4	0,1	0,4	0,81	Year	2	10,4	80,2	<0,001
	Residuals	42	0,1			CCP Group*Year	10	0,9	6,7	<0,001
						Residuals	42	0,1		

The conventional CCP groups grown at Saurasen yielded significantly less than their organic CCP group counterparts at Teilanger (A). In addition, at Saurasen, the conventional CQ group (3.9 t/ha) yielded significantly lower than CYQ (4.3 t/ha), and the CY group (4.1 t/ha) was comparable to the CQ group. In contrast, the organic OYQ and OY group yielded significantly more (both 5.2 t/ha) in comparison to OQ (4.7 t/ha) (A). Overall, there was a significant interaction between experimental season and CCP group (F=11.2; p<0,001) (Table 2.8).

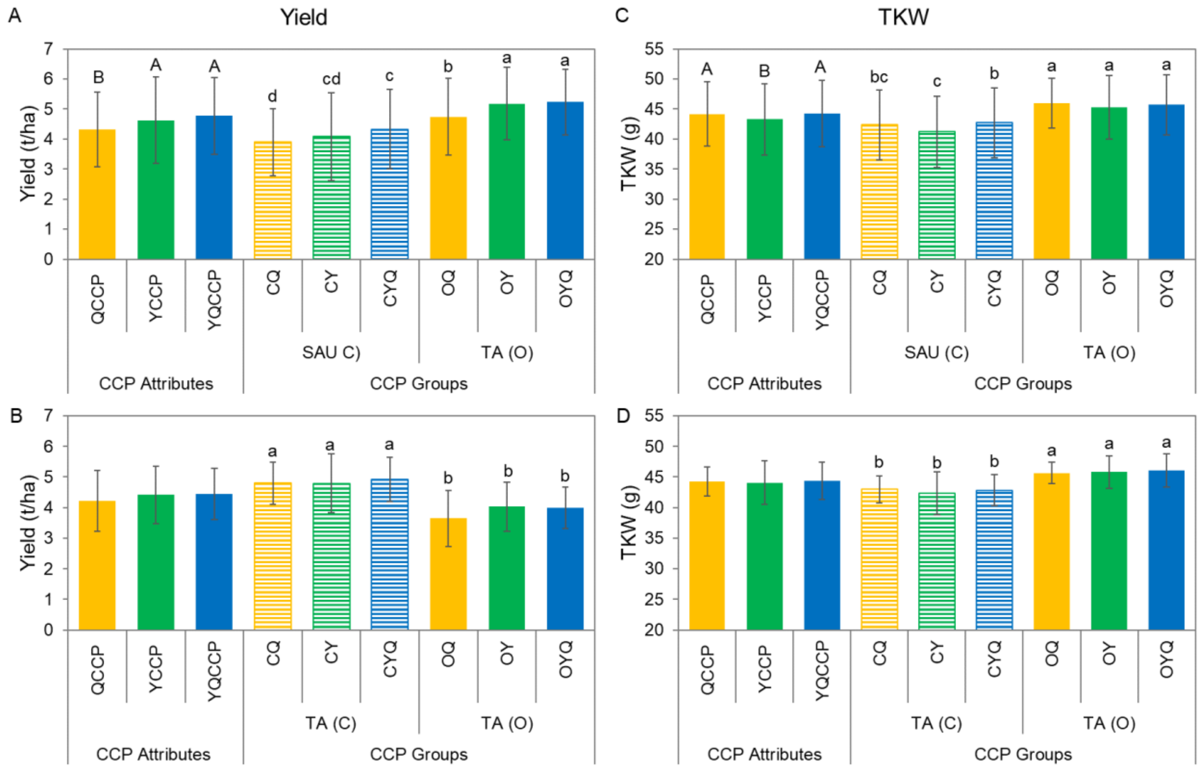

Figure 2.3 A: Mean yields (t/ha) of CCP attribute groups and CCP groups under organic (Teilanger=TA) and conventional (Saurasen=SAU) management for the five experimental seasons from 2005/06 to 2009/10. B: Mean yields (t/ha) of CCP attribute groups and CCP groups under organic (TA) and conventional (TA) management for the three experimental seasons from 2013/14 to 2015/16. C: Mean TKW (g) of CCP attribute groups and CCP groups under organic (Teilanger=TA) and conventional (Saurasen=SAU) management for seven experimental seasons from 2006/07 to 2012/13. D: Mean TKW (g) of CCP attribute groups and CCP groups under organic (TA) and conventional (TA) management for the three experimental seasons from 2013/14 to 2015/16. Differing capital letters indicate significant differences at $p<0.05$ within CCP attribute groups. Differing small letters indicate significant differences between CCP groups (ANOVA with Post-hoc HSD Test). Error bars indicate standard deviation. Conventional CCPs are indicated by bars with horizontal lines.

When grown on Teilanger from the F_{13} – F_{15}, the conventional CCP groups yielded significantly more than the organic CCP groups. However, neither the conventional nor the organic CCP groups differed significantly from each other within system (Figure 2.3 B). As before, CCP group and experimental season interacted in these later years ($F=6.7$; $p< 0.001$) (Table 2.8). The patterns for the single CCP entries were similar to the CCP groups with significant interaction effects between CCP entries and year within the two separate periods, however, no significant differences among parallel populations under either management system was found (data not shown).

As found for yield, differences among CCP groups for TKW were more pronounced in the F_6 – F_{12} when the conventional CCPs were grown at Saurasen (Figure 2.3 C, D).

The CCP YQ and Q attribute groups had significantly greater mean TKW compared to the CCP Y attribute group (44.2 g, 44.2 g and 43.3 g, respectively) from the F_6 to the F_{12} when the CCPs had been grown at both Saurasen and Teilanger. Such differences were no longer evident from the F_{13} – F_{15} when all CCPs were grown at Teilanger. However, in contrast to yields, TKW was consistently and significantly higher under organic management than under conventional management, independent of site (Figure 2.3 C, D, Table A 2.15).

For TKW, there was no significant interaction between CCP attribute group and year when the conventional CCPs were grown at Saurasen, however, this interaction became significant when all CCPs were grown at Teilanger from 2013/14 to 2015/16 (F=3.32; p=0.02) (Table A 2.15). Prior to 2013/14, the OQI (46.3g) and the CYQI (43.2g) population achieved the greatest mean TKW in comparison to the other CCP entries in their respective management system. At Teilanger, both the organic OYQI (47.7g) and the conventional CYQI (43.2g) populations achieved the greatest TKW values in their respective management system. Significant interaction effects between CCP entries and experimental seasons were found for the CCPs at both sites (Saurasen and Teilanger: F=1.7; p=0.03; Teilanger: F=4.8; p<0.001) (Table A 2.15).

2.4 Discussion

Across all years and under both management systems, the CCPYQs achieved the significantly highest yields, whilst the CCPQs the lowest, confirming a consistent influence of the parental genetics over time. Depending on year, the CCY populations yielded higher or lower than the CCYQ populations and only in 2011/12, after an extreme black frost event that had particularly affected the Y parents (Brumlop *et al*., 2017), did the OY populations yield lower than the OQ populations under organic management (no data available for conventional management). In that year, the OYQ populations yielded similarly to the OQ populations highlighting the compensatory capacity of the Q genetics to buffer the susceptibility of the Y genetics to black frost in the CCYQ population. Nevertheless, the strong selective effect of the black frost on the CCY genetics in early 2012 was a singular event and did not result in long-term changes of the YCCP populations general yield superiority as demonstrated by their higher yields in later years. The maintenance of the populations in large plots helped avoid genetic drift (Brumlop, 2017). Additionally, preliminary molecular analyses of the

CCPs over time suggest that this singular event did not change the overall genetic make-up of the populations (Weedon *et al*., unpublished).

Genetic effects on the populations were reflected in plant height in the F_5 and F_6, as well as in the F_{14} with the CCQ populations being consistently tallest and the CCY populations shortest, independent of management system. In contrast, differences in ear length were evident only in the F_5 and in the F_6 and were no longer found in the F_{14}. In the particularly dry season of 2013/14, yields were reduced in both systems, especially under organic management. With respect to diseases, the CCPs generally performed similarly to modern varieties despite their rather “old” genetics (release dates of the parents: 1934 to 2000) (Jones *et al*., 2010).

2.4.1 Foliar and foot diseases

Hovmøller *et al.* (2016) reported on three non-European stripe rust races present in Europe post-2011. The race “Warrior” was found to be widespread throughout Europe, whereas the races “Kranich” and “Triticale aggressive” tended to be more regionally spread and crop specific. Significant stripe rust presence was only recorded in Neu-Eichenberg from 2014 and it is assumed that at least two of the three races were present, namely “Warrior” and “Triticale aggressive”, as stipe rust was also found in the Triticale crops grown in Neu-Eichenberg in 2014 and 2015 (Weedon, personal observation).

The parental varieties of the CCPs were chosen mainly for their high yielding and baking qualities and performance under low-input conditions in Europe (Döring *et al*., 2015). It is not known whether foliar pathogen resistances were of great importance in parental varietal choice (Brumlop *et al*., 2017), although genetic distance between the parental varieties was carefully considered (Döring *et al*., 2015). Parental varieties, with apparent resistance to the local brown rust, had little to no resistances to the new stripe rust races present in 2014/15 and vice versa. The parental varieties Pastiche (Q), Renan (Q), Spark (Q), Wembley (Y) and to a degree Claire (Y), however, maintained low AUDPC values even with the change in the dominant foliar pathogen. Buerstmayr *et al.* (2014) reported on three quantitative trait loci (QTL) in the Austrian variety Capo, which were associated with both stripe and brown rust resistances and which were found at the same chromosome position, helping to explain the long-term resistance that Capo (varietal release in 1989) has managed to maintain. It is not known whether any of the CCP parental varieties hold these same QTLs, providing the CCPs with novel resistance sources to both stripe and brown rust. Nevertheless, the fact that all CCPs under both organic and conventional management had similar mean AUDPC and RAUDPC values over six experimental seasons in comparison to the pure line variety Capo demonstrates the ability of these heterogeneous wheat populations to compete with many commonly grown reference varieties.

Local selective forces may be very variable, especially with respect to biotic pressures. Brown rust in 2009 and stripe rust since 2014 varied strongly between fields, including large differences in disease severity on the reference varieties. While in 2009, the distance between the organic and conventional field, soil and microclimatic conditions were large, since 2013 the CCPs have been growing in adjacent fields with similar soil quality and within one 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, disease was stronger in the organic field, whilst in 2016 AUDPC values were similar across fields (Figure 2.1).

Differences among CCP groups or parallel CCPs for AUDPC ranking were rare. Only the conventional CY group displayed significantly higher foliar pathogen incidence in comparison to the CYQ group. It could be that the greater genetic diversity present in the YQ populations (crossing of all 20 parents) resulted in greater pathogen resistance variation and diversity, improving the adaptive capacity and resilience of the YQCCPs to their environment. However, the organic CCP groups did not follow the same trend. Depending if epidemics are singular or recurrent events, they may or may not affect the population genetic composition over time though. Evidence for poorer adaptation to stripe rust was observed in a CCYQ population that had been cultivated in Hungary from 2005 to 2013 (Chapter 4). In order to fully understand the differences found between the CCPs and their parallel populations, molecular analyses to look at changes in resistance gene frequencies between the CCPs in each management system and over time will be necessary. Overall the CCPs display advantages of increased intra-specific diversity with positive effects on foliar pathogen reduction and tolerance similar to what has been reported in other studies (Smithson & Lenne, 1996; Finckh *et al*., 2000; Finckh, 2008; Newton *et al*., 2009; Ratnadass *et al*., 2012).

2.4.2 Yields

Yields of the conventional CCPs were found to be significantly lower than the organic CCPs when the conventional CCPs were grown at Saurasen. Since 2013/14, the conventional CCPs have also been grown at Teilanger and have achieved higher overall mean yields in comparison to the organically managed CCPs. There was no significant interaction effect found between the CCP attribute group and management system at either site, indicating that there was not a CCP group more suited to a specific system and that generally, the YQCCP and YCCP groups tended to be higher yielding under both management systems and in both sites. This is in line with the expectations of the parental variety selection, particularly as the CCPQs were created on the basis of parents selected for high baking quality and not yield. There were, however, also significant interactions between CCP group, CCP entries and experimental seasons under both organic and conventional management, indicating 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 was reported by Brumlop *et al*. (2017), the extreme winterkill in the experimental year of 2011/12, resulted in the OQ CCPs out-yielding the OY CCPs due to their parental heritage. Similar results were found for the organic CCPs during the 2011/12 experimental year with the OYQ and OQ CCP groups achieving greater yields in comparison to the OY group. The reference varieties Achat and Capo out yielded all CCPs due to their good winter hardiness (Brumlop *et al*. 2017). These results are in contrast to the experimental year of 2014/15, which was characterised by extreme drought. In this year, both the organic and the conventional YCCP groups out yielded both the YQCCP and QCCP groups, most likely due the more modern parental variety genetics found in the YCCP groups. Yields of the parental varieties in 2014/15 showed a similar yield ranking pattern confirming the effects of parental genetic background in yield performance under these particular environmental conditions. Under organic management, the organic CCPs all out-yielded the reference varieties Achat and Capo. Similar results were reported by

Danquah & Barrett (2002b), whereby three composite cross barley generations out-yielded the well-known reference variety Atem in the experimental year of 1992, characterised by drought. However, under conventional management, the reference variety Capo had significantly greater yields in comparison to all conventionally managed CCPs. This most likely reflects the parental selection for varieties that are best suited to low-input conditions in Europe.

Jones *et al*. (2010) reported that the more modern parental varieties, mainly found in the CCY and CCYQ populations, yielded better under conventional conditions. This was found to be the case for the CCP groups under conventional conditions as well. The significant differences in yielding ability and stability between the two CY parallel populations may indicate differing selection pressures. The various CCPs were also analysed for yield stability (Chapter 3). The CYI population reacted much more strongly to environmental effects than all other conventional CCPs and it emerged as considerably less stable compared to CYII. Taken together, these results are strongly suggestive that the two conventional CY CCPs may have undergone divergent evolutions over time. Differentiation among populations and between generations can mainly be attributed to environmental pressures, plant-plant competition and plant-pathogen co-evolution, which makes specific selective forces difficult to pinpoint in this respect, however (Enjalbert *et al.,* 1998). Weather conditions were the same for each population in each generation, but localized differing environmental conditions such as soil quality (particularly challenging for the conventional CCPs prior to 2013/14), disease pressure and nutrient availability might have occurred. However, significant differences between parallel populations were based on few repeated samples within plots without true replications. Yield comparisons in replicated trials under conventional and organic conditions are under way to test all 12 CCPs for potential differences due to growing system and divergent evolution. Molecular studies will be necessary to confirm divergent evolutionary trajectories.

Overall, genetic effects of the parental varieties are still visible in terms of mean yield over all experimental seasons and management systems. In the comparison of yield variance between the CCPs within each management system, there seems to be a tendency towards lower yield variation in later generations, but more experimental seasons are necessary in order to confirm this trend. However, the trend towards lower yield variance in later generations in the conventionally managed CCPs is most likely coupled with the significant site effect. The CCPs under organic conditions were comparable to the reference varieties Achat and Capo, and achieved better yields mainly in experimental years that were characterised by drought or heat stress. In experimental seasons characterised by colder climatic conditions (2009/10 and 2011/12), the organic reference varieties had greater yields, which is likely to be indicative of their better overwintering capacity in comparison to the CCPs.

2.4.3 Thousand Kernel Weight

TKW tended to be greater in the CCQ and CCYQ populations and no significant interaction was found between the CCP attribute groups and the management system. Particularly under the poorer conditions of Saurasen, the CY group had significantly lower TKW in comparison to the CYQ group and these results were consistent when comparing the mean TKW of conventional CCP groups across all experimental seasons. The significant interaction effect between the CCP entries and experimental years indicates the plasticity of the individual CCP entries under differing experimental seasons and the fact that heritability of seed size is generally considered to be low (Silvertown, 1989). Differences between CCP groups are most likely due to parental genetic background, as well as inherent parental variety performance under differing management systems.

A number of studies report on the variability among composite cross populations with regard to agronomic and morphological traits and further support the fact that many of the composite cross populations are not evolving in parallel (Goldringer *et al*., 2001b; Stange *et al*., 2006; Steffan, 2008). The results of this present study also report some significant differences among populations and between generations for the phenotypic traits recorded, however, confirming divergent evolutions of the CCPs in Neu-Eichenberg is challenging due to rank inconsistencies within and across all experimental years. However, the significant differences between the conventional CYI and CYII populations for yield presents a possible example of a divergent trajectory between two genetically similar populations. The separate evolution for the agronomic trait of yield between parallel populations could be accredited to differing initial genetic variation, but would essentially indicate that these parallel populations had been subjected to different selective forces and as such had evolved separately, even within such a short time period. Local selection pressures contribute to separate population evolutions and changes in disease resistances, earliness and agronomic traits between populations are brought about by the biotic and physical environmental selection pressures of a growing site (Goldringer *et al*., 2001a).

2.5 Conclusion

Most of the differences found between the CCPs can be traced back to their parental genetics, as well as to the differing agronomic performance of these parental genes under differing management systems. Initial genetic variance between the CCPs cannot be overlooked and the apparently high outcrossing rate often found in heterogeneous populations (Enjalbert *et al*., 1998; Goldringer *et al*., 2001a; Finckh *et al*., 2009) 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 varieties in terms of foliar pathogen resistances and agronomic performance, particularly under organic conditions, and represent great germplasm potential capable of adaptation to changing environmental conditions. In order to understand the variation of evolutionary trajectories even in parallel populations, it is important to keep in mind that competition between genotypes within an heterogeneous population is a selective force itself, which is again influenced by changes in the genetic structure of the population, as well as environmental conditions (Le Boulc'h *et al*., 1994; Wolfe *et al*., 2006). This illustrates the complexity of heterogeneous population evolution, especially as many factors are involved in their evolutions from parental variety genetics, pathogen selection pressure, initial population genetic variance, environmental conditions and the selective force of the populations themselves through the various mechanisms of competition or cooperation (induced resistance), for example. For further in-depth studies molecular analyses should help to track and give insight into the separate evolutions of these CCPs within and between systems and over the generations, as was shown for early generations of these CCPs in the UK (Knapp *et al*., 2013).

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Appendix

Table A 2.9: Description of the development of the composite cross wheat populations growing in Neu-Eichenberg (C=Conventional, O=Organic, YQ=Yield x Quality, Q = Quality and Y = Yield).

Generation	Year	Composite cross wheat population development in Witzenhausen											
F_5*	2005/06	CYQ		OYQ		CQ		OQ		CY		OY	
F_6**	2006/07	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_7	2007/08	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_8	2008/09	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_9	2009/10	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{10}	2010/11	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{11}	2011/12	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{12}	2012/13	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{13}	2013/14	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{14}	2014/15	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII
F_{15}	2015/16	CYQI	CYQII	OYQI	OYQII	CQI	CQII	OQI	OQII	CYI	CYII	OYI	OYII

*YQ, Q and Y populations were split into organic (O) and conventional (C).

** CYQ, OYQ, CQ, OQ, CY, and OY were split into two parallel populations (I and II).

Table A 2.10: Mean RAUDPC values (Relative Area under the Disease Progress Curve) and standard deviation (SD) for the CCPs and reference varieties under organic management from 2008/09 to 2015/16.

RAUDPC for organically managed CCPs and varieties																		
Group	**Mean Group RAUDPC**	**SD**	**Entry**	**2008/09**	**SD**	**2009/10**	**SD**	**2010/11**	**SD**	**2013/14**	**SD**	**2014/15**	**SD**	**2015/16**	**SD**	**Mean RAUDPC**	**SD**	**Mean CCP RAUDPC**
			Achat	0,61	0,16	0,04	0,05	0,06	0,06	0,04	0,01	0,14	0,03	0,17	0,02	0,20 a*	0,25	-
			Akteur	-		-		-		0,07	0,03	0,23	0,07	-		-		-
			Astardo	-		0,02	0,04	0,04	0,03	-		-		-		-		-
			Batis	0,38	0,22	0,03	0,05	0,05	0,04	-		-		-		-		-
			Bussard	0,58	0,26	-		-		-		-		-		-		-
			Butaro	-		-		-		0,02	0,00	0,07	0,01	0,12	0,01	-		-
			Capo	0,44	0,14	0,01	0,02	0,04	0,03	0,02	0,00	0,11	0,03	0,15	0,03	0,14 abc	0,19	-
			Naturastar	-		-		-		0,26	0,05	0,18	0,03	-		-		-
			Scaro	-		-		-		0,02	0,00	0,25	0,05	-		-		-
			Skagen	-		0,02	0,03	0,06	0,06	-		-		-		-		-
			Tamaro	0,06	0,05	0,04	0,04	0,03	0,02	-		-		-		-		-
			Wiwa	-		-		-		-		0,10	0,02	0,14	0,03	-		-
OQ	0,14	0,17	OQI	0,48	0,19	0,08	0,11	0,03	0,02	0,03	0,00	0,18	0,09	0,22	0,04	0,16 ab	0,20	0,16 bc
			OQII	0,27	0,19	0,08	0,06	0,06	0,06	0,02	0,00	0,14	0,03	0,16	0,03	0,12 bc	0,13	0,12 abc
OY	0,12	0,14	OYI	0,20	0,15	0,04	0,03	0,06	0,06	0,04	0,00	0,16	0,02	0,17	0,04	0,09 c	0,10	0,09 c
			OYII	0,42	0,17	0,07	0,08	0,07	0,06	0,04	0,01	0,14	0,02	0,23	0,03	0,15 ab	0,17	0,15 ab
OYQ	0,15	0,17	OYQI	0,44	0,16	0,08	0,06	0,09	0,07	0,03	0,01	0,15	0,02	0,14	0,02	0,16 ab	0,17	0,16 a
			OYQII	0,40	0,17	0,05	0,06	0,04	0,03	0,04	0,01	0,17	0,03	0,26	0,05	0,13 bc	0,17	0,13 bc

Differing small letters indicate significant differences at p<0,05 between CCP entries and CCP groups over all experimental seasons (Kruskal H test)

*Differing small letters indicate significant differences at p<0,05 between entries over all experimental seasons (Dunnett's Modified Tukey-Kramer Test)

Table A 2.11: Mean RAUDPC values (Relative Area under the Disease Progress Curve) and standard deviation (SD) for the CCPs and reference varieties under conventional management from 2008/09 to 2015/16.

RAUDPC for conventionally managed CCPs and varieties

Group	Mean Group RAUDPC	SD	Entry	2008/09	SD	2009/10	SD	2010/11	SD	2013/14	SD	2014/15	SD	2015/16	SD	Mean RAUDPC	SD
			Achat	-		-		-		0,09	0,01	0,05	0,01	0,19	0,02	-	
			Akteur	-		-		-		0,36	0,04	0,13	0,03	-		-	
			Batis	-		0,10	0,12	0,07	0,09	-		-		-		-	
			Butaro	-		-		-		0,03	0,00	0,02	0,00	0,07	0,01	-	
			Capo	0,26	0,19	0,26	0,16	0,08	0,07	0,04	0,01	0,03	0,01	0,12	0,03	0,16 ab	0,16
			Herrmann	0,03	0,03	-		-		-		-		-		-	
			Impression	0,01	0,01	0,04	0,06	0,02	0,01	-		-		-		-	
			Skagen	-		0,05	0,07	0,03	0,03	-		-		-		-	
			Wiwa	-		-		-		-		-		0,08	0,01	-	
CQ	0,16 a	0,16	CQI	0,32	0,17	0,10	0,14	0,08	0,07	0,10	0,01	0,07	0,02	0,16	0,03	0,14 ab	0,15
			CQII	0,33	0,21	0,20	0,17	0,10	0,10	0,06	0,01	0,07	0,02	0,16	0,03	0,18 a	0,17
CY	0,17 a	0,17	CYI	0,30	0,21	0,19	0,17	0,07	0,05	0,09	0,03	0,08	0,02	0,17	0,03	0,16 ab	0,16
			CYII	0,28	0,21	0,25	0,19	0,11	0,08	0,12	0,02	0,05	0,01	0,16	0,02	0,19 a	0,17
CYQ	0,13 b	0,14	CYQI	0,20	0,18	0,12	0,14	0,07	0,06	0,10	0,03	0,08	0,02	0,16	0,02	0,12 b	0,12
			CYQII	0,33	0,20	0,07	0,10	0,09	0,07	0,15	0,05	0,06	0,01	0,15	0,03	0,13 ab	0,15

Differing small letters indicate significant differences at $p<0,05$ between CCP groups and entries over all experimental seasons (Dunnett's Modified Tukey-Kramer Test)

Table A 2.12: Combined foot disease index (DI), DI for *Pseudocercosporella herpotrichoides* (Pseudo.), DI for *Fusarium* spp. and DI for *Rhizoctonia cerealis* (Rhizoc.) within each experimental season for the a) organic and b) conventional CCPs and reference varieties. Mean foot disease index over all 6 experimental seasons is also given.

