Performance of Winter Wheat Cultivars in Organic and Conventional Farming Systems

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Summary

In the past decades, wheat (*Triticum aestivum* L.) breeding on a global scale was strongly focused on grain yield improvement to limit starvation. The introgression of semi-dwarfing genes for example improved the harvest index, which is the ratio of grain yield to total aboveground biomass. Accompanied by the increased input of mineral nitrogen (N) and phosphorus (P) fertilizers and the application of pesticides, it resulted in considerable yield increase. Focusing on yield improvement, wheat breeders tended to neglect to breed for cultivars achieving high grain yields at low nutrient supply, which means using available nutrients most efficiently. This development might have resulted in a shift of the optimum nutrient level for wheat cultivation and thus led to cultivars with an increasing demand for nutrient supply. Arbuscular mycorrhizal fungi (AMF) can contribute to nutrient supply of plants under nutrient limited conditions. It is hypothesized that breeding under high input conditions might result in cultivars that lost the ability to form AMF symbiosis. Herefrom the question arose whether those modern cultivars selected for high input farming are suitable for growing under the nutrient restricted conditions in organic farming.

This study assessed the need of specific breeding programs for organic farming. The general hypothesis was that cultivars selected under organic conditions are better suitable for organic farming than cultivars selected under conventional high input conditions. Two one year field studies were carried out in a total of seven environments with eight to ten wheat cultivars. Wheat cultivars were assessed in organic and conventional systems of the DOK long-term field trial in 2007, where different farming systems are compared since 1978. In 2008 these cultivars were assessed under practical farming conditions (replicated on-farm trials) at three organically managed farms in different pedo-climatic regions. In contrast to the fertile DOK site on loess soil, the organic farms were located at more marginal sandy or sandy loamy soils with a lower inherent yield potential. The main objectives were (i) to compare yield, baking quality and several parameters of nutrient use efficiency of modern winter wheat cultivars derived from organic and conventional breeding programs as well as old cultivars in organic and conventional systems of the DOK long-term field trial, (ii) to compare the performance of a set of these cultivars at three on-farm trials at organically managed farms at more marginal sites, (iii) to analyse phenotypic stability of selected traits and (iv) to assess the root colonization with arbuscular mycorrhizal fungi (AMF-RC) and the correlation between AMF-RC and nutrient concentration of P, Manganese (Mn) and Zinc (Zn) in plant tissue and in the grain, nutrient uptake and grain yield.

Grain yields were significantly higher under conventional than under organic conditions at the fertile DOK site in 2007. According to expectations, the conventionally bred cultivars achieved the highest yields under conventional conditions, whereas the organically bred cultivars could not outyield the conventionally bred cultivars in the organic systems. In contrast, the organically bred cultivars could slightly outperform the conventionally bred cultivars at the three marginal on-farm sites in 2008. Remarkably, the difference in grain yield was statistically significant at the lowest yielding site.

Baking quality parameters clearly increased from old to modern organically and conventionally bred cultivars in all test environments. Nitrogen use efficiency was higher under organic than under conventional conditions and increased with the year of release of the cultivars. Similar to the results obtained for grain yield, nutrient use efficiency of the organically bred cultivars was higher than of the conventionally bred cultivars at the marginal organic sites. However, this was not confirmed in the organic systems at the fertile DOK site.

No significant genotype x environment interactions for agronomically important traits were observed comparing the organic and conventional systems at the fertile DOK site in 2007. In contrast, significant interactions were detected among the three marginal on-farm trials in 2008 and in the combined analysis across all seven conventionally and organically managed sites. This emphasizes the importance of selection under the adequate target environments. Screening and selection should not only be performed under organic farming but various pedo-climatic conditions, including also more marginal soils.

Regarding the stability of grain yield and nutrient use efficiency, a cultivar suitable for organic farming should respond dynamically to the given environmental conditions. Such a dynamic behaviour would be expressed by a good performance under marginal conditions and a constant increase from the marginal sites to the fertile DOK sites. In contrast, a static stability is required for baking quality, i. e. the gluten index. For such a parameter, a genotype should achieve stable values across a wide range of environments. One organically bred cultivar was identified, which was stable for all three traits (yield, nutrient use efficiency, baking quality) simultaneously. However, it was not possible to relate the stability to the different breeding categories.

A promising approach to improve nutrient use efficiency of wheat could be achieved by breeding for improved AMF symbiosis. Root colonization of AMF (AMF-RC) was significantly higher in the organic than in the conventional systems but did not differ among the ten wheat cultivars at any of the seven sites. In one organically managed system and in the unfertilized control at the fertile DOK site, a positive correlation between AMF-RC and shoot P concentration at tillering was measured. No such correlation was obtained in the conventional system at the DOK site and at the marginal sites. These results indicate that higher AMF-RC might contribute to shoot P supply under organic conditions. However, the measured effect of the AMF-wheat symbiosis was only observed in early growth stages and was not reflected in improved P-uptake or grain yield at harvest. No consistent correlations were observed between AMF-RC and Mn and Zn. Molecular studies on AMF-diversity of a larger set of cultivars grown under low input conditions could shed more light on the co-evolution of wheat and AMF during breeding programs.

In conclusion, this study strongly indicates the need for organic selection environments at least in later generations of wheat breeding when selection for grain yield takes place. This study could not confirm the hypothesis that modern conventionally bred wheat cultivars might have lost the ability to form AMF symbiosis during breeding for high input conditions.

Zusammenfassung

Global betrachtet war die Steigerung der Erträge zur Bekämpfung von Hunger in den vergangenen Jahrzehnten das Hauptziel in der Weizenzüchtung (*Triticum aestivum* L.). Mit der Einführung von Verzwergungsgenen wurde der Ernteindex verbessert, der das Verhältnis Kornertrag zur oberirdischen Gesamtbiomasse darstellt. Begleitet von einer ansteigenden Zufuhr von Stickstoff- (N) und Phosphor- (P) Düngern und der Anwendung von Pestiziden hat dies zu einem beträchtlichen Ertragszuwachs geführt. Durch die jahrzehntelange Züchtung auf Hochertragssorten für den intensiven Anbau wurde möglicherweise das optimale Düngungsniveau im Weizenanbau verschoben und so indirekt auf Sorten mit einem höheren Nährstoffbedarf selektiert. Arbuskuläre Mykorrhiza können zur Nährstoffversorgung von Pflanzen vor allem unter nährstofflimitierten Bedingungen beitragen. Ergebnisse aus der Literatur lassen vermuten, dass die Züchtung unter nährstoffreichen Bedingungen dazu geführt haben könnte, dass moderne Sorten die Fähigkeit zur Kolonisierung mit arbuskulärer Mykorrhiza verloren haben. Aus dieser Situation heraus ergibt sich die Frage, ob Sorten, die aus solchen Züchtungsprogrammen hervorgegangen sind, für den biologischen Anbau geeignet sind.

Im Fokus dieser Arbeit stand die Beurteilung der Notwendigkeit spezifischer Züchtungsprogramme für den biologischen Landbau. Dabei wurde folgende Hypothese überprüft: Sorten, die unter biologischen Bedingungen gezüchtet worden sind, sind besser an die Bedingungen im biologischen Landbau angepasst als konventionell gezüchtete Hochleistungssorten. Zwei einjährige Feldstudien mit je acht bis zehn Winterweizensorten wurden in insgesamt sieben Umwelten durchgeführt. Eine erste Studie wurde 2007 im biologischen und konventionellen Verfahren im DOK-Langzeitversuch durchgeführt, in dem verschiedene Anbausysteme seit 1978 verglichen werden. In einer zweiten Studie wurden die Sorten 2008 unter Praxisbedingungen auf biologisch bewirtschafteten Betrieben in verschiedenen pedo-klimatischen Regionen der Schweiz geprüft. Im Gegensatz zum DOK-Langzeitversuch, einem fruchtbaren Löss-Standort, waren die Praxisbetriebe auf sandigen bis sandig-lehmigen Böden und hatten ein insgesamt geringeres Ertragspotenzial. Teilziele der Arbeit waren (i) der Vergleich der Erträge, der Backqualität und der Nährstoffeffizienz von modernen Winterweizensorten aus biologischen und konventionellen Züchtungsprogrammen sowie alten Sorten, angebaut unter biologischen und konventionellen Bedingungen im DOK-Langzeitversuch auf fruchtbarem Lössboden, (ii) der Vergleich der Leistung dieser Sorten auf drei biologisch bewirtschafteten Praxisbetrieben an Standorten mit geringem Ertragspotenzial, (iii) die Analyse der phänotypischen Stabilität der Sorten und (iv) die Bestimmung der Wurzelkolonisierung mit arbuskulärer Mykorrhiza unter Feldbedingungen sowie deren Korrelationen mit der Nährstoffkonzentration von Phosphor (P), Mangan (Mn) und Zink (Zn) im Pflanzengewebe und im Korn, mit der Nährstoffaufnahme ins Korn und mit dem Kornertrag.

Im DOK-Langzeitversuch waren 2007 die Kornerträge unter konventionellen Bedingungen deutlich höher als unter biologischen Bedingungen. Erwartungsgemäss erzielten die konventionell gezüchteten Sorten die höchsten Erträge innerhalb des konventionellen Anbauverfahrens während die biologisch gezüchteten Sorten keine Überlegenheit gegenüber den konventionellen Sorten in den biologischen Systemen zeigten. Im Gegensatz zu den Ergebnissen im DOK-Langzeitversuch, waren die Erträge der biologisch gezüchteten Sorten auf den drei biologischen Praxisbetrieben in 2008 leicht höher als die der alten und der konventionell gezüchteten Sorten. Signifikant gesichert war dieser Unterschied am Standort mit dem insgesamt tiefsten Ertragsniveau.

In allen geprüften Umwelten stieg die Backqualität deutlich von den alten zu den modernen biologisch und konventionell gezüchteten Sorten an. Unter biologischer Bewirtschaftung war die Stickstoffeffizienz aller Sorten generell höher als unter konventionellen Bedingungen und stieg auch mit dem Jahr der Zulassung der

Sorten an. Auf den ertragsschwächeren Praxisbetrieben war die Stickstoffeffizienz der biologisch gezüchteten Sorten höher als die der konventionell gezüchteten Sorten. Dies konnte in den biologischen Anbauverfahren am fruchtbaren DOK-Standort nicht bestätigt werden.

Im DOK-Langzeitversuch mit dem direkten Vergleich der biologischen und konventionellen Anbauverfahren traten keine signifikanten Genotyp-Umwelt-Wechselwirkungen für agronomisch wichtige Parameter auf. Im Gegensatz dazu wurden in 2008 zwischen den drei Praxisbetrieben und auch in der Gesamtanalyse über alle sieben Prüfumwelten in 2007 und 2008 signifikante Genotyp-Umwelt-Wechselwirkungen festgestellt. Dieses Ergebnis unterstreicht die grosse Bedeutung einer Selektion unter den jeweiligen Zielumwelten. Darüber hinaus zeigt diese Studie, dass Selektion nicht nur unter Biobedingungen stattfinden sollte, sondern an möglichst vielen und möglichst unterschiedlichen Standorten, die ein breites Spektrum der Anbausysteme innerhalb des Biolandbaus widerspiegeln.

In Bezug auf Kornertrag und Nährstoffeffizienz ist eine Sorte dann für den biologischen Anbau geeignet, wenn sie dynamisch auf gegebene Umweltbedingungen reagiert. In dieser Studie bedeutet dies eine konstante Zunahme des Kornertrags von den drei marginalen Standorten zu den Bio-Anbauverfahren im DOK-Langzeitversuch. Im Gegensatz dazu wird für Parameter der Backqualität wie z.B. der Feuchtkleberindex eine statische Stabilität benötigt. Dies bedeutet, dass eine Sorte das gleiche Ergebnis in verschiedenen Umwelten erzielt. Eine der biologisch gezüchteten Sorten zeigte gleichzeitig eine hohe Stabilität für die drei Parameter Kornertrag, Stickstoffnutzungseffizienz und Feuchtkleberindex.

Die Wurzelkolonisierung der Weizensorten mit arbuskulärer Mykorrhiza war unter biologischen Bedingungen höher als unter konventionellen Bedingungen. Ein signifikanter Sortenunterschied konnte aber nicht festgestellt werden. In einem biologischen System und in der ungedüngten Kontrolle zeigte sich im DOK-Langzeitversuch eine positive Korrelation zwischen der Wurzelkolonisierung und der P Konzentration im Spross bei der Bestockung. Im konventionellen System im DOK-Langzeitversuch und in den Praxisversuchen wurde keine Korrelation beobachtet. Dies könnte ein Hinweis sein, dass unter spezifischen biologischen Anbaubedingungen eine höhere Wurzelkolonisierung zu einer besseren P-Versorgung beitragen kann. Jedoch zeigte sich dieser Effekt nur in einem frühen Entwicklungsstadium und spiegelte sich nicht in einer höheren P-Aufnahme oder einem höheren Kornertrag wider. Auch konnten keine konsistenten Korrelationen zwischen der Mykorrhiza-Wurzelkolonisierung und den Konzentrationen von Mn und Zn festgestellt werden. Molekulargenetische Studien zur Diversität der arbuskulären Mykorrhizierung mit einer grösseren Anzahl von Sorten, die unter nährstoffarmen Bedingungen angebaut werden, könnten Aufschluss über die Co-Evolution von Weizen und Mykorrhiza im Verlauf der Züchtung geben.

Zusammenfassend zeigt diese Studie die Notwendigkeit, biologisch bewirtschaftete Flächen in Züchtungsprogramme für den Biolandbau einzuschliessen. Wichtig ist dies vor allem in fortgeschrittenen Generationen des Zuchtprogrammes, ab denen die Ertragsselektion stattfindet. Die Hypothese, dass die Fähigkeit von Weizen zur Mykorrhizierung bei modernen Hochleistungssorten verloren gegangen ist, hat sich nicht bestätigt.

1 INTRODUCTION

Current Challenges in Agriculture and the Contribution of Organic Farming

The challenge of modern agricultural systems is to ensure global food supply without further deforestation and environmental degradation. During the last decades, accelerated input of mineral nitrogen (N) and phosphorus (P) fertilizers and application of pesticides were the common way to increase crop yields. Thus, the demand for these fertilizers increased drastically (Tilman et al., 2002). The increase in fertilizer input resulted in a decrease of nutrient use efficiency both for N (Limon-Ortega et al., 2008) and for P (Egle et al., 1999). In the context of scarcity of resources and raising costs for mineral fertilizers there is an increasing request on strategies to improve nutrient use efficiency.

Strategies or landuse systems are needed that improve productivity and at the same time minimize environmental pollution and adverse impacts on biodiversity and associated ecological factors like soil fertility, pest control or pollination. Organic farming is regarded as a sustainable alternative to conventional agriculture as it has the potential to maintain biodiversity (Mäder et al., 2002; Hole et al., 2005), prevent soil degradation (Reganold et al., 1987; Tilman et al., 2002; Hepperly et al., 2006; Marriott and Wander, 2006; Fließbach et al., 2007), reduce the negative agricultural impacts on climate change (Nemecek et al., 2005; Pimentel et al., 2005; Niggli et al., 2008a; Niggli et al., 2008b) and contribute to global food supply (Badgley et al., 2007; Niggli et al., 2007; Scialabba, 2007). However, the productivity of organic farming needs to be improved.

The **productivity of organic compared to conventional farming** strongly depends on soil and climate conditions as well as on the choice of crops being compared. A meta-analysis showed that organic agriculture was particularly competitive under marginal environments that are common in developing countries (Badgley et al., 2007). In more fertile soils in temperate climate like in Switzerland, it was shown in a long-term trial that yields of the organic farming systems in a 7 year crop rotation were on average 20% lower than those of the conventional farming system (Mäder et al., 2002). In a long-term trial in Pennsylvania comparing manure and legume-based organic farming systems and conventional farming based on mineral fertilizers, it was found that organic and conventional systems had similar soybean and maize yields however, the organic systems had an huge increase in soil organic carbon in both systems (Hepperly et al., 2006).

Soil fertility is fundamental in determining the productivity of agricultural systems and strongly affected by various agricultural measures such as fertilization, crop rotation and soil management in general including soil cultivation. It is directly linked with processes of decomposition of crop residues and nutrient supply.

In organic farming systems, **nutrient supply** is based on organic material (manures, compost, crop residues or legumes) or slow-release sources (e.g. rock phosphate). Most materials incorporated into the soil in organic systems do not contain readily soluble nutrients. Therefore, there is a greater reliance on chemical and biological processes to release nutrients in plant available forms in the soil solution. Rotted or composted manure as used in organic farming have been shown to promote beneficial belowground processes if compared to synthetic fertilizers (Mäder et al., 2002). Quality and quantity of organic inputs has implications for the activity of soil microorganisms and the soil food web, biological processes of nutrient transformation and the accumulation of soil organic matter. A comprehensive study on the effect of farmyard manure and mineral fertilizers on below and aboveground biota revealed that organic fertilizers fostered biotic interactions within and between belowground and aboveground components indicating an improvement of sustainability (Birkhofer et al., 2008).

Long-term application of farmyard manure and slurry affects not only the microbial and faunal communities but also alters important soil properties such as the content of soil organic matter. **Soil organic matter** contributes to soil fertility as it helps to maintain the soil structure and to provide the resistance to structural degradation (Shepherd et al., 2002). Higher contents of soil organic matter were found in organically than in conventionally managed soils (Pimentel, 2006; Fließbach et al., 2007). Topsoil was found to be deeper and higher in organic matter content resulting in a reduced risk of soil erosion (Reganold et al., 1987). Higher aggregate stability was measured in organic than in conventional farming systems (Siegrist et al., 1998). Soil aggregate stability was strongly correlated with earthworm activity which was found to be higher under organic than under conventional management (Mäder et al., 2002).

The importance of the **crop rotation** design for nutrient cycling and conservation and weed, pest and disease control was shown by Stockdale et al. (2001). Diverse arable grass-rotations including legumes and cover crops improve the fixation of nitrogen and the sequestration of carbon in soils (van Eekeren et al., 2008). Prolonging the crop rotation led to a clear reduction of potato diseases caused by soilborne pathogens (Peters et al., 2003).

Soil cultivation techniques such as reduced tillage were shown to increase aggregate size (Jacobs et al., 2009) and aggregate stability (Emmerling, 2007) and thus preventing soil erosion. Moreover, this technique contributed to soil fertility through increased organic matter (Alvarez, 2005; Berner et al., 2008) and soil microbial biomass (Berner et al., 2008) or increased earth worm density (Tebrügge, 1999; Topoliantz, 2000; Chan, 2001). Reduced tillage was shown to be practicable also under organic farming conditions during six years (Berner et al., 2008; Krauss et al., 2009). Overall, higher yields compared to ploughing were recorded in this trial, and weed infestation was still acceptable.

Organic farming is a multi-targeted approach trying to incorporate all dimensions of soil fertility as indicated above. Most management practices in organic farming affect more than one component of the system. For example, mechanical weed control by cultivation stimulates mineralization of nitrogen at the same time. In contrast to conventional farming, it does not focus on individual impact measures. The “no till” technique used in conventional farming for example, efficiently prevents soil erosion but more herbicides and soluble mineral fertilizers are needed. Due to this multi-targeted approach, organic farming is - among the concepts of sustainable land use systems - a very consequent one.

1.1 Wheat Breeding

1.1.1 General Aspects of Wheat Breeding

Wheat (*Triticum aestivum* L.) emerged as a cultivated crop about 10,000 years ago. It is a hexaploid wheat and evolved through hybridization of Triticum dicoccum (tetraploid emmer wheat) with Aegilops tauschii (dipoloid wheat) (Shewry, 2009). Since that time, diversification of wheat has occurred through mutation and hybridization. Enhanced selection and breeding began in the 19th century accompanied by advances in improving plant health and grain yield (Worland and Snape, 2001). Nowadays, wheat is among the three most important staple crops and was grown on 223,6 Mio ha worldwide in 2008 (http://faostat.fao.org).

Yield Improvement

Wheat breeding during the last decades was strongly focused on grain yield improvement. Traditionally, this has been reached empirically by phenotypical selection for promising genotypes resulting in locally best adapted cultivars. However, major advances were made by specific changes for example in plant type and structure, in plant physiology, in durable disease resistance, and other changes in grain number and grain weight (Rajaram, 2001; Ortiz et al., 2007).

Plant height of wheat was significantly decreased by plant breeders from about 140 cm to 70-100 cm during the last decades (Worland and Snape, 2001). Reducing the plant height increased lodging resistance of wheat cultivars allowing much higher input of fertilizer and thereby increased yields considerably. Moreover, this development resulted in a shift of the harvest index (HI) due to the reduced straw biomass. The HI is the ratio of grain yield to total aboveground biomass and measures the success in partitioning assimilated photosynthate to harvestable product (Sinclair, 1998). The significant increase in HI from old to modern cultivars was often reported (Sticksel et al., 2000; Brancourt-Hulmel et al., 2003; Guarda et al., 2004; Acuna et al., 2005). Mainly responsible for changes in HI was the introduction of the dwarfing genes Rht1 and Rht2 from the Japanese Norin wheat in 1954 (Austin et al., 1980; Rajaram, 2001; Worland and Snape, 2001). Cultivars possessing dwarfing genes revealed higher yields when compared to cultivars without dwarfing genes as was shown by many studies (Brancourt-Hulmel et al., 2003; Guarda et al., 2004; Acuna et al., 2005; Fischer, 2007).

The incorporation of a single rye chromosome (wheat-rye translocation lines) introduced novel **disease resistance** genes to bread wheat and thus improved plant health and yield (Worland and Snape, 2001). For example the introduction of the Sr2 gene complex increased stem rust resistance (Braun et al., 1996).

Physiological aspects of winter wheat that strongly affect plant growth and grain yield are **the vernalisation and the photoperiodic sensitivity** and the early development of tillers and ears. Winter wheat usually requires at least 40-80 days of temperatures between 0° C and - 7° C to start the floral initiation. To manipulate flowering times, the plant's response to photoperiod has to be controlled. In temperate regions, when temperatures increase in spring and active growth starts, a photoperiod insensitive cultivar can immediately initiate its floral primordial and run up to flower. A photoperiod sensitive variety will remain vegetative until increasing day lengths in the spring satisfy the photoperiod requirements. This led to an extended grain filling and ripening period, resulting in higher yields and improved quality (Worland and Snape, 2001).

1.1.2 Breeding Categories for Winter Wheat

Inbred Lines

Wheat is a self-pollinating plant as the pollination takes place within the closed flower preventing natural cross-pollination. Cultivars of self-pollinating crops are generally homozygous progenies derived from crosses of two or several defined progenitors. They are commonly bred by classical pedigree breeding schemes (see detailed description below). Breeding starts with the choice of the most promising crosses of parental lines. The standard method for defined cross pollination employs hand emasculation and isolation of female parent followed by hand pollination with the pollen shedding ear of the selected male parent. The resulting F1 progeny is completely homogenous and heterozygote. During continued propagation by natural self pollination, the progenies of one cross will segregate while the homozygosity will increase with each generation. The F1 crossing progeny is propagated and harvested as bulk to obtain the F2 and F3 generation. From F3 – F6, single ear descendents are selected between and within families of one cross. The differentiation of individual line characteristics increases from F3 till the F5 as the level of homozygosity increases from 75 (F3) to 93.75% (F5). In the advanced generations (F5 – F8), the variability within the single ear progenies decreases and only a few successful genotypes remain as promising breeding lines during generations F7 – F12 (Fischbeck, 1985; Becker, 1993). The unique characters of a new cultivar have to be preserved by maintenance breeding.

Hybrid Breeding in Wheat

Hybrids are obtained by crossing two parental lines aiming for extraordinary high productivity, the so-called heterosis effect. The productivity of the F1 should be significantly higher than the mean productivity of the parental lines to call it heterosis. The parental lines are homozygote pedigree lines. If the parental lines were derived from highly differing gene pools, the hybrids will be extremely heterozygote resulting in high heterosis effects. The disadvantage of hybrids is that this heterosis effect is only realized in the first generation. Progenies of self pollinated hybrids are segregating resulting in heterogeneous and less productive crops. Therefore it is not possible for farmers to propagate their own seeds as hybrid seeds is less attractive as the heterosis effect is usually smaller as for outcrossing species like maize. It is also more difficult to prevent self pollination of wheat. For commercial production of hybrid seeds in wheat, the female parent needs to be male sterile. This can either be provoked by the application of gametozides or the incorporation of male sterility genes. Therefore, hybrids are of minor importance in wheat breeding up to now (Becker, 1993; Jung et al., 1999).

Composite Cross Populations

The development of the composite cross approach arose to increase genetic diversity within cultivars allowing genetic adaptation towards unforeseen biotic and abiotic stress factors. Composite cross populations are formed by assembling seed stocks with diverse evolutionary origins and by recombination of these stocks by large numbers of crossings. The F1 progenies of such crosses are propagated as one heterogenous bulk and subsequent natural selection follows for mass sorting of the progeny in successive natural cropping environments. Composite cross populations can provide dynamic gene pools, which in turn provide a means of conserving germplasm resources and also allow selection of heterogeneous crop varieties (Suneson, 1956; Paillard et al., 2000; Phillips and Wolfe, 2005; Finckh, 2007; Wolfe et al., 2008).

1.1.3 Stability and Adaptability Analysis in Plant Breeding: The Concepts of Phenotypic Stability

Successful new cultivars must achieve high values for yield and other agronomic traits. Moreover, they have to show their superiority not only in one environment but in a range of heterogeneous environments. Such cultivars provide high stability of the respective traits. Differences in stability between cultivars often show up in multi-location field trials due to the interactions between genotypes and environments, the so-called genotype x environment interactions. If the ranking of genotypes depends on the particular environmental conditions where they are grown, the interactions can be understood as a result of a differential reaction to environmental stress factors like drought or disease. However, only a minor part of the genotype x environment interactions can be attributed to clearly defined environmental effects. The major part of the genotype x environment interactions is just an inexplicable quantity in the statistical analysis of trials. The term “phenotypic stability” is often used in this context to refer to fluctuations in the phenotypic expression of a trait while the genotypic composition of the cultivars remains stable.

Depending on the goal and on the trait, two different concepts of stability exist, which are termed as the **static** and the **dynamic** concept of stability (Léon, 1985).

According to the static concept, a stable genotype possesses an unchanged and stable performance independently of environmental variations. This stable genotype shows little deviation from the expected character level. Applying this concept, the phenotypic stability is measured using the variance of a genotype across the tested environments. This environmental variance (EVS) of genotypes’ detects all deviations from the genotypic mean. Using the environmental variance, a desirable genotype will not react at all in changing environmental conditions. A genotype with minimum EVS is considered to be stable. Values for EVS should be low for traits such as resistance to pests and diseases, and quality parameters.

For yield, in contrast, a breeder aims at finding genotypes which are stable and high yielding, simultaneously, i.e. cultivars showing good performance under poor conditions as well as increased yield with increased fertilization level. This is reflected in the dynamic concept of the ecovalence (EVD) according to Wricke (1962). The EVD measures the contribution of a genotype to the genotype x environment interactions. A low EVD value indicates that the genotype reacts stable but dynamically to changing environmental conditions.

1.1.4 Suitability of Modern Wheat Cultivars for Organic Farming

Focusing on grain yield improvement for high input farming systems, wheat breeders generally neglected the improvement of nutrient use efficiency (Calderini et al., 1995), which means cultivars achieving high grain yields under low nutrient supply. Nutrient use efficiency was mentioned mainly in the context of low input agriculture in developing countries but was up to now not regarded as a problem in industrialized nations (Bonjean and Angus, 2001). This development might have resulted in a shift of the optimum N level for wheat cultivation and might have led to cultivars with an increasing N demand as stated in recent studies (Brancourt-Hulmel et al., 2003; Guarda et al., 2004; Sylvester-Bradley and Kindred, 2009). It is estimated that about 95% of organic agriculture is based on crop cultivars developed for conventional high input farming (Lammerts van Bueren et al., submitted). One of the main principles of organic farming, the relatively closed nutrient cycling based on farm resources, is limiting the nutrient input. Under the assumption that modern cultivars are increasingly dependent on nutrient input, they might be decreasingly suitable for organic farming.

In general, the most successful cultivars in conventional farming are tested for their suitability under organic farming conditions and the best ones are then propagated and distributed for the organic sector. The rational behind is that the organic sector is too small for own organic breeding programs and that the best cultivars from conventional breeding programs will also be the best choice for organic farming. However, the last assumption is lacking experimental data.

Most breeding programs are conducted in controlled environments with an optimum level of fertilizer supply and herbicide application to ensure that crop deficiencies are minimized. Placed on research stations for example the fertilizer input, crop rotations and plant protection strategies often do not mirror farmers' situation but represent uniform test environments reflecting most favourable growing conditions (Ceccarelli, 1996; Desclaux, 2005; Fossati et al., 2005; Ceccarelli and Grando, 2007). Ceccarelli and Grando (2007) found that unfavourable conditions seem to be very different from each other, while favourable conditions tend to be somewhat similar. In addition, commercial plant breeders generally focused on mainstream cultivars that are suitable for huge areas, rather than on locally adapted cultivars or cultivars suitable for specific growing conditions (Lammerts van Bueren et al., 1999; Rajaram and van Ginkel, 2001). This is in contrast to the requirements of cultivars for highly heterogeneous and unfavourable environments such as low input and organic farming systems.

In Europe, wheat cultivars for organic farming have to fulfil requirements of farmers, cereal processing industries and moreover consumers of organic products. Farmers expect high yielding cultivars with high tolerance against abiotic and biotic stress. Cereal processing industries especially rely on high technological baking quality. Consumers of organic products expect food of best sensory quality but moreover with high nutritional values and generally healthy products. The need of specific breeding programs for organic farming is intensively discussed within the organic sector (Lammerts van Bueren et al., 2002; Niggli, 2002; Kunz et al., 2006; Lammerts van Bueren et al., 2008; Wolfe et al., 2008). Consensus exists that breeding aims differ for organic and conventional farming.

Common breeding goals are high yields, disease resistance and high baking quality. However, there are additional traits which are relevant in organic farming only and therefore need to be improved by specific breeding efforts. For example, seed quality and seed health (especially resistance against common wheat bunt (Tilletia caries)) is most fundamental in organic farming as the use of chemic-synthetical seed treatments is not allowed. During plant establishment, the relevant traits are tillering capacity and regeneration ability after harrowing and a rapid nutrient uptake. Weed suppression ability is most fundamental in organic farming where no herbicides are allowed. Plant height and leaf posture can contribute to successful weed suppression. Cultivars have to be resistant or at least tolerant against diseases on the leaves and especially later on, on the ears (e.g. against Fusarium, Septoria and Tilletium fungi). From heading to maturity, cultivars require improved nutrient use efficiency (NUE) under limited nutrient conditions. This can be achieved e.g. by a well developed fine rooting system or a functioning symbiosis with soil microorganism such as arbuscular mycorrhizal fungi (AMF). Fundamental is also the ability to efficiently relocate nutrients from stems and leaves into the grain. Finally, grain yield stability seems to have a higher priority than the absolute yield amount. There are high requirements on the nutritional values and sensory quality of the grain and especially on the bread making quality under limited N supply (Kunz et al., 2006; Löschenberger et al., 2008).

The number of published field studies concerning the genetic improvement of wheat focused on organic farming are rare and studies including intrinsic organically bred cultivars are hardly to find. Field studies of wheat genotypes tested under organic farming were recently published by Carr et al. (2006), Murphy et al. (2007), Baresel et al. (2008) and Reid et al. (2009). While the studies of Murphy et al. (2007) and Reid et al. (2009) were carried out with cultivars derived only from organic breeding, the studies of Carr et al. (2006) and Baresel et al. (2008) mainly comprised conventionally bred cultivars. Experimental studies on maize breeding under organic compared to conventional farming systems were carried out by Burger et al. (2008), De Geus (2008) and Lorenzana and Bernardo (2008). However, recommendations whether to establish specific breeding programs for organic farming are not consistent among the studies. The contradictory results are discussed in detail in Chapter 4.4.1.

1.1.5 Wheat Breeding Programs in Organic Farming

Wolfe et al. (2008) defined three different types of breeding programs out of which cultivars for organic farming are released.

Wheat Breeding Programs for Conventional Agriculture (BFCA)

Selection is carried out under conventional farming conditions and the best cultivars of these programs are presumed to be the best under organic conditions as well. In these programs, conventionally bred wheat cultivars are just selected for organic growing conditions when the conventional breeding process has been completed. The French agricultural research institute (INRA) started an "organic winter wheat breeding program" in 2003. Cultivar tests under organic and conventional low input conditions revealed excellent performance of cultivars selected under low input conditions in the organic systems (Rolland et al., 2008). However, the conditions of low input agriculture are not comparable to conventional high input agriculture. A further example is the winter wheat breeding program of the Swiss breeding research station Agroscope Changins-Wädenswil, which focuses on integrated production systems applying herbicides but only limited amounts of insecticides and pesticides (Fossati, 2003).

Wheat Breeding Programs for Organic Agriculture (BFOA)

In breeding programs with special emphasize on organic farming, the specific breeding goals for organic farming are incorporated into the running conventional breeding program. Typically, crosses and early selection is conducted under conventional conditions but later breeding generations are evaluated at organically and conventionally managed sites. One example is the wheat breeding program for organic agriculture of the Austrian company Saatzucht Donau (see detailed description below) (Löschenberger et al., 2008). The first selection steps (F1 – F5) are carried out under conventional conditions (Figure 1 1). Bulk populations with individual ear selection is conducted in parallel under organic and under low input conditions in advanced generations (F6 – F7). Maintenance breeding as well as the production of prebasic and basic seeds are carried out under conventional conditions, followed by propagation of certified seeds under organic conditions.

Organic Plant Breeding (OPB) for Wheat

In organic plant breeding programs all steps of selection, propagation and maintenance are carried out under organic conditions and the breeding techniques used are in agreement with the principles of organic agriculture (Lammerts van Bueren, 2002). Such a program is for example carried out in Switzerland by Getreidezüchtung Peter Kunz (GZPK), Verein für Kulturpflanzenentwicklung (www.gz.peter-kunz.ch [Kunz et al., 2006]). Breeding and selection of cultivars is carried out exclusively on organic or more precisely bio-dynamic farms. The overall goal of that breeding program is the general improvement of quality of organic wheat cultivars. Other organic cereal breeding programs are also carried out in Germany by Getreidezüchtung Darzau (www.darzau.de), at Dottenfelder Hof (www.dottenfelderhof-forschung.de) and at the Keyserlink Institute (www.saatgut-forschung.de/index.htm). All these breeders are aligned in the Association of bio-dynamic plant breeders (www.abdp.org). Breeding for organic farming is also conducted at the Elm Farm Research Centre (www.efrc.com) in the UK. While most breeding programs are focused on classical pedigree breeding, the approach of developing composite cross populations (CCP) is used at Elm Farm.

Examples of Wheat Breeding schemes

The process of cultivar breeding from creating new diversity by crossing to selection and testing of promising lines, multilocation yield trials, multiplication of seeds, registration and official cultivar tests till the official release of the cultivar usually takes between ten and twelve years. In the following section, the breeding schemes of Saatzucht Donau (Figure 1 1) (Löschenberger et al., 2008) and of the Getreidezüchtung Peter Kunz (GZPK) (Kunz et al., 2006) will be described in more detail as they represent successful examples of wheat breeding for the organic sector. During the last few years, seven and ten winter wheat cultivars were released by Saatzucht Donau and GZPK, respectively and are grown at organic farms in Switzerland, Germany and Austria. The main differences between the breeding schemes of Saatzucht Donau and GZPK are the beginning of single ear selection, line selection, first scorings of important traits and the site management system. Saatzucht Donau is carrying out a Breeding Program for Organic Agriculture (BFOA), in which breeding is done at conventionally and organically managed sites. The breeding program of GZPK is carrying out Organic Plant Breeding (OPB), which means that all breeding sites are managed organically.

In both programs, intensive visual field selection for agronomic parameters such as early vigor, tillering capacity, plant height, complemented by a selection of promising seeds based on grain appearance starts in F4. At this step, Saatzucht Donau already starts analysing baking quality parameters such as grain protein content, Zeleny value and falling number, whereas GZPK starts assessing baking parameters with lines of F5 – F7 (Figure 1 1). Two years of yield trials, now under organic conditions are conducted by Saatzucht Donau in F6 at

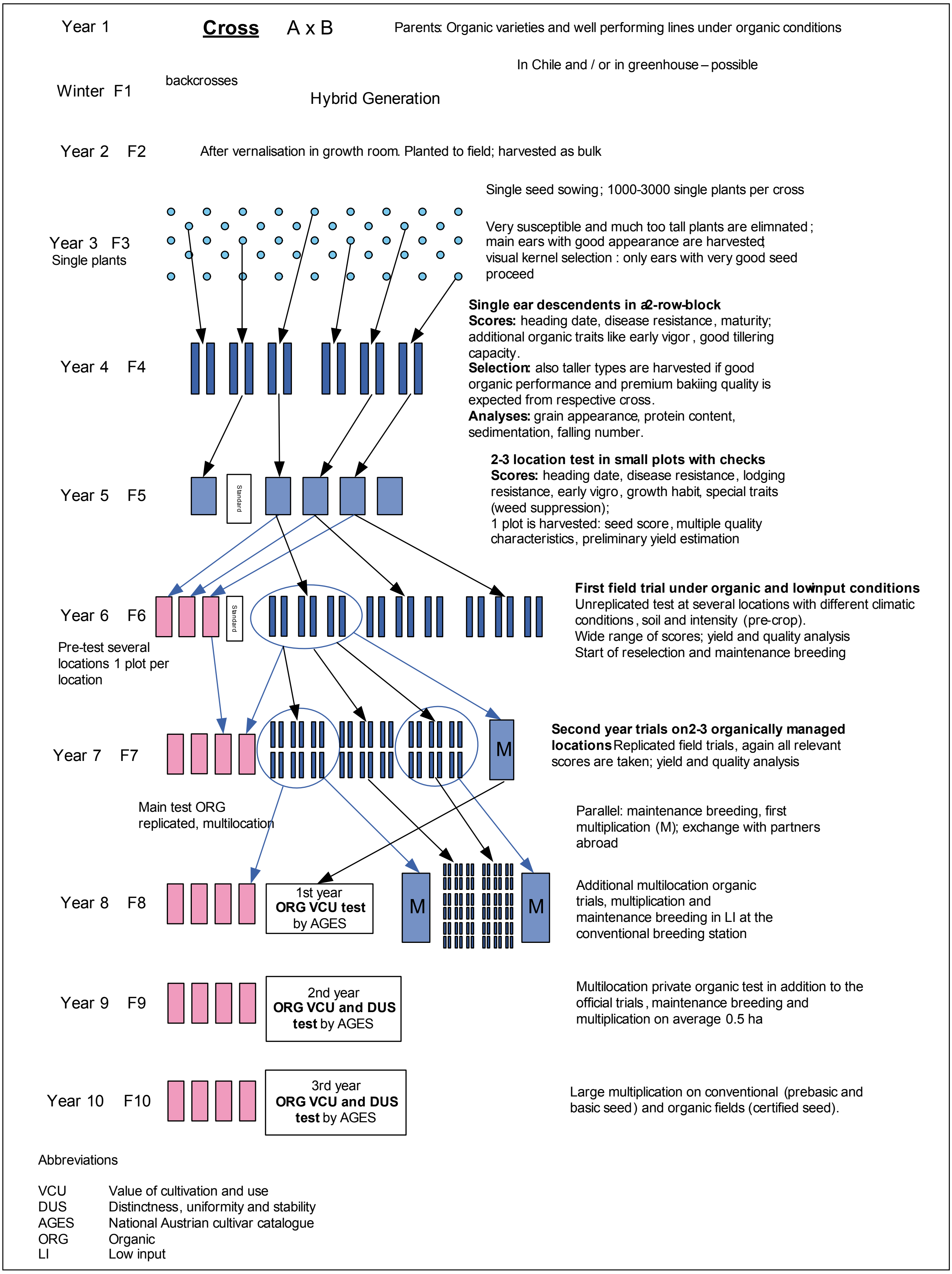

Fig. 1 1. Breeding scheme for organic winter wheat as mainly performed by Saatzucht Donau (modified after Löschenberger et al., 2008) several locations in different climatic environments. F8 is the beginning of official three-year trials for Austrian organic cultivar testing, accompanied by private tests under organic conditions at several locations. Prebasic and basic seed is multiplied on conventional fields; certified seeds are multiplied on organic fields. At GZPK, lines are selected at organic sites from F5 – F7. This is followed by multilocation tests during several years starting with a number of 380 lines and ending with about 32 promising advanced breeding lines. Each year, one or two cultivars were forwarded to the official Swiss cultivar testing.

1.1.6 Suitability of Molecular Breeding Tools for Organic Farming

Whether a cultivar is suitable or not for growing under organic conditions depends on the breeding aims within the breeding programs, the included breeding environments but also on the used breeding techniques. The reliance and the dependency on conventional seeds is also critical due to the increasing application of biotechnological methods in breeding. Organic farming is internationally based on the standards of the International Federation of Organic Farming Movement (IFOAM). The IFOAM standards however specify suitable and permitted methods of plant breeding, hereby explicitly banning methods such as genetic modification and protoplast fusion modification (IFOAM, 2006). With the advent of molecular markers it became possible to dissect quantitative inherited traits into single genes. For wheat the identification of such quantitative trait loci (QTL), using segregating populations of parents with contrasting phenotypes, has proven to be difficult due to the complex hexaploid genetics of wheat (Messmer et al., 1999; Tuberosa et al., 2002; Paillard et al., 2003). Presently, the implementation of marker assisted selection (MAS) into commercial wheat breeding programs is still limited and restricted to marker assisted backcross breeding for introgression of major genes from unadapted material or the pyramidization of resistance genes. However, with advanced marker technologies and new mapping techniques such as association mapping (Zheng et al., 2009) and tilling (targeting induced local lesions) (Slade et al., 2005; Parry et al., 2009) more QTL will be identified and useful for MAS. Rajaram and van Ginkel (2001), wheat breeders at the CIMMYT centre, the world leading institute for wheat breeding, recently stated that the overall goal of wheat breeding was yield improvement by technologies based on genetic engineering. Development of cultivars for zero-tillage and the use of transgenics to develop hybrid wheat in close collaboration with the breeding concern Monsanto are on the top priority list. A huge range of transformation techniques and potential applications in wheat breeding not only related to yield but moreover to quality traits and disease resistances and abiotic stress is given by Barsby et al. (2001). In future, not only the suitability of cultivars but moreover the suitability of applied technologies during the breeding process have to be considered when choosing cultivars for organic farming. These current developments in global wheat breeding put further pressure on the organic movement to establish own breeding programs.

1.2 Arbuscular Mycorrhizal Fungi

1.2.1 General Aspects of Arbuscular Mycorrhizal Fungi

The symbiosis between mycorrhizal fungi and plant roots is enormously widespread in natural ecosystems. Arbuscular mycorrhizal fungi (AMF) colonize roots of about 80% of land plant families (Brundrett, 2002). These fungi belong to the phylum Glomeromycota and can be clearly separated by rDNA analysis from other fungal groups (Schüssler et al., 2001). AMF contribute to an enhanced mineral nutrient uptake of the host in exchange for supply of carbohydrates. Due to this function, they might have played an important role for colonization of land by plants (Redecker et al., 2000; Schüssler et al., 2001).

Arbuscular mycorrhizal symbiosis consists of three important components: the plant root, the fungal structures within and between root cells and the extraradical mycelium in the soil. Infection sources in the soil are a prerequisite for root colonization. Spores, infected root fragments and hyphae can serve as inoculum. The relatively large spores (up to 500 µm in diameter) (Figure 1 2) can survive for long time in the soil. However, main infection sources are the hyphal network (Figure 1 3) and the infected root fragments. Within plant roots, arbuscules are formed as organs for nutrient exchange (Figure 1 3) and fungal vesicle for storage of lipids (Figure 1 4).

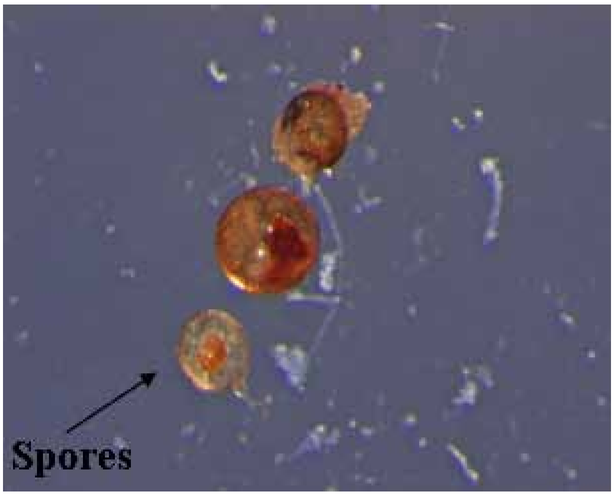

Figure 1 2 Spores of arbuscular mycorrhizal fungi isolated from DOK soil in December 2006 (Source: I. Hildermann)

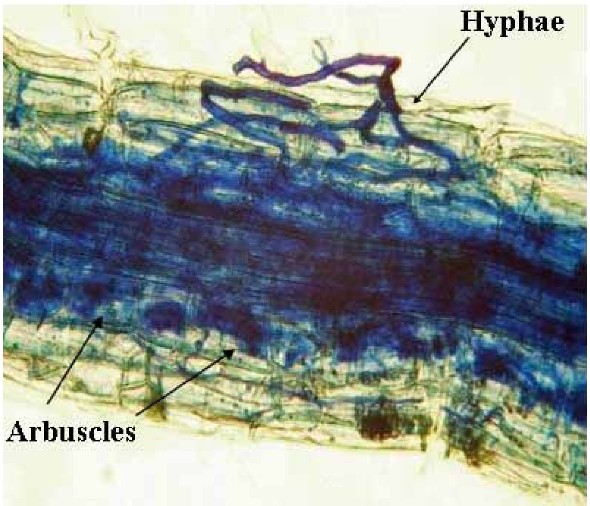

Figure 1 3 Hyphae and arbuscules of arbuscular mycorrhizal fungi in a winter wheat root stained with trypan blue; (Source: I. Hildermann)

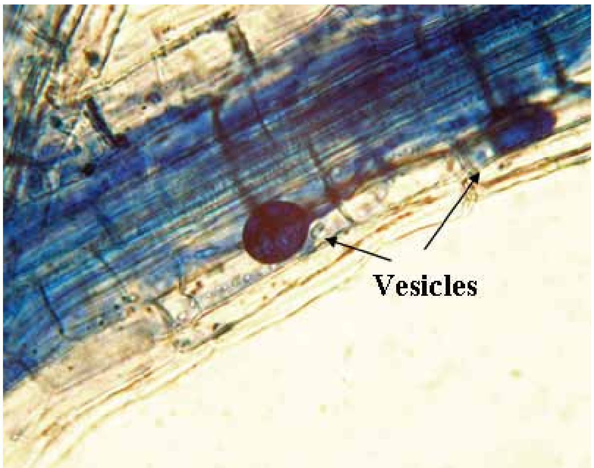

Figure 1 4 Vesicles of arbuscular mycorrhizal fungi in a winter wheat root stained with trypan blue; 200x magnified (Source: I. Hildermann)

1.2.2 Arbuscular Mycorrhizal Fungi in Agricultural Ecosystems

As AMF are part of the soil biota, these fungi play an important role for soil structure and soil fertility. Like other fungi, they contribute to soil stabilization by binding microaggregates to macroaggregates through their hyphae (Smith and Read, 2008) and through a sticking effect of the extracellular glycoprotein glomalin (Tisdall et al., 1997; Smith and Read, 2008). Beside these indirect benefits for plant growth, plants benefit directly from AMF as they can enhance tolerance to water stress (Rillig et al., 2001) and may furthermore increase resistance to certain root pathogens (Smith and Read, 2008).

Crop management such as fertilization (Hegde et al., 1999; Liu et al., 2007), tillage (Kabir, 2005; Berner et al., 2008), crop rotation (Oehl et al., 2003; Oehl et al., 2005) and plant protection can strongly influence AMF, both directly by destroying the hyphal nets during tillage or indirectly by creating favourable or unfavourable conditions for AMF. Among all these factors, plant available soil P is the main factor controlling the plant-fungus relationship (Gryndler et al., 2006). There is a negative correlation between plant available soil P and AMF-root colonization (AMF-RC) (Graham and Abbott, 2000; Sorensen et al., 2005; Gryndler et al., 2006; Smith and Read, 2008; Kahiluoto et al., 2009). As soil P is generally lower under organic than under conventional conditions (Gosling and Shepherd, 2005; Romanya and Rovira, 2009), AMF abundance and diversity was often found to be higher in organic systems (Kahiluoto et al., 2001; Oehl et al., 2003).

The support of nutrient uptake of the host plant by the external mycelium that explores larger soil volumes beyond the rhizosphere is considered to be the most important benefit of the symbiosis (Marschner and Römheld, 1998). The improvement of plant nutrition status as a result of the transport of slowly diffusing nutrient ions such as PO^{4-}, Zn^{2+} and Cu^{2+} by the external mycelium of AMF is well known (Marschner, 1993; Liu et al., 2007). AMF are able to make P sources of the passive pool of soil P accessible to plants and are thus a crucial component in plant nutrition, particularly in organic- and low input farming (Douds et al., 1993; Ryan et al., 1994; Douds, 1995; Mäder et al., 2000a; Oehl et al., 2003; Oehl et al., 2004; Ryan et al., 2004; Kahiluoto et al., 2009).