Entry	2008/09	2009/10	2010/11	2013/14	2014/15	2015/16	Mean DI (combined)	2008/09	2009/10	2010/11	2013/14	2014/15	2015/16	Mean DI (Pseudo.)	2008/09	2009/10	2010/11	2013/14	2014/15	2015/16	Mean DI (Fusarium)	2008/09	2009/10	2010/11	2013/14	2014/15	2015/16	Mean DI (Rhizoc.)
a) Organic																												
Achat	29,1	33,7	26,8	20,7	14,6	29,1	25,7	21,5	19,8	10,1	8,7	4,3	27,1	15,2	6,9	13,8	16,7	11,3	9,6	1,3	9,9	0,8	0,0	0,0	0,8	0,7	0,7	0,5
Akteur	-	-	-	22,6	9,0	-	-	-	-	-	8,5	2,1	-	-	-	-	-	13,5	6,2	-	-	-	-	-	0,6	0,7	-	-
Astardo	-	36,6	25,8	-	-	-	-	-	29,0	9,2	-	-	-	-	-	7,6	15,8	-	-	-	-	-	0,0	0,8	-	-	-	-
Batis	28,4	30,5	21,3	-	-	-	-	18,2	14,0	6,9	-	-	-	-	9,8	16,6	14,4	-	-	-	-	0,4	0,0	0,0	-	-	-	-
Bussard	22,0	-	-	-	-	-	-	15,4	-	-	-	-	-	-	6,1	-	-	-	-	-	-	0,5	-	-	-	-	-	-
Butaro	-	-	-	17,7	11,4	31,6	-	-	-	-	5,7	3,0	27,1	-	-	-	-	11,8	8,0	4,2	-	-	-	-	0,2	0,4	0,3	-
Capo	20,4	21,7	20,6	21,2	18,6	42,6	24,2	15,5	12,4	9,0	8,6	11,5	36,3	15,6	4,8	9,1	11,6	12,3	6,8	5,9	8,4	0,0	0,2	0,0	0,3	0,3	0,4	0,2
Naturastar	-	-	-	21,7	12,9	-	-	-	-	-	5,7	2,4	-	-	-	-	-	15,6	7,7	-	-	-	-	-	0,5	2,8	-	-
Scaro	-	-	-	24,7	12,9	-	-	-	-	-	13,6	2,3	-	-	-	-	-	10,3	8,6	-	-	-	-	-	0,8	1,9	-	-
Skagen	-	23,6	23,9	-	-	-	-	-	9,9	7,9	-	-	-	-	-	13,6	15,9	-	-	-	-	-	0,2	0,0	-	-	-	-
Tamaro	16,7	29,5	19,2	-	-	-	-	7,3	16,9	8,4	-	-	-	-	8,9	12,0	10,8	-	-	-	-	0,6	0,6	0,0	-	-	-	-
Wiwa	-	-	-	-	21,1	28,1	-	-	-	-	-	3,5	17,4	-	-	-	-	-	17,6	9,5	-	-	-	-	-	0,0	1,3	-
OQI	36,9	28,7	31,6	21,8	24,2	29,1	28,7	26,1	16,5	11,8	10,9	8,9	12,1	14,4	8,0	11,2	18,4	10,9	15,3	17,0	13,4	2,8	1,1	1,5	0,0	0,0	0,0	0,9
OQII	21,6	15,0	22,9	12,5	31,5	24,7	21,4	11,4	3,6	4,2	1,7	17,7	13,1	8,6	9,7	11,4	18,8	10,8	12,9	10,8	12,4	0,6	0,0	0,0	0,0	0,8	0,8	0,4
OYI	37,0	15,6	35,4	11,1	37,9	21,7	26,4	24,5	0,6	10,4	0,0	19,7	8,8	10,7	11,5	14,4	25,0	11,1	18,2	12,9	15,5	1,0	0,6	0,0	0,0	0,0	0,0	0,3
OYII	53,6	19,9	21,8	16,7	20,2	41,3	28,9	40,6	10,2	7,3	2,5	7,3	22,4	15,0	11,5	9,1	14,5	14,2	12,1	18,9	13,4	1,6	0,6	0,0	0,0	0,8	0,0	0,5
OYQI	42,9	22,3	26,5	22,1	19,2	41,8	29,1	27,2	15,2	7,6	11,0	5,8	25,7	15,4	13,0	7,0	18,9	11,0	13,3	16,0	13,2	2,7	0,0	0,0	0,0	0,0	0,0	0,5
OYQII	19,4	16,2	24,3	22,9	21,0	38,9	23,8	10,6	9,6	9,0	9,7	0,8	25,4	10,9	8,8	5,9	11,8	13,2	16,1	13,5	11,5	0,0	0,7	3,5	0,0	4,0	0,0	1,4
b) Conventional																												
Achat	-	-	-	30,9	18,6	28,0	-	-	-	-	24,4	8,2	17,5	-	-	-	-	6,5	9,3	10,4	-	-	-	-	0,0	1,1	0,0	-
Akteur	-	-	-	25,4	14,5	-	-	-	-	-	18,0	0,8	-	-	-	-	-	7,4	10,5	-	-	-	-	-	0,0	3,2	-	-
Batis	-	19,4	17,4	-	-	-	-	-	12,9	9,8	-	-	-	-	-	6,5	5,2	-	-	-	-	-	0,0	2,4	-	-	-	-
Butaro	-	-	-	44,7	9,3	41,1	-	-	-	-	41,3	1,2	20,3	-	-	-	-	3,3	6,5	19,3	-	-	-	-	0,0	1,6	1,6	-
Capo	45,9	30,7	19,2	42,6	12,0	54,7	34,2	43,2	27,6	8,2	40,2	4,3	36,9	26,7	2,7	3,1	9,9	1,6	5,4	17,8	6,8	0,0	0,0	1,0	0,8	2,3	0,0	0,7
Herrmann	24,4	-	-	-	-	-	-	23,3	-	-	-	-	-	-	1,1	-	-	-	-	-	-	0,0	-	-	-	-	-	-
Impression	39,0	14,8	23,9	-	-	-	-	36,0	9,3	12,1	-	-	-	-	1,3	5,2	9,8	-	-	-	-	1,8	0,3	1,9	-	-	-	-
Skagen	-	15,3	15,5	-	-	-	-	-	6,1	7,4	-	-	-	-	-	8,8	8,2	-	-	-	-	-	0,3	0,0	-	-	-	-
Wiwa	-	-	-	-	-	39,5	-	-	-	-	-	-	19,7	-	-	-	-	-	-	18,5	-	-	-	-	-	-	1,3	-
CQI	39,5	18,8	31,4	71,1	11,4	40,4	35,4	39,5	10,0	14,3	68,0	3,0	22,6	26,2	0,0	8,1	12,1	3,1	6,1	17,4	7,8	0,0	0,6	5,0	0,0	2,3	0,4	1,4
CQII	41,8	21,7	22,1	35,6	15,4	38,2	29,1	40,8	13,3	7,4	28,8	0,0	19,7	18,3	1,1	8,3	9,6	6,8	14,0	13,1	8,8	0,0	0,0	5,1	0,0	1,5	5,4	2,0
CYI	46,3	17,4	22,6	27,4	12,1	46,8	28,8	45,7	9,9	15,3	22,6	5,7	32,5	22,0	0,6	7,0	5,6	4,8	3,6	14,3	6,0	0,0	0,6	1,6	0,0	2,9	0,0	0,8
CYII	45,6	17,0	20,0	24,3	8,3	54,2	28,2	45,6	4,8	9,3	17,6	2,3	38,9	19,7	0,0	12,2	10,7	5,1	6,1	15,4	8,3	0,0	0,0	0,0	1,5	0,0	0,0	0,2
CYQI	47,2	20,0	31,8	36,7	21,1	50,6	34,6	45,6	7,3	17,4	33,6	8,6	29,1	23,6	1,7	11,8	5,3	3,1	12,5	21,6	9,3	0,0	0,9	9,1	0,0	0,0	0,0	1,7
CYQII	48,1	26,0	27,9	40,3	8,3	42,2	32,1	46,8	14,7	8,6	36,1	0,0	24,5	21,8	0,0	11,3	15,7	3,5	8,3	17,7	9,4	1,3	0,0	3,6	0,7	0,0	0,0	0,9

Table A 2.13: Mean squares (MS), F values and p values from analysis of variance for yield in the CCP entries, groups and reference varieties under organic and conventional management and for Thousand Kernel Weights (TKW) of the CCPs. Year represents the experimental seasons, Entry represents the CCP parallel populations and reference varieties, Group represents CCP groups and reference varieties and Site represents the two conventional sites (Saurasen and Teilanger).

	CCP entry and group yield analysis				**CCP entry and reference yield analysis**				**CCP entry and group TKW analysis**			
Organic	**DF**	**MS**	**F value**	**P value**	**DF**	**MS**	**F value**	**P value**	**Df**	**MS**	**F value**	**p value**
Entry	5	0,7	8,2	<0,001	7	0,5	4,7	<0,001	5	4,5	2,4	0,05
Year	8	23,1	273,3	<0,001	7	28,5	263,0	<0,001	9	156,5	84,1	<0,001
Entry*Year	40	0,2	2,2	0,01	49	0,3	2,3	<0,01	45	3,6	2,0	0,02
Residuals	42	0,1			48	0,1			42	1,9		
Group	2	1,3	11,7	<0,001	4	0,7	5,3	<0,001	2	1,3	0,5	0,60
Year	9	21,3	189,6	<0,001	7	28,5	214,4	<0,001	9	156,5	60,1	<0,001
Group*Year	18	0,2	2,0	0,02	28	0,3	2,3	<0,01	18	4,1	1,6	0,09
Residuals	72	0,1			72	0,1			72	2,6		
Conventional	**DF**	**MS**	**F value**	**P value**	**DF**	**MS**	**F value**	**P value**	**Df**	**MS**	**F value**	**p value**
Entry	5	0,4	10,0	<0,001	6	1,1	23,3	<0,001	5	8,2	3,6	<0,01
Site	1	7,9	197,5	<0,001	1	0,8	16,1	<0,001	1	28,9	12,7	<0,001
Year	6	16,1	400,9	<0,001	4	5,9	125,7	<0,001	8	423,3	185,5	<0,001
Entry*Site	5	0,2	4,6	<0,01	6	0,3	6,7	<0,001	5	3,3	1,5	0,22
Entry*Year	30	0,2	5,3	<0,001	24	0,2	3,8	<0,001	40	4,5	2,0	<0,01
Residuals	30	0,0			28	0,0			54	2,3		
Group	2	0,7	7,0	<0,01	3	1,9	15,9	<0,001	2	11,2	3,7	0,03
Site	1	5,8	56,3	<0,001	1	0,8	6,4	0,02	1	28,9	9,6	<0,01
Year	7	14,5	140,6	<0,001	4	5,9	49,6	<0,001	8	423,3	140,5	<0,001
Group*Site	2	0,2	1,8	0,18	3	0,4	2,9	0,04	2	2,1	0,7	0,50
Group*Year	14	0,2	2,1	0,02	12	0,2	1,3	0,25	16	5,2	1,7	0,06
Residuals	57	0,1			46	0,1			84	3,0		

Table A 2.14. Mean yields (t/ha) in each experimental season for each CCP. Mean entry yield (t/ha) over all experimental seasons (excl. 2005/06) are reported.

Entry	**2005/6**	**2006/7**	**2007/8**	**2008/9**	**2009/10**	**2010/11**	**2011/12**	**2012/13**	**2013/14**	**2014/15**	**2015/16**	**Mean entry yield (t/ha)**
Organic												
OQI	5,85	2,78	5,57	4,76	5,09	7,24	4,18		2,61	4,83	3,87 b	4,47 C*
OQII		2,69	5,27	5,22	6,13	7,36	3,94		2,66	4,57	4,38 ab	4,66 BC
OYI	6,29	3,51	5,76	5,21	5,89	7,18	3,41		3,16	4,96	4,25 ab	4,75 ABC
OYII		3,35	6,99	4,72	6,10	7,51	3,99		3,35	5,38	4,22 ab	4,93 AB
OYQI	5,62	3,59	6,28	4,93	6,13	7,76	3,91		3,43	4,29	4,59 a	4,95 AB
OYQII		3,78	6,45	5,00	6,43	7,52	4,31		3,25	5,10	3,99 b	5,01 A
Conventional												
CQI	4,98	2,29	3,26	5,02	4,33 bc			5,40	4,59	6,05	4,35	4,30 B*
CQII		2,24	3,70	4,90	3,91 c			5,52	4,49	5,98	4,58	4,26 B
CYI	5,30	1,95	3,62	5,60	3,87 c			6,09	4,67	6,42	3,58	4,27 B
CYII		2,04	3,13	5,64	4,84 ab			6,03	4,90	6,34	4,44	4,56 A
CYQI	5,16	2,29	4,47	5,32	4,67 ab			5,69	5,38	5,68	4,53	4,64 A
CYQII		2,18	3,92	5,56	5,24 a			6,17	4,18	6,31	4,51	4,59 A

Differing small letters indicate significant differences between CCP entries within one experimental season at p<0,05 (Kruskal-H Test)

*Differing capital letters indicate significant differences at p<0,05 between CCP entries excl. 2005/06 (ANOVA and HSD Posthoc Test)

Table A 2.15: Mean squares (MS), F values and p values from analysis of variance for TKW in the CCP attribute groups, CCP groups and CCP entries under organic and conventional management depending on the site. The analyses for the sites Saurasen (conv. CCPs) and Teilanger (org. CCPs) were based on data from 2006/07 to 2012/13 (Figure 2.3 C). The analyses for the site Teilanger were based on data from 2013/14 to 2015/16 (Figure 2.3 D). Year represents the experimental seasons, CCP Attribute Group represents CCQ, CCY and CCYQ and excluding management history, the CCP Group represents CCP groups (CQ, CY, CYQ, OQ, OY and OYQ) and CCP entries represents the 12 CCP parallel populations (org. and conv.).

	CCP Attribute Group TKW analysis					CCP entry and group TKW analysis				
Site		**Df**	**MS**	**F value**	**p value**		**Df**	**MS**	**F value**	**p value**
Saurasen and Teilanger	CCP Group	2	12,5	5,06	0,01	CCP Entry	11	42,30	18,36	<0,001
	Year	6	543,0	219,64	<0,001	Year	6	543,00	235,54	<0,001
	System	1	415,1	167,91	<0,001	CCP Entry*Year	66	3,90	1,69	0,03
	Group*Year	12	2,7	1,08	0,38	Residuals	48	2,3		
	Group*System	2	3,6	1,46	0,24					
	Year*System	6	12,8	5,20	<0,001	CCP Group	5	89,50	36,19	<0,001
	Group*Year*System	12	4,6	1,85	0,05	Year	6	543,00	219,64	<0,001
	Residuals	90	2,5			CCP Group*Year	30	5,50	2,21	0,01
						Residuals	90	2,50		
		Df	**MS**	**F value**	**p value**		**Df**	**MS**	**F value**	**p value**
Teilanger	CCP Group	2	0,7	0,24	0,78	CCP Entry	11	19,47	12,13	<0,001
	Year	2	95,8	31,77	<0,001	Year	2	95,84	59,72	<0,001
	System	1	173,4	57,46	<0,001	CCP Entry*Year	22	7,66	4,77	<0,001
	Group*Year	4	10,0	3,32	0,02	Residuals	36	1,60		
	Group*System	2	1,0	0,32	0,73					
	Year*System	2	25,8	8,55	<0,001	CCP Group	5	35,35	11,72	<0,001
	Group*Year*System	4	2,3	0,76	0,56	Year	2	95,84	31,77	<0,001
	Residuals	54	3,0			CCP Group*Year	10	10,08	3,34	0,001
						Residuals	54	3,02		

Table A 2.16: Mean squares (MS), F values and p values from analysis of variance for stem length (cm) in the CCP groups under organic and conventional management. Year represents the experimental seasons, Group represents CCP groups (CCQ, CCY and CCYQ) and site represents the two conventional sites (Saurasen and Teilanger).

System		Stem length (cm)			
		DF	**MS**	**F value**	**p value**
Organic CCPs	Group	2	4762	26,8	<0.001
	Year	2	2997	16,9	<0.001
	Group*Year	4	1548	8,7	<0.001
	Residuals	1161	178		
Conventional CCPs		**DF**	**MS**	**F value**	**p value**
	Group	2	4995	35,8	<0,001
	Site	1	257177	1840,9	<0,001
	Year	1	269	1,9	0,17
	Group*Year	2	95	0,7	0,51
	Group*Site	2	215	1,5	0,22
	Residuals	1161	140		

3. Heterogeneous winter wheat populations differ in yield stability depending on their genetic background and management system

Abstract

Twelve winter wheat composite cross populations (CCPs), based on three genetic backgrounds and maintained at the University of Kassel, Germany, under both organic and conventional management, were assessed for yield performance and yield stability in comparison to two modern pure line varieties over 6 to 8 experimental years. A number of stability parameters were chosen to represent both the static and dynamic concepts of stability in order to identify populations with either adaptation to specific environments or broad adaptation across environments. The genetic effects of the CCP parental varieties were clearly present when comparing CCP yield performance in both management systems. Compared to the pure line Capo, CCPs performed similarly under organic conditions, but considerably poorer under conventional conditions pointing to the adaptation of the parental materials to low input systems. CCPs with a broader genetic base achieved the greatest yield stability in comparison to CCPs based on fewer parents indicative of the buffering capacity of genetic diversity, particularly under more challenging environments. CCPs with a genetic background of high yielding parents reacted most strongly to the different environments and apparently diverged under conventional management over time. Possibilities to improve CCPs through the addition of new genetic material while maintaining the benefits of diversity to achieve higher and more stable yields, particularly in light of increasingly unpredictable climatic conditions are discussed.

3.1 Introduction

Increasingly uncertain climatic conditions threaten the security and stability of agricultural systems (Østergård et al., 2009; Döring et al., 2011) and a better understanding of genotype x environment interactions (GEI) is needed to shift the agricultural focus from manipulating environments to grow crops to creating crops that fit into the environment (Østergård et al., 2009; Lammerts van Bueren & Myers, 2011). Environmental interactions also include the effects of agricultural management systems (Lammerts van Bueren & Myers, 2011). GEIs play a pivotal role in assessing the yield stability of crops and the challenge of changing climatic conditions necessitates that new crop cultivars should have broad adaptability, stable agronomic performance over a range of environments and management systems and generally high yields (Akcura *et al*., 2006). Yield stability is an important selection criterion in varieties and plant material suited for organic and low-input agricultural systems, particularly due to the challenging environmental conditions found in these systems (Annicchiarico & Filippi, 2007; Döring *et al*., 2012; Dawson & Goldringer, 2012). Genotypes with better yield stability may have an advantage under these challenging conditions (Annicchiarico, 2002; Lammerts Van Bueren et al., 2011), particularly as GEIs are considered “a common limiting factor when stable genotypes are required” (Raggi *et al*., 2017).

A number of yield stability parameters are available in order to measure stability in crops. Yield stability is divided into a couple of concepts, the main two being the concept of static stability (Type I, homoeostasis, biological) (Becker & Leon, 1988) and dynamic stability (Type II, agronomic) (Lin *et al*., 1986). The static stability concept refers to genotypes, which generally tend to yield similarly across all environments and are thus relatively better yielding in unfavourable environments (Stagnari *et al*., 2013). According to Simmonds (1991), genotypes that show high stability in the static sense may be better suited to organic and low-input agricultural systems. Static stability parameters enable the selection of genotypes better suited to marginal environments characterized by high environmental stresses, which makes this stability concept particularly relevant for small-scale, subsistence farmers (Ceccarelli, 1996). The static stability concept makes use of specific GEIs, in order to find genotypes that are better suited to a given environment, thereby selecting for “more narrowly adapted varieties” (Cleveland, 2001). The dynamic concept of stability refers to a genotype whose mean response in an environment is parallel to the mean response of all genotypes in an environment. These genotypes tend to have low GEIs and are adaptable to a broader range of environments (Cleveland, 2001; Annicchiarico, 2002), which may also be an important characteristic valuable to organic agricultural systems depending on the range of environments. Plant breeding for conventional agriculture, for example, has focused on dynamic yield stability in order to produce varieties better adapted to diverse geographical environments and suited to less challenging environments that can be manipulated or managed through higher inputs (Frankel *et al*., 1995), so that genotype yield improves through improved environmental conditions (Eberhart & Russell, 1966).

A number of researchers have reported on the advantages of increased diversity, both inter- and intraspecific, for plant protection, yield stability and soil conservation (Østergård et al., 2009; Tooker & Frank, 2012; Finckh & Wolfe, 2015; Vidal et al., 2017). Furthermore, positive correlations between diversity and stability, as well as between diversity and productivity have been found (Tilman *et al*., 1996; Finckh *et al*., 2000; Moreau, 2010; Newton *et al*., 2010; Barot *et al*., 2017). Genetic diversity is needed to be able to react and adapt to highly unpredictable climatic conditions and changes and variations in soil, water and nutrient status (Döring *et al*., 2011). The High genetic Diversity approach is relevant to organic and low-input agricultural systems due to the comparatively large environmental variability found in these systems, where increased genetic diversity is better able to cope with higher biotic and abiotic stresses (Annicchiarico & Filippi, 2007; Döring *et al*., 2010; Dawson & Goldringer, 2012). These challenges, coupled with the additional pressure of plant genetic diversity loss, has driven novel breeding approaches such as Composite Cross Populations (CCPs) and other genotype mixtures, thereby increasing intra-field diversity. Literature on the effects of increased genetic diversity through the use of cultivar mixtures and CCPs and its stabilizing effect on yield has, however, been contradictory. Hockett *et al*. (1983) reported on inconsistent yield stability for a number of barley populations analysed across 16 environments. Clay & Allard (1969), working with barley varietal mixtures, reported that there was either no effect of increased diversity on yield stability or that although varietal mixtures resulted in a small yield advantage over the mean of their components, yield stability was found to be lower. In contrast, a number of researchers report on greater yield stability in more genetically diverse crop material in both barley (Pfahler & Linskens, 1979; Soliman & Allard, 1991; Finckh *et al*., 2000; Grando *et al*., 2001; Creissen *et al*., 2016; Raggi *et al*., 2017) and wheat (Dubin & Wolfe, 1994; Döring *et al*., 2015). Positive effects of genetically diverse cropping systems on yield stability in general have also been reported (Gaudin *et al*., 2015; Manns & Martin, 2018).

In this paper, we present the results of a yield stability analysis on a number of winter wheat CCPs and pure line varieties that were grown under both organic and conventional management for up to 8 experimental years. In 2002, three winter wheat CCPs were created through the crossing of 20 carefully selected parental varieties by the John Innes Centre and in collaboration with the Elm Farm Research Centre, UK (Döring *et al*., 2015; Brumlop *et al*., 2017). Since 2005, these three heterogeneous winter wheat populations have been multiplied annually at the University of Kassel, Neu-Eichenberg, under differing management systems (organic and conventional) and subject to natural selection. The specific aims of the research were to test: i) the suitability of the genetically diverse CCPs in terms of yield and yield stability in the differing management systems and ii) to compare the yield and yield stability of the CCPs to the modern pure line varieties used as references under differing management conditions.