1.2.3 Wheat and the AMF Symbiosis

Colonization of wheat roots (AMF-RC) was often reported to be low, ranging between 10 – 30% (Hetrick et al., 1996; Al-Karaki et al., 2004; Friedel et al., 2008). Beside the low AMF-RC, cereals might be generally less dependent on the AMF symbiosis compared to other agricultural crops. In a field study under temperate conditions, growth of 22 agricultural species in fumigated and unfumigated soils with good availability of P was compared (Plenchette et al., 1983). Cereals such as wheat and oat established AMF-RC but plant growth remained unaffected. In contrast, maize, carrots, tomatoes and potatoes showed positive growth response in unfumigated soils.

The low colonization rate and the lower dependency might be attributed to the root morphology of cereals. Generally, plants with coarse root systems like maize seem to benefit more from AMF symbiosis than the genotypes with fibrous root systems like wheat as stated in the reviews of Johnson et al. (1997) and Brundrett (2002) on the coevolution of roots and mycorrhizas of land plants. This was first mentioned by Baylis (1975) and was also confirmed by Hetrick et al. (1988) comparing root morphology of warm-season and cool-season tallgrass prairie plants. During the evolutionary process of plants, the root systems became increasingly finer with the finest roots becoming progressively thinner and more branched. Cereals generally develop long, fine-branched, rapid growing rooting systems allowing direct nutrient and water uptake from a large soil volume. In contrast, species which exhibit thick and less branched roots with a long life span, a well protected root cortex and a relatively slow root growth often provide optimal habitat for AMF that support the indirect nutrient and water uptake of the host (Brundrett, 2002; Smith and Read, 2008).

In wheat, AMF symbiosis contributed to improved P-uptake in shoots (Koide, 2000; Zhu et al., 2001) and in grain (Karagiannidis and Hadjisavva-Zinoviadi, 1998; Graham and Abbott, 2000; Kahiluoto et al., 2001; Al-Karaki et al., 2004; Li et al., 2006). Besides P, improved grain Zn-uptake due to AMF was shown by Karagiannidis and Hadjisavva-Zinoviadi (1998), Ryan et al. (2004) and Kahiluoto et al. (2001). However, most of these data are based on pot trials. Johnson et al. (1997; 2010) described the AMF symbiosis as being mutualistic or parasitic depending on the nutrient status of the soil. Mycorrhizal associations are beneficial (mutualistic) to plants, when the net costs of carbon (C) delivery to the fungi are less than the net benefits of nutrient uptake. This appears in soils that are deficit in both, N and P. However, in such a case, the C for P exchange will be limited by restricted carbohydrates production of the plant. At high N and low P availability, mutualistic benefits are predicted to be greatest as the high N supply increases the photosynthetic capacity of the host plant. The association is detrimental (parasitic) when the net costs exceed the net benefits. This appears in soils without limitations in N or P.

1.2.4 Breeding for Plant-Microbe Interactions

A promising approach to improve nutrient use efficiency of agricultural crops would be to breed for improved rhizosphere related traits such as the plant-microbe interaction with arbuscular mycorrhiza or plant growth promoting bacteria (PGPB). It is still not clear whether and to which extent there is an effect on rhizosphere related traits induced by breeding conditions. According to Drinkwater and Snapp (2007), the AMF symbiosis or plant-microbial interactions in general, could be less favourable for a crop under modern agricultural high input conditions as they strongly differ from the environmental conditions under which the symbiosis evolved. According to this hypothesis, breeding under organic low input conditions should lead to cultivars with a high functionality of the AMF symbiosis, while this potential might have been lost during selection under high input conditions. Therefore, differences in the AMF symbiosis are expected for cultivars derived from selection under different fertilization levels as represented in this study by old cultivars and cultivars derived from organic and conventional breeding programs.

In pot trials, Hetrick et al. (1992; 1993) observed higher colonization and responsiveness of wheat cultivars bred before 1950, i.e. before synthetic fertilizers were widely applied than of modern wheat cultivars. Also in pot trials, higher responsiveness of older wheat cultivars compared to recently released cultivars was reported by Manske (1989) and Zhu et al. (1989). Mazzola and Gu (2000) demonstrated in greenhouse trials that the increase in population size of rhizobacteria depended upon the wheat cultivar but not on the breeding programs.

Molecular studies using on hard red spring wheat cultivars (Fu et al., 2005) and oat cultivars (Grau Nersting et al., 2006) showed less number of alleles in modern cultivars than in old cultivars and landraces indicating a loss of genetic diversity during breeding. As mentioned, the AMF-symbiosis causes carbon costs to the plant and AMF can be parasitic in P rich environments, which might result in lower yields. Thus, breeders could have been selecting indirectly against high AMF-RC and breeding inadvertently for cultivars with less efficient microbe-plant interaction as hypothesized in the review of Lambers et al. (2006). It is hypothesized that alleles involved in the AMF-wheat symbiosis might have been lost during early selection in high P environments. Hetrick et al. (1995) identified individual genes responsible for a functioning AMF-wheat symbiosis. Such studies provide valuable information about the genetic basis of plant-microbe interactions. In the future, direct breeding for improved plant-microbe interaction might be possible by molecular tools. Efforts have already been made in mapping quantitative trait loci (QTLs) associated with rhizosphere traits. Via marker assisted selection, these QTLs could be reintroduced into cultivars (Wissuwa et al., 2009).

1.3 Aims of the Thesis

The debate on the suitability of modern winter wheat cultivars for organic farming provided the impetus for this thesis. The overall aim was to assess the need of specific breeding programs for organic farming under the general hypothesis that cultivars selected under organic conditions (direct selection) are better suitable for organic farming than cultivars selected under conventional conditions (indirect selection).

Within this thesis, two one-year field studies with eight to ten winter wheat cultivars derived from organic and conventional breeding programs and old cultivars were conducted in a total of seven environments including both organically and conventionally managed sites. In both studies, the same parameters were assessed: yield and yield components, baking quality, nutrient use efficiency for N and P and the AMF-root colonization in relation to nutrient concentration and nutrient uptake in plant shoots and grains and in relation to grain yield.

In 2007, ten winter wheat cultivars were tested in the DOK long-term system comparison trial (Figure 1 5 and Figure 1 6) to assess their performance under organic and conventional conditions at the same field site. In the DOK trial organic and conventional farming systems are compared under homogenous soil conditions since 1978. The experimental lay-out of the DOK trial (Figure 0 1), of the embedded cultivar test (Figure 0 2) and the sampling area (Figure 0 3) are presented in the Annex. The cultivar test in the DOK trial was published in detail in two papers. The results of grain yield and baking quality are presented in Chapter 2 (Hildermann et al., 2009). The results of nutrient use efficiency and the relation with the AMF symbiosis are presented in Chapter 3 (Hildermann et al., in revision).

In 2008, eight out of the ten wheat cultivars were tested at three marginal organically managed sites in order to examine the potential of these cultivars in a wider range of organic environments and especially under less fertile conditions than the DOK trial (Figure 1 7). In contrast to the DOK trial, the second experiment was carried out on-farm on sites differing in soil, climate and moreover precrops, weed management and fertilizer regimes. The experimental lay-out of the on-farm trials (Figure 0 4) is presented in the Annex. Chapter 4 presents the results of these on-farm trials and shows the combined analysis across the five organically managed sites of both experiments (Hildermann et al., submitted).

In a comprehensive analysis the need of specific breeding programs is discuss with respect to the results obtained in the two field experiments (Chapter 5.5) including socio-economic aspects of plant breeding is presented in Chapter 5.6.

The final conclusions and the outlook are given in Chapter 6.

The main objectives of the thesis are:

(1) To compare yield, baking quality and nutrient use efficiency of modern winter wheat cultivars derived from organic and conventional breeding programs as well as old cultivars **in organic and conventional systems of the DOK long-term system comparison trial at a fertile site** (Chapter 2 and 3),

(2) to compare yield, baking quality and nutrient use efficiency of these cultivars **at three organically managed on-farm trials at marginal sites** (Chapter 4),

(3) to analyse their phenotypic stability for grain yield, baking quality and nutrient use efficiency **across marginal and fertile organic sites** and (Chapter 4)

(4) to assess **AMF-root colonization** of these cultivars and the correlation between of AMF-root colonization and nutrient concentrations in shoots and in grain and straw at harvest, nutrient uptake and grain yield under field conditions (Chapter 3 and Chapter 4).

Figure 1 5 The DOK long-term field trial in Therwil (Basle-Land) in 1992, where organic and conventional farming systems are compared since 1978. N = unfertilized control (NOFERT); D1, D2 = bio-dynamic (BIODYN 1 and BIODYN 2); O1, O2 = bio-organic; K1, K2 = conventional farming with manure; M = conventional farming with mineral fertilizers only (CONMIN). The systems NOFERT, BIODYN 1 and BIODYN 2 and CONMIN were included in the cultivar trial.

Figure 1 6 DOK-field plots with winter wheat cultivars in June 2007. Front left: conventional farming with mineral fertilizers only (CONMIN), front right: unfertilized control (NOFERT); back left: bio-dynamic farming (BIODYN 2), back right: bio-dynamic farming (BIODYN 1)

Figure 1 7 Field plots of winter wheat cultivars of the on-farm trials at a bio-dynamically managed farm in Rheinau (site SH) in June 2008.

2 YIELD AND BAKING QUALITY OF WINTER WHEAT CULTIVARS IN DIFFERENT FARMING SYSTEMS OF THE DOK LONG-TERM TRIAL

This article has been published:

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2.1 Abstract

Background: A challenge in wheat (*Triticum aestivum L.*) breeding for organic farming is to provide high yielding cultivars with appropriate baking qualities under the limiting conditions of organic fertilizer input and without the use of pesticides. Cultivars are usually tested on organic and conventional farms. However, field properties may differ due to spatial variations of soils and micro-climate. In our study, we tested old, organically and conventionally bred cultivars in organic and conventional farming systems of the DOK long-term system comparison trial.

Results: Effects of cultivars and systems on yield and quality parameters were statistically significant. Genotype x system interactions were generally not observed. Grain yield across all cultivars increased from 4.2 Mg ha^{-1} under organic conditions up to 6.8 Mg ha^{-1} under conventional conditions, with protein contents of 90 g kg^{-1} and 117 g kg^{-1}, respectively. Conventionally bred cultivars yielded significantly more under conventional conditions than organically bred cultivars, whereas neither organically nor conventionally bred cultivars performed better under organic conditions.

Conclusion: Breeding for yield was successful, but only under high input conditions, where these successes were accompanied by rising inputs of external resources. The results of this study suggest that cultivar testing in long-term system comparisons can complement standard on-farm testing.

Keywords: Organic farming – Plant breeding – Winter wheat – Yield – Baking quality

2.2 Introduction

Wheat (*Triticum aestivum* L.) is a staple food in large parts of the world and was grown on 21.7 million ha worldwide in 2007 (FAO (www.faostat.fao.org)). Many attempts have been made to improve wheat production, with yield increase and resistance to lodging and fungal diseases as the main objectives. As a result, grain yields have risen rapidly, especially during the last 60 years. In industrialized countries, this wheat yield increase has generally been accompanied by an increased input of external resources such as mineral fertilizers and pesticides (Tilman et al., 2002). In addition to the intensification of agricultural practices, breeding efforts affecting plant morphology traits and yield components have led to higher yielding cultivars (cvs). Guarda et al. (2004) postulated earliness, reduced plant height, an increased harvest index and rising numbers of seeds m^{-2} as the most important changes.

The aim of organic farming is to produce healthy and environmentally friendly food by closing the nutrient cycle as much as possible and avoiding the use of synthetic mineral fertilizers and pesticides. The benefits of organic farming, such as lower external input of nutrients, maintenance of soil fertility, and enhanced biological activity and biodiversity above- and belowground, have been shown in many studies (Reganold et al., 2001; Bulluck et al., 2002; Mäder et al., 2002)

In Switzerland, the organic farming sector is constantly growing. 125,596 ha (12% of total agricultural land area) were organically farmed in 2006, thus making Switzerland one of the ten European countries with the highest percentage of organically farmed land (Willer et al., 2008). However, only 3% (2,373 ha) of the winter wheat (73,910 ha) was grown organically in 2006 (Bundesamt für Statistik, (ww.agr.bfs.admin.ch)). Although winter wheat is the most frequently grown cereal in organic farming in Switzerland, it is still a niche market of limited economic interest for breeding companies. For conventional wheat production, Swiss seed propagating cooperatives provided 17 registered cultivars. Despite this, out of the 13 cultivars recommended and propagated for organic wheat production in Switzerland, only six cultivars were developed in breeding programs conducted within organic farming systems. A similar situation is described in the Netherlands, where the limited area of organically farmed land appears to deter breeding companies from establishing special programs for organic purposes (Lammerts van Bueren et al., 2002). To be suitable for organic farming, cultivars must be able to tolerate certain unfavourable conditions typically linked with organic farming, e.g. the low soil nutrient status due to the slow release of organic fertilizers and the pressure from weeds, pests and diseases. Generally, wheat yields are lower under organic than under conventional conditions (Mäder et al., 2002; Ryan et al., 2004; L-Baeckstrom et al., 2006; Schwaerzel et al., 2006; Mäder et al., 2007; Mason et al., 2007; Murphy et al., 2007). Problems with weeds (Mason and Spaner, 2006) and diseases and in particular the lower input of nutrients (L-Baeckstrom et al., 2004; Murphy et al., 2007) are often stated as the main reasons. There is currently a lively debate on the question as to how the breeding environment influences the performance of wheat cultivars under organic or low input growing conditions. A study on wheat breeding for low input farming compared direct selection conducted under the target conditions vs. indirect selection conducted under conditions differing from the target environment, showing the first being more successful (Brancourt-Hulmel et al., 2005). Similar results were obtained in barley selection for low input conditions (Ceccarelli, 1996). For organic wheat production, it was shown that direct selection under organic conditions led to higher yields under organic growing conditions (Murphy et al., 2007).

Besides yield, baking quality is the most important trait for bread wheat breeding. L-Baeckstrom et al. (2004) found clear differences in baking quality between organically and conventionally grown wheat, with higher baking quality in the conventional system. In that ten-year study, limited nitrogen (N) in the organic systems caused most of the differences. In a Swiss study, in general lower values were observed for the rheological dough properties in organically grown cultivars compared to cultivars grown under conventional low input conditions, although the results of the baking tests were similar (Kleijer, 2006).

Hence a challenge in breeding for organic farming is the development of cultivars with suitable baking qualities that can also produce high yields under the limiting conditions of organic fertilizer input. Cultivar testing is normally performed on organically and conventionally managed farms. However, field properties at the compared sites may differ greatly due to spatial variations of soils and due to micro-climate heterogeneity. To our knowledge, comparative studies under homogenous site conditions within one experimental field plot design are lacking. We tested the performance of old, organically and conventionally bred cultivars in organic and conventional farming systems of the DOK long-term system comparison trial. The DOK long-term trial is one of the most rigorously examined system comparisons between organic and conventional farming systems in the world (Mäder et al., 2002; , 2006). Our hypothesis was that cultivars bred under low input conditions (old and organically bred cultivars) would perform better in the organic low input systems than conventionally bred cultivars because the former had been adapted to low input conditions during the breeding process. This hypothesis is in line with the opinion of Wolfe et al. (2008), who recently defined the desired characteristics of wheat cultivars for organic agriculture. We analyzed the most important parameters for wheat production during the growing period and after harvest, namely: plant density, plant height, yield, yield components and parameters related to baking quality.

2.3 Materials and Methods

2.3.1 Experimental Design

A field experiment with ten winter wheat cultivars grown under organic and conventional management conditions was performed in the DOK trial in 2006/2007. The DOK long-term trial was set up in 1978 at Therwil (7°33'E, 47°30'N) in the vicinity of Basel, Switzerland, by the Agroscope Reckenholz-Tänikon Research Station (ART) and the Research Institute of Organic Agriculture (FiBL), in order to compare two organic (bio-Dynamic and bio-Organic) and two conventional farming systems ("Konventionell" with and without manure) (Mäder et al., 2002). The soil is a haplic luvisol (sL) (typic Hapludalf) on deep deposits of alluvial loess. The climate is relatively dry and mild with a mean precipitation of 785 mm per year and an annual mean temperature of 9.5°C. The seven-year crop rotation was the same for all systems. From 1999 - 2006, the following crops were planted: potatoes, winter wheat 1, soybean, maize, winter wheat 2, grass-clover 1, grass-clover 2. In the conventional system, pesticides were only applied if economic thresholds for pests and diseases were exceeded, according to the integrated scheme of plant protection. In the organic farming systems, pests, weeds, and diseases were managed according to bio-dynamic guidelines. The field experiment was replicated four times.

Ten cultivars were tested in four replicates in two organic systems (BIODYN 1 and 2), a conventional system (CONMIN) and an unfertilized control (NOFERT), resulting in a total of 160 plots. These systems differed mainly in terms of fertilization and plant protection strategies. The organic systems represent mixed farms with arable land and livestock, CONMIN mimics a conventional system without livestock. The level of fertilization increased gradually from NOFERT to BIODYN 1 (0.7 livestock units ha^{-1}), BIODYN 2 (1.4 livestock units ha^{-1}) and CONMIN. The experimental design was a split-plot with the main factor systems and the secondary factor wheat cultivars. Soil samples at 20 cm depth were taken after wheat sowing on 5 December 2006. The main chemical soil characteristics are shown in Table 2 1.

System	pH	C_{org}	N_{min} [a]	P [b]	K [b]
	(H_2O)	(%)	(mg kg^{-1})	(mg kg^{-1})	(mg kg^{-1})
NOFERT	5.84 c	1.11 c	11.02 c	8.30 c	27.22 d
BIODYN 1	6.14 b	1.22 b	12.90 b	8.68 c	48.33 c
BIODYN 2	6.40 a	1.41 a	16.07 a	12.99 b	68.83 b
CONMIN	6.34 a	1.23 b	12.78 b	24.45 a	79.70 a
ANOVA					
P value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
LSD (d.f. = 3) [c]	0.12	0.08	2.71	1.86	5.64

[a] $N_{min} = NO_3 - N + NH_4 - N$

[b] measured in a double lactic acid extract

[c] LSD, least significant difference; d.f. degree of freedom

Table 2 1 Soil acidity, soil organic carbon content and soluble mineral elements in soil at beginning of the experiment in December 2006 (0 - 20 cm soil depth, n = 8)

Over four crop rotations (1978 - 2005) in the DOK trial, the Ntotal, phosphorous (P) and potassium (K) nutrient inputs were much higher in the conventional system than in the organic systems. The mean annual Ntotal input in the organic systems was 81% of the input in the CONMIN system. The organic system received 59% and 66%, respectively, of the amount of P and K fertilizers applied in the CONMIN system (Mäder et al., 2006).

In the 2006/2007 season, the BIODYN 1 and BIODYN 2 systems received split applications of 5/10 t ha^{-1} composted manure and 30/60 m^{-3} ha^{-1} slurry. The CONMIN system received only mineral fertilizers, split into three applications. This resulted in 33, 66 and 140 kg N_{total} ha^{-1} for the BIODYN 1, BIODYN 2 and CONMIN systems, respectively (Table 2 2).

	N_{tot} [kg ha^{-1}]	$N_{available}$* [kg ha^{-1}]
NOFERT	-	-
BIODYN 1 Composted manure (5 t) and slurry (30 m^{-3})	33	7
BIODYN 2 Composted manure (10 t) and slurry (60 m^{-3})	66	14
CONMIN Calcium ammonium nitrate (700 kg ha^{-1})	140	140

*$N_{available}$ (NH_4-N+NO_3-N)

Table 2 2 Nitrogen input to winter wheat plots via fertilisers as total and available N in 2006 - 2007

In the CONMIN system, weeds were controlled by applying 0.2 kg ha^{-1} of the herbicide Husar (50 g kg-1 Iodosulfuron-methyl-natrium and 150 g kg-1 Mefenpyr-diethyl) and 0.5 kg ha^{-1} Rasantan (22.5 g Amidosulfuron, 75 g Diflufenican and 375 g Bromoxynil a.i. kg^{-1}) on 3 March 2007. In addition, the CONMIN system received one application of the plant growth regulator Moddus (26.3% Trinexapac-ethyl) at the rate of 0.4 kg

ha^{-1} on 10 April 2007. The systemic fungicide Opera (13.3% Pyraclostrobin and 5% Epoxiconazol), was applied on 23 May 2007 at the rate of 1.75 L ha^{-1} for disease control.

Old, organically and conventionally bred cultivars developed between 1840 and 2006 were sown in the trial, resulting in a total of nine cultivars and one composite cross population (Table 2 3). In the composite cross population (CCP), a large number of cultivars from the UK were intercrossed and propagated as one bulk (Phillips and Wolfe, 2005). In the following text, the nine cultivars and the composite cross population are listed as ten cultivars. All cultivars had to be of bread wheat quality and suitable for the growing conditions in northwestern Switzerland. The old cultivars (Rouge de Bordeaux, Mont Calme 245 and Probus) were selected and released before 1950 and represent the era prior to intensification in agriculture. The so-called "organically bred" cultivars (Scaro, Sandomir and CCP) were derived from breeding programs in organic agriculture (as defined by Wolfe et al. (2008)), i.e., all breeding steps were carried out on organically managed sites. Moreover, selection and propagation techniques were also compliant with organic principles. The conventionally bred cultivars (Titlis, Caphorn, Antonius and DI 9714) originated from breeding programs for conventional agriculture. The cultivars Titlis and Antonius are also recommended for organic farming in Switzerland (FiBL (www.fibl-shop.org)). Four Swiss cultivars adapted to the local conditions (Mont Calme 245, Probus, Titlis and Scaro) represent the development in wheat breeding in Switzerland during the last century.

Cultivar	Abbreviation	Country of origin	Year of release	Origin / Breeder
Old cultivars/landraces				
Rouge de Bordeaux	**RB**	FR	1840	Institut National de la Recherche Agronomique (INRA), FR-75338 Paris Cedex 07
Mont Calme 245	**MC**	CH	1926	Nationale Genbank Agroscope Changins-Wädenswil (ACW), CH-1260 Nyon 1
Probus	**PR**	CH	1948	Nationale Genbank Agroscope Changins-Wädenswil (ACW), CH-1260 Nyon 1 / Agroscope Reckenholz-Tänikon (ART) - CH-8046 Zürich
Organically bred cultivars				
Scaro	**SC**	CH	2006	Sativa Rheinau AG, CH-8462 Rheinau, Getreidezüchtung Peter Kunz, CH-8634 Hombrechtikon
Sandomir	**SA**	DE	2009	Getreidezüchtung Darzau, Karl Josef Müller, DE-29490 Neu Darchau
Composite Cross Population	**CCP**	GB	not registered	The Organic Research Center, Elm Farm, GB-Hamstead Marshall, Newbury, Berkshire RG20 0HR
Conventionally bred cultivars				
Titlis (standard)	**TI**	CH	1996	Delley seeds and plants, CH-1567 Delley / Agroscope Changins-Wädenswil, CH-1260 Nyon 1
Antonius	**AN**	AT	2003	Delley seeds and plants, CH-1567 Delley/ Saatzucht Donau GesmbH. & CoKG, AT-2301 Probstdorf
DI 9714	**DI**	FR	not registered	Institut National de la Recherche Agronomique (INRA), FR-75338 Paris Cedex 07
Caphorn	**CA**	FR	2001	Delley seeds and plants, CH-1567 Delley/ Monsanto UK Ltd., GB-Cambridge

Table 2 3 Winter wheat cultivars planted in the DOK long-term experiment, their countries of origin and years of release

Winter wheat cultivars were sown after maize on 26 October 2006 in ten subplots (3 m x 1 m) on the margins of the 16 DOK plots (5 m x 20 m), thus comprising the four systems described above in all four replicates. BIODYN 1 plots were adjacent to BIODYN 2 plots, and NOFERT plots were adjacent to CONMIN plots. Sowing density was 420 germinating seeds m^{-2}, in accordance with organic farming recommendations. Seed density was the same in all systems and for all cultivars, as recommended for cultivar tests (Donner and Osman, 2006). The seed number was adjusted according to the results of a prior germination test. Germination of the cultivars ranged from 92% to 98%. Row spacing was 16.7 cm. The ten cultivars were randomly arranged in each replicate of the DOK experiment.

2.3.2 Initial Soil Analysis

Two soil samples per subplot were collected after sowing on 5 December 2006 at a depth of 20 cm, using an auger (Ø 3 cm). All ten samples of a strip of five subplots were combined in one mixed sample. We measured soil acidity in a water suspension, mineral nitrogen (N_{min} = NH_4-N + NO_3-N) photometrically in 0.01 M $CaCl_2$, soil organic carbon by wet combustion and phosphorous and potassium in double lactic acid (DL).

2.3.3 Plant Height and Plant Density

Plant heights were measured on ten plants per cultivar per subplot after plant emergence on 13 December 2006, at early heading on 18 April 2007, after ear emergence on 25 May 2007 and at the beginning of ripening on 27 June 2007. Plant density after emergence (18 December 2006), number of tillers per m^{-2} (13 April 2007) and number of ears m^{-2} (07 June 2007) were counted in two 0.5 m long rows per subplot.

2.3.4 Yield and Harvest Parameters

The subplots were harvested on 13 and 14 July 2007. Whole plants were sampled from the centre of each subplot in two 2.0 m long rows to determine fresh weight of straw and grain. Straw and grain samples were oven-dried at 40°C to constant weight in order to determine dry matter content (DM) and dry matter yield, thousand kernel weight (TKW), hectoliter weight (HLW), number of seeds per ear, weight of seeds per ear and parameters related to baking quality. Harvest Index (HI) was calculated with the formula grain yield (DM) / [grain yield (DM) + straw yield (DM)]. Nitrogen Harvest Index (NHI) was calculated with the formula N uptake grain / (N uptake grain + N uptake straw).

2.3.5 Quality Parameters of Wheat Grain

Quality parameters of wheat grain were measured according to the standard methods of the International Association for Cereal Science and Technology (ICC) AT-1030 Vienna (ICC (www.icc.or.at)). The Hagberg falling number (HFN), an indicator of sprouting resistance, was determined according to ICC STANDARD No. 107/1 in order to estimate alpha-amylase activity in cereal grains (Figure 2 1). The Zeleny value (ZV) was analyzed according to ICC STANDARD No. 116/1 (Figure 2 2 and Figure 2 3). Wet total gluten content (G_{tot}) and gluten index (GI) (ICC Standard No. 155) were analyzed using mixed samples of four replicates (Figure 2 4 and Figure 2 5). Gluten was separated from whole wheat flour by centrifugation. The gluten index determines the gluten characteristics, indicating whether the gluten is weak (Figure 2 6) or strong (Figure 2 7).

Figure 2 1 Determination of the falling number: Whole wheat flour with water with a stirrer inserted, is boiled in hot water. After 5 seconds the stirring begins automatically. The stirrer is automatically released in its top position after 60 seconds and is allowed to fall down under its own weight. The total time in seconds from the start of the instrument until the stirrer has fallen a measured distance is registered as the falling number. The flour is undergoing liquefaction due to alpha-amylase activity. The higher the alpha-amylase activity, the faster the liquefaction starts and the lower is the falling number. Rainy weather during harvest can cause sprouting leading to a development of the alpha-amylase enzymes. Alpha-amylase activity has direct impact on bread making quality. As little as 5 % sprouted grain, mixed with 95 % sound grain, can render the entire mixture unacceptable. Source: Getreidezüchtung Peter Kunz

Figure 2 2 Determination of Zeleny sedimentation value: Flour is suspended in bromphenyl-solution (right four cylinders) and afterwards in lactic acid (left four cylinders) during 5 min in each step. Source: Isabell Hildermann

Figure 2 3 Determination of Zeleny sedimentation value: The suspension is allowed to sediment during 5 min. The volume of the sediment is the Zeleny sedimentation value. Swelling of the gluten fraction of flour (gliadin and glutenin) affects the rate of sedimentation of a flour suspension in the lactic acid medium. A higher gluten content and better gluten quality decelerate sedimentation and result in higher sedimentation values. Source: Isabell Hildermann

Figure 2 4 Determination of total wet gluten: Preparation of dough from whole meal flour by adding a sodium chloride solution. Total wet gluten is isolated by washing this dough with the same solution removing the residual water by centrifugation and weighing the remainder. Source: Isabell Hildermann

Figure 2 5 Remaining wet gluten after washing. Wet gluten in wheat flour is a plastic-elastic substance consisting of gliadin and glutenin. Source: Getreidezüchtung Peter Kunz

Figure 2 6 Determination of Gluten Index (GI): Gluten after centrifugation. Centrifugation allows for determining the amount of weak and strong gluten. Amount of weak gluten of a wheat cultivar with a high portion of weak gluten resulting in low GI. Source: Getreidezüchtung Peter Kunz

Figure 2 7 Determination of Gluten Index (GI): Gluten after centrifugation. Amount of weak gluten of a wheat cultivar with a high portion of strong gluten resulting in high GI. Source: Getreidezüchtung Peter Kunz

2.3.6 Grain Crude Protein Content and N Concentration in Straw

Oven-dried grain and straw samples were coarse ground (Mikro Feinmühle Culatti, Type DCFH 48) and then fine ground with a swing mill (Retsch MM 200). N concentration was measured using a CHN analyzer (Leco CHN 100). Grain crude protein content (GCP) was calculated with unrounded N concentration values using the formula: GCP = N x 5.7.

2.3.7 Statistical Analyses

Analyses of variance were performed using the SPSS 13.0 software package (SPSS Inc. Chicago, Illinois 60606). The main effects – systems and cultivars – and their interactions were tested for significance by a two-way ANOVA. Significance between means was determined by least significant difference (LSD) values where $P < 0.05$. The JMP 5.0.1. software package (JMP release 5.0.1.2. SAS Institute Inc. Cary, NC) was used for performing multiple regressions and correlations. Redundancy analysis (RDA) for yield and yield components as well as for quality parameters was performed using CANOCO 4.5 (Biometris, Plant Research International, Wageningen, NL) (TerBraak and Smilauer, 2002). Effects of systems or cultivars were evaluated with the Monte Carlo permutation test. RDA identified the influence of either systems or cultivars on yield or quality parameters.

2.4 Results and Discussion

2.4.1 Plant Growth Development

Plant growth development, characterized by the parameters plant density after emergence, number of tillers and number of ears, is shown in Figure 2 8. Plant height is shown in Table 2 4. Cultivars and systems showed significant effects on plant density after emergence, number of tillers, number of ears (Figure 2 8) and on plant height; significant genotype x system interactions were not detected in a two-way-ANOVA. The numbers of ears m^{-2} were 21% and 53% greater in the BIODYN 2 and CONMIN systems, respectively as compared to NOFERT. According to Guarda et al. (2004), the number of ears m^{-2} is one of the most important factors influencing yield.

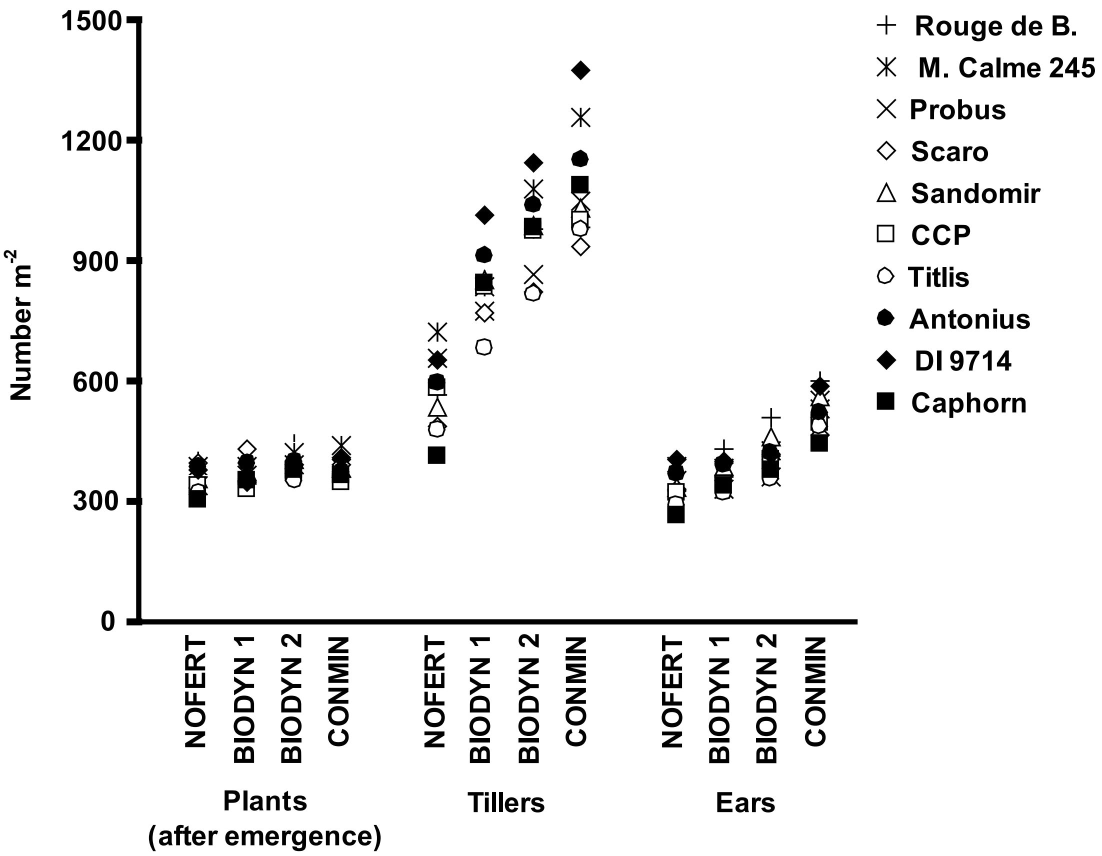

Figure 2 8 Plant density after emergence, number of tillers and number of ears of ten winter wheat cultivars in four farming systems (means, n = 4)

Plant height in June was strongly reduced relative to the year of release of the cultivars (Table 2 4). Across all systems, old cultivars grew as tall as 112 cm (cv Probus) or 126 cm (cv Rouge de Bordeaux). Conventionally bred cultivars grew only as tall as 70 cm (cultivar (cv) Caphorn) and 94 cm (cv Antonius), while organically bred cultivars were ranked in-between. Guarda et al. (2004) found a similar reduction of plant height in wheat for a series of cultivars released between 1900 and 1994. Plant height in April was positively correlated with grain yield ($r = 0.476$; $p < 0.0001$; $n = 160$). Rapid early growth, also known as early vigor, is important for good plant establishment and yields. The higher N input in the CONMIN system was expected to result in taller plants; however, this did not occur because plant growth regulators were applied in this system. The conventionally bred cv Antonius shows that tall plants can also achieve good grain yields under both low and high input conditions.

Due to overall low weed pressure in the DOK trial, the competitiveness of cultivars in terms of high plant height and tillering capacity for weed suppression (Drews et al., 2002; Korres and Froud-Williams, 2002) could not be analyzed.

	Plant height [cm]				
	Across all systems	NOFERT	BIODYN 1	BIODYN 2	CONMIN
	(n = 16)	(n = 4)	(n = 4)	(n = 4)	(n = 4)
Cultivar					
Rouge de B.	126.0	111.0	132.0	130.5	130.4
M. Calme 245	111.2	99.5	113.9	115.9	115.4
Probus	114.1	102.1	116.3	117.8	120.3
Scaro	93.9	84.3	96.9	99.1	95.3
Sandomir	108.8	93.8	112.0	115.5	114.1
CCP	85.3	73.9	84.6	93.0	89.7
Titlis	87.5	74.8	91.2	92.1	91.8
Antonius	94.0	81.6	96.0	100.7	97.9
DI 9714	71.5	62.6	70.1	76.0	77.1
Caphorn	69.6	61.3	71.4	72.0	73.6
	Across all cultivars				
	(n = 40)				
System					
NOFERT	84.5				
BIODYN 1	98.4				
BIODYN 2	101.2				
CONMIN	100.6				
ANOVA					
Cultivar					
P value	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
LSD (d.f. = 9)[a]	4.3	12.5	4.8	9.2	7.2
System					
P value	< 0.0001				
LSD (d.f. = 3)	2.7				
Cultivar x System					
P value (d. f. = 27)	n.s.[b]				

[a]d. f., degrees of freedom
[b] n.s. = not significant

Table 2 4 Plant height of ten winter wheat cultivars in four farming systems in June 2007

2.4.2 Yield and Yield Components

Grain and straw yield, HI and NHI were significantly affected by systems and cultivars (Table 2 5 and Table 2 6), whereas no significant genotype x environment interactions were detected in a two-way ANOVA. Higher N input rates resulted in higher yields of grain and straw. These results are in agreement with other studies comparing different levels of N fertilization (Sticksel et al., 2000; Levy et al., 2007). Accordingly, higher wheat yields were obtained under conventional than under organic conditions (Mäder et al., 2002; L-Baeckstrom et al., 2004, 2006; Schwaerzel et al., 2006; Mäder et al., 2007; Mason et al., 2007; Murphy et al., 2007). Averaged across all cultivars, grain yield was 4.2 Mg ha^{-1} in the organic system BIODYN 2 and 6.8 Mg ha^{-1} in the conventional system CONMIN, which represents an increase of 62%. The average yield in the BIODYN 2 system was in line with the long-term average of wheat yields of the organic systems in the DOK long-term experiment (Mäder et al., 2006; 2007). These results were comparable to the average wheat yield of 4.0 Mg ha^{-1} under organic farming conditions in Switzerland in 2005 (Rudmann and Willer, 2005). Conventional grain yields were much higher compared to previous results in the DOK trial (6.8 Mg ha^{-1} vs 4.8 Mg ha^{-1}) (Mäder et al., 2006), reflecting the increase of N applications to the CONMIN from appr. 75 kg ha^{-1} to 140 kg ha^{-1}. The higher yields in the CONMIN are also due to chemical plant protection. We observed an increasing trend in yields as a function of the year of release of the cultivars. The conventionally bred cv Antonius produced the highest yields across all systems (4.9 Mg ha^{-1}), which was 29% greater than the overall yield of the oldest cv Rouge de Bordeaux (3.8 Mg ha^{-1}).

A linear regression analysis of yield development by year of release of the cultivars revealed a greater increase in grain yield under conventional conditions (7.4 kg ha^{-1} yr^{-1} in CONMIN) than under organic conditions (1.7 kg ha^{-1} yr^{-1} in BIODYN 2). In contrast to other studies on wheat (Brancourt-Hulmel et al., 2005; Murphy et al., 2007) or on barley, (Ceccarelli, 1996) our results did not show that cultivars bred under low input conditions (old and organically bred cultivars) yielded higher under low input conditions. A different situation was found for conventional conditions, where conventionally bred cultivars yielded higher compared to old and organically bred cultivars. The deep loess soil at the DOK experiment site, which is characterized by a high inherent soil fertility, good water retention and low weed pressure, could account for these contradictory results.

Yield potential progress in wheat has been associated with an increased harvest index (Fischer, 2007), a trend also demonstrated in our data. Reduction in plant height, and therefore lower straw yields, accompanied by higher grain yields led to rising harvest indices of modern cultivars (Table 2 6). This is in line with many other studies (Brancourt-Hulmel et al., 2003; Guarda et al., 2004; Acuna et al., 2005). The harvest indices of organically bred cultivars (0.38 - 0.42) were in the range between those of the oldest cultivar Rouge de Bordeaux (0.32) and the conventionally bred cultivar Caphorn (0.49). Guarda et al. (2004) demonstrated that old wheat cultivars achieved the highest harvest indices under low input conditions and that modern cultivars reached their maximum harvest indices at high N input levels. This trend, however, was not confirmed by our data.

The N harvest index did not vary greatly between cultivars, indicating that the age of the cultivar had no significant influence on N harvest index (Table 2 6). The lowest values were obtained for the conventionally bred cvs DI 9714 (0.74) and Caphorn (0.75). This fact can be explained by the low N concentrations in the grain of these modern cultivars, which balances the higher grain yields.

Systems and cultivars had a significant effect on thousand kernel weight, hectoliter weight, weight of seeds per ear and number of seeds m^{-2} (Table 2 7 and Table 2 8). Significant interactions were not detected in a two-way ANOVA. Thousand kernel weight increased with nutrient input in the system. There is no general agreement in the literature regarding the influence of N input on thousand kernel weight. In contrast to our findings, Schwaerzel et al. (2006) found no differences between thousand kernel weights of organically and conventionally grown wheat. Guarda et al. (2004) even reported lower values in systems with higher N input. Results in the literature are also contradictory for changes in thousand kernel weight in comparisons of old vs. modern wheat cultivars. In our study, thousand kernel weight was generally higher for old cultivars. Across all systems, the highest values for thousand kernel weight were measured in the oldest cultivar Rouge de Bordeaux (48 g); the lowest values were measured in the conventionally bred cv Caphorn (36 g). This is in line with findings of one other study (Guarda et al., 2004). Other authors reported higher thousand kernel weights for modern cultivars vs. old cultivars (Brancourt-Hulmel et al., 2003; Underdahl et al., 2008).

Hectoliter weight increased from NOFERT to CONMIN. Averaged across all cultivars, hectoliter weight was 75.5 kg hL^{-1} in the BIODYN 2 organic system and significantly lower than in the CONMIN conventional system (78.7 kg hL^{-1}). This is consistent with the findings reported by Mason and Spaner (2006). In contrast, Schwaerzel et al. (2006) did not observe differences in hectoliter weight between organically and conventionally grown wheat. Differences in hectoliter weight between cultivars were generally low. Weight of seeds per ear and number of seeds m-2 rose from NOFERT to CONMIN (Table 2 8). Within the systems, the weight of seeds per ear increased from old to modern cultivars by about 20% in the organic systems, but by 47% in the conventional system. Numbers of seeds m-2 were similar in the NOFERT and BIODYN 1 systems, but increased by 7% and 47% in the BIODYN 2 and CONMIN systems, respectively.

The results of yields and yield components showed a trend similar to that in other studies comparing old

	Grain yield (DM) [Mg ha^{-1}]					Straw yield (DM) [Mg ha^{-1}]				
	Across all systems	**NOFERT**	**BIODYN 1**	**BIODYN 2**	**CONMIN**	**Across all systems**	**NOFERT**	**BIODYN 1**	**BIODYN 2**	**CONMIN**
	(n = 16)	(n = 4)	(n = 4)	(n = 4)	(n = 4)	(n = 16)	(n = 4)	(n = 4)	(n = 4)	(n = 4)
Cultivar										
Rouge de B.	3.8	2.1	3.2	4.0	6.0	7.9	4.4	7.1	9.2	10.7
M. Calme 245	4.4	2.8	3.8	4.4	6.5	7.3	5.1	6.4	7.5	10.3
Probus	3.8	2.6	3.3	3.6	5.9	7.1	4.7	6.3	7.0	10.5
Scaro	4.5	2.9	3.8	4.4	6.7	6.2	4.4	5.2	6.1	9.1
Sandomir	4.1	2.2	3.3	4.1	6.9	6.7	3.8	6.2	7.4	9.3
CCP	4.3	2.4	3.6	4.2	6.8	5.8	3.8	5.3	6.2	7.9
Titlis	4.4	2.6	4.0	4.1	7.0	6.5	3.8	5.7	6.8	9.6
Antonius	4.9	3.5	4.3	4.7	7.3	7.0	4.6	5.8	7.3	10.0
DI 9714	4.3	2.9	3.5	4.0	6.8	5.1	3.6	4.1	5.2	7.5
Caphorn	4.9	2.7	4.4	4.4	8.1	5.1	2.9	4.8	5.3	7.2
	Across all cultivars					**Across all cultivars**				
	(n = 40)					(n = 40)				
System										
NOFERT	2.7					4.1				
BIODYN 1	3.7					5.7				
BIODYN 2	4.2					6.8				
CONMIN	6.8					9.2				
ANOVA										
Cultivar										
P value	< 0.0001	n.s.	0.0039	n.s.	0.0044	< 0.0001	n.s.	0.0002	< 0.0001	< 0.0001
LSD (d.f. = 9)[a]	0.4	-	0.6	-	1.0	0.6	-	1.1	1.2	1.4
System										
P value	< 0.0001					< 0.0001				
LSD (d.f. = 3)	0.2					0.4				
Cultivar x System										
P value (d. f. = 27)	n.s.[b]					n.s.				

[a] d. f., degrees of freedom
[b] n.s. = not significant

Table 2 5 Yield (DM) of grain and straw of ten winter wheat cultivars in four farming systems. Results of one-way and two-way ANOVA and interactions are shown. LSD is provided in case of significant ANOVA ($P < 0.05$)

	Harvest Index					N-Harvest Index				
	Across all systems	NOFERT	BIODYN 1	BIODYN 2	CONMIN	Across all systems	NOFERT	BIODYN 1	BIODYN 2	CONMIN
	(n = 16)	(n = 4)	(n = 4)	(n = 4)	(n = 4)	(n = 16)	(n = 4)	(n = 4)	(n = 4)	(n = 4)
Cultivar										
Rouge de B.	0.32	0.31	0.31	0.30	0.36	0.78	0.60	0.80	0.84	0.88
M. Calme 245	0.37	0.36	0.37	0.37	0.39	0.84	0.72	0.87	0.87	0.89
Probus	0.35	0.36	0.34	0.34	0.36	0.81	0.70	0.81	0.85	0.87
Scaro	0.42	0.40	0.42	0.42	0.43	0.81	0.69	0.87	0.83	0.86
Sandomir	0.38	0.37	0.35	0.36	0.42	0.83	0.66	0.86	0.88	0.90
CCP	0.41	0.39	0.40	0.40	0.46	0.76	0.62	0.77	0.80	0.85
Titlis	0.41	0.40	0.41	0.38	0.42	0.83	0.67	0.88	0.84	0.91
Antonius	0.42	0.43	0.43	0.39	0.42	0.85	0.78	0.89	0.86	0.89
DI 9714	0.45	0.45	0.46	0.43	0.47	0.74	0.65	0.71	0.77	0.82
Caphorn	0.49	0.48	0.48	0.46	0.53	0.75	0.57	0.81	0.74	0.89
	Across all cultivars					**Across all cultivars**				
	(n = 40)					(n = 40)				
System										
NOFERT	0.39					0.67				
BIODYN 1	0.40					0.83				
BIODYN 2	0.38					0.83				
CONMIN	0.43					0.88				
ANOVA										
Cultivar										
P value	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	n.s.	< 0.0001	n.s.	n.s.
LSD (d.f. = 9)[a]	0.02	0.05	0.04	0.05	0.05	0.05	-	0.07	-	-
System										
P value	< 0.0001					< 0.0001				
LSD (d.f. = 3)	0.01					0.03				
Cultivar x System										
P value (d. f. = 27)	n.s.[b]					n.s.				

[a] d. f., degrees of freedom
[b] n.s. = not significant

Table 2 6 Harvest index and N harvest index of ten winter wheat cultivars in four farming systems. Results of one-way and two-way ANOVA and interactions are shown. LSD is provided in case of significant ANOVA ($P < 0.05$)

	Thousand kernel weight [g]					Hectolitre weight [kg hl^{-1}]				
	Across all systems	NOFERT	BIODYN 1	BIODYN 2	CONMIN	Across all systems	NOFERT	BIODYN 1	BIODYN 2	CONMIN
	(n = 16)	(n = 4)	(n = 4)	(n = 4)	(n = 4)	(n = 16)	(n = 4)	(n = 4)	(n = 4)	(n = 4)
Cultivar										
Rouge de B.	47.9	37.8	50.1	51.7	51.8	76.5	68.8	78.4	78.8	79.9
M. Calme 245	42.5	34.4	42.7	44.3	48.5	74.6	70.1	75.3	75.3	77.6
Probus	39.5	32.8	40.4	41.4	43.2	76.8	73.1	77.4	77.8	78.6
Scaro	40.2	31.5	40.7	42.8	46.0	77.9	73.9	78.4	78.8	80.7
Sandomir	37.0	29.0	36.7	39.3	42.8	76.7	72.3	76.3	77.2	81.1
CCP	38.0	28.9	39.4	40.1	43.3	71.5	65.1	71.8	72.4	76.5
Titlis	40.6	31.2	41.6	43.3	46.2	75.5	70.5	76.0	75.8	79.5
Antonius	41.6	37.0	41.4	42.7	45.2	77.5	75.8	76.8	77.3	80.3
DI 9714	41.5	32.0	43.9	43.8	46.3	71.9	66.3	72.1	72.6	76.7
Caphorn	36.0	26.2	37.9	37.2	42.7	69.2	60.7	70.7	69.3	76.0
	Across all cultivars (n = 40)					**Across all cultivars** (n = 40)				
System										
NOFERT	32.1					69.7				
BIODYN 1	41.5					75.3				
BIODYN 2	42.7					75.5				
CONMIN	45.6					78.7				
ANOVA										
Cultivar										
P value	< 0.0001	n.s.	< 0.0001	< 0.0001	< 0.0001	< 0.0001	n.s.	< 0.0001	< 0.0001	< 0.0001
LSD (d.f. = 9)[a]	2.0	-	2.2	2.5	2.5	2.3	-	1.3	2.6	1.4
System										
P value	< 0.0001					< 0.0001				
LSD (d.f. = 3)	1.3					1.5				
Cultivar x System										
P value (d. f. = 27)	n.s.[b]					n.s.				