3.2 Materials and methods

3.2.1 Experimental material and field site

In 2002, three composite cross populations (CCPs) were created in the UK through the complete half-diallel crossing of 20 parental varieties. The parental varieties (varietal release dates between 1934 and 2000) were chosen based on their agronomic performance under low-input conditions in Europe, as well as to ensure a wide genetic basis for the CCPs (Jones *et al*., 2010; Döring *et al*., 2015). The first CCP was created through the crossing of twelve high baking quality parental varieties, thereafter referred to as CCPQ (Quality). The second CCPY was based on the crosses of nine high yielding parental varieties (Yield) with the parental variety Bezostaya, regarded as both high yielding and as having good baking quality, having been crossed into both the CCPQ and CCPY populations. The third CCP was created through the crossing of 8Y x 11Q parental varieties and Bezostaya with all others and is therefore referred to as CCPYQ (Yield x Quality). Four male sterile lines were included in the initial crosses in order to encourage outcrossing within the CCPs and the F_2 seeds of these initial crosses were bulked and multiplied at four sites across the UK until the F_4 (for detailed description see Döring *et al*., 2015; Brumlop, 2017; Chapter 2). Since 2005 (F_5), the three CCPs have been grown at the experimental research station of the University of Kassel in Neu-Eichenberg, Hessen, under both organic (O) and conventional (C) management. In 2006/07, each CCP was split in equal parts in order to create two parallel populations per CCP under each management system (6 CCPs per system), bringing the total number of CCPs to twelve (parallel populations indicated by I and II).

The twelve CCPs have been multiplied annually in Neu-Eichenberg in plots of at least 150m^2 since 2006/07 at the experimental research fields of the Department of Ecological Plant Protection (51°22'24.7"N and 9°54'12.5"E), with a mean annual precipitation of 684mm (2000-2013), mean annual temperature of 9.3°C (2000-2013) and altitude of 247m above sea level. The organically managed CCPs were grown from 2005/06 in a field (Teilanger) classified as having fine loamy loess soil (Haplic Luvisol) with 76 soil points according to the German soil grading system (0-100) (Wildhagen, 1998). Initially, the conventional CCPs were grown on a field (Saurasen) located at about 500m distance from Teilanger (2005/06-2012/13). Saurasen is characterised as a sandy loam loess soil (Stagnic Luvisol) with 52 soil points (Wildhagen, 1998). However, in 2013/14 the conventional CCPs were relocated to a conventionally managed field on Teilanger, thereby ensuring similar soil quality for both management systems.

The organic CCPs have been managed without the addition of fertilizers, fungicides, pesticides or herbicides and follow a two-year grass-clover mixture. Row spacing was generally 30cm to allow for weed control through harrowing at tillering and/or hoeing at later stages if needed (see Bertholdsson *et al*. 2016 for further details). The conventional populations on Saurasen were rotated annually with grass-clover and the pre-crop for the conventionally managed CCPs on Teilanger was either maize or a green manure. No fungicides or insecticides were applied, but herbicide was generally used once a year in early spring. A split application of mineral nitrogen fertilizer at a rate of 125kg/ha was applied during the growing season (50kg and 75kg/ha at each application, respectively). At stem elongation, growth regulators were applied in 2008 and 2009, but not in 2010 or thereafter. A number of currently relevant pure line varieties were grown in smaller plots neighbouring the CCPs for comparison in both the organic and conventionally managed systems. Under organic management, the reference varieties Achat and Capo were grown in 8 experimental years with the CCPs since 2007/08. However, under conventional management only the variety Capo was used most often as a reference variety since 2008/09 (6 experimental years). Both

Achat and Capo are commonly grown varieties known for baking quality (E class varieties according to the German wheat classification system).

3.2.2 Stability parameters and statistical analysis

Stability indices based on grain yield values for the CCPs and reference varieties were calculated separately for each management system. The CCPs are referred to as CCP entries when referred to as a group or by their individual names (e.g. CYQI – conventionally managed CCPYQ I) and the reference varieties by their names Achat and Capo. The experimental years are treated as environments (Env.) and the CCP entries and reference varieties are referred to as genotypes (Gen.) when a genotype x environmental interaction (GEI) is discussed. The yield stability indices of the organically managed CCPs and Achat and Capo were calculated based on a dataset of eight experimental years (2007/08-2011/12 and 2013/14-2015/16), whereas the dataset of the conventional CCPs and Capo was based on 6 experimental years (2008/09-2009/10 and 2012/13-2015/16). Although the conventionally managed CCPs changed site, the yield stability analysis was conducted across all experimental years with site only taken into account for the grain yield analysis. Grain yield in each management system was analysed separately using an ANOVA and included the main effects of experimental entries and years as fixed factors and the interaction between them. The grain yield analysis of the conventionally managed entries included the additional main effect of location (site) as a fixed factor.

Environmental variance (EV_i) as a stability index falls under the Type I stability concept of static stability. Genotypes that achieve low EV_i values are considered stable as their grain yields show very little variation across environments and hence no strong GxE interactions (Roemer, 1917; Becker & Leon, 1988). However, genotypes that indicate good static stability by achieving constant yields across environments may yield better under challenging environments indicating suitability to specific environments. The stability index environmental variance (EV_i) was calculated by:

$$EV_i = \sum \frac{(X_{ij} - \bar{X}_i)^2}{e - 1}$$

With X_{ij} representing the yield response of the entry *i* in the environment *j*, $\bar{X}_i$ as the entry mean yield across all environments and *e* representing the number of environments.

A yield reliability index (I_i) proposed by Kataoka (1963) combines both genotype mean yield and EV_i to combine the advantages of genotypes with better grain yield and low yield variation across environments. The index calculates the lowest yield that a genotype will achieve based on a probability *P*, which is fixed and dependent on a farmer's aversion to risk or a particular environment (Annicchiarico, 2002). Döring *et al*. (2015) used the fixed P=0.75 in order to calculate I_i for a number of CCPs and their mixtures. This *P* value allows for the lowest yield that could be expected in 75% of cases and has been recommended for modern agricultural systems with favourable climatic conditions (Eskridge, 1990; Döring *et al*., 2015). I_i was calculated by:

$$I_i = X_i - Z_{(P)}\sqrt{EV_i}$$

where $Z_{(P)}$ equals the fixed factor 0.675 based on P=0.75, X_i represents the entry mean across all environments and EV_i is the previously calculated environmental variance.

Wricke's ecovalence (W^2) (1962) is a measure of dynamic stability (Type II stability), where a stable genotype shows a low GEI by achieving a yield response similar or parallel to the mean yield response of all genotypes (Annicchiarico, 2002). This index measures the GEI effect of genotypes across environments with an index value closest to 0, indicating the highest stability with no GEI. Wricke' ecovalence W^2 was calculated by:

$$W^2 = \sum\nolimits_{ij} (X_{ij} - \bar{X}_i - \bar{X}_j + \bar{X})^2$$

where X_{ij} represents the genotype (*i*) yield in environment *j*, $\bar{X}_i$ is the genotype mean yield across environments, $\bar{X}_j$ is the mean yield in environment *j* and $\bar{X}$ is the grand mean.

A genotype superiority index (P_i) was proposed by Lin & Binns (1988), which assesses a genotypes yield performance in comparison to the maximum yield response in multiple environments. Lower values for P_i indicate yield performance superiority, an indication that a genotype’s yield response is close to the maximum yield achieved in an environment and as such is indicative of general adaptability.

P_i was calculated by:

$$Pi = \sum \frac{(X_{ij} - M_j)^2}{2e}$$

where X_{ij} is the genotype (*i*) yield response in environment *j*, *M* is the maximum/best response in environment *j* and *e* the number of environments. P_i can be extrapolated further into:

$$Pi = \left[\overbrace{e(\bar{X}_i - \bar{M})^2}^{1} + \overbrace{\sum_{j=1}^{e}(X_{ij} - \bar{X}_i - \bar{M}_j + \overline{M})^2}^{2}\right]/(2e)$$

where $\bar{X}_i$ is the mean yield of genotype *i* over all environments and $\bar{M}$ is the mean of the maximum responses over all environments. The first part of the equation (1) calculates the sum of squares (SS) for the genetic effects of P_i (genetic deviation), whilst the second part of the expanded equation (2) gives the SS of the GxE interaction in the comparison of differing genotypes (GEI deviation) (Lin & Binns, 1988). According to Lin and Binns (1988), the GEI deviation should not be used as a selection criterion for stability *per se*, but should rather be used as an additional tool to assess specific environmental adaptation.

Additionally, linear regression of the mean yield performance of each entry on the mean environmental yield performance (mean of all experimental entries per year) was performed in order to calculate the regression coefficient (b_i) (Finlay & Wilkinson, 1963). As proposed by Finlay & Wilkinson (1963), the regression coefficient of each experimental entry was then plotted against the genotype mean yield response (LOG10) in order to gain insight into genotype yield stability, both static (b_i<1) and dynamic (b_i=1).

An AMMI (Additive Main Effect and Multiplicative Interaction) analysis was performed on the organically managed CCPs and reference varieties on a dataset of six experimental years (Env.) (2008/09-2011/12, 2013/14 and 2015/16). The number of environments were reduced from the original dataset due to missing replicated grain yield values needed for the analysis. No AMMI analysis was performed for the conventional CCPs due to the resulting small number of experimental years available (4 experimental years), as a result of unreplicated grain yield values. The AMMI (Additive Main Effect and Multiplicative Interaction) analysis combines an ANOVA (analysis of variance analysis) for the genotype and environment main effects with principal component analysis (Gollob, 1968; Mandel, 1971; Zobel *et al*., 1988) and was carried out with the statistical software R (Version 3.3.3, 2017.03.06) using the AMMI function in the R package *agricolae* (de Mendiburu, 2015). AMMI analysis allows for the quantification of the GEI and the visualization of patterns and relationships between genotype entries and environments through the AMMI Biplot (Zobel *et al*., 1988). The ANOVA allows for the compartmentalization of the yield variance into three components, namely the genotype, environment and GEI deviations from the grand or model mean. Thereafter multiplication effect analysis separates the GEI deviations into different interaction principal component axes (IPCA) (Farshadfar *et al*., 2011). For the ANOVA calculation, the main effects of experimental entries (Gen.) and experimental years (Env.) were used as fixed factors, as well as the interaction between them for grain yield values, whilst the replicates were included as the random effect.

Additionally, using the AMMI function in the R package *agricolae* (de Mendiburu, 2015), the AMMI stability value (ASV), proposed by Purchase *et al*. (2000), provides a quantitative stability value based on the AMMI model and is calculated by:

$$ASV = \sqrt{\left[\frac{IPCA1_{sumofsquare}}{IPCA2_{sumofsquare}}\left(IPCA1_{score}\right)\right]^2 + \left(IPCA2_{score}\right)^2}$$

As described by Farshadfar *et al*. (2011), ASV “is the distance from zero in a two dimensional scattergram of IPCA1 (interaction principal component analysis axis 1) scores against IPCA2 scores”. Genotypes with lower ASV values are considered more stable due to their closer proximity to the centre of the axes and their lower GEIs (stability across environments). Genotypes that achieve low ASV values may be considered more stable; however, their yields may be low. An additional yield stability index (YS_i) could be calculated using the ranking of ASV values combined with yield ranking (*RS*), as proposed by Kang (1988). This yield stability index allows for the selection of genotypes characterized by both high stability and yield by ranking genotypes in terms of their ASV values and mean grain yield from best (1) to worst and summing the two ranks to provide the yield stability index (YS_i) (Farshadfar *et al*., 2011). YS_i was calculated with the following formula:

$$YS_i = RASV + RY$$

where *RASV* represents the ASV ranking and *RY*, the yield ranking. Genotypes that achieve low YS_i values indicate varieties that shown stability across environments whilst achieving high yields.

3.3 Results

3.3.1 Climatic data

The mean annual temperature (Sept.-Aug.) from 2005/06 to 2015/16 was 0.6°C higher compared to the long-term annual average temperature of 9°C recorded from 1971-2000. The warmest seasons recorded were 2013/14 and 2015/16 (10°C), whilst the coolest experimental season was 2012/13 (8.4°C) (see Chapter 2, Table 2.2). There has been a general shift in precipitation patterns and drier late winter-early spring periods (particularly in February and March) have become more prevalent in the last decade. The driest experimental seasons were 2005/06 (540 mm) and 2014/15 (588 mm), with the wettest season recorded in 2009/10 (791 mm) (see Chapter 2, Table 2.2). A number of extreme climatic events have been recorded for the experimental station, including a severe black frost occurrence in early February of 2011/12, which was followed by above average temperatures and little precipitation in February and March. These conditions led to severe drought stress and winterkill (for more details see Brumlop *et al*. 2017). Lower than average precipitation from November to February were also experienced in the experimental seasons of 2013/14 and 2014/15. This drought period was extended into the late spring and early summer months (May and June) in the experimental season of 2014/15, resulting in a very dry season with a total seasonal precipitation of 588 mm (Sept.-Aug.) (see Chapter 2, Table 2.2).

3.3.2 Organic CCPs and reference varieties

Across all seasons, the OYQ and OY CCPs did not yield significantly different from Achat and Capo, only OQI yielded lower (Figure 3.1 A). The reference varieties Achat and Capo achieved the highest mean grain yield over the eight experimental years (Figure 3.1 A, Table A 3.5); however, in terms of environmental variance (EV_i), indicative of the static stability concept, Capo and the OYI CCP achieved the lowest value, indicating best stability (Figure 3.1 B). The same was true for the lowest yielding OQI. For yield reliability I_i, which combines both mean grain yield and EV_i, the reference variety Achat and the OYQII CCP achieved the best stability values, while the OYQII and OYQI achieved the lowest ecovalence (W^2) values, indicating better dynamic stability in comparison to the reference varieties and the other CCP entries (Figure 3.1).

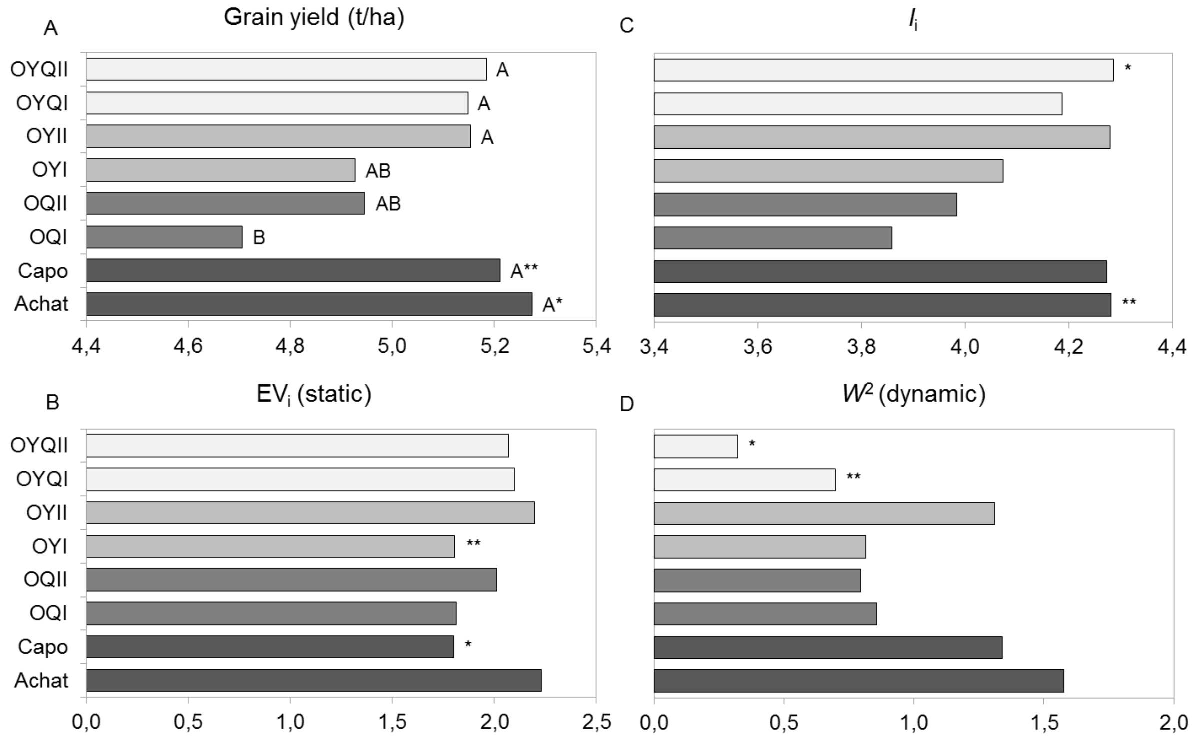

Figure 3.1: A) Mean grain yield, B) environmental variance (EV_i), C) yield reliability index (I_i) and D) ecovalence (W^2) for the organically managed CCP entries and reference varieties over eight experimental years. * denotes the best performing entry, ** denotes the next best performing entry. Differing capital letters indicate significant differences at $p<0.05$ between entries over all experimental seasons.

In terms of stability based on the genotype regression coefficient (b_i) (Finlay & Wilkinson, 1963), the OYQII CCP was best adapted to all environments (Figure 3.2 A) with a slope (b_i) closest to 1. All entries, except for the variety Achat, achieved slopes below 1, indicating above average stability in the static sense and more specific adaptation to unfavourable environments. The slope of the entries OQI, OQII, OYI, OYII and Capo correlated with the low EV_i values of those entries, indicating low yield variation over all environments (Figure 3.2 A, Figure 3.1 C).

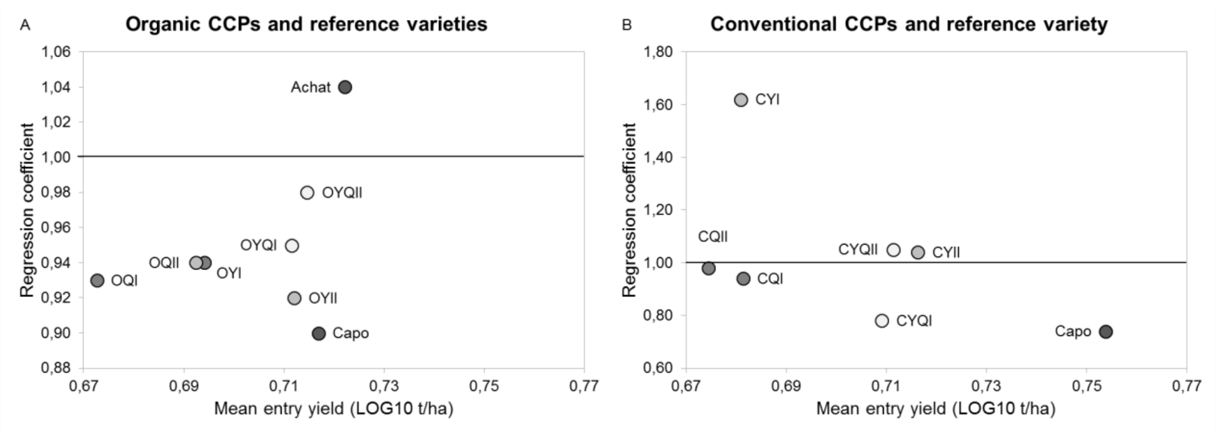

Figure 3.2: The regression coefficient (b_i) plotted against the mean entry yield (LOG10 t/ha) for A) all organic CCP entries and reference varieties over eight experimental years and B) all conventional CCPs and reference variety over six experimental years (Finlay & Wilkinson, 1963).

The lowest superiority index (P_i) value was found in the OYQII CCP, followed by Achat and OYII (Table 3.1). Lower P_i values indicate smaller distances from maximum yields and therefore “greater yield superiority” (Döring *et al*., 2015). However, the contribution of GEI deviation to P_i for Achat and OYII (45 and 49%, respectively) was considerably greater than that of OYQII (23%). This indicates that these entries show a likelihood towards greater GEI interaction and adaptation to specific environments. This is supported by the divergent regression coefficient values (Figure 3.2 A) and greater ecovalence (W^2) values (Figure 3.1 D). Higher P_i values were found for OQI, OQII and OYI indicative of their lower yields in comparison to the other entries, however, the contribution of the genetic deviation to P_i was considerably greater indicating more general adaptation, particularly as the W^2 values of these entries were also low.

Table 3.1: Superiority index (P_i), genetic and GEI deviations of P_i and percentual contributions of the deviations to P_i for organic CCP entries and reference varieties over eight experimental years. Best value is marked in bold.

System	Experimental years	Entry	P_i (*1000)	P_i genetic	P_i GxE	P_i genetic %	P_i GxE %
Organic	8	Achat	143	78	65	55	45
		Capo	245	128	117	52	48
		OQI	479	422	57	88	12
		OQII	397	277	120	70	30
		OYI	373	249	124	67	33
		OYII	160	82	78	51	49
		OYQI	244	136	108	56	44
		OYQII	**119**	92	28	77	23

Table 3.2: Analysis of variance for grain yield of the organic CCP entries and reference varieties (Gen.) across six experimental years (Env.) used for the AMMI analysis. The percentual contribution of the main effects relative to the total Sum of Squares (SS) for the model (Model=Env+Gen+Env*Gen) are given. Additionally, AMMI Stability Values (ASV) and their ranking, yield ranking and Yield stability index (YS_i) values for each entry are given based on the AMMI analysis.

Organic entries (6 environments)

	Df	**SS**	**% of model SS**	**% of GxE SS**	
Model	53	202,56			
Env	5	189,99	94		
Rep(Env)	6	0,91	0		
Entry (Gen.)	7	3,77	2		
Env*Gen	35	7,89	4	4	
Entry		**ASV value**	**ASV ranking**	**Yield ranking**	**YS_i**
Achat		1,16	8	2	10
Capo		0,93	7	1	8
OQI		0,69	4	8	12
OQII		0,25	1	6	7
OYI		0,84	6	7	13
OYII		0,46	3	5	8
OYQI		0,81	5	3	8
OYQII		0,35	2	4	6

In the AMMI model, based on a dataset of six experimental years, the main effect of environment (experimental years) contributed the greatest share to yield variance relative to the total SS of main effects (Model=Env+Gen+Env*Gen) (94 %) (Table 3.2), while experimental entries (Gen.) and GxE accounted for 2 % and 4 %, respectively. The larger GEI effects, in comparison to the genotype effect, indicates the presence of entries particularly suited to specific environments.

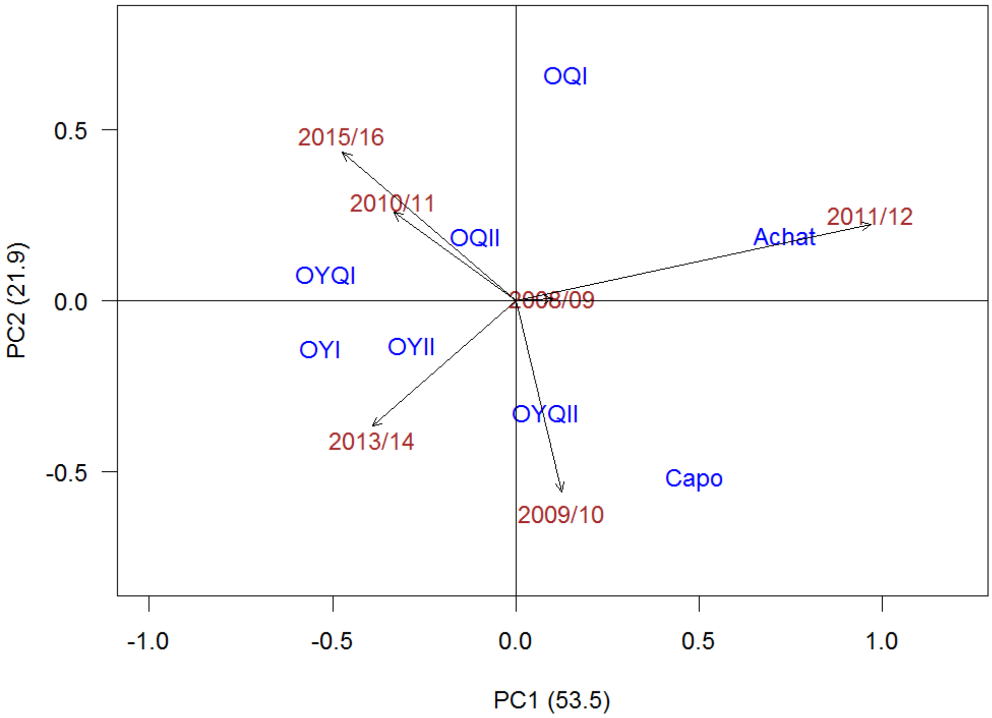

Figure 3.3:AMMI2 Biplot of the first two AMMI interaction (PCA) scores for the organic CCP entries and reference varieties (blue) in six experimental years (red).