[a] d. f., degrees of freedom
[b] n.s. = not significant

Table 2 7 Thousand kernel weight and hectoliter weight of ten winter wheat cultivars in four farming systems. Results of one-way and two-way ANOVA and interactions are shown. LSD is provided in case of significant ANOVA (P < 0.05)

	Weight of seeds per ear [g]					Number of seeds per m² [no m⁻²]				
	Across all systems	**NOFERT**	**BIODYN 1**	**BIODYN 2**	**CONMIN**	**Across all systems**	**NOFERT**	**BIODYN 1**	**BIODYN 2**	**CONMIN**
	(n = 16)	(n = 4)	(n = 4)	(n = 4)	(n = 4)	(n = 16)	(n = 4)	(n = 4)	(n = 4)	(n = 4)
Cultivar										
Rouge de B.	1.0	0.9	0.9	1.0	1.2	9404	8656	6128	9347	13485
M. Calme 245	1.3	1.1	1.3	1.3	1.5	12840	11917	11113	12308	16023
Probus	1.3	1.1	1.3	1.2	1.5	12555	11511	10293	10844	17572
Scaro	1.4	1.2	1.4	1.5	1.6	13641	12376	13045	13577	15567
Sandomir	1.1	0.9	1.2	1.1	1.3	12244	11105	12604	12786	12481
CCP	1.3	1.0	1.3	1.3	1.7	13654	11533	11645	12937	18502
Titlis	1.5	1.2	1.5	1.6	1.7	13510	11121	11863	13153	17903
Antonius	1.6	1.5	1.6	1.5	1.7	15832	14320	14520	14593	19896
DI 9714	1.4	1.0	1.3	1.3	1.8	14659	12826	12208	12154	21448
Caphorn	1.5	1.0	1.6	1.5	2.0	15448	12222	14144	14397	21029
	Across all cultivars (n = 40)					**Across all cultivars** (n = 40)				
System										
NOFERT	1.1					11759				
BIODYN 1	1.3					11756				
BIODYN 2	1.3					12610				
CONMIN	1.6					17391				
ANOVA										
Cultivar										
P value	< 0.0001	0.0026	0.0005	< 0.0001	< 0.0001	< 0.0001	n.s.	0.0020	n.s.	0.0203
LSD (d.f. = 9)[a]	0.1	0.2	0.3	0.2	0.2	2050	-	3421	-	5324
System										
P value	< 0.0001					< 0.0001				
LSD (d.f. = 3)	0.1					1296				
Cultivar x System										
P value (d. f. = 27)	n.s.[b]					n.s.				

[a] d. f., degrees of freedom
[b] n.s. = not significant

Table 2 8 Weight of seeds per ear and number of seeds per m⁻² of ten winter wheat cultivars in four farming systems. Results of one-way and two-way ANOVA and interactions are shown. LSD is provided in case of significant ANOVA (P < 0.05) and modern cultivars. The increase in grain yield was associated with increases in harvest index, the number of grains m^{-2} and the weight of the seeds per ear. In a multiple regression analysis with yield as the target variable, the weight of the seeds per ear and the number of ears m^{-2} had the strongest impact on yield. Together they accounted for 76% of the total variation in yield (Table 2 9). For durum wheat, it has been demonstrated that yield differences are due primarily to the number of seeds m^{-2} and secondarily to the weight of the seeds (Arduini et al., 2006).

Grain yield model (n = 160)					
			Parameter estimate	***p*-value**	**Cumulative r^2**
Intercept			-5.469	< 0.0001	
Seeds per ear	Harvest	[g]	2.015	< 0.0001	0.4963
Number of ears	June 2007	[no m^{-2}]	0.009	< 0.0001	0.7639
Plant density	Dec 2006	[no m^{-2}]	-0.006	< 0.0001	0.7962
Plant height	Apr 2007	[cm]	0.070	< 0.0001	0.8165
Plant height	May 2007	[cm]	-0.039	< 0.0001	0.8324
Hectolitre weight	Harvest	[kg hl^{-1}]	0.060	0.0003	0.8455
Ear size	June 2007	[cm]	0.192	0.0106	0.852

Table 2 9 Multiple regression model explaining influence of parameters on grain yield across all farming systems and all winter wheat cultivars. The following parameters were included in the regression model: number of plants in December, number of tillers, tillers per plant, number of ears, ears per plant, plant height in December, plant height in April, plant height in May, ear size in May, plant height in June, ear size in June, seeds per ear, number of seeds per ear, number of seeds m^{-2}, thousand kernel weight and hectolitre weight. Seeds per ear and number of ears m^{-2} accounted for 76% of the yield variation in the experiment

2.4.3 Quality Parameters

Baking quality is highly dependent on protein quantity and also protein quality. Grain crude protein content, Zeleny value, total gluten content, gluten index and falling number are the parameters generally used to predict final behaviour during the baking process.

Grain crude protein content was 108, 94, 90 and 117 g kg^{-1} in the NOFERT, BIODYN 1, BIODYN 2 and CONMIN systems, respectively (Table 2 10). Contents were relatively low compared to previous findings in the DOK trial (between 128 and 145 g kg^{-1} in BIODYN 2 and between 131 and 145 g kg^{-1} in CONMIN) (Mäder et al., 2007). Wheat samples from the 2003 DOK trial contained between 130 (BIODYN 2) and 160 g kg^{-1} (CONMIN) protein (Langenkämper et al., 2006). Grain protein increased with nitrogen input from BIODYN 1 to BIODYN 2 and CONMIN, which is in line with other studies (Guarda et al., 2004; Levy et al., 2007). In NOFERT, grain protein content was unexpectedly high due to low grain yields connected with small grain size. While grain protein content was higher in the conventional systems than in the organic systems in our study, similar to the findings of L-Baeckstöm et al. (2004), other authors report no differences in protein content between farming systems (Ryan et al., 2004; Mason et al., 2007). In the study of Ryan et al. (2004) however, wheat was planted following N-fixing legumes, resulting in generally higher nitrogen supply, whereas wheat followed maize at the end of the crop rotation in our study. The old cultivars achieved the highest protein contents across all systems, and the differences were significant. Protein dropped from 114 (cv Probus) to 93 g kg^{-1} (cv Caphorn) relative to the year of release of the cultivars, which is in close agreement with previous findings (Calderini et al., 1995; Smith and Gooding, 1999; Guarda et al., 2004; Acuna et al., 2005). In BIODYN 2 (73 g kg^{-1}) and in CONMIN (102 g kg^{-1}), the lowest grain protein content was measured for cv Caphorn. In BIODYN 2 (103 g kg^{-1}) and in CONMIN (140 g kg^{-1}), the highest grain protein content was measured for cv Probus.

Zeleny values were higher in modern compared to old cultivars (Table 2 11). The lowest values across all systems were measured for the oldest cultivars Rouge de Bordeaux (25.5 mL) and Mont Calme 245 (19.6 mL) and for the CCP (37.6 mL). The other cultivars did not differ significantly, achieving values between 55.8 mL (cv Antonius) and 60.5 mL (cv Scaro). The high values in the modern cultivars indicate that lower grain protein contents were compensated for by a quality improvement in protein composition, as also postulated by Guarda et al. (2004).

	Grain crude protein content [g kg^{-1}]				
	Across all systems	**NOFERT**	**BIODYN 1**	**BIODYN 2**	**CONMIN**
	(n = 16)	(n = 4)	(n = 4)	(n = 4)	(n = 4)
Cultivar					
Rouge de B.	108.5	113.1	103.1	100.5	117.1
M. Calme 245	103.6	110.4	96.7	90.5	116.9
Probus	113.8	107.7	104.5	103.2	140.0
Scaro	101.1	106.0	92.8	92.7	112.9
Sandomir	101.6	109.9	96.3	80.8	119.5
CCP	98.4	104.3	88.7	90.3	110.5
Titlis	103.4	111.5	91.9	90.1	120.2
Antonius	103.4	107.8	93.1	92.3	120.6
DI 9714	95.8	99.6	85.4	88.8	109.3
Caphorn	92.9	107.8	88.4	73.3	102.1
	Across all cultivars				
	(n = 40)				
System					
NOFERT	107.8				
BIODYN 1	94.1				
BIODYN 2	90.2				
CONMIN	116.9				
ANOVA					
Cultivar					
P value	< 0.0001	n.s.	< 0.0001	0.0326	< 0.0001
LSD (d.f. = 9)[a]	0.6	-	0.7	1.6	1.2
System					
P value	< 0.0001				
LSD (d.f. = 3)	0.4				
Cultivar x System					
P value (d. f. = 27)	n.s.[b]				

[a]d. f., degrees of freedom
[b] n.s. = not significant

[a]d. f., degrees of freedom
[b] n.s. = not significant

Table 2 10 Grain crude protein content of ten winter wheat cultivars in four farming systems. Results of one-way and two-way ANOVA and interactions are shown. LSD is provided in case of significant ANOVA (P < 0.05)

	Zeleny value	Gluten total #	Gluten index #	Falling number
	[mL sedimentation]	[g kg^{-1} DM]		[s]
Cultivar (n = 16)				
Rouge de B.	26	279	15	291
M. Calme 245	20	258	14	326
Probus	60	273	74	311
Scaro	61	230	97	362
Sandomir	57	245	87	359
CCP	38	222	79	203
Titlis	59	243	91	375
Antonius	56	228	98	308
DI 9714	57	186	98	347
Caphorn	56	182	98	264
System (n = 40)				
NOFERT	50	244	72	296
BIODYN 1	45	209	78	316
BIODYN 2	43	202	80	326
CONMIN	57	283	71	320
ANOVA				
Cultivar				
P value	< 0.0001	-	-	< 0.0001
LSD (d.f. = 9)[a]	3			19
System				
P value	< 0.0001	-	-	< 0.0001
LSD (d.f. = 3)	2			12
Cultivar x System				
P value (d. f. = 27)	0.0013	-	-	< 0.0001

For gluten total and gluten index n = 40 (mixed samples of 4 replicates), ANOVA could not be calculated
[a]d. f., degrees of freedom

Table 2 11 Baking quality parameters of ten winter wheat cultivars in four farming systems. Results of one-way and two-way ANOVA and interactions are shown. LSD is provided in case of significant ANOVA (P < 0.05)

Parallel to the results for protein contents, there was a decrease of the total gluten contents with respect to the year of release of the cultivars, with the highest values (35%) obtained for cv Probus in the CONMIN system and the lowest values (16%) obtained for cv Caphorn in the BIODYN 2 system. The quality of gluten expressed as gluten index is a parameter, well suited to predict baking quality of wheat. The development of total gluten (quantity) and the quality of gluten (gluten index) can be used to trace breeding efforts. Breeding efforts had strong effects on the composition of gluten in wheat (Figure 2 9). While modern cultivars had the lowest total gluten contents, the gluten index was highest for conventionally bred cultivars. As a result, almost 100% of the total gluten was strong gluten for conventionally bred cvs Antonius, DI 9714 and Caphorn. Averaged across all systems, the organically bred cultivars still had between 8 g kg^{-1} DM (cv Scaro) and 50 g kg $^{-1}$ DM (CCP) of weak gluten, which is 3.4 and 22.2% of total gluten. A study on Italian durum wheat revealed a similar trend among cultivars of different breeding eras (Motzo et al., 2004). Increasing gluten indices were measured in modern durum wheat cultivar, which is postulated as an improvement of quality compared to old cultivars.

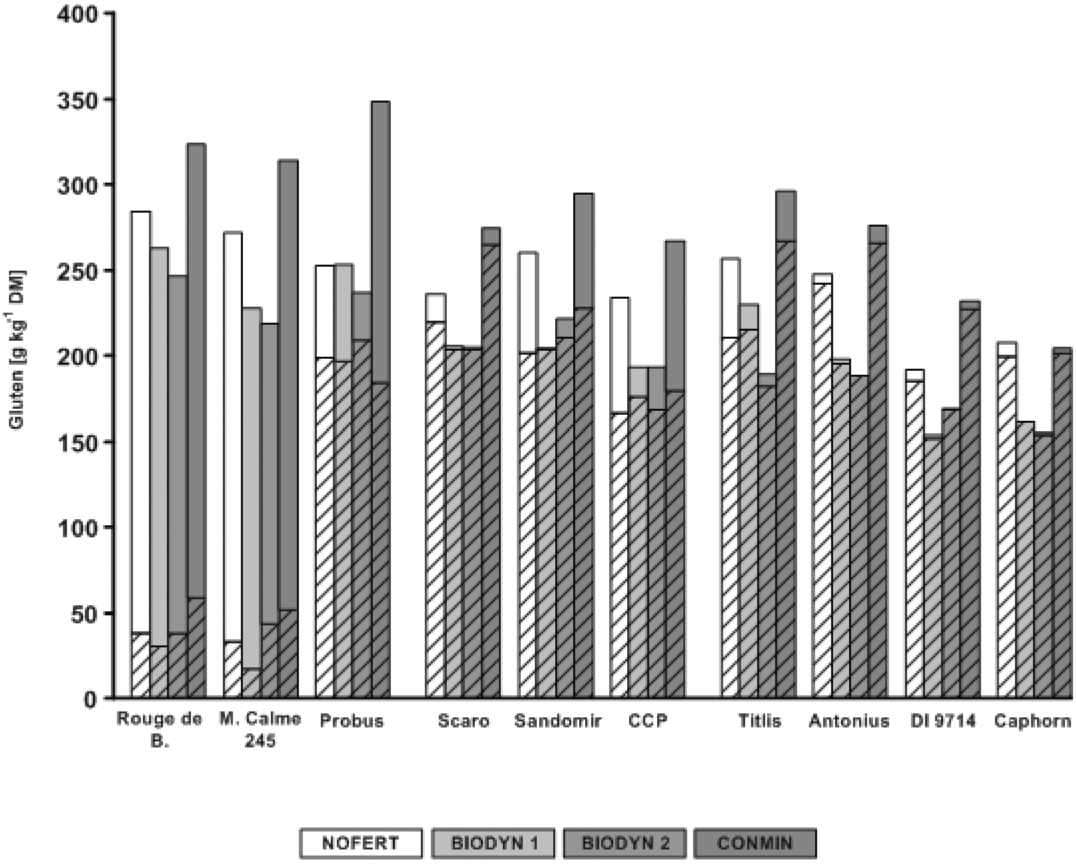

Figure 2 9 Total gluten content, divided into strong (hatched) and weak (not hatched) gluten of ten winter wheat cultivars in four farming systems (means, n = 4)

It turned out that the systems showed similar patterns for grain crude protein content, Zeleny value and total gluten content: high values were achieved in the NOFERT control and in the CONMIN system, and low values were achieved in the BIODYN 1 and BIODYN 2 organic systems. Nitrogen accumulated in NOFERT due to low grain numbers and weights; in CONMIN due to the input of mineral N fertilizers. In Table 2 12, the correlation matrix for grain yield and quality parameters is presented for the systems BIODYN 2 and CONMIN. Grain crude protein was positively correlated with the quantitative parameter total gluten under conventional ($r = 0.68$; $p < 0.0001$) as well as under organic conditions ($r = 0.45$; $p < 0.0001$) (Table 2 12). However, there was no positive correlation between grain protein content and Zeleny value or Gluten index, which are parameters that evaluate the quality of protein. Because grain protein content influences other baking quality parameters such as Zeleny value, gluten quantity and quality, attention is often paid to the (frequently negative) correlation between grain yield and grain protein content. In our study as well as in other studies (Kibite and Evans, 1984; Brancourt-Hulmel et al., 2005; Oury and Godin, 2007), grain yield was weakly but negatively correlated with protein content. Correlation was significant in the conventional system. In contrast to our findings, where correlation was slightly stronger under conventional conditions, Brancourt-Hulmel et al. (2005) found that correlation was stronger at low nutrient levels.

	Grain yield (DM)	Hectolitre weight	Zeleny value	Falling number	Gluten total	Gluten Index	Grain crude protein
Grain yield (DM)	1.0	-0.12	0.29 *	-0.16	-0.61 ***	0.50 ***	-0.33 **
Hectolitre weight	-0.02	1.0	0.10	0.47 ***	0.47 ***	-0.003	0.28 *
Zeleny value	-0.04	0.01	1.0	0.36 **	-0.36 **	0.86 ***	0.12
Falling number	-0.02	0.49 **	0.28	1.0	0.30 *	0.13	0.32 **
Gluten total	-0.21	0.71 ***	-0.32	0.24	1.0	-0.70 ***	0.68 ***
Gluten Index	0.03	-0.25	0.85 ***	-0.02	-0.53 ***	1.0	-0.26 *
Grain crude protein	-0.16	0.28 *	-0.09	0.26	0.45 ***	-0.27	1.0

[a] Correlations above the diagonal represent values of the CONMIN conventional system, while correlations below the diagonal represent values of the BIODYN 2 organic system; *r* values significant at * $P < 0.05$, ** $P < 0.01$ or *** $P < 0.001$.

Table 2 12 Correlation matrix (r values) of grain yield, hectolitre weight, Zeleny value, falling number, total gluten content, gluten index and grain crude protein content (n = 40)a

2.4.4 Redundancy Analysis

A redundancy analysis was conducted to summarize yield and yield components (Figure 2 10) as well as quality parameters (Figure 2 11). The influence of systems (34%) and cultivars (19%) explained 52% of the variability of the model for yield and yield components. Yield was mainly determined by the nutrient gradient within the systems, as indicated by the horizontal distribution of the four systems and the ten cultivars. CONMIN, a system in which 140 kg N ha^{-1} yr^{-1} is applied to wheat, had the strongest impact (33%), whereas the low input systems had only minor influence (NOFERT: 6%; BIODYN 1: 5%; BIODYN 2: 1%). The ordination of the cultivars indicated an affinity of the conventionally bred cvs Caphorn, Antonius and DI 9714 and the conventional system CONMIN and of the oldest cv Rouge de Bordeaux and the low input systems NOFERT and BIODYN 1. The cvs Mont Calme 245 (1926) and Probus (1948) and the organically bred cv Sandomir were grouped next to the organic system BIODYN 2. The organically bred cv Scaro, the composite cross population and the conventionally bred cv Titlis did not show a clear affinity for any one of the systems.

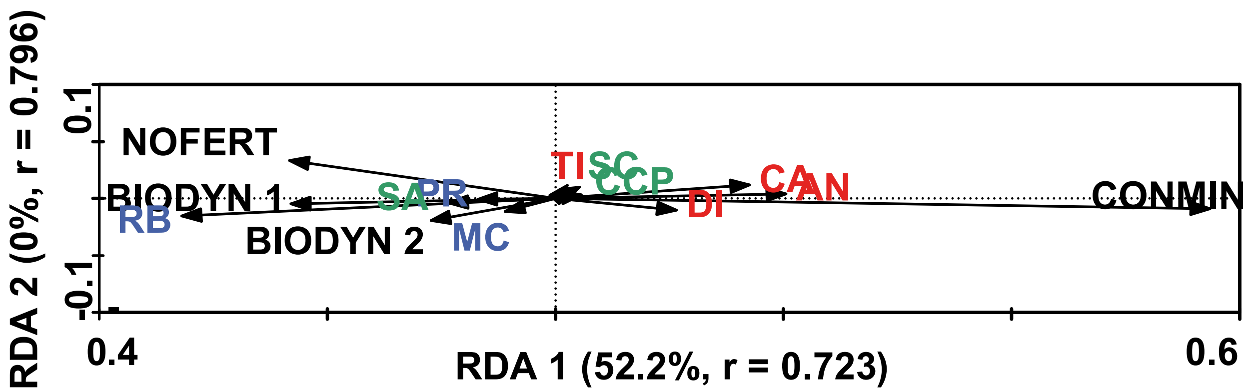

Figure 2 10 Constrained ordination of the first two canonical axes as determined by a redundancy analysis (RDA) of yield and yield components (plant density after emergence m^{-2}, number of tillers m^{-2}, number of ears m^{-2}, plant height (Dec, May, June), ear length (May, June), weight of seeds per ear, number of seeds m^{-2}, thousand kernel weight, yield of grain and straw, dry matter content of grain and straw) of ten winter wheat cultivars and four systems. Vector directions indicate maximum variation due to the corresponding factor, and vector length indicates the strength of correlation. Breeding background of cultivars is indicated by colours: old cultivars (blue), organically bred cultivars (green), conventionally bred cultivars (red)

The influence of systems and cultivars explained 79% of the variability in the quality model. In contrast to the situation for yield, cultivar characteristics had a major influence (75%) on quality, whereas only 4% of the variability could be attributed to the systems and therefore to the nutrient input. Systems are grouped closely in the centre of the graph, underscoring their minor influence. Only the NOFERT unfertilized control had a slightly higher impact (6%). The two oldest cultivars Rouge de Bordeaux and Mont Calme 245 grouped separately, but there was no further grouping of the cultivars by breeding background.

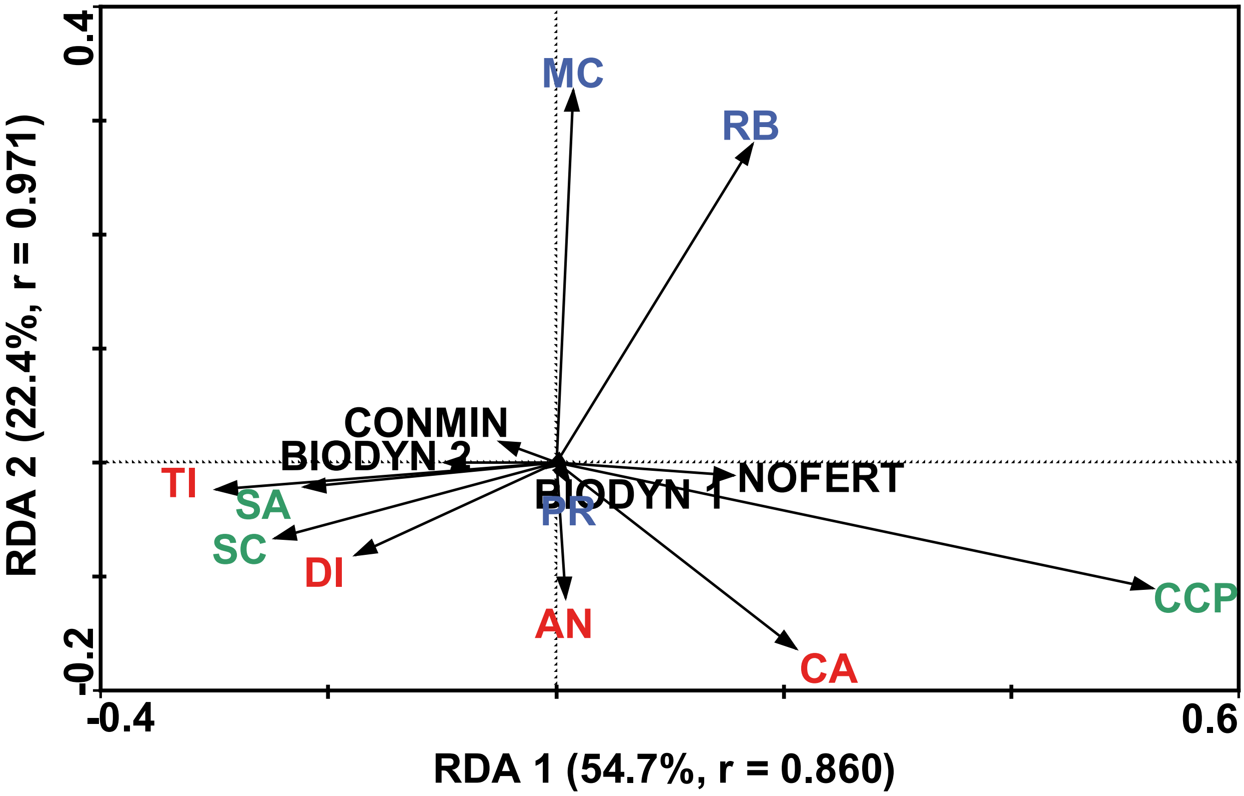

Figure 2 11 Constrained ordination of the first two canonical axes as determined by a redundancy analysis (RDA) of quality parameters (grain protein content, Zeleny value, Hagberg falling number, gluten content total, gluten index) of ten winter wheat cultivars and four systems. Vector directions indicate maximum variation due to the corresponding factor, and vector length indicates the strength of correlation. Breeding category of cultivars is indicated by colours: old (blue), organically bred (green), conventionally bred (red) cultivars

2.5 Conclusions

We tested the hypothesis that cultivars bred under low input conditions (old and organically bred cultivars) would outperform conventionally bred cultivars in the organic low input systems, as the former were adapted to low input conditions during the breeding process. Generally, we observed significant effects of cultivars and systems on all tested parameters. However, the expected genotype x system interactions did not appear. While conventionally bred cultivars produced the highest yields under conventional conditions, the organically bred cultivars did not produce the highest yields under organic conditions. The hypothesis can therefore not be corroborated. Under conventional farming conditions, yields strongly increased relative to the year of release of the cultivars, whereas the same set of cultivars showed only a minor increase under organic farming conditions. Under low input and nutrient-limited organic conditions, modern cultivars could not perform to the full extent of their genetic potential, irrespective of whether the breeding took place under conventional or organic farming conditions. The results imply that breeding for yield during the last century was successful, but only under high input conditions, wherein the development was accompanied by increasing inputs of external resources such as mineral fertilizers and fungicides. One of the goals of organic farming is the maintenance of a resilient system in the soil, in order to produce healthy products without exploiting natural resources. Besides concerns for environmental protection, product safety and quality, organic agriculture must strive to increase yields and quality in order to meet the challenge of supplying food. Moreover, increasing yields would improve the economic situation for organic farmers. The sharp differentiation of both factors (cultivars and systems) shows that the applied methodological approach, namely the testing of cultivars within a long-term, replicated system comparison in which system-immanent effects of separate cultivar trials such as soil heterogeneity and micro-climate are excluded, can provide reliable results. Such trials can therefore complement on-farm testing performed on larger plots, in which the resistance of cultivars to pests and diseases may be observed more adequately.

Acknowledgements

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3 NUTRIENT USE EFFICIENCY AND ARBUSCULAR MYCORRHIZAL ROOT COLONIZATION OF WINTER WHEAT CULTIVARS IN DIFFERENT FARMING SYSTEMS OF THE DOK LONG-TERM TRIAL

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3.1 Abstract

Background: For organic farming, cultivars are required with high nutrient use efficiency under nutrient limited conditions. Arbuscular mycorrhizal fungi (AMF) are known to contribute to nutrient uptake under low input conditions. We compared nutrient use efficiency (NUE) of old and modern organically and conventionally bred cultivars in organic and conventional systems and assessed AMF-root colonization (AMF-RC) in relation to nutrient concentrations.

Results: Cultivars and systems had a statistically significant effect on nitrogen (N) and phosphorus (P) concentrations and NUE parameters, whereas no genotype x environment interactions appeared. In contrast to N and P uptake, the NUE parameters were higher under organic than under conventional conditions. NUE for N increased with the year of release of cultivars. In the organic systems, the organically bred cultivars could not outperform the conventionally bred cultivars in grain yield and NUE parameters. AMF-RC was higher in the organic than in the conventional system, but did not differ among cultivars.

Conclusion: Cultivars achieving high NUE in the organic systems were found among modern cultivars, irrespective of the breeding program. Nutrient conditions during breeding program did not affect AMF-RC. No clear evidence was found that AMF symbiosis contributed more to nutrient concentrations under low input than under high input conditions.

Keywords: Organic farming - plant breeding - winter wheat - nutrient use efficiency - arbuscular mycorrhizal fungi

3.2 Introduction

The challenge of modern agricultural systems is to ensure global food supply by minimizing adverse effects on the environment. During the last century, accelerated input of mineral nitrogen (N) and phosphorus (P) fertilizers and application of pesticides were common ways to increase yields. As a result, the demand for these fertilizers increased drastically (Tilman et al., 2002). The production of mineral N fertilizer is highly energy intensive. The production of P fertilizer from phosphate rock causes severe environmental pollution during the mining process. P resources are severely limited and are predicted to be exhausted within the next 40 years (Cordell et al., 2009). In the context of resource scarcity and environmental pollution, there is a need to develop sustainable and nutrient use efficient farming systems. Organic farming, based on the use of animal manure and organic fertilizers, on nutrient cycles, which are as closed as possible and on broad crop rotations, including cover crops and green manure, aims to maintain soil fertility, which is fundamental for sustainability (Reganold et al., 2001; Mäder et al., 2002; Tilman et al., 2002; Niggli et al., 2008b). As nitrogen use efficiency (Nit-UE) decreases with increasing nutrient input, Nit-UE has been found to be higher under organic than under conventional conditions (van Delden, 2001; L-Baeckstrom et al., 2006). However, the availability of N and P is often a limiting factor in plant growth in organic farming and as a result restricts yields (L-Baeckstrom et al., 2004; Murphy et al., 2007). It is therefore necessary to breed cultivars that are best adapted to organic low input conditions.

During the last century, breeding efforts focused mainly on the improvement of yields under high external input conditions. Although several studies have shown improved nutrient use efficiency (NUE) of modern wheat cultivars compared to older cultivars (Calderini et al., 1995; Ortiz-Monasterio et al., 1997; Foulkes et al., 1998; Guarda et al., 2004), old cultivars and cultivars derived from organic low input breeding programs might be better adapted to organic farming, as the selection has taken place under low input conditions.

Actually, there are three different types of breeding programs out of which cultivars for organic farming are released (Wolfe et al., 2008). In breeding programs for conventional agriculture (BFCA), selection is carried out at conventionally managed sites. The best cultivars are presumed to be the best under organic conditions as well. In breeding programs for organic agriculture (BFOA), crosses and early selection are generally conducted under conventional conditions. Later breeding generations are selected at organically managed sites. In organic plant breeding programs (OPB), all steps of selection, propagation and maintenance are carried out under organic conditions. Moreover, the breeding techniques used comply with the principles of organic agriculture. The three organically bred cultivars included in this experiment are all derived from OPB.

Traits with higher priority in organic than in conventional breeding programs are for instance tillering capacity or regeneration ability after harrowing, weed suppression ability, resistance or at least tolerant against diseases on the leaves and on the ears. Nutrient use efficiency under limited nutrient conditions can be achieved by e.g. a well developed fine rooting system or a functioning symbiosis with soil microorganism such as arbuscular mycorrhizal fungi (AMF). Finally, grain yield stability has a higher priority than the absolute amount (Kunz et al., 2006; Löschenberger et al., 2008). It has been demonstrated for winter wheat (Murphy et al., 2007) and for spring wheat (Reid et al., 2009) that direct selection in organic plant breeding programs was more successful for increase in grain yield in organic farming, than indirect selection in breeding programs for conventional agriculture. This was not confirmed in our recent study. There, the organically bred cultivars did not outperform the conventionally bred cultivars under organic conditions (Hildermann et al., 2009).

Especially in organic farming, where the external input of nutrients is limited, the establishment of a functional symbiosis with arbuscular mycorrhizal fungi (AMF) could be a promising strategy for improving NUE. AMF are of particular importance in organic and in low input agroecosystems. AMF can enhance resistance to certain root pathogens, (Hegde et al., 1999; Liu et al., 2007) can stabilize soil aggregates by their intricate extraradical mycelial network and can enhance water stress tolerance (Ruiz-Lozano et al., 2006). Moreover, it is known that AMF can contribute to plant nutrition by delivering immobile nutrients such as P, zinc (Zn) or Manganese (Mn) (Thompson, 1987; Marschner, 1993; Kahiluoto et al., 2009). In wheat, it was demonstrated that AMF contributed to the uptake of shoot P (Karagiannidis and Hadjisavva-Zinoviadi, 1998; Graham and Abbott, 2000; Zhu et al., 2001; Al-Karaki et al., 2004; Li et al., 2006), grain P (P-G) (Karagiannidis and Hadjisavva-Zinoviadi, 1998) and grain Zn (Zn-G) (2003; Ryan et al., 2008).

Agricultural measures such as fertilization, plant protection, crop management and tillage affect AMF, as was shown in the DOK trial and in other studies (Johnson, 1993; Boddington and Dodd, 2000; Mäder et al., 2000a; Oehl et al., 2003). Organic sources of nutrients (farmyard manure, compost and crop residues) as used in organic farming and slow releasing mineral fertilisers such as rock phosphate may even promote AMF (Ryan et al., 1994). AMF species diversity and abundance but also AMF-root colonization (AMF-RC) has been found to be higher at organic (Ryan et al., 1994; Mäder et al., 2000a; Oehl et al., 2003) or low input (Kahiluoto et al., 2009) sites than at conventional sites. In a long-term trial, AMF contribution to soil quality parameters such as microbial biomass or decomposition activity, was higher in the low input than in the high input system (Kahiluoto et al., 2009). Same authors showed in a bioassay with flax and clover an enhanced contribution of AMF to plant growth and P uptake in the low input system compared to the high input system.

To exactly determine AMF-contribution to nutrient uptake and plant growth, AMF effectiveness has to be assessed, which requires a non-mycorrhizal control. Due to the ubiquity of AMF in most ecosystems, the establishment of such a control in field trials is challenging. Usually it is done by soil fumigation (Kahiluoto et al., 2001), which does not comply with the guidelines and regulations of the organic systems of the DOK long-term trial. To obtain information on the AMF-symbiosis, AMF-RC was measured in this study. It is known, that there is no linear correlation between AMF-RC and AMF-effectiveness (Kahiluoto et al., 2009). Therefore, the results based on AMF-RC have to be carefully interpreted. Nevertheless, Hetrick et al. (1992) proposed AMF-RC in field studies as a potential activity indicator of AMF symbiosis as it is a necessary precondition for the plant to benefit from the symbiosis. In controlled pot trials, these authors found higher AMF-RC correlated with higher effectiveness of old compared to modern wheat cultivars.

In the present study, ten winter wheat cultivars derived from organic (OPB) and conventional (BFCA) breeding programs and old cultivars were tested in organic and conventional systems of the DOK field experiment. In contrast to studies comparing cultivars on neighbouring organically and conventionally managed farms, this test was conducted under similar soil and climatic conditions at a homogenous field site. Parameters related to plant growth, yield and technological baking quality aspects are published in Hildermann et al. (2009) Here, we present the results for nutrient use efficiency for N and P and assessments related to AMF symbiosis. The objectives of the study were (i) to compare NUE parameters and AMF-RC of wheat cultivars derived from divers breeding programs in organic and conventional systems with different fertilization levels and (ii) to determine the correlation between AMF-RC and nutrient (P, Mn, Zn) concentration and uptake of winter wheat cultivars at different developmental stages.

3.3 Materials and Methods

Experimental design

A field experiment with ten winter wheat cultivars grown under organic and conventional farming conditions was performed in the DOK trial in 2006/2007. Information on the DOK long-term trial is given in Mäder et al. (2002) A detailed description of the experimental layout and design of the winter wheat experiment is published in Hildermann et al. (2009). Therefore, we will only give a short overview of the experiment here.

Ten cultivars were tested with four replicates in two organic systems (BIODYN 1 and BIODYN 2), a conventional system (CONMIN) and an unfertilized control (NOFERT), resulting in a total of 160 subplots. These systems differed mainly in terms of fertilization and plant protection strategies, whereas the crop rotation was the same in all systems. From 1999 – 2009, it comprised potatoes, winter wheat 1, soybean, silage maize, winter wheat 2, grass-clover 1, grass-clover 2. The organic systems represent mixed farms with arable land and livestock; CONMIN mimics a conventional system without livestock. The level of fertilization increased gradually from NOFERT to BIODYN 1 (0.7 livestock units ha^{-1}), BIODYN 2 (1.4 livestock units ha^{-1}) and CONMIN. The experimental design was a split-plot with systems as main block and cultivars as subplots. Soil samples were taken at a depth of 20 cm on 5 December 2006. The main soil chemical characteristics are shown in Table 3 1.

System	pH (H_2O)	C_{org} (%)	N_{min}[a] (mg kg^{-1})	P[b] (mg kg^{-1})	K[b] (mg kg^{-1})	Ca[c] (mg kg^{-1})	Mg[b] (mg kg^{-1})	Cu[c] (mg kg^{-1})	Fe[c] (mg kg^{-1})	Mn[c] (mg kg^{-1})	Zn[c] (mg kg^{-1})
NOFERT	5.84 c	1.11 c	11.02 c	8.30 c	27.22 d	1422.50 c	165.50 c	4.73 a	179.65 a	67.76 c	5.68 b
BIODYN 1	6.14 b	1.22 b	12.90 b	8.68 c	48.33 c	1640.00 b	178.25 c	4.53 a	159.81 b	75.84 ab	6.78 a
BIODYN 2	6.40 a	1.41 a	16.07 a	12.99 b	68.83 b	1885.00 a	197.13 b	4.38 a	136.31 c	82.34 ab	7.01 a
CONMIN	6.34 a	1.23 b	12.78 b	24.45 a	79.70 a	1681.25 bc	319.25 a	4.51 a	133.99 c	73.44 bc	6.50 b
ANOVA											
P value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.017	<0.0001	<0.0001	<0.0001

[a] $N_{min} = NO_3 - N + NH_4$ [b] measured in a double lactic acid extract [c] HCl / H2 SO_4

Table 3 1 Soil acidity, soil organic carbon content and soluble mineral elements in the soil at the beginning of the experiment in December 2006 (0-20 cm soil depth), means, n=32. Different letters indicate differences based on Tukey-Kramer test

In the 2006/2007 season, BIODYN 1 and BIODYN 2 received split applications of 5/10 t ha^{-1} composted manure and 30/60 m^3 ha^{-1} slurry (not aerated). CONMIN received only mineral fertilizers, split into three applications. This resulted in 33, 66 and 140 kg N_{total} ha^{-1} for BIODYN 1, BIODYN 2 and CONMIN, respectively, which corresponded to 7, 14 and 140 kg ha^{-1} $N_{available}$, respectively.

Ten winter wheat cultivars developed between 1840 and 2006 were examined in the DOK trial, including one composite cross population, in which a large number of cultivars from the UK were intercrossed and propagated as one bulk (Phillips and Wolfe, 2005). In the following text, the nine cultivars and the composite cross population (CCP) are listed as ten cultivars. The cultivars can be classified into three old (Rouge de Bordeaux, Mont Calme 245, Probus), three organically bred (Scaro, Sandomir, CCP) and four conventionally bred cultivars (Titlis, Antonius, DI 9714, Caphorn) (Table 3 2).

Winter wheat cultivars were sown after maize on 26 October 2006 in ten subplots (3 m x 1 m) on the margins of the 16 DOK plots (5 m x 20 m). The cultivars were randomly arranged in each replicate of the DOK experiment.

Cultivar	Country of origin	Year of release	Origin / Breeder
Old cultivars/landraces			
Rouge de Bordeaux	FR	1840	Institut National de la Recherche Agronomique (INRA), FR-75338 Paris Cedex 07
Mont Calme 245	CH	1926	Nationale Genbank Agroscope Changins-Wädenswil (ACW), CH-1260 Nyon 1
Probus	CH	1948	Nationale Genbank Agroscope Changins-Wädenswil (ACW), CH-1260 Nyon 1 / Agroscope Reckenholz-Tänikon (ART) - CH-8046 Zürich
Organically bred cultivars			
Scaro	CH	2006	Sativa Rheinau AG, CH-8462 Rheinau, Getreidezüchtung Peter Kunz, CH-8634 Hombrechtikon
Sandomir	DE	2009	Getreidezüchtung Darzau, Karl Josef Müller, DE-29490 Neu Darchau
Composite Cross Population	GB	not registered	The Organic Research Center, Elm Farm, GB-Hamstead Marshall, Newbury, Berkshire RG20 0HR
Conventionally bred cultivars			
Titlis (standard)	CH	1996	Delley seeds and plants, CH-1567 Delley / Agroscope Changins-Wädenswil, CH-1260 Nyon 1
Antonius	AT	2003	Delley seeds and plants, CH-1567 Delley/ Saatzucht Donau GesmbH. & CoKG, AT-2301 Probstdorf
DI 9714	FR	not registered	Institut National de la Recherche Agronomique (INRA), FR-75338 Paris Cedex 07
Caphorn	FR	2001	Delley seeds and plants, CH-1567 Delley/ Monsanto UK Ltd., GB-Cambridge

Table 3 2 Winter wheat cultivars planted in the DOK long-term experiment, their countries of origin and years of release

Initial soil analysis

Two soil samples (0-20 cm) per subplot (total of 160 subplots) were collected using an auger (Ø 3 cm). Ten samples of a strip of five subplots were combined in one bulked sample resulting in a total of 32 bulked samples. Soil acidity was measured in a water suspension, mineral nitrogen (N_{min} = NH_4-N + NO_3-N) photometrically in 0.01 M $CaCl_2$ and soil organic carbon by wet combustion. Phosphorus and potassium were measured in double lactic acid (DL) and Ca, Mg, Cu, Fe, Mn and Zn in HCl / H_2SO_4.

Soil pH was similarly high in BIODYN 2 and CONMIN, whereas it was lower in BIODYN 1 and NOFERT (Table 3 1). Organic carbon, indicating humus content, was highest in BIODYN 2. Soil P was lowest in NOFERT and increased to BIODYN 1, BIODYN 2 and CONMIN. While soil P, potassium (K) and magnesium (Mg) increased with the input of fertilizers, copper (Cu) and iron (Fe) decreased. Soil mineral nitrogen (Nmin) was higher in BIODYN 2 than in CONMIN. The values suggest that mineralization in the cool season was still high in BIODYN 2 due to the previous application of manure and higher soil life activity in that system, as was reported by Mäder et al. (2002).

3.3.1 Root and Shoot Sampling

To analyse AMF-RC, root samples (0-20 cm) were taken with an auger (Ø 4 cm) according to Mäder et al. (2000a) The corresponding above-ground shoots were sampled to analyse N, P, Mn and Zn. The first sampling took place on 20 April 2007 at the end of tillering (Zadoks scale 30). The second sampling took place on 16 May 2007 at flowering (Zadoks scale 65). Soil-root samples were deep frozen at -25°C until the roots were washed out. After washing, the roots were stored in a 70% ethanol solution. Shoots samples were oven-dried at 40°C until constant weight, coarsely ground in a mill (Mikro Feinmühle Culatti, Typ DCFH 48, Culatti AG, CH-8005 Zürich) and afterwards finely ground in a swing mill (Retsch MM 200 Retsch GmbH, DE-42781 Haan).

3.3.2 AMF Root Colonization

The roots were cleared and stained according to a modified method of Phillips and Hayman (1970). Roots were cleared in 2.5% KOH, and fungal structures stained with 0.05% Trypan blue. The percentage of root length colonized by AMF (AMF-RC) was assessed using a dissecting microscope (Leica M205 C, Leica Microsystems (Suisse) SA, 1020 Renens, Switzerland) at a magnification up to 100 x. 150 intersections were counted according to the grid-line intersect method modified after Giovannetti et al. (1980).

3.3.3 Analysis of N, P, Zn and Mn

Nitrogen concentration in shoots, straw and grain was measured with a CHN analyser (Leco CHN 100, LECO Instrumente GmbH, DE-41199 Mönchengladbach). P, Mn and Zn were analysed using wave length dispersive X-ray fluorescence spectroscopy. 2.0 g of the ground material was pelleted into tablets with a diameter of 20 mm and a thickness of 4 mm without binding agents, modified after Hutton et al. (1977) and Norrish et al. (1977) Measurements were carried out on a Bruker-axs SRS-3000 with a rhodium tube (Bruker AXS GmbH, DE-76187 Karlsruhe).

3.3.4 Nutrient Use Efficiency Parameters

Grain, straw and total uptake (aboveground) and utilization efficiency was calculated for the elements N and P. Total available N (Ntav) was calculated as mineral nitrogen in the top soil at 5th December plus available N applied as fertilizers. N uptake efficiency and use efficiency were additionally calculated. These parameters were not calculated for P as it is not possible to determine plant available P analogously to N available from soil and from fertilizers. The components, symbols, units and their definitions are given in Table 3 3.

Nit-UE was defined after Moll et al. (1982) as the ration of grain yield (DM) to N supply (as total available N) and is in that way applied in field studies (Le Gouis et al., 2000; Muurinen et al., 2006). This definition does not comprise additional factors influencing plant N such as mineralization from humus, crop residues and manures or leaching, which are difficult to measure. According to Le Gouis et al. (2000), N uptake efficiency (NUpE) and N utilization efficiency (NUtE) reflect main parameters of nutrient use efficiency. NUpE describes the ability of the plant to extract N from the soil, NUtE reflects the ability to transform the extracted N into grain yield, and Nit-UE reflects the ability to produce grain yield in response to N supply.

Component	Symbol	Unit	Definition
Nitrogen			
N total fertilizer	N_{tf}	kg N ha^{-1}	N supply as contained in fertilizers
N available fertilizer	N_{avf}	kg N ha^{-1}	N available (NH_4 - N + NO_3 - N) in fertilizers
N mineral soil	N_{min}	kg N ha^{-1}	N mineral (NH_4 - N + NO_3 - N) in the soil
Total available N	N_{tav}	kg N ha^{-1}	N available in fertilizers + N mineral in the soil
Shoot N at tillering	N-Ti	g N kg^{-1} DM	Shoot N concentration at tillering
Shoot N at flowering	N-Fl	g N kg^{-1} DM	Shoot N concentration at flowering
Straw N	N-S	g N kg^{-1} DM	Straw P concentration
Grain N	N-G	g kg^{-1} DM	Grain N concentration
Grain N uptake	N-Gup	kg N ha^{-1}	Grain yield (DM) * Grain N concentration
Straw N uptake	N-Sup	kg N ha^{-1}	Straw yield (DM) * Grain N concentration
Total N uptake	N-Tup	kg N ha^{-1}	Grain N uptake + Straw N uptake
Nitrogen uptake efficiency	NUpE	kg N kg^{-1} N	Total N uptake / Total available N
Nitrogen utilization efficiency	NUtE	kg DM kg^{-1} N	Grain yield (DM) / Total N uptake
Nitrogen use efficiency for grain yield	Nit-UE	kg DM kg^{-1} N	Grain yield (DM) / Total available N
Phosporus			
Shoot P at tillering	P-Ti	g P kg^{-1} DM	Shoot P concentration at tillering
Shoot P at flowering	P-Fl	g P kg^{-1} DM	Shoot P concentration at flowering
Straw P	P-S	g P kg^{-1} DM	Straw P concentration
Grain P	P-G	g P kg^{-1} DM	Grain P concentration
Grain P uptake	P-Gup	kg P ha^{-1}	Grain yield (DM) * Grain P concentration
Straw P uptake	P-Sup	kg P ha^{-1}	Straw yield (DM) * Grain P concentration
Total P uptake	P-Tup	kg P ha^{-1}	Grain P uptake + Straw P uptake
Phosphorus utilization efficiency	PUtE	kg DM kg^{-1} P	Grain yield (DM) / Total P uptake
Manganese and Zinc			
Total Mn uptake	Mn-Tup	kg Mn ha^{-1}	Grain Mn uptake + Straw Mn uptake
Total Zn uptake	Zn-Tup	kg Zn ha^{-1}	Grain Zn uptake + Straw Zn uptake

Table 3 3 Components, their symbols, units and definitions as related to nitrogen and phosphorus use efficiency

3.3.5 Statistical Analyses

Statistical data analyses were performed using the JMP 5.0.1 software package (SAS Institute Inc. Cary, NC, USA). Data were checked for normal distribution by the Shapiro-Wilk test. Data that were not normally distributed (N-S, P-S, P-Sup) were log-transformed. For presentation, data were back-transformed. Analysis of variance was performed on the whole data set using a multifactorial model with systems, cultivars and field replicates as factors. The interactions between systems and cultivars were also tested. To test the significance of the effect of the breeding category, an ANOVA with the main effects breeding category and systems and their interactions was conducted. With significant model effects, a Tukey Kramer (HSD) post hoc test for multiple comparison was performed to compare sample means. The correlation between two parameters was calculated by Spearman's rank correlation coefficient.

3.4 Results and Discussion

3.4.1 Nitrogen and Phosphorus Concentrations in Shoots, Straw and Grain

Shoot N (g N kg^{-1}) decreased from tillering (N-Ti = 22.7 g kg^{-1}) to flowering (N-Fl = 9.2 g kg^{-1}) in all treatments and in all winter wheat cultivars (Table 3 4). This decrease during growing season is in line with results on soft wheat (Justes et al., 1994; Ziadi et al., 2008) and on durum wheat (Dordas, 2009). Generally, N concentrations in the different measured plant parts (shoot N at tillering and flowering and N in grain (G-N) and straw at harvest (S-N)) were higher in NOFERT and CONMIN than in the organic systems (Table 3 4). N-concentrations are similar to those observed in spring wheat (Ziadi et al., 2008), whereas Justes et al. (1994) found much higher N-Ti concentrations (42 – 52 g kg^{-1}) for winter wheat. In NOFERT, this was a concentration effect due to low shoot biomass and grain yield (Table 3 6); in CONMIN it was due to the high N supply resulting in increase in grain yield with high G-N compared to BIODYN 1 and BIODYN 2 (Hildermann et al., 2009). N concentrations in all plant parts hardly differed between the two organic systems, although BIODYN 1 received only half of the amount of organic fertilizers than BIODYN 2. However, total available N differed less and accounted for 39 kg ha^{-1} in BIODYN 1 compared to 55 kg ha^{-1} in BIODYN 2.