The AMMI2 Biplot (Figure 3.3) accounted for 75 % of the yield variation and the CCPs OQII, OYQII and OYII were found to be the most stable entries in terms of dynamic stability (no strong interaction with a specific environment), as indicated by their low ASV scores (Table 3.2) and proximity to the centre of the axes. The experimental year of 2008/09 was the most stable environment, located in the centre of the axes and indicative of the lowest yield variation in comparison with all years. The reference variety Achat was the least stable in terms of ASV values. It had the best yield in the year 2011/12 after the bare frost (Table A 3.5). In terms of YS_i, combining both mean yield and ASV ranking, the OYQII CCP achieved the best YS_i value (smallest value), followed by OYQI, OYII and the reference variety Capo; however, Capo tended towards a higher ASV value indicating adaptation to specific environments (static stability) (Table 3.2) and a positive interaction to the experimental year 2009/10 (Figure 3.3).

3.3.3 Conventional CCPs and references

A significant site effect was found for mean yield of the experimental entries over the six experimental years with significantly greater yields found at Saurasen than at

Teilanger (5.2 and 5.0t/ha, respectively) (Table A 3.6). A significant interaction effect between experimental entries and site was also present, indicating differential yield ranking of the experimental entries depending on the site (Chapter 2, Table A 2.5). The reference variety Capo and the CCP CYII achieved the greatest grain yields over all experimental years with 5.7t/ha and 5.2t/ha, respectively (Figure 3.4 A). The lowest yields were achieved by CQII (4.7t/ha) and CYI (4.8t/ha) (Figure 3.4 A). Capo and CYQI had the lowest EV_i values indicating the highest stability, whilst the CYI CCP had the highest variability in grain yield over the experimental years, indicated by its higher EV_i value (Figure 3.4 B). Capo and CYQI had the best yield reliability score (I_i), whilst the CCP CYI the poorest (Figure 3.4 C), indicating low mean grain yield and high yield variation across multiple environments. The greatest values for the dynamic stability measure (W^2) were found in the CYII and CQI CCPs, indicating that these CCPs did not differ greatly in their mean yield performance in relation to the mean environmental yield over the experimental years. The CCPs CYI and CYQII had the highest values for W^2, tending towards a greater GEI (Figure 3.4 D).

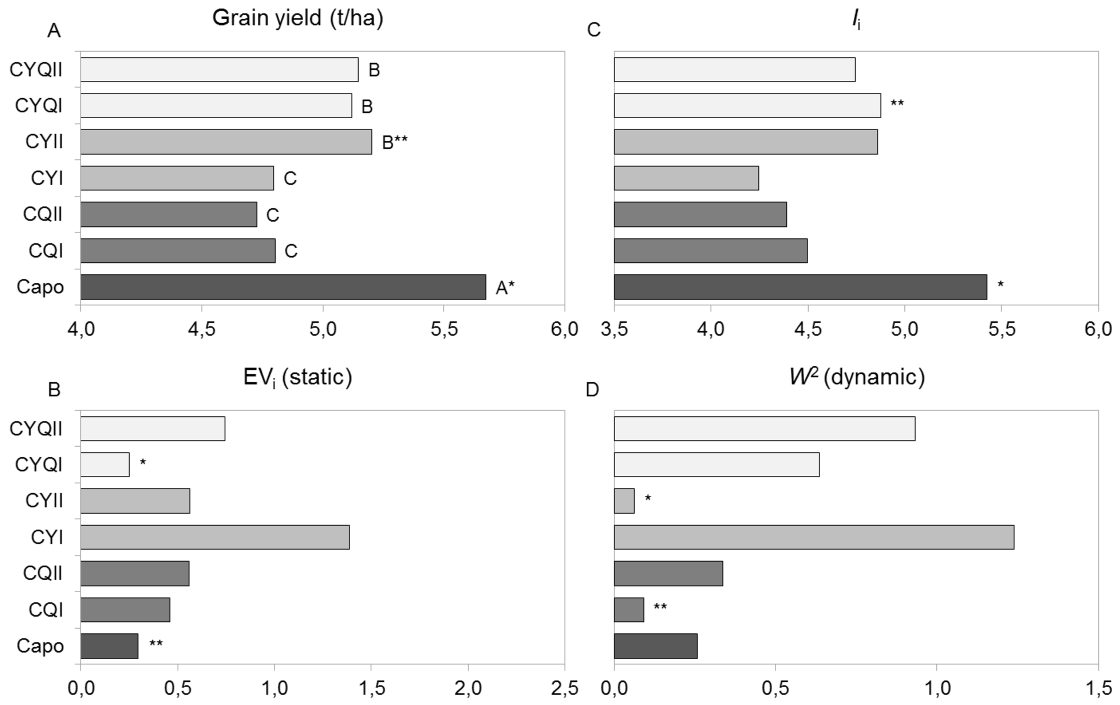

Figure 3.4: A) Mean grain yield, B) environmental variance (EV_i), C) yield reliability index (I_i) and D) ecovalence (W^2) for the conventionally managed CCP entries and reference varieties over six experimental years. * denotes the best performing entry, ** denotes the next best performing entry. Differing capital letters indicate significant differences at $p<0.05$ between entries over all experimental seasons.

The CCPs CYII and CYQII tended towards a slope close to 1 (Figure 3.2 B), as did the CCPs OQI and OQII. However, CYII and CYQII yielded highest amongst the conventional CCPs (Figure 3.4 A), while OQI was especially low yielding amongst the organic CCPs (Figure 3.1 A). The reference variety Capo and the CCP CYQI had b_i values below 1, indicating above average yield stability and adaptation to less favourable environments, particularly Capo, which achieved a significantly greater mean yield than the conventional CCPs. This trend towards adaptation to more specific environments (greater GEI) is also supported by the lower EV_i values achieved by both entries. The CYI CCP showed a very strong adaptation to more favourable environments with a slope of 1.6; however, this CCP indicates general instability with poor values for both EV_i and W^2, as well as a low mean yield (Figure 3.4 A, B, D).

The reference variety Capo achieved an exceptionally low P_i value indicating its greater yield superiority in comparison to the other entries (Table 3.3). The CYII achieved the best P_i values amongst the CCPs, which in contrast to Capo, had a greater share of genetic deviation contributing to the P_i value. The CYQI and CYQII CCPs tended towards similar P_i values (214 and 240, respectively), followed by the CQ CCPs. The CYI CCP showed the poorest values for P_i, as well as a high contribution of the GEI deviation to the superiority index value.

Table 3.3: Superiority index (P_i), genetic and GEI deviations of P_i and percentual contributions of the deviations to P_i for the conventional CCP entries and reference variety Capo over six experimental years. Best value is marked in bold.

System	Experimental years	Entry	P_i (*1000)	P_i genetic	P_i GxE	P_i genetic %	P_i GxE %
Conventional	6	Capo	**2**	0,27	1	17	83
		CQI	382	368	14	96	4
		CQII	451	421	30	93	7
		CYI	511	300	211	59	41
		CYII	140	100	40	71	29
		CYQI	214	181	33	84	16
		CYQII	240	118	122	49	51

3.3.4 Association between stability parameters under differing management systems

A significant positive correlation was found between grain yield (GY) and the yield reliability index I_i (index combining both mean yield and EV_i), whilst a significant negative correlation was found between grain yield (GY) and P_i under both organic and conventional management (Table 3.4). Under organic management, a significant negative correlation was found between P_i and I_i; however, under conventional management the significant correlation between these two stability parameters was positive.

Table 3.4: Spearman rank correlation between mean performance and stability parameters for grain yield of the organically managed CCPs and reference varieties (8 experimental years) and the conventionally managed CCPs and reference variety (6 experimental years). Contrasting correlations between the management systems are marked in bold.

	Organic CCPs and reference varieties						**Conventional CCPs and reference variety**					
	GY	b_i	I_i	P_i	EV_i	W^2	GY	b_i	I_i	P_i	EV_i	W^2
GY	-	**0,30**	0,93**	-0,90**	0,64'	**0,38**	-	**-0,21**	0,79*	-0,86*	-0,11	**-0,21**
b_i		-	**0,40**	**-0,51**	0,57	**-0,32**		-	**-0,71'**	**0,61**	0,96**	**0,46**
I_i			-	**-0,98*** **	**0,52**	**0,10**			-	**0,96** **	**-0,68**	**-0,39**
P_i				-	**-0,64'**	0,02				-	**0,54**	0,54
EV_i					-	0,07					-	0,39
W^2						-						-

*p<0,05; **p<0,01; ***p<0,001; 'p<0,10, numbers in **bold** indicate contrasting correlations between mgmt. systems
GY=grain yield, b_i=regression coefficient, I_i=yield relaibility index, P_i=yield superiority index, EV_i=environmental variance and W^2=Wricke's ecovalence

A significant positive correlation was found between b_i and EV_i only under conventional management. There tended to be moderate correlations between a number of yield stability parameters of the same stability concept, although these were not statistically significant. Under organic management, there was no correlation found between EV_i and W^2 (both differing stability concepts) and between W^2 and the two stability parameters P_i and I_i (0.02 and 0.10, respectively) (Table 3.4). Under conventional management, however, higher, albeit not statistically significant correlations occurred between EV_i and W^2 (0.39) and between W^2 and the two stability parameters P_i and I_i (0.54 and -0.39, respectively).

3.4 Discussion

The aim of this study was to assess the yield performance and yield stability of various CCPs against reference varieties over a number of experimental years, as well as to determine the suitability of the heterogeneous wheat populations in terms of yield stability and yield under differing management systems.

3.4.1 Yield stability of CCPs and reference varieties under differing management systems

Under organic management, no particular differences for yield stability between the parallel CCPs were found, although the CCQ populations tended towards the lowest yields, as expected based on their genetic background for high baking quality, rather than yielding ability. Similar results for lower yields of the CCQ populations in comparison to the other CCP groups have been reported by Brumlop *et al*. (2017) and in Chapter 2. Kang (1998) recommended more than eight environments in order to calculate a reliable stability analysis. Eight environments were available for the CCPs and reference varieties under organic management; however, for the AMMI analysis only six environments were available. Despite only six experimental years, the results of the AMMI analysis were similar to the results of the other stability parameters and can be used as an additional basis to find genotypes indicative of yield stability across environments and above average yields.

The OYQII population achieved above average yields and had the greatest stability (highest number of top ranks for the various stability parameters) with low GEI (greater dynamic stability). Whilst the regression coefficient (b_i) has been included as a stability parameter in this study, Becker & Leon (1988) report that due to a number of criticisms of the measure, it is best used as an additional evaluation tool with which to describe a genotype’s adaptation and response to unfavourable environments. Bearing this in mind, the OYQII CCP tended towards a slope closest to 1 and as such indicated good adaptation to all environments. The CCYQ populations are the most genetically diverse due to their parental makeup (20 parental varieties) and as such have the advantage of a larger parent set with both high yielding and high baking quality characteristics. Döring *et al*. (2015) found similar results when comparing the grain and protein stability of the same CCPs under differing management systems. Both the CCY and CCYQ populations tended towards lower (better) EV_i values for grain yield in comparison to the mean and mixture of their respective parental varieties across both organic and conventional environments (Döring *et al*., 2015). Greater yield stability of barley CCPs over a number of reference varieties has also been reported by Soliman & Allard (1991), indicating the potential use of CCPs to create cultivars characterised by little to no GEI. Creissen *et al*. (2016) working on winter barley mixtures, found increased yield stability of two barley mixtures over two pure lines varieties for the dynamic stability measure W^2. The reference variety Capo in our study also displayed a high degree of yield stability, tending towards adaptation to unfavourable environments (greater GEI) and high stability in terms of environmental variance (EV_i, static stability) and I_i, particularly in comparison to the CCPs under conventional management.

The mechanisms of compensation, complementation and facilitation have been given as ecological processes, which may increase stability in genetically diverse populations (Phillips & Wolfe, 2005; Döring *et al*., 2011, 2015; Creissen *et al*., 2016). Although the exact mechanisms that inferred better stability to the OYQII CCP in particular are unknown, the German CCPs showed remarkable resilience and compensation effects in the experimental year of 2011/12 (Brumlop *et al*., 2017), when the severe black frost in February 2012, followed by a drought described above occurred. There was a high degree of winterkill in in the CCP parental varieties, which had been grown in plots neighbouring the populations. Although only four of the parental varieties (mainly from the Q CCPs) survived reasonably well due to good winter hardiness, the CCPs, characterized by greater genetic diversity, recovered sufficiently enough to achieve a mean trial yield of 4.2 t/ha. Creissen *et al*. (2013) showed that in genotype mixtures in *Arabidopsi*s, seed yield stability in the mixtures was maintained through the mechanism of compensation. This compensatory effect for seed yield was pronounced under abiotic stress, and could have provided the OYQ populations, which are more genetically diverse, an advantage under the more challenging conditions of the organic management system. According to Annicchiarico & Filippi (2007) and Lammerts van Bueren & Myers (2012), organic systems are considered more challenging due to higher abiotic and biotic pressures. In organic systems, there are few immediate control options when dealing with insect pests and pathogens. Additionally, abiotic stresses such as low N availability under organic conditions, particularly in early spring, make the growing conditions in organic and low-input systems more challenging (Dawson *et al*., 2008; Messmer *et al*., 2012). While no pathogen or insect control was applied in both management systems described here, nutrient dynamics were likely different in the two systems. Climatic conditions in Neu-Eichenberg over the last few years have been characterised by more frequent drought periods between late winter and early spring. This has resulted in lower soil biological activity and thus N mineralisation during this critical growth period and likely led to overall more stressful abiotic conditions for wheat under organic management. Slower mineralisation and lower N inputs in the organic system, particularly under drought stress, leads to earlier senescence. In addition to early maturation, which leaves plants unable to make use of later rain periods for grain filling, N sources during grain filling under organic management are often limited (Baresel *et al*., 2008; Osman *et al*., 2012). These greater challenges found in the organic system may be mitigated by greater intra-specific diversity, as is the case with the OYQ CCPs and greater yield stability.

Under conventional management, the reference variety Capo was found to be the most stable genotype, followed by the CYII and CYQI CCPs. The CCY and CCYQ CCPs were the same CCPs reported by Döring *et al*. (2015) for their better yield stability in comparison to their respective parental variety mixtures and means. A comprehensive analysis of the parental varieties by Jones *et al*. (2010) reports on the advantage of the Y parental set under conventional management due to their later release date (more modern varieties) and better adaptation to agricultural systems with higher N inputs. The modern genetic base found in the CYII population and the CYQI (crossed with yield parental set) may have given them a yield advantage, as well as a yield stability advantage under conventional conditions. The high yielding parental varieties were found to yield better under conventional management and were less suitable for organic systems characterised by higher abiotic and biotic stress (Jones *et al*., 2010).

Interestingly, in the comparison of the conventional CCY parallel populations, the CYI CCP yielded significantly lower than the CYII population (Figure 3.4 A). Additionally, the CYI CCP showed greater instability in both the static and dynamic sense, suggesting potentially divergent evolutionary trajectories. The slope of the regression analysis for CYI was very steep, indicating below average stability and an adaptation to more favourable conditions. Similar differential trajectories for mean yield were also found between the two parallel CY populations, with the CYI achieving both the highest and the lowest yield across eight experimental seasons from 2006/07-2009/10 and 2012/13-2015/16 (Chapter 2).

The conventionally managed CCPs and reference variety could only be analysed for their yield stability over six years, reducing the strength of the yield stability assessment (Kang, 1998). Additionally, the CCPs and reference variety changed location to another field in 2013/14. A significant difference was found for mean yield of all experimental entries between the two locations, as well as a significant interaction effect between the conventional experimental entries and locations (Chapter 2); however, it is unsure as to the significance of the location change on CCP yield stability evolution, which could not be taken into account in this study. Goldringer *et al*. (2001a,b) reported on the divergent evolution of French wheat CCPs subjected to differing locations. Also, results from a study of the effects of growing the CCYQs in differing environments (locations) over a number of years suggest changes to both foliar pathogen resistances and morphological traits (Chapter 4), making location an important consideration. However, as yield stability analyses are generally calculated across multiple locations and years, the significant mean yield difference between the locations was not taken into consideration. Additionally, dividing the datasets between the two locations would have reduced the number of environments further, making a yield stability analysis in this respect meaningless.

The significantly lower yields of the conventionally managed CCPs in comparison to the pure line variety Capo highlights the importance of introducing new genetic material into the CCPs. The parents of the CCPs were chosen specifically for their performance under low-input conditions in Europe (Jones *et al*., 2010; Döring *et al*., 2015; Brumlop *et al*., 2017) and as such are most likely unable to take advantage of the higher N-inputs found in current conventional systems. Therefore, the addition of elite pure lines into CCPs, as proposed by Döring *et al*. (2015), may help to improve yields, particularly in conventional systems. Additionally, Knapp *et al*. (2013) reported on the “reversion to wild type” and loss of alleles related to dwarfing in wheat CCPs from the UK, but based on the same genetic background as the CCPs in this study. This is particularly relevant as the trade-off between competitive ability in the form of plant height has been negatively correlated with agronomic performance (Goldringer *et al*., 2001a; Knapp *et al*., 2013; Döring *et al*., 2015). This competitive ability may result in lower yields due to greater investment in biomass rather than in kernel number and weight, and can increase the risk of lodging, further reducing grain yields (Denison, 2012; Döring *et al*., 2015). For these reasons, the application of plant growth regulators to reduce height is recommended for CCPs under conventional management.

3.4.2 Relation of stability parameters

The significant positive correlation between grain yield and the yield reliability index I_i under both conventional and organic management indicates no trade-off between yield and stability, as greater stability for I_i is indicated by increasing values. The negative correlation between grain yield and superiority P_i is in line with this, as lower values indicate greater stability for P_i. Therefore both P_i and I_i could be used as stability measures that select for both stable and high yielding genotypes. However, only under organic management, were low to moderate positive correlations found between grain yield and the EV_i and W^2 stability parameters, indicating a potential trade-off between better grain yield and yield stability under more challenging conditions, although the correlations were not significant. This however, illustrates the advantages of using a number of stability parameters in order to ensure adequate criteria for genotypes in specific environments (Temesgen *et al*., 2015). There were moderate to high correlations between a number of parameters based on the same stability concept, such as between b_i, which can indicate both static and dynamic stability, and the EV_i and W^2 stability measures. Similar results have been reported by a number of researchers (Duarte & de O. Zimmermann, 1995; Temesgen *et al*., 2015; Kanouni *et al*., 2015). Importantly, not all stability parameters were correlated, indicating a differential stability evaluation, which may aid selection depending on the genotype characteristics desired. Differences in the correlations between stability parameters in differing management systems illustrate the differing GEI and the strong genetic component involved in these interactions (Stagnari *et al*., 2013), particularly when one considers the divergent correlations found under differing management systems between P_i and I_i (Table 3.4).

3.5 Conclusion

Under organic management, the YQ CCPs with their wider genetic base tended towards better yield stability and above average yields in comparison to the other CCP groups and reference varieties. This wider genetic background tended to be advantageous in the buffering of higher abiotic and biotic stresses, which characterise organic and low-input systems (Döring *et al*., 2011). Thus, the importance of parental selection in the adaptation and suitability of CCPs to specific environments cannot be understated (Jones *et al*., 2010; Döring *et al*., 2011, Chapter 2). The challenging and often marginal environments of organic and low-input agriculture necessitate the inclusion of stability parameters that quantify static stability (Stagnari *et al*., 2013) and the importance of multiple trial environments is evident. Yield stability and yield performance of the conventionally managed CCPs were lower than those of the reference variety Capo, indicative of the parental selection criteria for performance in organic and low-input systems, rather than in management systems characterised by higher N-inputs. However, populations from both the conventional CCYQ and CCY achieved relatively good stability, although they were lower yielding in comparison to Capo. As the breeding of heterogeneous crop populations is an approach supported mainly by organic farmers, researchers and breeders, little effort or demand has pushed for the creation of genetically diverse populations better suited to conventional systems. Improving CCPs for conventional systems may also involve the admixing of elite breeding lines as suggested by Döring *et al* (2015). However, CCPs, particularly under organic management, show great potential not only in terms of yield performance, but also in general yield stability.

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Appendix

Table A 3.5: Mean yields (t/ha) in each experimental season for each organically managed CCP and reference varieties. Mean entry yield (t/ha) over all experimental seasons is also given.

Mean yield (t/ha) of organically managed CCPs and references									
Entry	**2007/08**	**2008/09**	**2009/10**	**2010/11**	**2011/12**	**2013/14**	**2014/15**	**2015/16**	**Mean yield (t/ha)**
Achat	6,66	5,32	6,46	7,35	5,20	2,85	4,16	4,33	5,27 A*
Capo	5,71	5,52	6,56	7,31	4,80	3,48	4,21	3,85	5,21 A
OQI	5,57	4,76	5,09	7,24	4,18	2,61	4,83	3,87	4,71 B
OQII	5,27	5,22	6,13	7,36	3,94	2,66	4,57	4,38	4,94 AB
OYI	5,76	5,21	5,89	7,18	3,41	3,16	4,96	4,25	4,93 AB
OYII	6,99	4,72	6,10	7,51	3,99	3,35	5,38	4,22	5,15 A
OYQI	6,28	4,93	6,13	7,76	3,91	3,43	4,29	4,59	5,15 A
OYQII	6,45	5,00	6,43	7,52	4,31	3,25	5,10	3,99	5,18 A
Mean annual yield (t/ha)	6,09 B**	5,09 C	6,10 B	7,40 A	4,22 D	3,10 E	4,69 C	4,19 D	

*Differing capital letters indicate significant differences at p<0,05 between entries over all seasons (ANOVA and HSD Posthoc Test)

**Differing capital letters indicate significant differences at p<0,05 between experimental seasons (ANOVA and HSD Posthoc Test)

Table A 3.6: Mean yields (t/ha) in each experimental season for each conventionally managed CCP and the reference variety Capo. Mean entry yield (t/ha) and mean location yield (t/ha) over all experimental seasons are also given. SD represents standard deviation.

Mean yield (t/ha) of conventional CCP and reference entries												
Entry	**2008/09**	**SD**	**2009/10**	**SD**	**2012/13**	**2013/14**	**SD**	**2014/15**	**2015/16**	**SD**	**Mean entry yield (t/ha)**	**SD**
Capo	5,92	0,3	5,10	0,3	6,2	5,54	0,3	6,6	5,42	0,2	5,67 a	0,5
CQI	5,02	0,1	4,33	0,2	5,4	4,59	0,6	6,1	4,35	0,2	4,80 c	0,6
CQII	4,90	0,1	3,91	0,1	5,5	4,49	0,2	6,0	4,58	0,2	4,73 c	0,7
CYI	5,60	0,2	3,87	0,1	6,1	4,67	0,0	6,4	3,58	0,0	4,80 c	1,1
CYII	5,64	0,1	4,84	0,2	6,0	4,90	0,1	6,3	4,44	0,3	5,20 b	0,7
CYQI	5,32	0,2	4,67	0,0	5,7	5,38	0,0	5,7	4,53	0,3	5,12 b	0,5
CYQII	5,56	0,1	5,24	0,1	6,2	4,18	0,0	6,3	4,51	0,2	5,15 b	0,8
Mean annual yield (t/ha)	5,42 B*		4,57 D		5,87 A	4,82 C		6,19 A	4,49 D			
Conventional sites												
Saurasen											5,17 A**	
Teilanger											4,96 B	

Differing small letters indicate significant differences at p<0,05 between all CCP and reference entries (ANOVA and Post-hoc HSD Test)

*Differing capital letters indicate significant differences at p<0,05 between all experimental seasons (ANOVA and Post-hoc HSD Test)

**Differing capital letters indicate significant differences at p<0,05 between conventional sites (ANOVA and Post-hoc HSD Test)

4. Composite cross wheat populations show stability and local adaptation despite rapidly changing environmental conditions

Abstract

A winter wheat composite cross population (CCPYQ) was created in the UK in 2001 through the crossing of 20 parental varieties, characterized by either high yield or baking quality. Since 2005 (F_5), the CCYQ population has been grown in Germany and Hungary, as well as remaining in the UK. In 2008 (F_8), eight project partners developed a cycling pattern in order to create travelling CCPs, originating from either Germany, Hungary or the UK. One CCP was grown by each partner under either organic or low-input conditions for one year and subsequently sent to the next partner, thereby creating cycling CCPs with vastly different histories. In 2013, all eight cycling CCPs and the three non-cycling CCPs that had been maintained in Germany, Hungary and the UK were included in a two-year experiment at the University of Kassel, Germany. In 2013/14, the eleven CCPs (F_{13}) and three pure line varieties were compared for their agronomic performance and morphological characteristics in a replicated trial. In 2014/15, saved seed of the F_{13} CCPs were grown together with harvested seed of the CCPs from the first experimental year (F_{14}) and the same three pure line varieties in order to compare two generations in one environment. In the second experimental year, agronomic performance and baking quality of the experimental entries was compared, as well as the effect of differing seed weight at sowing on agronomic parameters. Results from the two-year trial indicate that the CCPs remain relatively similar to one another for most agronomic parameters, whether exposed to differing growing environments or having remained static at one location. With the exception of the Hungarian non-cycling CCP, the CCPs were not significantly affected by stripe rust. This CCP also diverged in terms of a higher degree of awnedness, as well as superior ability to maintain yield under severe drought conditions in 2015. Additionally, one cycling CCP diverged from all others for kernel colour that appeared connected to higher protein content while small divergences for stem length were found. Differing seed weight at sowing affected some agronomic parameters such as thousand kernel weight, plant height and harvest index under drought conditions, but not under less stressful conditions. In both experimental years, the CCPs were comparable to the pure line varieties in terms of agronomic performance and under the drought conditions

of 2015, no reference variety had a yield advantage over any of the CCPs. These results indicate the potential of CCPs to compete with pure line varieties and the capacity of heterogeneous wheat populations to buffer environmental stresses.