Differences for N-Ti, N-Fl and N-S between cultivars derived from the three different breeding categories were small but statistically significant. The conventionally bred cultivars achieved the highest shoot N concentrations, whereas N-G of the old cultivars (18.9 g kg^{-1}) was higher than N-G of the organically (17.8 g kg^{-1}) and the conventionally bred modern cultivars (17.5 g kg^{-1}). Similarly, other studies (Calderini et al., 1997; Smith and Gooding, 1999; Guarda et al., 2004; Acuna et al., 2005) reported on decreased N-G in modern wheat cultivars compared to old cultivars. This decrease indicates that breeding for improved grain yield negatively affected N-G due to a dilution effect.

Similar to N, shoot P decreased during the growth period from tillering (P-Ti = 2.8 g kg^{-1}) to flowering (P-Fl = 1.4 g kg^{-1}). The P concentrations for the different growing stages were similar to other studies (Ziadi et al., 2008; Dordas, 2009). P-Ti increased with increased fertilizer input from NOFERT to CONMIN (Table 3 4). Also P-Fl and grain P (P-G) was highest in the CONMIN system whereas straw P (P-S) was highest in the unfertilized control NOFERT. An increase in P concentration with increased fertilizer input was observed for wheat shoots, (Egle et al., 1999; Ziadi et al., 2008; Dordas, 2009) wheat grain (Ryan et al., 2004; Mäder et al., 2007; Dordas, 2009) and rye grains (Kahiluoto et al., 2009).

Significant effects of cultivars were observed for P-Fl, P-S and P-G. P-Fl was higher in the conventionally than in the organically bred and old cultivars. However, differences in P-G were not significant between breeding categories (Table 3 4). This is in contrast to the findings of other studies (Calderini et al., 1995; Murphy et al., 2008), wherein P-G was lower in modern cultivars compared to older cultivars. Our results indicate that by focusing on yield improvement during breeding, grain N concentration decreased, whereas grain P concentration remained stable. No significant correlations were observed between shoot N and P concentrations at tillering and flowering stage and the final grain concentration.

	Shoot N Tillering	Shoot N Flowering	Straw N	Grain N	Shoot P Tillering	Shoot P Flowering	Straw P	Grain P
	N-Ti	N-Fl	N-S	N-G	P-Ti	P-Fl	P-S	P-G
	(g N kg^{-1})	(g N kg^{-1})	(g N kg^{-1})	(g N kg^{-1})	(g P kg^{-1})	(g P kg^{-1})	(g P kg^{-1})	(g P kg^{-1})
Cultivar								
(Across systems; n = 16)								
Rouge de B.	19.4 b	8.0 a	2.4 bcd	19.0 ab	2.5 a	1.2 bcd	0.20 abc	2.9 c
M. Calme 245	21.2 ab	8.6 bc	2.1 d	18.2 bcd	3.0 a	1.4 abc	0.13 bc	2.3 d
Probus	21.9 ab	9.0 bc	2.9 ab	19.8 a	2.5 a	1.1 cd	0.04 d	3.6 a
Scaro	21.2 ab	9.0 bc	2.3 bcd	17.7 bcde	2.4 a	1.1 d	0.12 bc	3.3 abc
Sandomir	22.0 ab	8.9 bc	2.2 cd	18.5 abc	3.0 a	1.4 abcd	0.10 c	3.4 ab
CCP	21.1 ab	9.2 abc	2.9 ab	17.3 cde	2.8 a	1.5 ab	0.22 ab	2.9 c
Titlis	22.8 ab	9.4 abc	2.7 abc	18.1 bcd	2.7 a	1.4 abc	0.13 bc	3.2 abc
Antonius	23.4 ab	9.1 bc	2.1 d	18.1 abc	3.0 a	1.4 abcd	0.18 abc	3.1 bc
DI 9714	23.3 ab	9.7 ab	3.3 a	16.8 de	2.9 a	1.5 a	0.30 a	3.2 abc
Caphorn	24.0 a	10.7 a	3.4 a	16.7 e	2.5 a	1.6 a	0.17 abc	3.0 bc
System								
(Across cultivars; n = 40)								
NOFERT	29.2 a	11.1 a	4.2 a	18.9 a	0.9 d	1.3 b	0.24 a	3.1 b
BIODYN 1	20.7 b	7.3 b	2.0 c	16.5 c	2.7 c	1.3 b	0.11 b	2.9 b
BIODYN 2	16.9 c	6.7 b	2.0 c	16.2 c	3.2 b	1.3 b	0.12 b	3.0 b
CONMIN	21.2 b	11.5 a	2.8 b	20.4 a	4.0 a	1.6 a	0.13 b	3.4 a
Breeding category								
OLD (n = 48)	20.8 b	8.5 b	2.4 b	18.9 a	2.6 a	1.3 b	0.11 b	2.9 a
ORG (n = 48)	21.4 b	9.0 b	2.5 b	17.8 b	2.7 a	1.3 b	0.14 ab	3.2 a
CONV (n = 64)	23.6 a	9.7 a	2.8 a	17.5 b	2.8 a	1.5 a	0.19 a	3.1 a
ANOVA								
Cultivar								
P value (d. f. = 9)	0.035	0.0001	0.0001	0.0001	0.08	< 0.0001	< 0.0001	< 0.0001
System								
P value (d.f. = 3)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Cultivar x System								
P value (d. f. = 27)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Breeding category								
P value (d.f. = 2)	< 0.0001	< 0.0001	0.0099	< 0.0001	n.s.	< 0.0001	0.0003	0.046
Breeding category x System								
P value (d.f. = 11)	n.s.	n.s	n.s.	n.s.	n.s.	n.s.	n.s.	n.s

d. f., degrees of freedom

Table 3 4 Nitrogen and phosphorus concentrations in shoots at tillering and flowering, and in straw and in grain of ten winter wheat cultivars, four systems and three breeding categories. Results of two-way ANOVAs and interactions are shown. Different letters indicate differences based on Tukey-Kramer test

3.4.2 Nitrogen Uptake and Nitrogen Efficiency Components

Systems affected all components of N uptake and N efficiency. Cultivars and breeding categories affected grain N uptake (N-Gup), NUtE and Nit-UE but there were no significant differences in total N-uptake (N-Tup). Significant cultivar x system or breeding category x system interactions were not detected. The ANOVA results are presented in Table 3 5.

N-Gup, straw N uptake (N-Sup) and as a consequence N-Tup increased gradually as a result of N input to the systems. This was similarly reported in studies comparing increasing N input, (Calderini et al., 1995; Ortiz-Monasterio et al., 1997; Delogu et al., 1998; Le Gouis et al., 2000; Guarda et al., 2004) comparing organic and conventional farming (van Delden, 2001; L-Baeckstrom et al., 2006) and comparing different levels of N-fertilization within organic farming (Baresel et al., 2008). N-Sup in NOFERT was higher than N-Sup in the organic systems, indicating an inefficient N translocation from shoots to grain. This is also confirmed by low grain yield resulting in low values for NUtE in that system.

Differences between cultivars were observed for N-Gup. N-Gup was highest for the conventionally bred cv Antonius (91.5 kg ha^{-1}) and lowest for the old cv Rouge de Bordeaux (72.9 kg ha^{-1}). Generally, the conventionally bred cultivars revealed highest N-Gup (82.4 kg ha^{-1} vs 77.1 kg ha^{-1}). However, multiple comparisons between breeding categories were not significant according to the Tukey Kramer HSD test.

Calculated across all systems, we observed a slight increase in N-Gup of 0.03 kg ha^{-1} yr^{-1} (r = 0.35), with the year of release of the ten cultivars. These values are lower than values reported by Calderini et al. (1995) (0.72 kg ha^{-1} yr^{-1}) on trials with an input of 160 or 230 kg N and by Guarda et al. (2004) (0.67 – 0.82 kg ha^{-1} yr^{-1}) on trials with an input of 80 and 160 kg N. When calculated for BIODYN 2 and CONMIN separately, the increase in N-Gup was 0.09 kg ha^{-1} yr^{-1} (r = 0.56) in CONMIN, whereas no increase was observed in BIODYN 2. Similarly, grain yield of cultivars increased strongly relative to year of release in CONMIN, whereas there was only a minor increase in BIODYN 2 (Hildermann et al., 2009). These results confirm the close correlation between grain yield and grain N uptake (in our study: r = 0.95; $p < 0.0001$), also postulated in Triboi et al. (2006).

In contrast to N uptake, the N efficiency components NUpE, NUtE and Nit-UE generally decreased as a function of N input and were lowest in the conventional system CONMIN (Table 3-5). The results reflect improved NUpE and Nit-UE with decreasing N supply and improved NUtE by applying organic fertilizers at low doses. L-Baeckstrom et al. (2006) also found higher Nit-UE in organic than in conventional farming systems. Lower Nit-UE due to an increase in N input was reported in several other studies (Ortiz-Monasterio et al., 1997; Delogu et al., 1998; Guarda et al., 2004; Limon-Ortega et al., 2008) and generally stated in a recent review (Dawson et al., 2008). However, also examples of lower efficiencies in organically fertilized treatments than in urea treatments can be found (Limon-Ortega et al., 2008).

Significant differences between cultivars were found for NUtE and Nit-UE. NUtE ranged from 40.1 (cv Mont Calme 245) to 49.8 kg DM kg^{-1} N (cv Caphorn). Nit-UE, ranged from 66.2 (cv Rouge de Bordeaux) to 89.3 kg DM kg^{-1} N (cv Antonius). In general, Nit-UE and NUtE increased with the year of release of the cultivars and were highest in the conventionally bred cultivars in line with findings of other studies (Calderini et al., 1995; Ortiz-Monasterio et al., 1997; Guarda et al., 2004).

Nit-UE and NUtE can be improved by increasing the harvest index (HI), which corresponds to an increase in grain yield by a reduction of plant height and therefore straw yield (Hildermann et al., 2009). NUtE did not differ between the tall organically and the shorter conventionally bred cultivars. However, the conventionally bred cultivars achieved the highest Nit-UE (Table 3 5) indicating a better transformation of fertilizer into grain yield. Taller plants are preferably grown under organic conditions because of better weed suppression (Mason and Spaner, 2006). As an exception among the conventionally bred cultivars, cv Antonius is a tall growing cultivar. This cultivar achieved the highest Nit-UE and highest grain yields and represents therefore a cultivar suitable for organic farming.

	Grain yield		Grain N uptake		Straw N uptake		Total N uptake		N uptake efficiency		N utilization efficiency		N use efficiency for grain yield	
	GY		N-Gup		N-Sup		N-Tup		NUpE		NUtE		Nit-UE	
	(Mg ha^{-1})		(kg N ha^{-1})		(kg N ha^{-1})		(kg N ha^{-1})		(kg N kg^{-1} N)		(kg DM kg^{-1} N)		(kg DM kg^{-1} N)	
Cultivar														
(Across systems; n = 16)														
Rouge de B.	3.8	b	72.9	b	19.1	a	92.0	a	1.62	ab	41.1	bc	66.2	c
M. Calme 245	4.4	b	80.3	ab	16.4	a	99.9	a	1.72	ab	40.1	c	78.7	abc
Probus	3.8	ab	78.8	ab	20.7	a	96.7	a	1.73	ab	46.6	a	69.5	c
Scaro	4.5	ab	80.2	ab	16.5	a	96.7	a	1.73	ab	47.2	a	80.5	abc
Sandomir	4.1	b	77.5	b	15.0	a	92.5	a	1.56	b	45.4	ab	70.2	bc
CCP	4.3	ab	74.8	b	18.1	a	92.9	a	1.61	ab	46.6	a	74.0	bc
Titlis	4.4	ab	81.9	ab	18.3	a	100.2	a	1.70	ab	45.9	ab	77.9	abc
Antonius	4.9	a	91.5	a	15.4	a	107.0	a	1.90	a	48.0	a	89.3	a
DI 9714	4.3	ab	73.8	b	18.1	a	91.9	a	1.62	ab	48.1	a	76.7	abc
Caphorn	4.9	a	82.2	ab	17.4	a	99.9	a	1.73	ab	49.8	a	84.1	ab
System														
(Across cultivars; n = 40)														
NOFERT	2.7	d	49.8	c	17.6	b	67.4	c	2.45	a	39.5	b	96.0	a
BIODYN 1	3.7	c	61.3	b	11.5	d	72.7	c	1.85	b	51.4	a	94.8	a
BIODYN 2	4.2	b	68.0	b	14.5	c	82.6	b	1.50	c	51.2	a	76.5	b
CONMIN	6.8	a	138.5	a	26.4	a	165.0	a	0.96	d	41.5	b	39.5	c
Breeding category														
OLD (n = 48)	4.0	b	77.14	a	18.73	a	95.85	a	1.69	a	42.7	b	71.5	b
ORG (n = 48)	4.3	b	77.53	a	16.51	a	94.14	a	1.63	a	46.4	a	74.9	b
CONV (n = 64)	4.6	a	82.39	a	17.28	a	99.71	a	1.74	a	47.9	a	81.7	a
ANOVA														
Cultivar														
P value (d. f. = 9)	< 0.0001		0.001		n.s.		n.s.		n.s.		< 0.0001		< 0.0001	
System														
P value (d. f. = 3)	< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001	
Cultivar x System														
P value (d. f. = 27)	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.	
Breeding category														
P value (d. f. = 2)	< 0.0001		0.040		n.s.		n.s.		n.s.		< 0.0001		< 0.0001	
Breeding category x System														
P value (d. f. = 11)	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.	

d. f., degrees of freedom

Table 3 5 Grain yield, grain, straw and total nitrogen uptake, N uptake efficiency, N utilization efficiency and N use efficiency for grain yield of ten winter wheat cultivars, four systems and three breeding categories. Results of two-way ANOVAs and interactions are shown. Different letters indicate differences based on Tukey-Kramer test

3.4.3 Phosphorus Uptake and Phosphorus Utilization Efficiency

Analysis of variance showed significant effects of cultivars and systems on grain P uptake (P-Gup), straw P uptake (P-Sup), total P uptake (P-Tup) and phosphorus utilization efficiency (PUtE). No significant cultivar x system interactions were detected. The breeding categories affected P-Gup, P-Tup and PUtE. Significant breeding x system interactions were detected for P-Tup. The ANOVA results are presented in Table 3 6.

The results for P uptake and PUtE showed similar patterns as the results obtained for N uptake and NUtE. P-Gup and P-Tup increased with P input to the systems. P-Sup was higher in NOFERT than in the organic systems. P-Gup ranged from 8.1 (NOFERT) to 23.3 kg ha^{-1} (CONMIN). Similarly, Dordas (2009) reported that P-Gup in durum wheat was 8.4 kg ha^{-1} in a unfertilized control and 11 – 18 kg ha^{-1} in farming systems with different N and P inputs.

In contrast to the N uptake parameters, the conventionally and organically bred modern cultivars achieved significantly higher P-Gup and P-Tup than old cultivars (Table 3 6) which is in line with Calderini et al. (1995) Cv Antonius (15.7 kg ha^{-1}) again achieved the highest P-Gup.

As was shown for N, increased P input diminished PUtE, and organic fertilizer had a positive effect on PUtE: PUtE was higher in BIODYN 1 and BIODYN 2 than in CONMIN and NOFERT (Table 3 6). Similar reductions of PUtE relative to fertilizer input were shown in Egle et al. (1999)

There were no significant differences between the other cultivars for PUtE. The old cultivars had the significantly highest PUtE. However, this was due to an exceptionally high value for cv Mont Calme 245 with its relatively high grain yield and low grain-P (Table 3 6). These findings deviate from NUtE and do not confirm the results of Calderini et al. (1995) showing that PUtE increased from old to modern wheat cultivars.

We found a moderate correlation between NUtE and PUtE when calculated across all cultivars and all systems (r = 0.429; p < 0.0001) allowing simultaneous selection for both nutrients.

	Grain P uptake		**Straw P uptake**		**Total P uptake**		**P utilization efficiency**
	P-Gup (kg P ha^{-1})		P-Sup (kg P ha^{-1})		P-Tup (kg P ha^{-1})		PUtE (kg DM kg^{-1} P)
Cultivar (Across systems; n = 16)							
Rouge de B.	11.3	c	1.45	a	12.7	bc	297.8 b
M. Calme 245	10.4	c	0.93	ab	11.4	c	398.6 a
Probus	14.2	ab	0.30	c	14.5	abc	276.0 b
Scaro	14.8	ab	0.71	b	15.1	ab	297.4 b
Sandomir	14.3	ab	0.66	b	14.9	ab	280.1 b
CCP	12.6	bc	1.22	ab	14.0	abc	313.0 b
Titlis	14.2	ab	0.79	ab	15.3	ab	295.6 b
Antonius	15.7	a	1.20	ab	16.9	a	299.4 b
DI 9714	14.3	ab	1.44	a	15.8	a	281.8 b
Caphorn	14.8	ab	0.78	b	15.8	a	313.9 b
System (Across cultivars; n = 40)							
NOFERT	8.1	d	0.97	ab	9.2	d	293.5 b
BIODYN 1	10.8	c	0.63	c	11.7	c	323.6 a
BIODYN 2	12.4	b	0.81	bc	13.4	b	318.8 a
CONMIN	23.3	a	1.15	a	24.3	a	285.6 b
Breeding category							
OLD (n = 48)	11.9	b	0.78	a	12.7	c	327.7 a
ORG (n = 48)	13.9	a	0.84	a	14.6	b	297.9 b
CONV (n = 64)	14.7	a	1.03	a	16.0	a	296.6 b
ANOVA							
Cultivar							
P value (d. f. = 9)	< 0.0001		< 0.0001		< 0.0001		< 0.0001
System							
P value (d. f. = 3)	< 0.0001		< 0.0001		< 0.0001		0.0001
Cultivar x System							
P value (d. f. = 27)	n.s.		n.s.		n.s.		n.s.
Breeding category							
P value (d. f. = 2)	< 0.0001		n.s.		0.001		0.006
Breeding category X System							
P value (d. f. = 11)	n.s.		n.s.		0.040		n.s.

d. f., degrees of freedom

Table 3 6 Grain, straw and total phosphorus uptake and P utilization efficiency across all systems, cultivars and breeding categories. Different letters indicate differences based on Tukey-Kramer test

3.4.4 AMF-Root Colonization (AMF-RC)

AMF-RC differed significantly between the four systems at tillering and at flowering stage (Figure 3 1). At tillering, AMF-RC was significantly higher in the organic systems BIODYN 1 and BIODYN 2 than in the unfertilized control NOFERT and in the conventional system CONMIN. While AMF-RC increased in CONMIN during growth period as described in other studies (Al-Karaki et al., 2004; Covacevich et al., 2007), it remained almost constant in the other systems. Maybe AMF-RC started earlier in less fertilized conditions. The higher AMF-RC in BIODYN 2 when compared to CONMIN supports former findings in the DOK trial on wheat, vetch-rye and grass-clover (Mäder et al., 2000a) and also the results of an Australian study comparing the wheat-AMF symbiosis in organic and conventional farming (Ryan et al., 2004). While these results are in line with the hypothesis that AMF-RC declines with the intensification in P-fertilization as demonstrated in many other studies (Graham and Abbott, 2000; Kahiluoto et al., 2001; Marschner et al., 2005; Covacevich et al., 2007; Ryan et al., 2008; Kahiluoto et al., 2009), the low AMF-RC in the unfertilized control NOFERT (unfertilized since 30 years) was very unexpected. Therefore, we checked additional soil parameters.

Interestingly, across all systems and cultivars, AMF-RC was correlated with the C_{org} content at tillering ($r = 0.51$; $p < 0.001$) and at flowering stage ($r = 0.60$; $p < 0.001$). The ranking of the C_{org} content within the systems was similar to the observed AMF-RC. C_{org} was significantly higher in BIODYN 2 than in BIODYN 1, CONMIN and NOFERT. The low AMF-RC in NOFERT, a system with decreasing soil fertility, may be explained by the low C_{org} content, thus indicating a generally low microbial biomass. However, there are examples of sandy dunes with extremely low contents of C_{org} and still high AMF-RC (Sigüenza et al., 1996).

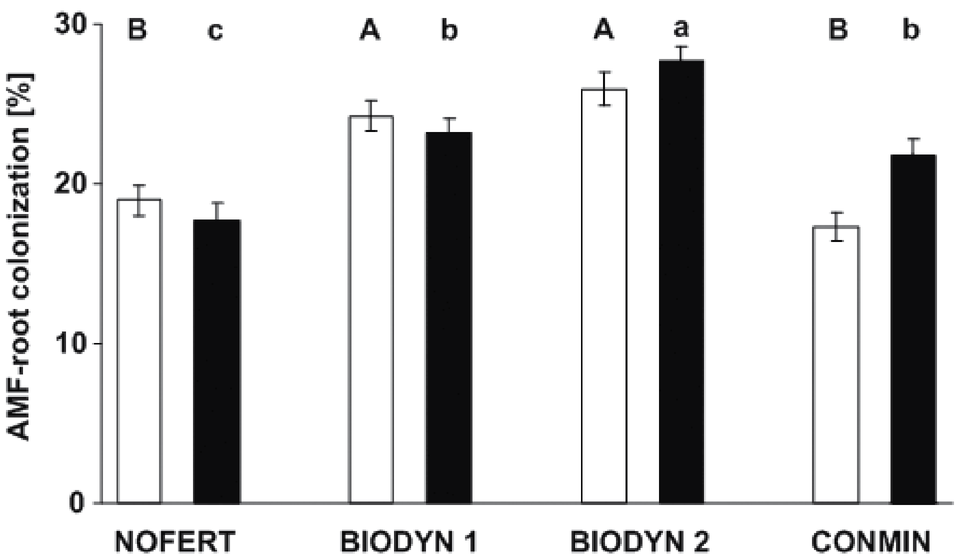

Figure 3 1 AMF-root colonization in four farming systems across ten cultivars (n=40) at tillering (white) and flowering stage (black). Bars represent standard error of means. Different letters indicate differences based on Tukey-Kramer test

Across all systems, AMF-RC of the ten cultivars ranged from 19% (cv Probus) to 25% (cv Scaro) (Figure 3 2). There is no clear agreement in literature on the degree of AMF-RC in wheat. In an earlier wheat study in the DOK trial, AMF-RC was only between 4 and 8%. (Mäder et al., 2000a) Values of AMF-RC in the range of our study were found by Hetrick et al., (1996) Zhu et al., (2001) Al-Karaki et al., (2004) Li et al. (2005) and Friedel et al., (2008) whereas AMF-RC ranged between 20 and 60% in other studies (Marschner et al., 2005; Ryan et al., 2005; 2008).

AMF-RC did not differ significantly among wheat cultivars across all systems and within the four systems, neither at tillering nor at flowering stage. At tillering, AMF-RC ranged from 19.4% (cv Probus) to 24% (cv DI 9714), and at flowering from 20% (cv Titlis) to 25.4% (cv Scaro). Our data did not show any effect of the breeding categories on AMF-RC. Especially in the context of the effect of the breeding environment on AMF-RC, the differences in AMF-RC among wheat cultivars are still under discussion (Wissuwa et al., 2009). Most studies report on results obtained in pot trials, as mycorrhizal response or growth benefits are difficult to assess in field studies due to the difficulties in including a non-mycorrhizal control (Kahiluoto et al., 2001). In contrast to our data, Hetrick et al. (1992; 1993) observed higher AMF-RC in wheat cultivars released before 1950 than in modern cultivars. Moreover, mycorrhizal response was lower in modern than in old cultivars (Manske, 1989; Zhu et al., 2001). As in our study, no differences in AMF-RC between two cultivars were found in a pot trial (Li et al., 2006). In a field study, slightly significant differences were observed in AMF-RC among twelve winter wheat cultivars. However, it was irrespective of the year of cultivar release (old and modern conventionally bred cultivars) (Friedel et al., 2008).