4.1 Introduction

Unpredictable and increasingly variable climatic conditions have highlighted the importance of developing new and innovative strategies for crop breeding and management (Østergård *et al*., 2009). The success of these strategies will largely be determined by better elucidation of genotype x environment x management interactions, changing the focus of agriculture from environmental manipulation through high external inputs to breeding crops better suited to particular environments (Østergård *et al*., 2009; Lammerts van Bueren & Myers, 2011). As environmental and agronomic conditions are heterogeneous between and within locations, diversity within varieties or crop populations should increase adaptability to the changing and variable range of growing environments. It is essential that such varieties and populations also provide a diverse range of qualities in order to meet the needs of farmers across environments (Wolfe *et al*., 2006). Evolutionary breeding through the use of Composite Cross Populations (CCPs), for example, has been gaining ground due to climatic uncertainties, increasing biotic and abiotic pressures, as well as plant diversity loss (Phillips & Wolfe, 2005; Goldringer *et al*., 2001a; Finckh & Wolfe, 2015; Dwivedi *et al*., 2017). CCPs and other genotype mixtures result in greater intra- and inter-varietal diversity within the agricultural landscape and ensure a “wider adaptation” capacity for crop varieties (Döring *et al*., 2011a,b).

Results for both barley and wheat indicate that heterogeneous populations are a promising option often comparable or superior to modern pure line varieties for both yield and yield stability (Allard, 1960; Soliman & Allard, 1991; Dubin & Wolfe, 1994; Goldringer *et al*., 2001a; Danquah & Barrett, 2002a; Brumlop *et al*., 2017; Raggi *et al*., 2017, Chapter 2, Chapter 3). Additionally, changes in phenotypical traits under differing environments and diverging evolutionary trajectories of genetically similar French wheat populations indicate the potential and capacity of genetic diversity to enable and facilitate adaption to specific environments (Le Boulc’h *et al*., 1994; Goldringer *et al*., 1998, 2001a,b). Increases in resistance gene frequencies to plant pathogen pressure in genetically diverse populations have also been reported for barley CCPs (Jackson et al., 1978; Saghai Maroof et al., 1983; Webster et al., 1986; Danquah & Barrett, 2002b), as well as for wheat CCPs (Le Boulc'h *et al*., 1994; Paillard *et al*., 2000a,b). These results support the hypothesis that genetic diversity can improve crop resilience and performance and provide greater buffering capacity under challenging conditions (Østergård *et al*., 2009; Döring *et al*., 2011; Döring *et al*., 2015; Dwivedi *et al*., 2017).

As the effects of climate change on crop agronomic performance are difficult to quantify, particularly in short-term trials, a unique opportunity arose within a European network working together on wheat CCPs since 2005 (F_5). A wheat (*Triticum aestivum* L.) CCP was created through a collaboration between the John Innes Centre and Elm Farm Research Centre (UK) in 2001 (see Chapter 1, Döring *et al*., 2015 and Brumlop *et al*., 2017 for further details). The wheat CCP CCYQ (YQ = Yield x Quality) originated through the crossing of eleven high baking quality parents with eight high yielding parents (88 crosses). The variety "Bezostaya", which is considered both high yielding and of high baking quality, was inter-crossed with the 19 parental varieties and these additional crosses included in the population (107 crosses in total for the CCP). Crosses of the 19 Y and Q parents with one of four naturally male sterile lines were also bulked into the 107 crosses for the population to enhance further outcrossing in later generations (Döring *et al*., 2015; Brumlop, 2017). Since 2005, bulked progenies of this population have been grown and maintained in the UK, Hungary and Germany. Since the F_8 (2008/09), a pattern was developed by eight partners to submit the CCP (CCPYQ) that had been maintained in the UK, Hungary and Germany since 2005 to changes in environment every year in order to simulate climate variation by „cycling" the populations. The CCPs were grown under organic or low-input conditions in a plot >100m^2 at one site and sent to the next cycling partner the following year (Figure 4.1). The original partners (UK, Hungary and Germany) also maintained their original "non-cycling" populations for comparison. Each partner involved in the cycling experiment multiplied and forwarded the received population on to the following partner since 2008/09 (F_8) until the F_{13} (2012/13) (Figure 4.1).

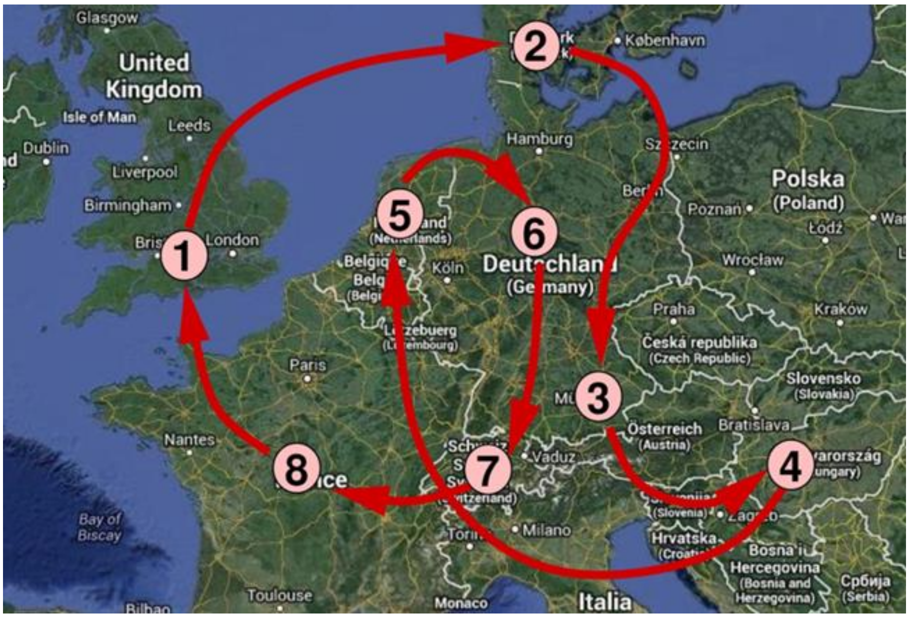

Figure 4.1: Cycling pattern developed between the eight partners for the CCYQ populations (see Table 4.1 for more details). Germany, Hungary and the UK have also maintained a non-cycling CCYQ for comparison.

This resulted in three “non-cycling” (i.e. home) populations and eight travelling or “cycling” populations that all originated from one base population (same bag of seed) in 2005. These 11 CCPs were compared at the University of Kassel, Germany, in a two-year trial. The aims of the two-year experiment conducted at the University of Kassel were i) to compare the eleven CCPs, exposed to vastly different climatic conditions in eight sites across Europe over time since 2008/09, in one site (Germany), for their performance (agronomic and baking quality) and phenotypic diversity. ii) To quantify both agronomic and morphological changes to both non-cycling (home) and cycling CCPs in order to describe specific adaptations depending on a CCPs history. iii) In 2014/15, the second experimental year, saved seed from 2013 (F_{13}) and harvested seed from 2014 (F_{14}) were sown, in order to compare two generations in one growing season and to ensure that the differences between populations were not in fact due to differing seed size. iv) To compare the agronomic performance and baking quality of the CCPs to a number of modern pure line varieties.

The following questions were addressed in this study:

1) Do CCPs exposed to changing environments differ from one another and to the home CCPs in terms of agronomic performance and baking quality?

2) Are the CCPs comparable to modern pure line varieties and do the CCPs have an advantage over pure line varieties under weather extremes i.e. drought conditions of 2014/15?
3) Are there effects of differing seed weight on the agronomic performance of the CCPs (F_{13} and F_{14})?

4.2 Materials and Methods

4.2.1 Field site and experimental design

The trials were carried out in the two experimental seasons of 2013/14 and 2014/15 at the research fields of the Department of Ecological Plant Protection in Neu Eichenberg (51°22’24.7”N and 9°54’12.5”E), mean annual precipitation (2000-2013): 684mm, mean annual temperature (2000-2013): 9.3°C, altitude: 247m above sea level. The soil is classified as fine loamy loess soil (Haplic Luvisol) scoring 76 points according to the German soil point system (0-100) (Wildhagen, 1998). The fields have been managed organically since 1984 without the use of synthetic fertilizers or pesticides.

In the first experimental year of 2013/14, seed from the eight cycling CCPs, as well as seed from the three non-cycling CCPs (F_{13}) (Table 4.1), were received from all partners and sown in the same field in a randomised complete block design with four replications. In addition, three modern pure line varieties Achat, Akteur and Capo were included as references (14 experimental entries). In 2014/15, saved seed of all CCPs from 2013 (F_{13}) and harvested seed of all CCPs from 2014 (F_{14}) were included with the same three reference varieties in a randomized complete block design with four replicates (25 experimental entries) (Table 4.1). The experimental fields were organically managed and the pre-crop for both experimental years was a two-year grass-clover mixture. The wheat was sown at 350 germinable kernels/m^2 and the rows were spaced 30cm apart to allow for weed control through harrowing and/or hoeing.

Table 4.1: List of the CCPs (F_{13} and F_{14}), their origin and cycling history grown in Neu-Eichenberg in the experimental year 2013/2014 and 2014/15. The F_{14} CCPs were harvested in the autumn of 2014 from the first experimental trial year.

CCP Code		**Origin**	**Cycling (Yes/No)**	**Cycling History***
F_{13}	**F_{14}**			
D13NC	D14NC	DNC	No	Since the F_5 in Germany (non-cycling)
DK13	DK13	D	Yes	D09-CH10-F11-UK12-DK13
HU13	HU13	D	Yes	D08-CH09-F10-DK11-TUM12-HU13
TUM13	TUM13	D	Yes	D08-CH09-F10-UK11-DK12-TUM13
HU13NC	HU13NC	HUNC	No	Since F_5 in Hungary (non-cycling)
F13	F13	HU	Yes	HU09-NL10-D11-CH12-F13
UK13	UK13	HU	Yes	HU08-NL09-D10-CH11-F12-UK13
UK13NC	UK13NC	UKNC	No	Always in the UK (non-cycling)
CH13	CH13	UK	Yes	UK08-TUM09-HU10-NL11-D12-CH13
D13	D13	UK	Yes	UK08-DK09-TUM10-HU11-NL12-D13
NL13	NL13	UK	Yes	UK09-DK10-TUM11-HU12-NL13

*Partner codes and institutes: CH = FIBL, Switzerland; D = Uni. Kassel, Germany; DK = University of Copenhagen, Denmark; F = INRA, France; HU = Centre for Agricultural Research, Hungary; NL = Louis Bolk Institute, The Netherlands; TUM = Technical University of München; UK = The Organic Research Centre, United Kingdom. NC = Non-cycling population.

Plot sizes in both experimental seasons were 16.5m^2 (11x1.5m). The wheat was sown on the 31.10.2013 and on 29.10.2014. Soil samples taken at two depths (0-30cm and 30-60cm) per replicate block shortly after sowing indicated a mean mineral nitrogen availability (kg N/ha) in the two soil levels of 49kg N/ha in 2013 and 54kg N/ha in 2014. Soil samples were taken and analysed according to the VDLUFA standards (VDLUFA, 1991).

4.2.3 Data processing and statistics

The calculation of a mean NGLA% over all three leaf levels was done through the weighting of the F leaf by the factor of 4, and the F-1 and F-2 leaves weighted by the factor of 3 (Brumlop *et al.*, 2017). The higher weighting of the flag leaf takes into account its greater contribution to total grain yield in comparison to lower leaves, as reported by Lupton (1969). Using the mean NGLA% of both assessment dates, the Area under the Disease Progress Curve (AUDPC) was calculated (Shaner & Finney, 1977), as well as the Relative Area under the Disease Progress Curve (RAUDPC) in accordance with Fry (1978). RAUDPC was calculated as follows:

$$RAUDPC = \frac{AUDPC_i}{AUDPC_{max}}$$

in which AUDPC_i= AUDPC of the *i*th genotype is divided by $\mathrm{AUDPC}_{\max}$ = the maximum potential AUDPC value of all genotypes in one trial (total no. of days in assessment period multiplied by maximum NGLA% of 100).

Using the severity classes described by Bockmann (1963), a foot disease severity index (DI) could be calculated as a general disease index for all three pathogens combined or for each foot rot pathogen separately, using the calculation as follows:

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

in which $x_1 \ldots x_3$ are the number of plant stems with the disease scores 1 to 3, respectively, and *n* is the total number of stems assessed.

Data analysis was done using the statistical software R (Version 3.3.3, 2017.03.06). The arcsine transformation was used to transform percentage data, where after data was tested for normal distribution of the residuals through QQ plots and the Shapiro-Wilk Test. Data were then tested for homogeneity of variance using the Levene Test for parametric and the Fligner-Killeen Test for non-parametric data sets. As ANOVA is considered a robust test against minor violations to data normality, data sets that were normally distributed or had minor deviations from normality, but that indicated homogeneity of variance, were tested using a univariate ANOVA and subsequent Post-hoc Tukey HSD Test (R package *agricolae*; de Mendiburu, 2015). For data that was found to be normally distributed, but that indicated heterogeneity of variance, a Welch's ANOVA and Post-hoc Games-Howell Test was calculated (R package *userfriendlyscience*; Gjalt-Jorn, 2017). In data sets that displayed neither normality, nor homogeneity of variance, a non-parametric Kruskal Wallis H Test and pairwise comparison with Holm correction were used.

Grain yield, TKW, stem length, AUDPC values, degree of awnedness and other agronomic parameters were analysed in separate models for each generation in each experimental year using the main effects of experimental entries and CCP origin groups (DNC, D, HUNC, HU, UKNC, UK) as fixed factors and replicate blocks as a random effect. In 2014/15, the F_{13} and F_{14} CCP entries and reference varieties were compared for a number of agronomic and morphological parameters in separate models using the experimental entries as the fixed factor and the replicate blocks as the random effect. In the comparison of the F_{13} and F_{14} CCP entries only in 2014/15, the main effects of CCP entries and generation were used as fixed factors, as well as the interaction between them for a number of measured traits, whilst the replicate block was included as the random effect. Comparisons for a number of agronomic parameters between the differing generations across both experimental seasons for both CCP entries only and all experimental entries were additionally performed using the experimental entries as the fixed factor. For the calculation of correlations between agronomic parameters within each generation, as well as the correlations between TKW at sowing and agronomic parameters, data was tested for normality and either a Pearson Product-Moment correlation or Spearman's rank correlation performed.

4.2.2 Assessments

In each experimental year, grain yields (t/ha^1) and thousand kernel weight (TKW) (g) were recorded and adjusted to 14% moisture content. During the growing season of both experimental years, plant growth stages were recorded according to the BBCH decimal code for growth stages (Witzenberger *et al*., 1989; Lancashire *et al*., 1991), based on the most frequently occurring BBCH stage on 20 to 30 plants, recorded 6 times per plot in order to adequately record growth stages at the specific assessments.

Foliar diseases caused by fungal pathogens were assessed twice during the growing season in both experimental years (2013/14 and 2014/15). Non-green leaf area (NGLA) was recorded in % (1-100%) on the flag leaf (F), the leaf below the flag leaf (F-1) and the F-2 leaf. The first foliar leaf assessment was carried out on all three leaf levels at BBCH stages 45-55 (26.05.2014, 29.05.2015) and the second assessment completed at BBCH 60-70 (16.06.2014, 17.06.2015), which included only two leaf levels due to leaf dieback in the F-2. In both experimental years, an average NGLA % per leaf level was estimated from an area of neighboring plants of approximately 25cm in length. NGLA of CCPs and reference varieties was assessed 6 times per plot and across all replicate blocks. The two main foliar leaf diseases observed were also recorded at each assessment date.

In addition to foliar disease, foot diseases were assessed at the beginning of July per CCP entry and pure line variety (BBCH 70-75) in the experimental year of 2013/14 only. A minimum of 30 plants with roots were pulled from five to six points per plot and across all replicate blocks. Soil residue and the outer stem sheath were removed and the lower stems were assessed for foot diseases (*Fusarium* spp., *Pseudocercosphorella herpotrichoides* and *Rhizoctonia cerealis*) according to a pictorial key (Bayer CropScience, 2013). Root rot symptom severity was assessed according to Bockmann (1963). Healthy plant stems were awarded the score of 0, plants with <50% of the stem diameter showing symptoms were awarded a score of 1, plants showing disease symptoms >50% of the stem diameter were scored as 2 and rotten or broken stems (caused by *P. herpotrichoides* only) were awarded a score of 3.

Morphological assessments were done by cutting 3 x 0.5m rows of mature plants from each plot (total area per plot: 0.450m^2). The plants were removed as close to the ground as possible and number of ears, stem length (from stem base to start of ear), ear length (from start of ear to tip of ear, awn length not included) and degree of awnedness were recorded. From these samples, total biomass and kernel weight were also recorded in order to calculate Harvest Index (HI) and kernel number per ear.

Protein content (%) was recorded for all CCP entries and reference varieties in both generations and in both experimental years. Protein content (%) was calculated according to seed nitrogen content (% N x 5.7), which was analysed using the Elementar Analysator vario MAX (Elementar Analysesysteme GmbH, Hanau, DE). In addition, a number of baking quality parameters were assessed for all F_{14} CCPs and reference varieties in 2014/15. Hagberg Falling Number (HFN) (ICC Method no. 107), sedimentation value (Zeleny) (ICC Method no. 116), wet gluten content (%) (ICC Method no. 106/2) and water absorption capacity (%) (ICC Method no. 179) were analysed by Aberham Laboratories, Großaitingen, DE. The analysis of baking volume (ml/100g flour) was based on an internal test developed by Aberham Laboratories using wholemeal flour and the addition of malt flour in order to stabilize the loaf crust only when HFN values were too high (personal communication, Dr. Aberham).

4.3 Results

4.3.1 Weather

Both experimental seasons were characterised by dry winters and springs with the exception that in May of 2013/14, enough rain fell during the critical period of flowering to prevent serious damage. In 2013/14, the dry months over winter and into early spring were coupled with higher than average temperatures, particularly between January and April. In 2013/14, the mean temperature was 10°C (Oct. to Aug.) and the total precipitation for the same period was 620mm. The drought in the second experimental year of 2014/15 was uninterrupted from November to June with a total seasonal precipitation between October and June of 298 mm leading to extremely early maturation so that the 95 mm that fell in July had no effect on yield (Figure 4.2). Monthly temperatures in 2014/15 were generally similar to the long-term average (1971-2000), except for higher than average temperatures from mid-June to August (Figure 4.2).

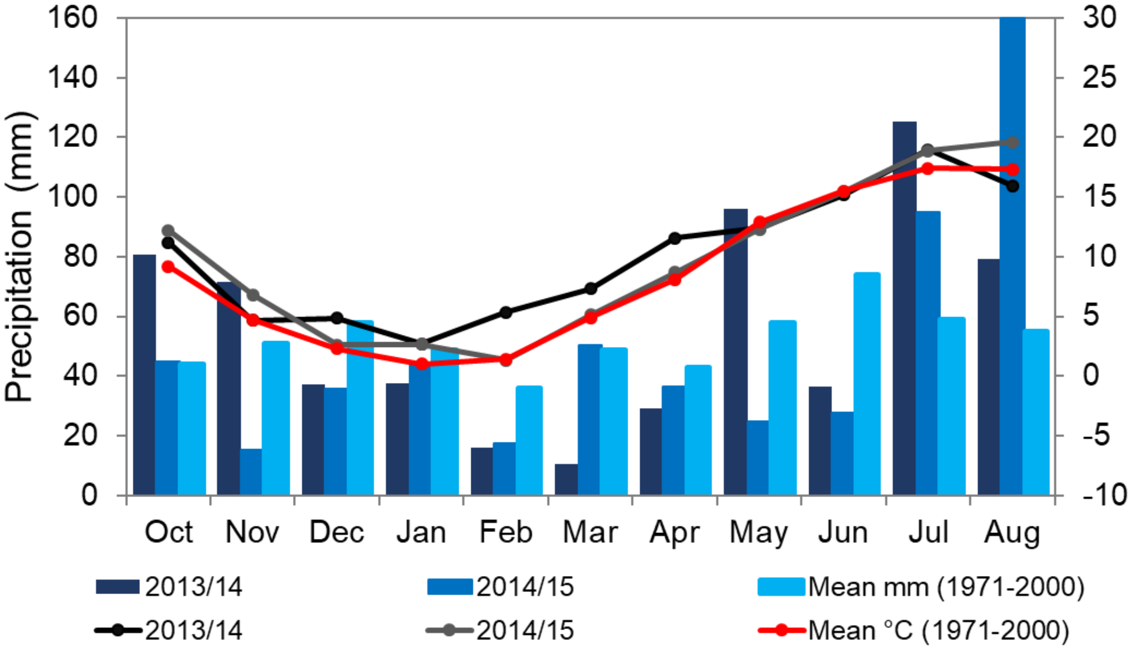

Figure 4.2: Mean monthly temperatures (°C) and mean monthly precipitation (mm) for the experimental years of 2013/14 and 2014/15. The long-term monthly mean for Göttingen (1971-2000) for both temperature and precipitation is given.

4.3.2 Grain yield and yield components

Significant replicate block effects were observed for the CCP entries for a number of agronomic parameters in both 2013/14 and in 2014/15 (Table 4.2). In 2013/14, there were block effects present for yield, TKW, number of ear bearing tillers per m^2, kernels per ear, HI and stem length. However, AUDPC and percentage of awnleted ears per m^2 did not differ significantly among replicate blocks. In 2014/15, significant replicate block effects were present for yield, number of ear bearing tillers per m^2 and AUDPC (Table 4.2).

Table 4.2: Mean squares (MS), F values and p values from analysis of variance for agronomic parameters of the CCP entries in both experimental years. Generation represents the two generations F_{13} and F_{14} (2014/15), Entry represents the CCP entries and Block represents the replicate blocks. Significant Entry and Block effects are marked in bold for 2013/14. For 2014/15, Entry, Gen. and Block effects are only marked in bold if there is no significant Entry x Gen. interaction effect.

2013/14								**2014/15**							
	Yield				**TKW**				**Yield**				**TKW**		
	Df	**MS**	**F value**	**p value**	**MS**	**F value**	**p value**		**Df**	**MS**	**F value**	**p value**	**MS**	**F value**	**p value**
Entry	10	0,31	2,58	**0,02**	7,64	5,35	**<0,001**	Entry	10	0,17	1,81	0,08	4,39	5,22	<0,001
Block	3	0,76	6,28	**<0,01**	10,80	7,56	**<0,001**	Generation	1	0,03	0,29	0,59	5,44	6,46	0,01
Residuals	30	0,12			1,42			Block	3	0,90	9,78	**<0,001**	0,86	1,03	0,39
								Entry*Gen.	10	0,12	1,27	0,27	2,24	2,66	**<0,01**
								Residuals	63	0,09			0,84		
	Ear bearing tillers/m^3				**Kernels per ear**				**Ear bearing tillers/m^3**				**Kernels per ear**		
Entry	10	2401	1,35	0,25	4,95	1,80	0,10	Entry	10	1408	0,82	0,61	11,23	2,89	<0,01
Block	3	11306	6,36	**<0,01**	14,49	5,29	**<0,01**	Generation	1	109	0,06	0,80	3,06	0,79	0,38
Residuals	30	1777			2,74			Block	3	12490	7,31	<0,001	4,52	1,16	0,33
								Entry*Gen.	10	3795	2,22	**0,03**	7,93	2,04	**0,04**
								Residuals	63	1708			3,89		
	HI				**AUDPC**				**HI**				**AUDPC**		
Entry	10	0,0006	3,60	**<0,01**	0,004	2,47	**0,03**	Entry	10	0,0014	6,75	**<0,001**	0,009	2,68	**<0,01**
Block	3	0,0024	14,64	**<0,001**	0,002	1,06	0,38	Generation	1	0,0004	2,02	0,16	0,001	0,37	0,55
Residuals	30	0,0002			0,001			Block	3	0,0020	5,01	**<0,01**	0,059	18,06	**<0,001**
								Entry*Gen.	10	0,0003	1,34	0,23	0,003	1,03	0,43
								Residuals	63	0,0002			0,003		
	Stem length				**Awnleted ears**				**Stem length**				**Awnleted ears**		
Entry	10	65,96	4,63	**<0,001**	0,028	6,80	**<0,001**	Entry	10	43,43	5,14	**<0,001**	0,0356	15,50	**<0,001**
Block	3	87,87	6,17	**<0,01**	0,006	1,46	0,25	Generation	1	21,15	2,50	0,12	0,0000	0,01	0,94
Residuals	30	14,24			0,004			Block	3	15,89	1,88	0,14	0,0001	0,05	0,99
								Entry*Gen.	10	11,42	1,35	0,22	0,0035	1,50	0,16
								Residuals	63	8,45			0,0023		

Total yields were significantly greater in 2013/14 (F_{13} only) (mean yield of 4.7 t/ha) in comparison to both the F_{13} and F_{14} of 2014/15 (mean yield 4.2 t/ha) (Table A 4.6). Significant differences between CCP entries and reference varieties were only found in 2013/14. Both the greatest and the smallest yields of 2013/14 were achieved by reference varieties Capo (5.6 t/ha) and Akteur (3.7 t/ha), respectively (Figure 4.3). Yields of seven out of eleven CCP entries were not significantly different from Capo. The CCP entries in 2013/14 all yielded similarly to one another with the UKNC and DK13 CCPs yielding the highest (5.04 and 5.03 t/ha, respectively) and D13, the lowest (4.2 t/ha) (Figure 4.3, Table A 4.6).

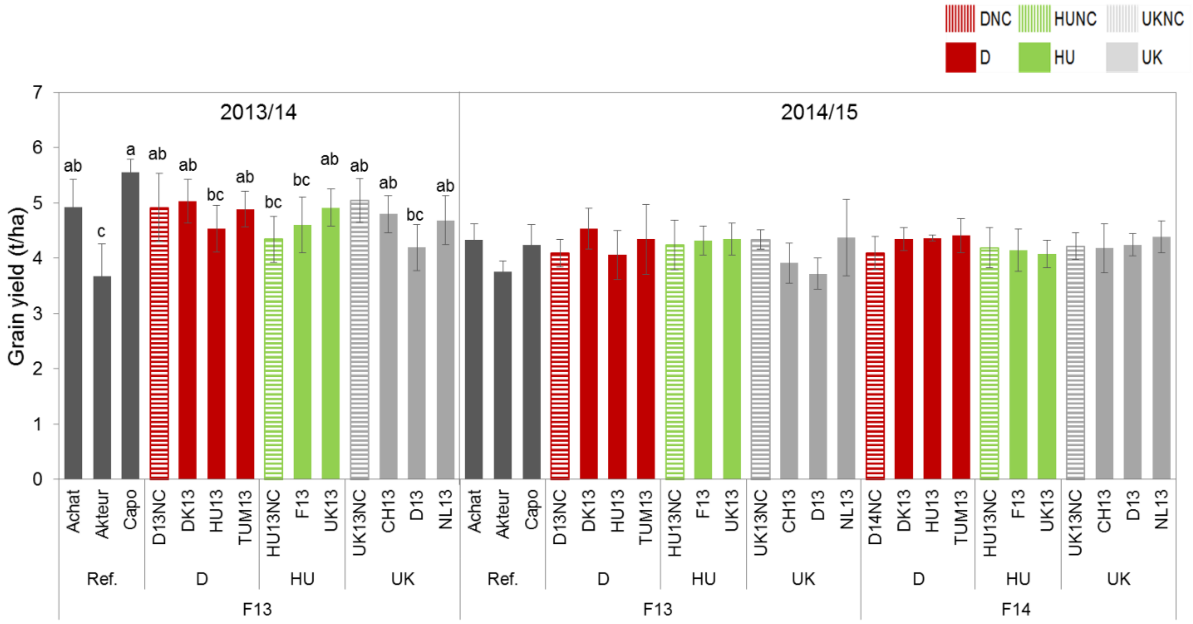

Figure 4.3: Total grain yields (t/ha) for the experimental years of 2013/14 and 2014/15. Error bars denote standard deviations. Differing small letters indicate significant differences between the F_{13} CCP entries and reference varieties within 2013/14 ($p<0.05$).

In 2014/15, no significant differences in yield were found between the CCP entries and reference varieties when comparing both within individual generations and across generations (Figure 4.3, Table A 4.6). Within the F_{13} CCPs, the greatest yield was achieved by DK13 (4.5 t/ha) and the lowest by D13 (3.7 t/ha). Between the F_{14} CCPs, the greatest yield was achieved by the TUM13 CCP (4.4 t/ha) and the lowest yield by the UK13 CCP (4.1 t/ha). No significant differences in grain yield were found between the two generations in 2014/15 and there was no interaction effect found between CCP entries and generations (Table 4.2).

TKW (g) values ranged from 48.1g (Achat) to 41.7g (HU13NC) in the experimental year of 2013/14. There were significant differences found for TKW values between the HU13NC CCP and the CCPs D13NC (45.9g), UK13 (44.9g) and CH13 (45.2g) (Table A 4.6). In the F_{13} in the experimental year of 2014/15, significant differences between CCPs were still present with the greatest TKW found in the non-cycling D13NC (45.7g) and the lowest in CCP D13 (42.5g). In the F_{14} of 2014/15, significant differences for TKW values between the CCPs were no longer present with the DK13 CCP achieving the greatest TKW value (45.9g) and UK13NC, the smallest (44.2g). There was a significant difference found for mean TKW between the two generations of CCPs in 2014/15 (F_{13}: 44.5g; F_{14}: 43.9g), as well as a significant interaction effect between the CCP entries and the generation (Table 4.2). TKWs were positively associated with yield, but the correlation was only significant in the F_{14} (Table 4.3 A).

Significant differences between the CCP entries for kernel number per ear were only found in the F_{13} of 2014/15. In 2013/14, kernel numbers per ear ranged from 27 (Akteur) to 32 (F13 CCP). In 2014/15, kernel numbers per ear were overall lower but similar among generations. In the F_{13} of 2014/15, kernels per ear ranged from the lowest value of 23 (HU13) to the highest of 29 in NL13. The NL13 CCP was found to have significantly more kernels per ear in comparison to HU13, TUM13 (25), F13 (25) and CH13 (25). Kernel number per ear in the F_{14} of 2014/15, ranged from the lowest found in the D13NC (22) to the greatest in the F13 (28) (Table A 4.6). No significant interaction effect was found between the CCP entries and generation (Table 4.2). Kernel number per ear was positively correlated with yield, but this correlation was only significant in the F_{14} of 2014/15 (Table 4.3 A).

No significant differences were found for ear-bearing tillers per m^2 between CCP entries in any generation or experimental year, however a significant interaction effect (F=2.22, p=0.03) was found between the CCP entries and the generations in 2014/15 (Table 4.2). Additionally, no significant difference in mean ear-bearing tillers per m^2 between the two generations in 2014/15 was found. Ear-bearing tillers per m^2 and yield correlated significantly in each generation and in each experimental year (Table 4.3 A).

Table 4.3: A) Correlation coefficients (R) for various agronomic parameters for the reference varieties and CCP entries of the F13 and F14 in the experimental years of 2013/14 and 2014/15. Significant correlations are indicated in bold. B) Correlation coefficients (R) for various agronomic parameters and TKW at sowing for CCP entries of the F_{13} and F_{14} in the experimental year of 2014/15. Significant correlations are marked in bold.

A.

F_{13} (2013/14)

	Yield	TKW	Ears/m^2	Kernel no.	HI	Stem length	AUDPC	Protein (%)
Yield	-	0,18	**0,39****	0,15	-0,10	**0,54*****	**-0,45*****	-0,23
TKW	-	-	-0,17	0,04	0,15	-0,03	0,21	-0,22
Ears/m^2	-	-	-	-0,12	**-0,34****	**0,46*****	-0,16	0,11
Kernel no.	-	-	-	-	**0,60*****	-0,14	-0,11	**-0,46*****
HI	-	-	-	-	-	**-0.54*****	-0,02	-0,31*
Stem length	-	-	-	-	-	-	-0,19	0,01
AUDPC	-	-	-	-	-	-	-	**0,32***
Protein (%)	-	-	-	-	-	-	-	-

F_{13} (2014/15)

	Yield	TKW	Ears/m^2	Kernel no.	HI	Stem length	AUDPC	Protein (%)
Yield	-	0,15	**0,47*****	0,21	0,25	0,19	-0,03	0,11
TKW	-	-	-0,01	-0,18	-0,13	0,15	0,21	-0,08
Ears/m^2	-	-	-	-0,20	**0,34***	0,19	0,09	**-0,28***
Kernel no.	-	-	-	-	**0,60*****	-0,06	-0,11	0,11
HI	-	-	-	-	-	**-0,39****	-0,02	-0,24
Stem length	-	-	-	-	-	-	-0,12	0,02
AUDPC	-	-	-	-	-	-	-	0,12
Protein (%)	-	-	-	-	-	-	-	-

F_{14} (2014/15)

	Yield	TKW	Ears/m^2	Kernel no.	HI	Stem length	AUDPC	Protein (%)
Yield	-	**0,26***	**0,40****	**0,28***	0,25	**0,48*****	-0,01	-0,08
TKW	-	-	-0,05	0,18	0,19	0,20	0,24	-0,14
Ears/m^2	-	-	-	-0,26	0,02	0,12	-0,03	-0,16
Kernel no.	-	-	-	-	**0,60*****	-0,08	0,02	-0,20
HI	-	-	-	-	-	**-0,29***	0,17	**-0,42****
Stem length	-	-	-	-	-	-	-0,13	-0,05
AUDPC	-	-	-	-	-	-	-	0,23
Protein (%)	-	-	-	-	-	-	-	-

*p<0,05, **p<0,01, ***p<0,001

B.

			2013/14					
Gen.	**Yield**	**TKW**	**Ears/m^2**	**Kernel no.**	**HI**	**Stem length**	**AUDPC**	**Protein (%)**
F_{13}	0,08	**0,36***	-0,01	-0,27	-0,19	0,22	**0,32***	0,12
			2014/15					
F_{13}	-0,01	0,14	0,01	-0,25	**-0,43****	**0,41****	0,02	-0,14
F_{14}	-0,10	0,15	0,06	-0,08	-0,13	0,02	0,05	-0,02

*p<0,05, **p<0,01

Harvest Index (HI) values in 2013/14 ranged from the lowest in the CCP D13 (0.38) to the highest in NL13 of 0.42 (Table A 4.6). In the F_{13} of 2014/15, the CCP NL13 still maintained the highest HI (0.42) and HU13 and Capo, the lowest with 0.38 and 0.37, respectively. In the F_{14} of 2014/15, the F13 CCP achieved the greatest HI value of 0.42, differing significantly to CH13 (0.38), Capo (0.37), D13NC (0.37) and D13 (0.37) (Table A 4.6). No significant difference was found for mean HI values between the two generations of 2014/15, however a significant interaction effect was present between CCP entries and the generations (Table 4.2). In both experimental years, HI values and yield were not correlated. Correlations between HI values and number of ear-bearing tillers per m^2 were significant and positive in each generation and experimental year (Table 4.3 A).

4.3.3 Foot and foliar disease

Foot diseases were low in 2013/14 and absent in the very dry 2014/15. The dominating foot disease pathogens of 2013/14 were *Fusarium* spp. (total mean DI of 14.8), followed by *Pseudocercosporella herpotrichoides* (total mean DI of 10.9) and *Rhizoctonia cerealis* (total mean DI of 0.6) (Table A 4.7). No significant differences were found between any of the CCP entries and reference varieties for any of the individual foot diseases indices or for the combined foot disease incidence. The combined foot disease index (total mean DI 25.6) in 2013/14 was low to moderate with the greatest combined DI found in the cycling D13 population (DI 31.3) and the lowest in the cycling CCP UK13 (Table A 4.7).

The main foliar disease observed in both experimental years was stripe rust caused by *Puccinia striiformis. Septoria* spp. and *Dreschlera tritici-repentis* were also present, although less frequently than stripe rust. Foliar disease pressure was lower in 2013/14, with AUDPC ranging from 175 (Akteur) to 42 (Capo) (Table A 4.6), than in 2014/15, when AUDPC ranged from 338 (Akteur) to 176 (Capo). NGLA values in 2013/14 ranged from 2 to 13% (1st assessment) and from 7 to 14% (2nd assessment). In 2014/15, NGLA values at the 1st assessment ranged from 4 to 11% and from 10 to 33% at the 2nd assessment.

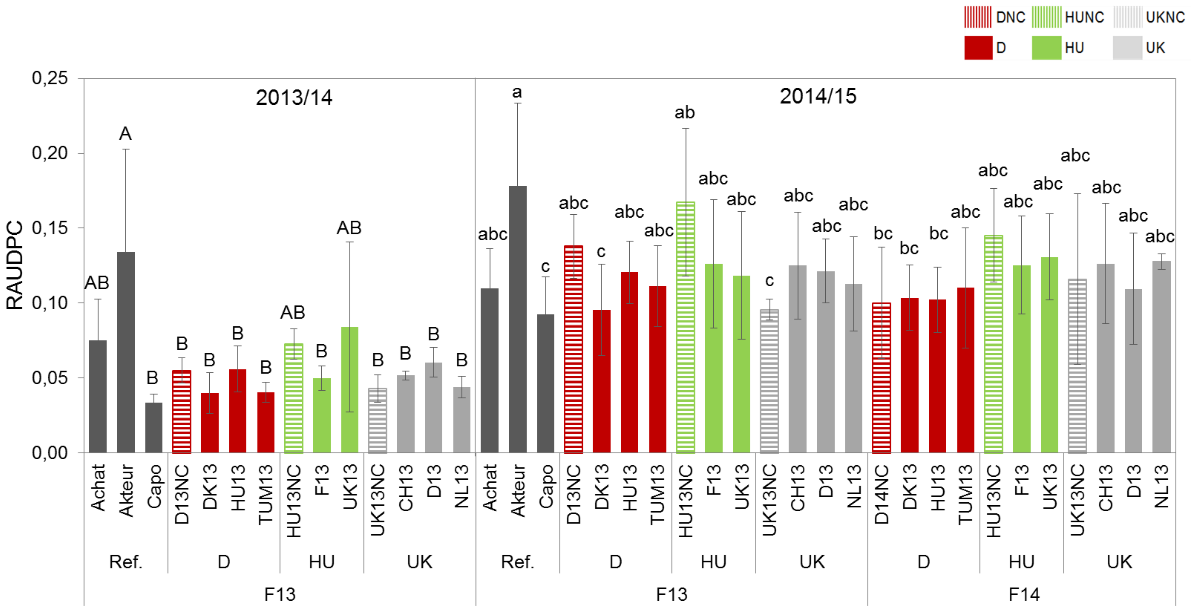

Figure 4.4: RAUDPC values (Relative Area Under the Disease Progress Curve) for the experimental years of 2013/14 and 2014/15. Error bars denote standard deviations. Differing capital letters indicate significant differences between the F_{13} CCP entries and reference varieties within 2013/14 ($p<0.05$). Differing small letters indicate significant differences between the F_{13} and F_{14} CCP entries and reference varieties within 2014/15 ($p<0.05$).

In 2013/14, no significant differences were found between CCP entries for foliar disease values. However, apart from the non-cycling HU13NC (RAUDPC=0.07 and AUDPC=94) and the cycling UK13 (0.08 and 109, respectively), from Hungarian origin, all other CCPs had significantly lower RAUDPC and AUDPC values in comparison to the most susceptible reference variety Akteur (0.13 and 175, respectively) (Figure 4.4, Table A 4.6). Despite the lower overall disease levels, yield correlated negatively with AUDPC in 2013/14 only ($p<0,001$; $R = -0,45$) (Table 4.3 A).

In 2014/15, significant differences for RAUDPC and AUDPC values were only found between CCP entries in the F_{13}. The Hungarian non-cycling F_{13} HU13NC (0.17 and 318) had significantly greater RAUDPC and AUDPC values in comparison to the non-cycling F_{13} UK13NC (0.10 and 182) and cycling F_{13} DK13 (0.10 and 182) CCPs. These two CCPs had similar low RAUDPC and AUDPC values to the reference variety Capo (0.09 and 176), and all three entries had significantly lower foliar disease values in comparison to the reference variety Akteur (0.18 and 338). There were no significant differences between the F_{13} and F_{14} CCP entries for either AUDPC and RAUDPC values in 2014/15 (Table A 4.6, Figure 4.4).

4.3.4 Effect of differing seed size on agronomic parameters in 2014/15

As seed of the F_{13} CCPs were sent from various partners, TKWs differed for each population. The TKWs ranged from the smallest of 42g (NL13 CCP) to 47g (UK13 CCP) (SD of TKW at sowing F_{13}: 1.42; F_{14}: 1.38). In contrast, the range of TKW for the F_{14} (i.e. as harvested in 2014) was much smaller, ranging from 45g to 47g (see above). In both years, significant correlations between TKWs at sowing and agronomic parameters were found for the F_{13}, but not for the F_{14} in 2015. In 2013/14, positive significant correlations were present between TKW at sowing, AUDPC and TKW values (Table 4.3 B). CCPs with greater TKW at sowing also tended to have greater TKWs at harvest. This correlation is supported by the moderate negative correlation between TKW at sowing and kernel number per ear, whereby fewer kernels per ear generally correlates with higher TKW values. In the drought year of 2014/15, a significant negative correlation between TKW at sowing and HI values and stem length was found for the F_{13} CCPs (Table 4.3 B). For the F_{13} in both years, TKW at sowing reduced kernel number per ear, albeit not significantly.

4.3.5 Effect of differing CCP origins on agronomic parameters

Populations that travelled did not differ significantly from their non-travelling original populations for yield (data not shown) and yield components. Although some significant differences were found between differing CCP groups, these were not consistent within each generation and experimental year. The grouping of the CCPs according to their origin and management history (cycling/non-cycling) indicated a significant difference for HI only in the F_{14} of 2014/15 when grown from seed of similar weight. In the F_{14}, the HI of the DNC CCP (0.37) was significantly lower to the mean HI of the HU cycling CCPs (0,41) and the UKNC CCP (0.41) (Figure 4.5 A). In both years, differences among the F_{13} populations in TKW followed similar trends with DNC having the largest TKW and HUNC the smallest (Figure 4.5 B). While in 2013/14, TKW at sowing correlated significantly with TKW at harvest (Table 4.3 B), this was not the case for the F_{14} in 2014/15. Despite the fact that seed weight of the DNC had been largest in the F_{14}, at harvest it was among the smallest, whilst the cycling CCP group of German origin (D) achieved the greatest mean TKW, significantly greater than the German non-cycling CCP (DNC), the UK non-cycling CCP (UKNC) and the UK cycling CCPs (UK) (Figure 4.5 B). No significant differences were found between CCP origin groups for number of ears per m^2 within the generations and experimental years (Figure 4.5 C). However, in 2015, when disease pressure due to stripe rust was overall higher, the HUNC CCP (F_{13}) had significantly higher AUDPC in comparison to the CCPs that had travelled (D, HU, UK) and the UKNC CCP. For the F_{14} the pattern was similar, but not significant (Figure 4.5 D).

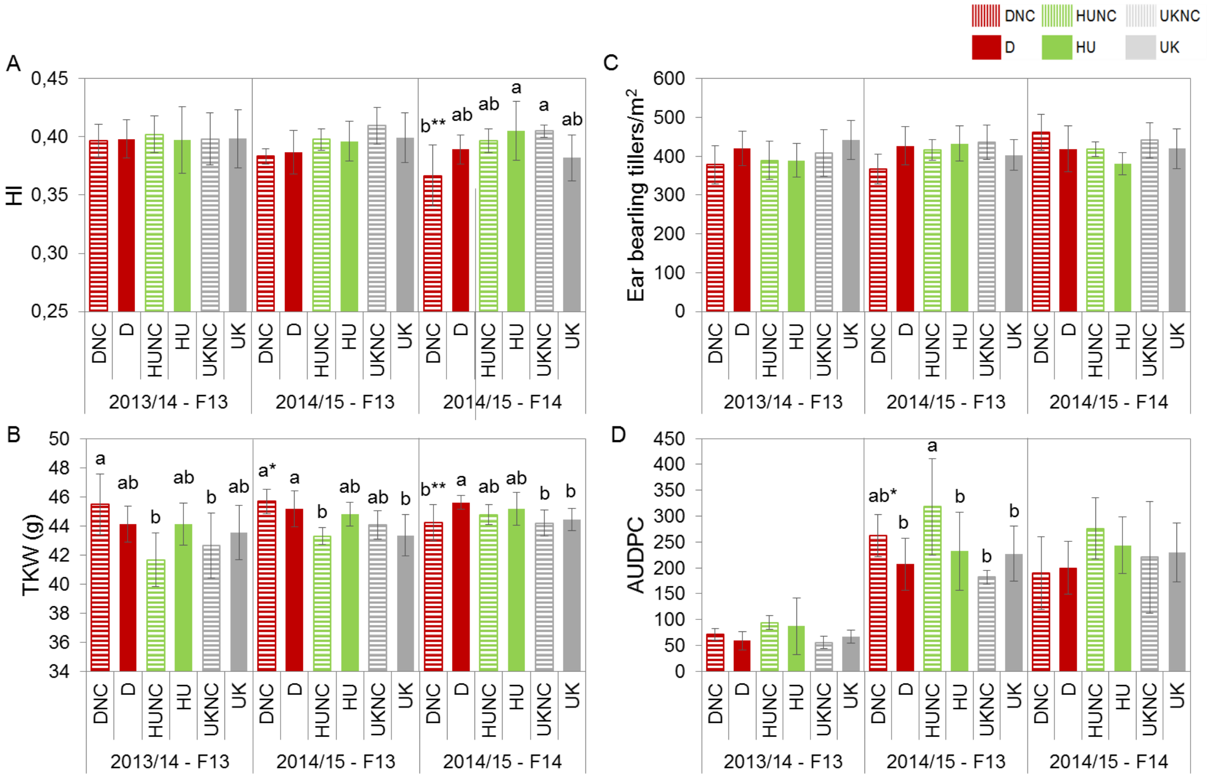

Figure 4.5: HI, number of ear-bearing tillers per m^2, TKW (g) and AUDPC values per CCP origin groups for each generation and experimental year. Differing small letters indicate significant differences between the CCP origin groups within the F_{13} of 2013/14 ($p<0,05$). *Differing small letters indicate significant differences between the CCP origin groups within the F_{13} of 2014/15 ($p<0.05$). **Differing small letters indicate significant differences between the CCP origin groups within the F_{14} of 2014/15 ($p<0.05$).

4.3.6 Stem and ear length

The reference variety Capo was consistently the tallest entry over both experimental years and the reference variety Akteur, the shortest. The mean stem length (cm) of all CCP entries and reference varieties was significantly longer in F_{13} of 2013/14 (93cm) in comparison to F_{13} and F_{14} of 2014/15 (88 and 89cm, respectively) (Table 4.4). Significant differences between CCP entries were present in the F_{13} generation of both experimental years for mean stem length, but no longer in the F_{14} (Table 4.4).

Table 4.4: Mean stem length (cm) for the CCP entries and reference varieties per generation and in each experimental year. Differing letters indicate significant differences between entries within a generation and experimental year (p<0.05).

Origin	**Entry**	**Stem length (cm)**			**Ear length (cm)**		
		2013/14	**2014/15**		**2013/14**	**2014/15**	
		F_{13}	**F_{13}**	**F_{14}**	**F_{13}**	**F_{13}**	**F_{14}**
References	Achat	87 cd	84 cd	84 cd	9,2 a	7,8 ab	7,8
	Akteur	82 d	79 d	79 d	9,1 ab	8,0 a	8,0
	Capo	102 a	95 a	95 a	8,0 b	7,2 b	7,2
D	D13NC	92 abcd	90 abc	88 abc	8,5 ab	7,7 ab	7,6
	DK13	93 abcd	88 abc	90 abc	8,6 ab	7,7 ab	7,8
	HU13	92 abcd	86 bcd	90 abc	8,6 ab	7,7 ab	7,1
	TUM13	97 abc	91 ab	92 abc	8,5 ab	7,5 ab	7,9
HU	HU13NC	95 abc	87 bc	88 abc	8,4 ab	7,5 ab	7,8
	F13	90 bcd	84 cd	87 bcd	8,1 b	7,3 ab	7,6
	UK13	95 abc	92 ab	88 abc	8,4 ab	7,5 ab	7,6
UK	UK13NC	94 abc	87 bc	88 abc	8,3 ab	7,5 ab	7,4
	CH13	99 ab	91 abc	90 abc	8,6 ab	7,4 ab	7,6
	D13	100 a	91 ab	94 ab	8,3 ab	7,6 ab	7,5
	NL13	86 cd	84 cd	87 abcd	8,3 ab	7,6 ab	7,5
	Mean	93 A*	88 B	89 B	8,5 A*	7,6 B	7,6 B
	CCP mean	94 A**	88 B	89 B	8,4 A**	7,5 B	7,6 B

Mean ear length of the CCP entries and reference varieties was longer in 2013/14 (8,5cm), than in either generation of 2014/15 (7,6cm) (Table 4.4). No significant differences for mean ear length were found between the CCP entries in either generation or experimental year.

4.3.7 Ear morphology

Within each generation in each experimental year, significant differences were found between CCPs of the same origin for percentage awned number of ears per m^2 with no significant generation effect (Table 4.2). Over all generations in both experimental years, significant differences between CCP entries were found only for the percentage awned ear-bearing tillers per m^2 (Figure 4.6).

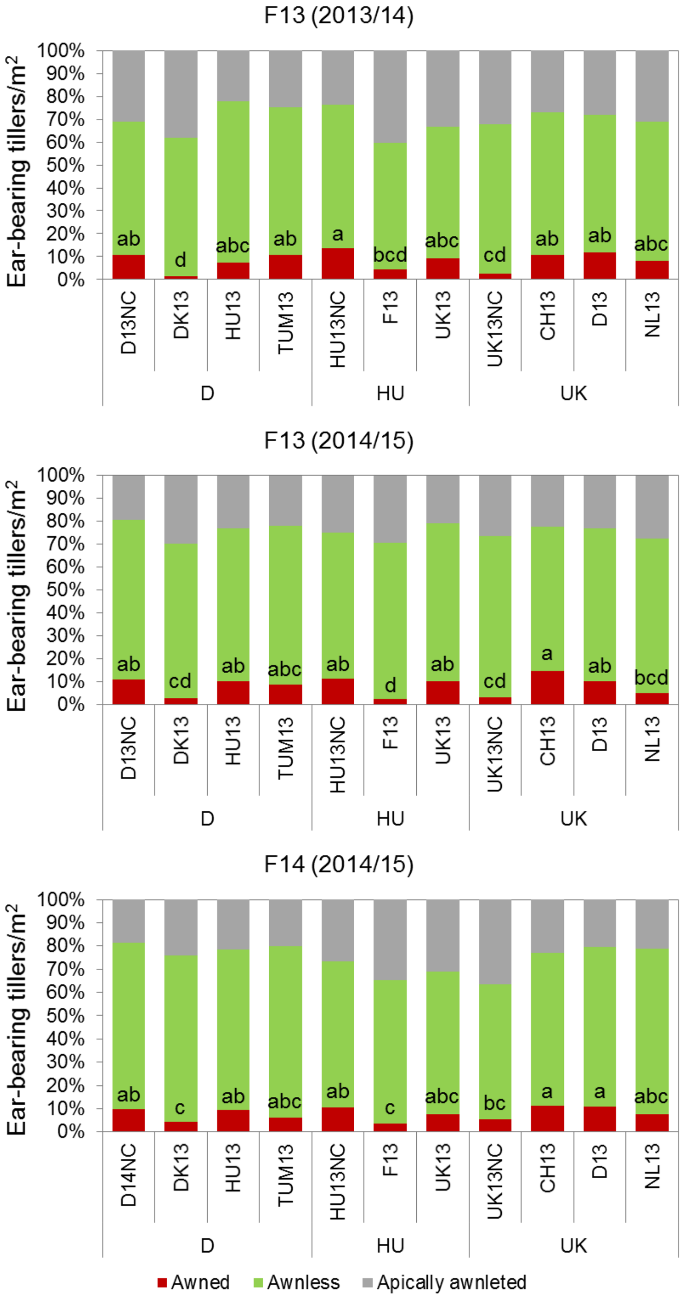

Figure 4.6: Percentage of awned, awnless and apically awnleted ear-bearing tillers per m^2 for all generations and experimental years (n=180 plants). Differing letters indicate significant differences for awned ears within a generation and for each experimental year.

In 2013/14, the percentage of awned ears per m^2 ranged from 1% in the CCP DK13 to 14% in the HU13NC CCP while in the F$_{13}$ of 2014/15, the percentage of awned ears per m^2 ranged from around 2% in the CCP F13 to almost 15% in the CH13 CCP. Similarly, in the F$_{14}$ of 2014/15, awned ears ranged from 4% (F13 CCP) to 11% (CH13 CCP) (Figure 4.6).

4.3.8 Baking quality

Protein content was low in both years reflecting the dry and very dry spring conditions. Significant differences between CCP entries and reference varieties for protein content (%) were found in the F_{13} of 2013/14 and F_{14} of 2014/15, however, there were no significant differences for mean protein yield (kg N/ha) in either generation and over both experimental years (Table 4.4). Over both experimental years, the reference variety Akteur achieved the greatest protein content, whilst for the CCPs over all generations, the CCPs D13 and HU13NC tended towards the best protein content, UK13NC and F13, the lowest.

Table 4.4: Protein content (%) and protein yield (kg N/ha) for the CCP entries and reference varieties per generation and in each experimental year. Differing letters indicate significant differences between entries within a generation and experimental year ($p<0.05$).

Origin	**Entry**	**Protein content (%)**			**Protein yield (kg N/ha)**		
		2013/14	**2014/15**		**2013/14**	**2014/15**	
		F_{13}	**F_{13}**	**F_{14}**	**F_{13}**	**F_{13}**	**F_{14}**
References	Achat	9,3 c	10,0	10,0 ab	460 ab	433	433
	Akteur	10,9 a	10,7	10,7 a	400 b	401	401
	Capo	9,3 c	9,7	9,7 b	516 a	411	411
D	D13NC	9,7 bc	9,7	9,8 ab	475 ab	398	403
	DK13	9,6 bc	9,5	9,5 b	485 ab	431	414
	HU13	9,6 bc	9,5	9,6 b	434 ab	386	420
	TUM13	9,9 bc	10,0	9,9 ab	483 ab	436	436
HU	HU13NC	10,1 b	10,0	9,7 b	439 ab	425	409
	F13	9,5 bc	9,9	9,3 b	440 ab	429	389
	UK13	9,8 bc	9,7	9,8 ab	484 ab	420	401
UK	UK13NC	9,4 c	9,7	9,4 b	472 ab	420	397
	CH13	9,6 bc	10,1	9,8 ab	459 ab	395	410
	D13	10,2 b	10,1	10,1 ab	427 ab	376	430
	NL13	9,5 bc	9,5	9,7 b	446 ab	419	424
	Mean	9,7 ns*	9,9	9,8	459 A*	413 B	413 B
	CCP mean	9,7 ns**	9,8	9,7	459 A**	412 B	412 B

Colour coding was used in order to differentiate between poor, moderate and good ratings for the various baking parameters based on the recommendations of Kompetenzzentrum Ökolandbau Niedersachsen (2005) and as applied by Brumlop *et al*. (2017) (Table 4.5). Water absorption capacity is considered good above 58%, whilst anything below 54% is considered a poor rating affecting shelf life, reducing dough volume and negatively affecting dough proof times. In terms of wet gluten content (%), any value less than 23 % is considered a poor rating and any value over 27% can be classified as good or acceptable. Poor ratings for sedimentation are values under 22ml, whilst good values are indicated over 28ml. The Hagberg Falling Number (HFN) is measured in seconds, whereby a poor rating is considered anything less than 180 seconds and a good rating from 240-280 seconds. However, any HFN values over 280 seconds are also poorly rated. The baking volume was measured using wholemeal test loaves with a poor loaf volume found below 330ml and good baking volume found above 350ml (Dr. Aberham, personal communication, Brumlop *et al.*, 2017).

Table 4.5: Baking quality parameters for the F_{14} entries (2014/15) including water absorption (%), wet gluten content (%), sedimentation value (Zeleny, ml), Hagberg Falling Number (seconds) and baking volume (ml/100g flour). Differing letters indicate significant differences between the entries ($p<0.05$). Colour codes: Red=poor/low, orange=moderate and green=good/high rating (according to Brumlop et al. 2017).

Gen.	**Origin**	**Entry**	**Water absorption (%)**	**Wet gluten (%)**	**Sedi. value (Zeleny)**	**HFN (sec.)**	**Baking volume (ml/100g flour)**
F_{14} (2014/15)	Ref	Achat	60,5 abc	21,9 ab	31,8 ab	370,3 a	306,0
		Akteur	62,3 a	24,3 a	35,8 a	373,0 a	318,5
		Capo	62,4 a	21,4 ab	31,0 abc	312,5 b	278,2
	D	D14NC	60,5 abc	21,7 ab	25,8 cde	276,8 bc	302,8
		DK13	59,7 c	19,8 b	24,3 de	303,5 bc	297,2
		HU13	60,1 bc	20,2 b	22,8 de	260,0 bc	299,5
		TUM13	59,8 c	21,3 ab	22,0 e	280,8 bc	280,5
	HU	HU13NC	59,9 c	20,5 ab	25,8 cde	261,3 bc	294,8
		F13	59,3 c	18,6 b	21,5 e	249,0 c	278,8
		UK13	60,5 abc	20,9 ab	25,0 de	270,5 bc	300,7
	UK	UK13NC	60,0 bc	20,0 b	21,5 e	283,3 bc	294,4
		CH13	62,0 ab	20,8 ab	25,3 de	287,0 bc	306,7
		D13	60,6 abc	22,3 ab	28,0 bcd	288,0 bc	309,8
		NL13	60,1 bc	20,1 b	22,8 de	289,8 bc	283,3

In terms of water absorption capacity, all experimental entries achieved good values. Significant differences were found between CCP entries and reference varieties for water absorption capacity values, which ranged from the greatest in the reference varieties Akteur and Capo (62,3 and 62,4%, respectively) to the lowest in the F13 CCP (59,3%). In contrast, none of the entries achieved satisfactory wet gluten content, with the majority of the CCPs achieving lower values than the reference varieties (Table 4.5). Sedimentation values (ml) were found to be better in the three reference varieties, particularly Akteur (35,8ml), in comparison to the CCP entries. The D13 CCP achieved the best sedimentation value of 28ml, while the F13 and UK13NC CCPs were considered the most poorly rated, both achieving a value of only 21,5ml. The best HFN values were found in six of the CCPs (values ranged from 249-277ml); whilst the reference varieties achieved HFN values considered too high that their values are poorly rated. Baking volume was considered poor for all entries including the reference varieties. The greatest baking volume was achieved by the reference variety Akteur (319ml), followed by the CCPs D13 (310ml) and CH13 (307ml). The F13 CCP achieved the lowest baking volume of 278ml, although differences between entries were not significant (Table 4.5).

4.4 Discussion

Generally, the CCPs, both cycling and non-cycling were similar to one another for most agronomic parameters. However, some differences between CCPs in differing generations or between experimental years for a number of parameters help to dissect effects of variable seed size at sowing versus effects of drought on performance versus genetic divergence. Such differences also indicate that a degree of diversity and a high plasticity for response to environment is present among the CCPs. Under the drought conditions of 2014/15, the CCPs achieved the same yields as the reference varieties, whilst in 2013/14 four out of eleven CCPs were outyielded by the variety Capo while seven CCPs, Capo and Achat achieved higher yields than Akteur. Thus, only under the less stressful conditions in the first year, at least one of the reference varieties (Capo) could take advantage of its more modern genetics. In contrast, the excellent buffering capacity of genetic diversity in the face of stress protected the CCPs from stripe rust in the first year and from drought in the second.

4.4.1 Disease

Post 2011, three new non-European races of stripe rust (*Puccinia striiformis*) have made a dramatic appearance throughout Europe (Hovmøller *et al*., 2016) and first showed up at the experimental site in Germany in 2013/14. Mean disease measured as non-green leaf area (NGLA) was low in 2013/14. The higher NGLA in the second experimental year may most likely be due to the extended drought conditions experienced from November to June, whereby plants were physiologically stressed and as such may have had a higher predisposition to disease (Duveiller *et al*., 2007) and/or start to senesce earlier. Exposure of most cycling CCPs, as well as the non-cycling UK CCP, to the new stripe rust races before 2013/14 may have resulted in variable changes in resistance frequencies in comparison to the Hungarian non-cycling population. Changes in foliar pathogen resistance frequencies have been reported for wheat (Le Boulc'h *et al*., 1994; Paillard *et al*., 2000b; Porcher *et al*., 2004) and barley (Jackson *et al*., 1978; Webster *et al*., 1986; Ibrahim & Barrett, 1991; Danquah & Barrett, 2002b) populations dependent on the respective disease pressure. Apart from the HU13NC population, all CCPs had comparable AUDPC values to the pure line variety Capo, which is considered to be resistant to stripe rust (Buerstmayr *et al*., 2014). Disease severity in the CCPs at the experimental site in comparison to the susceptible varieties Akteur and Naturastar has been low over the past 11 generations whenever serious diseases occurred (Chapter 2). The YQ populations used in the experiment are a cross of all 20 parental varieties thus representing a high genetic diversity protecting the populations successfully from disease.

4.4.2 Yields and yield components

The drought conditions of 2014/15 reduced yields significantly in comparison to the first year. The most prominent reduction occurred in the highest yielding reference variety Capo (25%), which is in stark contrast to the first year when Capo had significantly outyielded four CCPs. In 2014/15, six out of 11 CCPs yielded even slightly more than Capo. Similar results have been reported for three CC barley populations which outyielded the reference variety Atem in an experimental year characterized by drought (Danquah & Barrett, 2002a). Raggi *et al*. (2017) report on the success of a barley CCP in terms of yield and yield stability in comparison to a number of line selections and reference varieties. The yield stability and good agronomic performance of the CCP was attributed to the unpredictability and changing environmental conditions of the breeding station during population development over 9 years, which would have selected for genotypes better suited to “contrasting climatic conditions” (Raggi *et al*., 2017). The Hungarian non-cycling population, which in the first experimental year was one of the lowest yielding CCPs, maintained its yield while yields of the other CCPs dropped during the dry second experimental year. This may indicate that this non-cycling population subjected to drier continental environmental conditions may have some advantages in terms of drought tolerance in comparison to the other CC populations, particularly as this population also had the highest disease incidence and still managed to perform well in terms of yield. The F_{11} of the German non-cycling CCPs had been included in other trials in 2011/12 and 2012/13 together with the same references and a mixture of their parental varieties (Brumlop *et al*., 2017). The CCPs outyielded their parental mixture, whilst CCP yields were equivalent to those of Achat, Akteur and Capo in the experimental year of 2012/2013 (mean yield 6.0 t/ha). However, whilst the CCPs were highly superior to their parental mixture when facing a severe black frost in 2011/12, they were out yielded by Achat and Akteur, but not Capo, in this year due to the superior winter hardiness of the reference varieties, a feature that apparently needs improvement in the CCPs.

Generally, genetic changes in CCPs tend to be dramatic in early generations due to selective pressures, but these selective pressures also lead to a loss of diversity through the selection of improved genotypes best suited to the prevailing environmental conditions. CCP evolution in later generations therefore results in slower and less dramatic changes; hence the tendency towards smaller variance in terms of agronomic performance and in phenotypical traits from the 10th generation onwards (Qualset, 1968; Goldringer *et al*., 2001a,b). The cycling and non-cycling CCPs were overall similar for agronomic traits with the exception of resistance to stripe rust and drought in the Hungarian non-cycling CCP and the higher protein content in the cycling D13 CCP. This may indicate that in general the CCPs were already stable for agronomic traits when the cycling experiment started in the F_8 and as such may have entered the later evolutionary phase where genetic changes are slower and less dramatic. Longer adaptive periods or strong selective pressure such as the recent stripe rust epidemic may be needed in order to cause divergent evolutions for agronomic traits.

The differences among CCPs in both F_{13} generations in both experimental years were no longer present in the F_{14} of 2014/15 grown from seed produced in the same field. Seed size heritability is considered to be low (Silvertown, 1989) and variation in seed size and number tends to be a result of phenotypic plasticity, which is thought to be adaptive, especially as the result of environmental variation (Vaughton & Ramsey, 1998; Lehtilä & Ehrlén, 2005). In terms of kernel number per ear, a significant interaction effect between CCP entries and generation in 2014/15 again highlights the plasticity of the CCPs in terms of seed number variation. It may also indicate stability for these two characteristics within the populations. A longer time period with higher selection pressures may be needed in order to evoke permanent changes for these two traits. Such changes have been found between generations in a number of dynamically managed French wheat populations (Goldringer *et al.,* 2001b).

Differences in HI values among CCPs corresponded mainly to the differences in CCP stem length; however, differences for HI values were not consistent in each generation and experimental year. No significant difference was found for mean HI values between the two generations in 2014/15, although a significant correlation between TKW at sowing and both HI and straw length were found in the F_{13} of 2014/15, but not in 2013/14. Thus in the drought year, CCPs with lower TKW at sowing tended to have higher HI values achieving a greater grain yield to total biomass yield ratio. This is mainly due to the positive correlation between TKW at sowing and stem length, which indicated that CCPs with larger TKW values tended to be taller and have greater biomass, reducing HI values.

Significant positive correlations were found in the F_{13} of both experimental years between HI values and number of ear-bearing tillers per m^2, which was no longer found in the F_{14} of 2014/15. This indicates that despite the differing environmental conditions of the experimental seasons, seed weight at sowing may have played a determinant role in the correlation between HI and ear bearing tillers per m^2. However, although the correlation was significant in both experimental years, it was negative in 2013/14 and positive in 2014/15 (F_{13}). As HI represents the ratio of grain yield to total plant biomass, the negative correlation between HI and number of ears/m^2 found in 2013/14 indicates that greater plant biomass in the form of ears per m^2 reduced HI values as resources were invested into plant biomass rather than grain yield (kernel number and TKW). However, in the drought conditions of 2014/15, a higher number of ears per m^2 were correlated with higher HI values, reflecting the more challenging growing conditions of the season and the advantage of an increased number of ears per m^2 to contribute to grain yield, thereby increasing HI values.

Number of ears per m^2 was significantly correlated with yield for all generations in both experimental years. However, only in the F_{14} of 2014/15, did TKW at harvest have a significant positive correlation with yield. This could not be attributed to TKW at sowing as a significant correlation regarding TKW at sowing and at harvest was only found for the F_{13} of 2013/14. However, a significant generation effect found for TKW in 2014/15 is indicative of differences for mean TKW values between the two generations and is likely relevant for the significant correlation found between TKW and yield in the F_{14}. A high response plasticity of the CCPs for TKW values has been reported previously (Chapter 2), particularly as the environmental conditions prevalent during seed formation, which have been very heterogeneous based on the significant replicate block effects, considerably affect the quality and number of offspring produced (Roach & Wulff, 1987; Valencia-Diaz & Montana, 2005). Yield and kernel number per ear were also only significantly correlated in the F_{14} of 2014/15, however, the F_{13} of the same experimental year showed a similar correlation coefficient, indicative that in this case the correlation is likely environment dependent. Protein content was significantly correlated with kernel number in the F_{13} of 2013/14 and with ears per m^2 in the F_{13} of 2014/15. This may have pointed to differing growth stages important for final protein content, which would have been affected by the differing climatic conditions; however, in the F_{14} of 2014/15, protein content was significantly correlated with HI values, making interpretation of the results difficult and highlighting the complexity of dissecting environmental effects from differing seed weight at sowing.

4.4.3 Stem and ear length and ear morphology

Stems and ears of the CCPs (F_{13}) in 2013/14 were significantly longer in comparison to the average stem length of the F_{13} and the F_{14} of the second experimental year. This can be attributed to the more favourable environmental conditions of the first experimental year. There was no significant difference found for mean stem length between the two generations in 2014/15. In this year, TKW at sowing and stem length correlated for the F_{13} CCPs but not for the F_{14}, however. Sown seed size varied little for the F_{14} and thus explain the lack of correlation. Similarly, significant differences between CCPs for mean stem length were no longer found in the F_{14}. However, the fact that differing seed size had an effect on stem length in the F_{13} in the second, but not in the first year, suggests an interaction with climatic conditions. Seed size has been positively correlated with plant fitness (Smith & Fretwell, 1974) and Stanton (1984) reported on the positive effects of seed size on growth rate and flower number in wild radish plants; however, these effects were only present in competitive environments. Under the challenging climatic conditions of 2014/15, the differences in seed size at sowing in the F_{13} CCPs affected stem length (plant growth rate). This effect was not present in the F_{14} CCPs as seed size was more similar. Differences in the mean stem length between CCPs were present only in the F_{13} of both experimental years, although these differences were not found to be consistent. Goldringer *et al*. (1998, 2001a,b) reported on the increased plant height in French winter wheat populations over a number of generations due to competition for light. Additionally, Knapp *et al*. (2013) found that allele frequencies related to dwarfing decreased in winter wheat populations with the same parental genetics and the negative effects of strong competitive ability (such as plant height) on agronomic performance has been discussed by many researchers (Goldringer *et al*., 2001a; Denison, 2012; Knapp *et al*., 2013; Döring *et al*., 2015). The negative effects of strong competitive ability through plant height are highlighted by the low HI values and grain yield for the CCP D13.

Particularly reduced frequencies of awned ears in comparison to their origin populations (non-cycling) and other CCP entries were present in the DK13, F13 and UK13NC CCPs. In contrast, the HU13NC CCP tended towards a higher number of awned ears per m^2. This suggests divergent evolutions for the morphological trait of awned ears per m^2 in the relatively short period of five generations. Significant site effects for this morphological trait were also reported in a number of dynamically managed French wheat populations. Three out of four French wheat populations had a significantly greater number of awned ears in comparison to their original population after 8 years of multiplication at two sites (Goldringer *et al*., 1998, 2001a). Awns are associated with better drought tolerance as awns can contribute significantly to photosynthesis, which is essential in drought conditions where leaves may no longer be able to fulfill this capability due to early senescence (Blum, 1986). The HUNC CCP was grown in a continental climate characterized by warmer summer temperatures. In contrast to the other CCPs, the yield of the Hungarian non-cycling CCP did not differ over the two years and was apparently not affected by the drought conditions of 2014/15, despite the significantly greater disease pressure. Thus, the different environmental conditions under which the CCPs have been grown may have selected for ear awnedness, particularly under drier conditions contributing to the population’s ability to cope better with drought stress.

4.4.4 Baking quality

The genetic background of the CCP entries is based on both high baking quality and high yielding varieties and whilst yield may be subject to natural selection (Murphy *et al*., 2005; Phillips & Wolfe, 2005b), baking quality parameters are not considered to be shaped by natural selection (Murphy *et al*., 2005). In 2013, the German non-cycling CCPs and CCPs based on the 12 high quality parents of the CCPs tested in our study, were found to have similar baking volume, protein content and HFN values as the same reference varieties as used in this study (Brumlop *et al*., 2017). This highlights the importance of parental variety choice in the creation of high baking quality CCPs. Although the baking volume values were poor in 2015 for all experimental entries, again no significant differences were found between the CCPs and the reference varieties. Interestingly, the CCP D13, which has a high frequency of darker coloured ears and kernels, had the best protein content of all CCP entries and the highest loaf volume along with all the other baking quality parameters. Darker coloured kernels have been associated with higher protein values (Frey, 1967) and Döring *et al*. (2011b) using a colour sorter to separate darker and lighter kernels in a wheat CCP, found that the darker grain fraction had a protein content 1,6% greater than the lighter kernel fraction. The darker kernels and better baking quality parameter values in the CCP D13 again point to a divergent evolution for a morphological trait that had apparently occurred within five generations

4.5 Conclusion

Results from the study indicate that the non-cycling populations have remained similar to one another, except for some divergence for the HUNC CCP, which tended towards a higher degree of awnedness, higher susceptibility to stripe rust and an apparent yield advantage under drought conditions. Constantly changing environmental conditions did not confer an agronomic advantage to the cycling CCPs and they all remained quite similar in terms of agronomic parameters. However, some morphological differences were observed between the CCPs regarding degree of awnedness and stem length. Additionally, the cycling D13 CCP had achieved better values for the baking quality parameters and indicated differential kernel colour. These phenotypic changes were often significant and took place in the short time span between five and eight years.

Understanding the exact selection pressures for these morphological traits is difficult as detailed environmental information was not available for every site and year in which a population was grown. Nevertheless, general tendencies such as an increased number of awned ears in a population maintained in a continental environment may indicate an adaptive capacity to more extreme climatic conditions. Genetically diverse populations submitted to changing environments may also have had an advantage in terms of disease resistance, as these populations could be exposed to new pathogen races, allowing for selection within populations for new resistances.

A slow adaptation to an ever-changing environment is to be expected as the cycling populations only have one season to adapt before moving on to the next environment. According to Patel *et al*. (1987), large environmental variances, such as those experienced by the cycling CCPs, will allow for slow population evolutions as genotype diversity is preserved through the differing genotypes that thrive and reproduce under particular, but changing, environments. This, as mentioned by Döring *et al*. (2011a), provides “a buffer against the environmental fluctuations through compensatory effects”. In more stable environments, selection pressures may be stronger, enabling quicker divergent population evolutions according to the local selection pressures such as pathogen presence, interspecific competition or nutrient availability. In this way specifically suited genotypes will be favoured in a specialised environment, thereby also reducing the genetic diversity of the population (Patel *et al*., 1987; Le Boulc’h *et al*., 1994; Goldringer *et al*., 2001a; Horneburg & Becker, 2008; Döring *et al*., 2011a). However, as discussed by Döring *et al*. (2011a), subjecting heterogeneous crop populations to differing environments and their evolutionary forces, enables the populations to change and adapt to best suit a targeted environment with little interference from mankind.

Differing seed size at sowing due to varying multiplication sites disappeared after one year under the same management system, thereby ruling out genetic divergence of the CCPs for this phenotypical trait. The effects of differing seed weight at sowing on agronomic parameters appear to interact with the environment, as correlations were not consistent between the two experimental years. Although phenotypical differences between the CCP entries and generations due to differing seed weight at sowing were small, it would be of value to ensure that variances of seed weight and quality between experimental entries be kept low to ensure that only genetic differences between entries are reported.

The low number of significant differences found for agronomic traits indicate that the changing environmental effect on the cycling populations may have a stabilizing effect, or is somewhat limited. This suggests either population stability for these traits or indicates that selection pressures were not strong enough to implement changes within the CCPs overtime. However, it is clear that heterogeneous crop populations show great potential in terms of agronomic performance, particularly under conditions where higher biotic and abiotic pressures exist, and provide an interesting alternative to monocultural cropping systems.

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Appendix

Table A 4.6: TKW (g), kernel number per ear, ear-bearing tillers/m^2, HI, yield (t/ha) and AUDPC values for the CCP entries and reference varieties per generation and in each experimental year. Differing small letters indicate significant differences between entries within a generation and experimental year ($p<0.05$). *Differing capital letters indicate significant differences of the mean values for the CCP entries and reference varieties between generations and experimental years ($p>0.05$). **Differing capital letters indicate significant differences of the mean values for CCP entries only between generations and experimental years ($p<0.05$). ns = not significant.

Origin	Entry	TKW (g)			Kernel no. per ear			Yield (t/ha)		
		2013/14	2014/15		2013/14	2014/15		2013/14	2014/15	
		F_{13}	F_{13}	F_{14}	F_{13}	F_{13}	F_{14}	F_{13}	F_{13}	F_{14}
References	Achat	48,1 a	48,0 a	48,0 a	31	27 ab	27	4,9 ab	4,3	4,3
	Akteur	46,6 ab	42,9 d	42,9 c	27	26 abc	26	3,7 c	3,8	3,8
	Capo	46,2 abc	46,0 ab	46,0 ab	30	26 abc	26	5,6 a	4,2	4,2
D	D13NC	45,9 abcd	45,7 abc	44,2 bc	29	27 ab	22	4,9 ab	4,1	4,1
	DK13	44,9 bcde	45,0 bcd	45,9 ab	31	27 ab	27	5,0 ab	4,5	4,4
	HU13	43,3 cdef	44,4 bcd	45,6 b	29	23 c	25	4,5 bc	4,1	4,4
	TUM13	44,1 bcdef	46,1 ab	45,4 b	29	25 bc	25	4,9 ab	4,3	4,4
HU	HU13NC	41,7 f	43,3 cd	44,8 bc	30	26 abc	26	4,3 bc	4,2	4,2
	F13	43,3 def	45,0 bcd	44,7 bc	32	25 bc	28	4,6 bc	4,3	4,1
	UK13	45,0 bcde	44,7 bcd	45,6 b	28	26 abc	26	4,9 ab	4,3	4,1
UK	UK13NC	42,7 ef	44,1 bcd	44,2 bc	30	27 ab	27	5,0 ab	4,3	4,2
	CH13	45,2 abcde	44,7 bcd	44,6 bc	30	25 bc	24	4,8 ab	3,9	4,2
	D13	43,4 cdef	42,5 d	44,5 bc	28	26 abc	25	4,2 bc	3,7	4,2
	NL13	42,0 f	42,9 d	44,2 bc	30	29 a	26	4,7 ab	4,4	4,4
	Mean	44,5 *ns**	44,7	45,0	30 A	26 B	26 B	4,7 A	4,2 B	4,2 B
	CCP mean	43,8 B**	44,4 AB	44,9 A	30 A	26 B	26 B	4,7 A	4,2 B	4,2 B

Origin	Entry	Ear bearing tillers/m^2			HI			AUDPC		
		2013/14	2014/15		2013/14	2014/15		2013/14	2014/15	
		F_{13}	F_{13}	F_{14}	F_{13}	F_{13}	F_{14}	F_{13}	F_{13}	F_{14}
References	Achat	390 ab	410 ab	410 ab	0,43 a	0,41 ab	0,41 ab	98 ab	209 bc	209 ab
	Akteur	325 b	337 b	337 b	0,40 abc	0,38 ab	0,38 abc	175 a	338 a	338 a
	Capo	394 ab	379 ab	379 ab	0,41 abc	0,37 b	0,37 bc	43 b	176 c	176 b
D	D13NC	399 ab	368 ab	462 a	0,39 c	0,38 ab	0,37 c	72 b	262 abc	190 b
	DK13	443 ab	429 a	388 ab	0,41 abc	0,40 ab	0,39 abc	52 b	182 c	197 ab
	HU13	397 ab	412 ab	428 ab	0,40 abc	0,38 b	0,39 abc	73 b	229 abc	194 ab
	TUM13	421 ab	439 a	442 ab	0,39 c	0,38 ab	0,39 abc	53 b	211 bc	209 ab
HU	HU13NC	389 ab	417 ab	418 ab	0,40 abc	0,40 ab	0,40 abc	94 ab	318 ab	276 ab
	F13	380 ab	434 a	374 ab	0,40 abc	0,41 ab	0,42 a	65 b	240 abc	238 ab
	UK13	398 ab	432 a	388 ab	0,39 c	0,39 ab	0,39 abc	109 ab	225 abc	249 ab
UK	UK13NC	408 ab	436 a	442 ab	0,40 abc	0,41 ab	0,41 ab	56 b	182 c	220 ab
	CH13	443 ab	393 ab	407 ab	0,39 bc	0,39 ab	0,38 bc	67 b	238 abc	240 ab
	D13	454 a	414 ab	402 ab	0,38 c	0,39 ab	0,37 c	79 b	230 abc	208 ab
	NL13	426 ab	401 ab	449 a	0,42 ab	0,42 a	0,40 abc	57 b	215 bc	243 ab
	Mean	405 *ns**	407	409	0,40 A*	0,39 AB	0,39 B	78 B*	232 A	228 A
	CCP mean	415 *ns***	416	418	0,40 *ns***	0,39	0,39	71 B**	230 A	224 A

Table A 4.7: Disease Index (DI) for all CCP entries and reference varieties in the experimental year of 2013/14. The DI for *Pseudocercosporella herpotrichoides* (DI Pseudo.), *Fusarium* spp. (DI Fusarium), *Rhizoctonia cerealis* (DI Rhiz.) and the combined total DI are given.

Origin	**Entry**	**DI combined**	**DI Pseudo.**	**DI Fusarium**	**DI Rhiz.**
References	Achat	29,45	17,44	11,79	0,67
	Akteur	26,03	10,00	16,45	0,21
	Capo	21,74	7,29	13,61	0,83
D	D13NC	27,62	12,30	15,75	0,61
	DK13	27,37	11,87	15,84	1,88
	HU13	29,39	14,90	14,30	1,13
	TUM13	24,85	9,93	15,11	0,39
HU	HU13NC	22,42	5,65	16,12	1,06
	F13	27,65	13,47	14,98	0,19
	UK13	21,12	6,71	14,61	0,00
UK	UK13NC	23,28	7,88	15,81	0,00
	CH13	23,04	9,23	14,48	0,21
	D13	31,28	19,35	12,29	0,42
	NL13	23,40	6,93	16,99	0,38
Mean		**25,62**	**10,93**	**14,87**	**0,57**

5. General Discussion

Future sustainable agricultural systems will need to implement a number of strategies in order to increase food production and safeguard biodiversity, while simultaneously reducing inputs. Climate change, the dwindling reserves of non-renewable resources and the damaging effects of environmental pollution have highlighted the importance of alternative self-regulating and resilient agricultural systems, able to deal with greater abiotic and biotic stresses. While organic agriculture has long had sustainability as a goal, there is much room for improvement, particularly in terms of breeding crops for high diversity and productivity, but also for low-input cropping systems of the future. The current limiting framework of “political and economic structures”(Weiner, 2017) often impedes the application of agroecological approaches that have been argued to be the only way to achieve sustainable food production (Dwivedi *et al*., 2017; McIntyre *et al*., 2009; Kiers *et al*., 2008). Composite cross populations (CCPs) are of great interest not only for their agronomic performance and yield stability, but also for selecting for improved wheat quality in organic systems while maintaining intraspecific genetic diversity for optimal resilience to biotic and abiotic stresses.

5.1 The agronomic potential of evolutionary breeding

As reported by Jones *et al*. (2010), depending on the management system under which they were grown, CCP parental varieties performed better in terms of yield, protein value and proportion of green leaf area (GLA of flag leaf). The high yielding parental variety group showed a significant positive relationship between GLA values and varietal release date at all four conventional sites, but not at the organic sites. This indicates that the high yielding parental varieties, which include more modern cultivars (earliest varietal release date 1985 for variety High Tiller Line) in comparison to the high baking quality parental varieties, behaved differently in terms of GLA values depending on the management system. In this same CCP parental variety experiment, there was a significant negative correlation between the incidence of *Septoria* spp. and yield, which was found only for the CCYQ and CCY parental groups under organic management (Jones *et al*., 2010). These results from Jones *et al*. (2010) indicated that varieties with later release dates (mainly found in the CCY group) were less suitable for low-input and organic systems, which were characterised by higher abiotic and biotic pressures.

Research results on the German wheat CCPs indicate that, under organic management, yields and yield stability of both the CCYQ and CCY populations are comparable to currently grown pure line varieties used in organic agriculture (Brumlop *et al*., 2017; Weedon *et al*., 2017a; Chapter 2, 3 and 4). However, significant differences between the CCQ populations and the other CCPs indicate that parental genetics still play a dominant role and that parental variety selection is paramount to success, depending on the agronomic traits and performance desired. The CCQ populations, created through the crossing of high baking quality parents, show promise in terms of grain protein content and other baking parameters (Brumlop *et al*., 2017), having maintained these quality characteristics over a number of generations. The results of Chapter 4 indicate that a number of CCYQ populations, having been subjected to changing environmental conditions since the F_8, also exhibited good grain protein and similar baking parameter values to a number of reference varieties, due to the inclusion of high baking quality parental varieties in their creation. In terms of foliar pathogens, CCPs were comparable to a number of reference varieties under both organic and conventional management (Brumlop *et al*., 2017; Chapter 2, 4). Results from Chapter 2 indicated changes in ranking in the individual parental varieties for AUDPC and RAUDPC values between 2008/09 during a brown rust epidemic and 2014/15 during a stripe rust epidemic. This highlights the high diversity within the parental varieties for foliar pathogen resistances, particularly as a number of parental varieties indicated resistance to both brown and yellow rust. The change in ranking between the experimental seasons reflects the changes in foliar pathogen dominance on the one hand, but also indicates that a wide range of foliar pathogen resistances are present in the CCPs due to their parental varieties. Although foliar pathogen resistances in the parental varieties were not likely to have been a major selection criterion, through the recombined parents there is a diverse range of foliar pathogen resistance combinations present in the CCPs. Thus, even though the parental varieties were not previously exposed to the new virulent races of yellow rust, the CCPs resistance level and diversity proved adequate to withstand newly introduced pathogen races such as occurred with stripe rust after 2010 (Hovmøller *et al*., 2016; Ali *et al*., 2017).

An apparent management system effect on the CCPs, indicated differences in seedling root and shoot weight between organically and conventionally managed CCPs after 5 years under differing management systems (Bertholdsson *et al*., 2016). Thus, compared to conventionally managed CCPs, the organically managed CCPs had developed larger above- and belowground systems attributed to early vigour, adapting not only to greater weed pressure, but also to lower available soil N found under organic management (Messmer *et al*., 2012). Our current research (field research from 2014-2017) within the BMBF-funded project INSUSFAR (www.insusfar.de, last access January 2018), indicates that differentiation for yield response under differing N inputs has evolved among a number of organically managed CCPs within 11 generations (Weedon *et al*., 2017b; Weedon *et al*. 2017c). This highlights that there is genetic variability of nutrient use efficiency (NUE) available within the CCPs and that they are capable of adaptation to differing management and/or environmental conditions. Genotypes that are more efficient in N uptake in early growth stages where soil N is the limiting factor, are better adapted to systems with limited N resources such as organic conditions (Dawson *et al*., 2008; Baresel *et al*., 2008; Messmer *et al*., 2012). In the above mentioned INSUSFAR experiments, the organically managed CCPs also had significantly greater biomass (ears per m^2 and biomass weight), in comparison to a number of currently grown pure line varieties found in both conventional and organic agriculture (Weedon *et al*., 2017b; Weedon *et al*. 2017c; Wersebeckmann, 2017). We could also show that parameters of early vigour in the field such as ground cover (%) at tillering correlated significantly with ears per m^2 (Wersebeckmann, 2017). This supports the earlier hydroponic results for the organically managed CCPs described above (Bertholdsson *et al*., 2016). Comparison between organically and conventionally managed CCPs are underway in the INSUSFAR field trials from the 2017/18 experimental season. The above-mentioned traits of early vigour and greater above- and belowground biomass contribute to weed suppression through shading and competition, as well as to stable soil organic matter (Lammerts Van Bueren *et al*., 2002; Wolfe *et al*., 2008; Osman *et al*., 2012). Greater investment in vegetative biomass has been considered a trade-off to grain yield (Denison, 2012), and may also increase the risk of lodging (Döring *et al*., 2015). However, yields of CCPs grown at the University of Kassel under organic conditions have remained comparable or better than pure line varieties and have shown greater yield stability (Weedon & Finckh, 2015; Weedon *et al*., 2016, Chapter 2, 3). Additionally, results from Chapter 4 show that harvest indices for a number of CCYQ populations are similar to conventionally bred pure line varieties, indicating that CCP investment in vegetative biomass does not occur, in this case, at the expense of grain yield.

A management systems effect is also apparent in the CCPs in the sense that CCPs under conventional management are not as successful in terms of yield and yield stability as their organically managed counterparts in comparison to the reference variety Capo (Chapter 2, 3). This is mainly attributed to the parental variety choice specifically for performance in low-input systems in Europe (Jones *et al*., 2010). Thus, the reference variety Capo, outyielded all conventionally managed CCPs (Chapter 2). However, under conventional conditions, the conventional CYII population, as well as both conventional CCYQ CCPs, tended towards high yield stability, similar to the reference variety Capo (Chapter 3). Both in terms of yield and yield stability, apparent divergent evolutionary trajectories between the two parallel conventional CY CCPs indicate both initial genetic variability, as well as possible differing selection pressures, which enabled separate evolutions (Chapter 3). These divergent trajectories are indicative of the inherent capacity of genetically diverse populations to change and evolve under differing environments overtime.

5.2 Challenges to the implementation of evolutionary breeding

Heterogeneous populations face challenges with respect to variety registration, particularly according to the DUS criteria (distinctness, uniformity and stability) implemented for varietal and plant breeder protection through the UPOV agreement (UPOV, 2002; Dwivedi *et al*., 2017; Raggi *et al*., 2017). The result of these strict criteria has made the breeding and selling of diversified germplasm legally challenging (Brumlop *et al*., 2013; Winge, 2015; Dwivedi *et al*., 2017). However, under the Council Directive 2014/150/EU, heterogeneous populations of wheat, oats, maize and barley may be marketed until December 31st 2018 (European Commision, 2014). Although, this directive allows for the marketing of heterogeneous crop populations, it is most likely that breeders and farmers will face similar challenges as those facing the organic seed industry, particularly as heterogeneous crop populations have been proposed and supported by the organic and low-input agricultural sector (Döring *et al*., 2015; Raggi *et al*., 2017). According to Döring *et al*. (2012), the organic seed sector is faced with a number of challenges including lack of varieties best suited to organic conditions, lack of information on the agronomic performance of many organic cultivars, as well as the low volume of certified organic seed available. As these problems face the organic sector in general, it is most likely that the marketing and provision of seed of heterogeneous crop populations will face similar challenges.

Dwivedi *et al*. (2017) discuss the merits and importance of diversifying diet, as well as food systems. In this respect, heterogeneous crop populations may gain significant standing in achieving these aims. Rahmanian *et al*. (2014) report on the suitability of wheat CCPs for consumers with gluten intolerances. In the UK, baking quality and sensory testing has been done with a couple of wheat CCPs originating from the same source as the ones grown at the University of Kassel. Baking quality of the CCPs were comparable to a number of commercially-used wheat varieties in terms of loaf height and Hagberg Falling Number (Winkler *et al*., 2013a). Additionally, two of the UK wheat CCPs showed significantly higher micronutrient values for Mg and Zn in comparison to the benchmark variety (Solstice) (Winkler *et al*., 2013b). Research by Vindras-Fouillet *et al*. (2014) on sensory testing and nutritional qualities of French wheat populations indicate the need to further support the breeding of such heterogeneous wheat populations and the need to select for unique and “improved sensory and nutritional qualities”, particularly adapted for organic and low-input systems. Their work indicated that wheat populations with a darker grain colour were favoured by the sensory panels and that such characteristics could be used as a selection criterion in order to fulfil this breeding goal.

The use of heterogeneous crop populations is likely to be hindered by the fact that processors and actors throughout the value chain have little experience with diversified materials. In the case of baking wheat, for example, millers mix a number of varieties together after quality testing in order to create the desired flour blends for bakers. However, lack of experience with such heterogeneous wheat populations makes acceptance difficult and daunting. A marketing concept, which has been suggested within the EIP-AGRI project (Agricultural European Innovation Partnership) led by Dottenfelder Bio-Saat GmbH, includes the use of a specific “Diversity” label, to indicate products stemming from heterogeneous populations. This may help to educate consumers and aid acceptance, as has been done through the “Bioverita” label (www.bioverita.ch, last access January 2018), conceived for the specific promotion of organically bred crop varieties. Heterogeneous wheat populations, for example, present not only a novel breeding concept, but a novel marketing concept as well.

Presently, the use of CCPs is particularly advantageous for farmers, which are able to process the populations themselves, providing a unique product to a direct market in the form of farm shops and box schemes. However, the wider acceptance of genetically diverse populations throughout the value chain and down to the consumer is a challenge that needs to be addressed. Additionally, the financing for breeding of genetically diverse crop populations should not be neglected. Dialogue between breeders and farmers in terms of financing and support options are critical to ensure success for both breeding and farmer acceptance.

As evolutionary breeding and the use of heterogeneous crop populations has been supported and developed mainly for the organic and low-input agricultural sector (Döring *et al*., 2015; Raggi *et al*., 2017; Dwivedi *et al*., 2017), the breeding of CCPs for the conventional sector is not well known. It is not clear whether a market will exist for heterogeneous crop populations in conventional agriculture. However, the societal and environmental pressures to reduce agricultural inputs such as fertilizers, pesticides and herbicides may make CCPs and other genetically diverse populations more interesting to conventional farmers of the future as the breeding focus for such systems shifts to crop plants characterised by “nutrient economy and local environmental fitness” (Fess *et al*., 2011).

5.3 General outlook

The parental varieties were released between 1934 and 2000 (Jones *et al*., 2010), and as such the CCPs have missed out on considerable breeding progress made post 2000. In spite of the older genetics, however, the CCPs, particularly under organic management, have performed very well in terms of yield, yield stability, foliar pathogen resistances and baking quality parameters in comparison to commonly grown reference varieties. This does not mean, however, that CCPs should be excluded from genetic improvement and the mixing of elite lines into CCPs has already been recommended by Döring *et al*. (2015). Admixing of currently successful pure line varieties into CCPs is an additional option open to farmers with the added advantage that this approach is quick, simple, and cheap and can easily be performed on-farm. In the current INSUSFAR project, an improved CCP (iCCP), created by crossing three pure line varieties into a CCYQ population, is to be tested against its “unimproved” counterpart, other CCPs and a number of modern pure line varieties.

Overall, the agronomic stability of CCPs contributes to food security under changing and challenging climatic conditions, helping to reduce both the environmental impacts of agriculture and agrichemical inputs using an ecological innovation. As the baking qualities and agronomic performance of winter wheat CCPs have been shown to be comparable to pure line varieties and the newly introduced EU legislation has reduced the legal hurdles to growing and marketing heterogeneous populations, the implementation of CCPs throughout the value chain should be pursued. The acceptance of CCPs has great societal relevance by enhancing participation and sustainability through the introduction of a system that explicitly involves farmers and processors in a participatory way as breeders and stewards of genetic resources and agricultural sustainability, as well as enabling consumers to support such systems. This will help to support local social identity and empowerment and contributes greatly to the current trend towards localized consumption and food sovereignty. Breeding and selecting for heterogeneous crop populations contributes to the dynamic management and development of genetic resources and provides genetic material for farmer participatory approaches to breeding and selection for sustainable agricultural systems of the future.

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„Hiermit versichere ich, dass ich die vorliegende Dissertation selbständig, ohne unerlaubte Hilfe Dritter angefertigt und andere als die in der Dissertation angegebenen Hilfsmittel nicht benutzt habe. Alle Stellen, die wörtlich oder sinngemäß aus veröffentlichten oder unveröffentlichten Schriften entnommen sind, habe ich als solche kenntlich gemacht. Dritte waren an der inhaltlichen Erstellung der Dissertation nicht beteiligt; insbesondere habe ich nicht die Hilfe eines kommerziellen Promotionsberaters in Anspruch genommen. Kein Teil dieser Arbeit ist in einem anderen Promotions-oder Habilitationsverfahren durch mich verwendet worden.“

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„I hereby give my assurance that I completed this dissertation independently without prohibited assistance of third parties or aids other than those identified in this dissertation. All passages that are drawn from published or unpublished writings, either word-for-word or in paraphrase have been clearly identified as such. Third parties were not involved in the drafting of the materials contents of this dissertation; most specifically I did not employ the assistance of a dissertation advisor. No part of this thesis has been used in another doctoral or tenure process.”