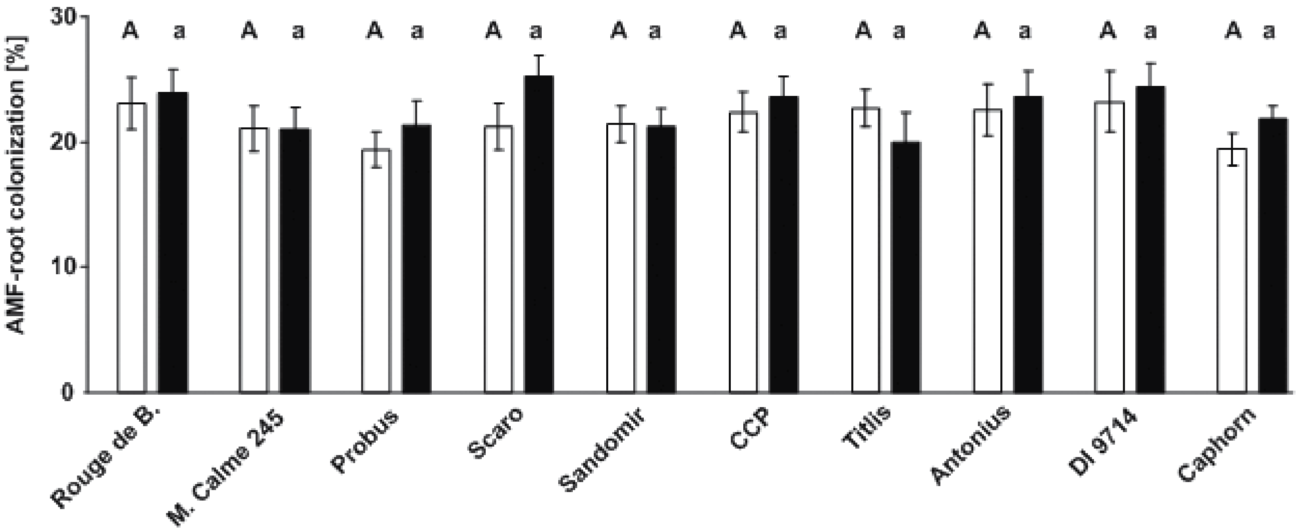

Figure 3 2 AMF-root colonization of ten cultivars across four farming systems (n=4) at tillering (white) and at flowering stage (black). Bars represent standard error of means. Different letters indicate differences based on Tukey-Kramer test

3.4.5 Correlation between AMF-RC and P, Mn and Zn Concentrations

Johnson et al. (1997) described the AMF symbiosis as being mutualistic and parasitic depending on the nutrient status of the soil. Mycorrhizal associations are beneficial (mutualistic) to plants, when the net costs of carbon delivery to the fungi are less than the net benefits of nutrient uptake. The association is detrimental (parasitic) when the net costs exceed the net benefits. For the nutrient limited systems NOFERT, BIODYN 1 and BIODYN 2, we expected a positive correlation between AMF-RC and nutrient concentrations due to AMF mediated nutrient supply. For the high input system CONMIN, we expected no or even a negative correlation as plant available nutrient might not be a limiting factor.

To test this hypothesis, correlations were calculated between AMF-RC and P, Mn and Zn concentrations at various plant stages and P, Mn and Zn total uptake (Table 3 7). We found significant positive correlations between shoot P and AMF-RC at tillering in NOFERT and BIODYN 2, but not in BIODYN 1 and CONMIN. AMF-RC at flowering was also significantly correlated with P-Fl in the organic system BIODYN 2. This indicates that in BIODYN 2 a higher colonization rate contribute to improved P supply. However, the measured effect of the AMF-wheat symbiosis in BIODYN 2 at early growth stages was not reflected in improved P-uptake or grain yield at harvest. Generally, no significant correlations were found between AMF-RC at tillering and flowering and grain yield in the four tested systems, except for slightly negative correlations in system BIODYN 2 (Table 3 7). For Mn, significantly negative correlations were found between AMF-RC and Mn concentrations in shoots and in straw and also Mn-Tup; however, only in the unfertilized control NOFERT. No significant correlations were found between AMF-RC and Zn concentrations and Zn-Tup. These findings are in contrast to Ryan et al. (2008) who observed a positive correlation under organic conditions between AMF-RC and Zn-G and a negative correlation between AMF-RC and P-G (Ryan et al., 2008). Several studies also report on a negative correlation between AMF-RC and Mn-G (Karagiannidis and Hadjisavva-Zinoviadi, 1998; Ryan et al., 2004; 2008).

Johnson et al. (1993; 1997) observed parasitism of AMF not only under high fertilization but also under extremely limited conditions of P and N. This could explain the inconsistent results and the absence of a positive correlation of AMF-RC and nutrient uptake or grain yield in our study.

	AMF-root colonization (%)							
	NOFERT		BIODYN 1		BIODYN 2		CONMIN	
	Tillering	Flowering	Tillering	Flowering	Tillering	Flowering	Tillering	Flowering
P								
Tillering	0.53 ***	#	- 0.06	#	0.49 ***	#	0.03	#
Flowering	0.25	'0.10	0.06	0.05	0.36 **	0.42 ***	0.18	- 0.09
Straw	0.10	- 0.09	0.01	0.28	0.16	0.43 ***	0.25	0.21
Grain	- 0.15	0.07	- 0.03	- 0.07	0.01	0.10	0.03	0.11
P-Tup	0.06	-0.08	-0.06	0.20	-0.24	0.22	0.11	0.26
Mn								
Tillering	-0.57 ***	-0.46 **	- 0.20	- 0.02	0.23	0.18	- 0.01	- 0.08
Flowering	-0.56 ***	-0.35 **	- 0.32 *	- 0.11	- 0.28	- 0.25	- 0.18	- 0.05
Straw	-0.59 ***	- 0.38 **	0.03	- 0.02	0.38 **	0.10	0.01	- 0.13
Grain	- 0.15	- 0.15	- 0.11	- 0.27	0.19	0.27	- 0.16	0.20
Mn-Tup	-0.49 **	-0.38 *	-0.04	-0.15	0.21	0.26	-0.15	0.16
Zn								
Tillering	- 0.33	- 0.13	- 0.05	- 0.02	- 0.05	0.12	0.02	0.12
Flowering	- 0.17	- 0.16	- 0.10	- 0.05	- 0.02	0.20	- 0.06	0.02
Straw	- 0.15	- 0.06	0.26	0.28	0.15	0.28	0.01	0.02
Grain	0.01	0.12	- 0.11	- 0.27	- 0.02	0.22	- 0.08	0.15
Zn-Tup	0.16	0.01	-0.03	-0.02	-0.24	0.17	0.08	0.27
GY	0.18	-0.13	0.07	0.23	-0.31 *	-0.01	0.19	0.21

= not calculated

*Table 3 7 Correlation matrix (r) of AMF root colonization at tillering and flowering stage and P, Mn and Zn concentrations in shoots at tillering, flowering, in straw and in grain at harvest and of P, Mn and Zn total uptake. r values significant at following P-levels: *0.05, **0.01, ***< 0.001*

3.5 Conclusion

The objective of the study (i) to compare NUE parameters and AMF-RC of wheat cultivars derived from divers breeding programs in organic and conventional systems with different fertilization levels and (ii) to determine the correlation of AMF-RC to nutrient (P, Mn, Zn) concentration and uptake of winter wheat cultivars at different developmental stages. While N and P uptake parameters and grain yield increased with nutrient input, nutrient use efficiency was higher in the organic systems than in the conventional system. Nit-UE differed within cultivars, but there was no cultivar x system interactions. The ranking of the cultivars was therefore similar for the four systems that differed strongly in management and nutrient level. There was a clear trend towards higher Nit-UE of modern (organically and conventionally bred) cultivars when compared to old cultivars. No evidence was found that breeding under organic conditions resulted in higher NUE or higher grain yield of these cultivars compared to conventionally bred cultivars. As there was considerable genetic variation in NUE within the cultivars, cultivars for organic low input farming should be carefully selected.

AMF-RC was higher in the organic than in the conventional system. However, our data did not show that the breeding conditions affected AMF-RC of wheat cultivars. No clear evidence was found that AMF symbiosis contributed more to nutrient uptake in the organic systems than in the conventional system.

Acknowledgment

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4 CULTIVAR X SITE INTERACTIONS OF WINTER WHEAT UNDER DIVERSE ORGANIC FARMING CONDITIONS

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4.1 Abstract

Most modern wheat cultivars used in organic farming have been developed in breeding programs for conventional farming. However, in the last two decades, organic breeding programs have been established. Which of these programs are most suitable to organic farming? Eight cultivars derived from organic and conventional breeding programs and old cultivars were tested at three marginal sites of Swiss organic farms. The results were compared to a previous study conducted in two more fertile organic systems of the DOK-system comparison trial. The main objectives of the study were (i) to compare yield, baking quality and nutrient use efficiency parameters at the three marginal sites, (ii) to analyse phenotypic stability of the main parameters across the three marginal and the two fertile sites, (iii) to prove the influence of seed origin (derived from organic versus conventional seed propagation) and (iv) to assess mycorrhizal colonization in relation to nutrient uptake.

At the marginal sites, there was a slight trend towards higher grain yields of the organically bred cultivars. This difference was statistically significant at the lowest yielding site. However, no such trend could be observed across marginal and fertile test environments. Nitrogen use efficiency of the organically bred cultivars was highest at the marginal sites, however no differences of baking quality index were observed between the breeding categories. Only minor influence of seed origin was observed. No differences of root colonization with arbuscular mycorrhizal fungi between the cultivars were observed and also no correlations between root colonization and shoot and grain nutrient concentrations and grain yield were detected.

Cultivars suitable for organic farming should not only achieve high yields but also high baking quality and nutrient use efficiency, as did the organically bred cultivar Scaro. Our results stress the importance of conducting selection and testing of cultivars in the scope of multi-location trials covering a wide range of the target conditions of organic farming.

Keywords: Organic farming - organic plant breeding - yield – baking quality – nutrient use efficiency – arbuscular mycorrhiza – seed origin – ecovalence – heritability

4.2 Introduction

The importance of modern organic farming systems has increased during recent years. Not only in Europe but worldwide, there is a rising awareness of the environmental impact of agricultural systems and of the nutritional quality of food. Cereals, including wheat, are the most important crops grown organically in Europe. This development raised the demand for wheat cultivars (cvs) adapted to the conditions specific to organic farming.

During the last decades, breeding efforts for wheat were strongly focused on the increase of grain yield and to a lesser extent on improvement of nutrient use efficiency (NUE) (Calderini et al., 1995). This might have resulted in a shift of the optimum N level for wheat cultivation and might have led to cultivars with an increasing demand for N supply, as stated in recent studies (Brancourt-Hulmel et al., 2003; Guarda et al., 2004; Sylvester-Bradley and Kindred, 2009). Recently released cultivars might therefore be less suitable for organic farming. Compared to the situation in conventional farming, the options for balancing environmental conditions in organic farming are strongly restricted because the input of nutrients is limited and no soluble chemical fertilizers and synthetic pesticides are used. Cultivars are therefore required that are able to adapt to the stressful, less controlled and hence highly variable organic farming environments. These differences between organic and conventional farming systems result in contrasting breeding aims. There are traits that are obviously more important for wheat production in organic farming, such as tillering capacity and regeneration ability after harrowing, rapid nutrient uptake, weed suppression ability, plant height, and resistance or at least tolerance to diseases on the leaves and especially on the ears (Wolfe et al., 2008). Cultivars suitable for organic farming also require improved nutrient use efficiency. This is achieved, for example, by a well developed rooting system and a functioning symbiosis with soil microorganism such as arbuscular mycorrhizal fungi (AMF), and also the ability to relocate nutrients from stems and leaves into the grain. Grain yield stability under adverse conditions is considered more important than the absolute amount. In addition, there are high requirements in terms of nutritional value and an excellent processing and sensory quality of the grain (Kunz et al., 2006; Lammerts van Bueren et al., 2008; Löschenberger et al., 2008; Wolfe et al., 2008).

Recently, wheat cultivars have been released from breeding programs for organic agriculture conducted e.g. in Switzerland (Kunz et al., 2006), Austria (Löschenberger et al., 2008) and Germany. However, answering the question as to whether breeding programs for organic farming provide better adapted cultivars remains difficult, and contradictory results have been published (Carr et al., 2006; Murphy et al., 2007; Burger et al., 2008; De Geus et al., 2008; Lorenzana and Bernardo, 2008; Reid et al., 2009).

In our previous experiment, three old, four conventionally and three organically bred winter wheat cultivars were tested in the DOK long-term trial in 2007, which enabled their performance in organic and conventional farming systems to be studied (Hildermann et al., 2009; in revision). We found little difference in the performance of organically and conventionally bred cultivars when used in organic systems at two fertilization levels (BIODYN 1 and BIODYN 2) on the fertile loess soil of the DOK trial in Therwil. However, organic farms are often situated on less fertile sites than the DOK trial. Therefore, in the follow-up study presented here, a cultivar test with eight out of the ten cultivars was established in 2008 on three organically managed farms on marginal sites. As in the previous experiment, the following parameters were analysed: yield, yield components and baking quality parameters as well as nitrogen (N) and phosphorus (P) use efficiency and the symbiosis with AMF. Additionally, we assessed the influence of seed origin (derived from organic versus conventional seed propagation) on important parameters.

First of all, this paper presents the results from the cultivar test on the three marginal on-farm sites. Secondly, we calculated the phenotypic stability of yield, baking quality and nutrient use efficiency for a wide range of organic farming environments in Switzerland based on the results obtained at these marginal sites and those obtained at the organically managed more fertile DOK sites in 2007. The main objectives of the study were (i) to compare yield, baking quality and nutrient use efficiency parameters at the three marginal on-farm sites, (ii) to analyse phenotypic stability of the main parameters across the marginal and the fertile sites, (iii) to prove the influence of seed origin (derived from organic versus conventional seed propagation) and (iv) to assess mycorrhizal colonization in relation to nutrient uptake.

4.3 Material and Methods

4.3.1 Experimental Design at the Marginal Sites

The experiment comprising the factors experimental site, winter wheat cultivar and seed origin (organic vs conventional seeds) was conducted in the 2007/2008 season on three organically or more precisely, bio-dynamically managed farms. The mixed arable farms were located in Rheinau ((SH), Canton Zurich), Fehraltorf ((ZH), Canton Zurich) and Vielbringen-Worb ((BE), Canton Berne) in three different agro-climatic regions across Switzerland (Tab. I). The SH site is characterized by sandy soil and low precipitation (< 700 mm), whereas the ZH and BE sites have high precipitation (> 1200 mm) and generally higher disease pressure from Septoria (*Stagonospora nodorum, Septoria tritici*), powdery mildew (*Blumeria graminis*) and leaf rust (*Puccinia tritici*).

The experiment included eight cultivars, which can be grouped into two old cultivars (Mont Calme 245, Probus), three cultivars derived from organic breeding programs (Scaro, Sandomir and a composite cross population (CCP)) and three cultivars derived from conventional breeding programs (Titlis, Antonius, Caphorn) (Hildermann et al., 2009). The seven cultivars and the composite cross population are listed as eight cultivars. Seeds were derived from a previous cultivar test in a bio-dynamic (BIODYN 2) and a conventional system (CONMIN) of the DOK long-term systems comparison trial (Hildermann et al., 2009), in order to assess the influence of seed origin.

As the experiment took place on-farm, crop rotation, tillage, fertilization and weed management was conducted according to the individual farmers' practices. Potatoes were grown before winter wheat at BE, whereas nitrogen-fixing legumes were grown as previous crops at SH (lucerne) and at ZH (grass-clover). At the SH site, approximately 54 kg available N ha^{-1} was applied as slurry split into two applications. No fertilizers were applied at the ZH and BE sites. On the three farms, nitrogen was supplied from manure applied to the rotational crops, and also from nitrogen fixed by the rhizobia of the leguminous crops in the rotation.

The experiment was set up as a block design with four replicates and with seed origin as sub-blocks, resulting in 64 plots per site. Cultivars were distributed randomly in each replicate. Sowing density was 400 viable seeds m^{-2}. The number of seeds was adjusted according to a prior germination test, where germination capacity ranged between 94 and 100%. Seeds were treated for common wheat bunt (Tilletia caries) with Tillecur (84.5% mustard powder, Andermatt Biocontrol, CH-6146 Grossdietwil). Cultivars were sown at BE on 14 October, at SH on 3 October and at ZH on 13 October 2007 in 4.13 m^{-2} subplots with a row spacing of 22 cm. Plant height and number of ears were determined in June. Whole plots were harvested at BE on 25 July, at SH on 16 July and at ZH on 26 July.

4.3.2 Initial Soil Analysis

Soil samples at the marginal sites were taken on 1 April 2008 to analyse chemical and physical soil properties. To analyse soil mineral nitrogen (Nmin), ten samples per field site were taken with an auger (Ø 3.5 cm) down to a depth of 90 cm and bulked into two sub-samples. Another five soil samples per replicate were taken down to a depth of 20 cm and bulked to measure P and K, soil acidity, soil organic carbon content and the clay and silt content. Soil acidity was measured in a water suspension, N_{min} ($N_{min} = NH_4\text{-N} + NO_3\text{-N}$) photometrically in 0.01 M $CaCl_2$, and P and K were measured in a 1:10 NH_4-Acetate-EDTA extract. Soil organic carbon (C_{org}) content was analyzed by titration after wet oxidation; the clay and silt contents were analyzed according the pipette method (Table 4 1).

Soil pH (H_2O) was 5.0 at BE and 6.0 at SH and ZH. Corg, a measure for humus content, was lowest at SH (1.3% C_{org}), intermediate at BE (1.6% C_{org}) and highest at ZH (2.1% C_{org}) (Table 4 1). Nmin measured in April was generally low and only 2.3 kg ha^{-1} at SH, which is a very sandy site. It was higher at BE (13.1 kg ha^{-1}) and at ZH (17.0 kg ha^{-1}). Due to a cold winter and spring, soils stayed cool throughout the spring and there was probably hardly any mineralization before soil sampling. As legumes were the previous crops at SH and ZH, N release during the growing period could be expected at these sites, whereas little N release could be expected at the BE site. Soil P was higher at the SH site (107.2 mg kg^{-1}) than at the ZH (38.6 mg kg^{-1}) and BE (26.3 mg kg^{-1}) sites. Soil potassium was lowest at BE (117.3 mg kg^{-1}) and similar at SH (157.5 mg kg^{-1}) and ZH (160.4 mg kg^{-1}).

	Pre-crop	Annual mean temperature	Precipitation	Soil texture	Clay	Silt	C_{org}	pH	Nmin[a] * 0-90 cm ** 0-20 cm	P[b]	K[b]
		(°C)	(mm)		(%)	(%)	(%)	(H_2O)	(kg ha^{-1})	(mg kg^{-1})	(mg kg^{-1})
BE	potatoes	7.9	1200	sandy loam	18.4	27.0	1.6	5.0	13.1*	21.9	117.3
SH	lucerne	8.5	700	sand with gravel	13.6	19.0	1.3	6.0	2.3*	89.3	157.5
ZH	grass-clover	8.5	1300	sandy loam	25.7	33.0	2.1	6.0	17.0*	32.1	160.4
BIODYN 1	maize	9.5	785	alluvial loess	16.0	72.0	1.2	6.1	12.9**	8.70	48.30
BIODYN 2	maize	9.5	785	alluvail loess	16.0	72.0	1.4	6.4	16.1**	13.00	68.80

[a] $N_{min} = NO_3 - N + NH_4 - N$

[b] Measured in a double lactic acid extract

Table 4 1 Pre-crops, annual mean temperature and precipitation and soil properties of the five sites

4.3.3 Root and Shoot Sampling

Root samples to determine AMF root colonization were taken between the 3rd and the 10th of June 2008 at the flowering stage (Zadoks scale 65). Four root samples per plot were taken at a depth of 20 cm with an auger (Ø = 4.0 cm) and bulked. Corresponding above-ground shoots were sampled to measure N and P concentrations. Root-soil samples were deep-frozen at −25° C until the roots were washed out from the soil. After washing, the roots were stored in a 70% ethanol solution. Shoot samples were oven-dried at 40° C until constant weight, coarsely ground in a mill (Mikro Feinmühle Culatti, Typ DCFH 48, Culatti AG, CH-8005 Zürich) and afterwards finely ground in a swing mill (Retsch MM 200 Retsch GmbH, DE-42781 Haan).

4.3.4 AMF Root Colonization

The roots were cleared and stained using a modified method of Phillips and Hayman (1970). Roots were cleared in 2.5% KOH, and fungal structures were stained with 0.05% Trypan blue. The percentage of root length colonized by AMF (AMF-RC) was assessed using a dissecting microscope (Leica M205 C, Leica Microsystems (Suisse) SA, CH-1020 Renens) at a magnification up to 100x. 150 intersections were counted according to a modified grid-line intersect method of Giovannetti and Mosse (1980).

4.3.5 Nitrogen and Phosphorus Concentrations and Calculation of Nutrient Use Efficiency Parameters

Concentrations of N in the shoots (N-Fl), straw (N-S) and grain (N-G) were measured by a CHN analyzer (Leco CHN 100, LECO Instrumente GmbH, DE-41199 Mönchengladbach). Shoot P concentration (P-Fl) was analyzed using wave length dispersive X-ray fluorescence spectroscopy on a Bruker-axs SRS-3000 with a rhodium tube (Bruker AXS GmbH, DE-76187 Karlsruhe). 2.0 g of the ground material was formed into tablets with a diameter of 20 mm and a thickness of 4 mm without binding agents, according to a modified method of Hutton and Norrish (1977) and Norrish and Hutton (1977). Grain, straw and total uptake were calculated for N and P (N-Gup, N-Sup, N-Tup, P-Gup, P-Sup, P-tup. Additionally, utilization efficiency of N (NUtE) and P (PUtE) was calculated as grain yield / total N or P uptake. Components, abbreviations, units and definitions are given in Table 4 2.

Component	Symbol	Unit	Definition
Nitrogen			
N mineral soil	N_{min}	kg N ha^{-1}	N mineral (NH_4 - N + NO_3 - N) in the soil
Shoot N at flowering	N-Fl	g N kg^{-1} DM	Shoot N concentration at flowering
Straw N	N-S	g N kg^{-1} DM	Straw N concentration
Grain N	N-G	g kg^{-1} DM	Grain N concentration
Grain N uptake	N-Gup	kg N ha^{-1}	Grain yield (DM) * Grain N concentration
Straw N uptake	N-Sup	kg N ha^{-1}	Straw yield (DM) * Grain N concentration
Total N uptake	N-Tup	kg N ha^{-1}	Grain N uptake + Straw N uptake
Nitrogen utilization efficiency	NUtE	kg DM kg^{-1} N	Grain yield (DM) / Total N uptake
Phosporus			
Shoot P at flowering	P-Fl	g P kg^{-1} DM	Shoot P concentration at flowering
Straw P	P-S	g P kg^{-1} DM	Straw P concentration
Grain P	P-G	g P kg^{-1} DM	Grain P concentration
Grain P uptake	P-Gup	kg P ha^{-1}	Grain yield (DM) * Grain P concentration
Straw P uptake	P-Sup	kg P ha^{-1}	Straw yield (DM) * Grain P concentration
Total P uptake	P-Tup	kg P ha^{-1}	Grain P uptake + Straw P uptake
Phosphorus utilization efficiency	PUtE	kg DM kg^{-1} P	Grain yield (DM) / Total P uptake

Table 4 2 Components, their symbols, units and definitions as related to nitrogen (N) and phosphorus (P) use efficiency.

4.3.6 Grain Yield, Yield Components and Baking Quality Parameters

Straw and grain samples were oven dried at 40 °C to constant weight in order to determine dry matter (DM) content and yield, thousand-kernel weight (TKW), hectolitre weight (HLW), and parameters related to baking quality.

Grain crude protein content was calculated with unrounded N concentration values using the formula GCP = N x 5.7. Zeleny value (ZV) was analysed according to ICC standard No. 116/1, falling number (Falling number) according to ICC Standard No. 107/1, wet gluten and Gluten index (GI) according to ICC Standard No. 155. A baking quality index (BQI) was calculated based on values for GCP, ZV, FN, gluten content and water uptake according to a formula of Kunz et al. (2006) commonly used in the breeding program for organic agriculture at the Getreidezüchtung Peter Kunz.

4.3.7 Statistical Analyses

Analyses of variance (ANOVA) for the eight winter wheat cultivars and two seed origins at three sites were performed using the JMP 5.0.1 software package (SAS Institute Inc. Cary, NC, USA). Normal distribution of the data was checked by the Shapiro-Wilk test. Not normally distributed data (P-S) were log-transformed for analysis, but back-transformed means are presented in the tables and figures. An ANOVA was performed on the whole data set using a multifactorial model with the factors sites, cultivars, seed origin and replicates, including site x cultivars interactions. A second ANOVA was carried out with the main factors breeding category and sites, including breeding category x site interactions. With significant model effects, a Tukey Kramer post hoc test at a p-level of 0.05 was performed to compare sample means. For each parameter, ANOVAs were initially performed across all three sites, and then for each of the three sites separately in a second step. Correlations between parameters were calculated by Spearman's rank correlation coefficient.

4.3.8 Comparing Marginal (BE, SH, ZH) and Fertile Sites (BIODYN 1 and BIODYN 2)

The results of the performance of the eight cultivars at the three marginal sites in 2008 were compared with the results at the two bio-dynamic systems (BIODYN 1 (0.7 LU ha^{-1}) and BIODYN 2 (1.4 LU ha^{-1}) of the previous DOK trial in 2007 as described in detail in (Hildermann et al., 2009; in revision). The combined data were analyzed using PLABSTAT, a computer program for analysis of plant breeding experiments (Utz, 2005). ANOVAs, correlations and broad-sense heritability (h^2) were calculated across the five sites. To estimate the stability and adaptability of the cultivars, the static and the dynamic concepts were applied as described by Becker and Leon (1988). The environmental variance (EVS) shows whether or not a cultivar reacts to changing environmental conditions (static concept). A genotype with minimum variance under different environments was considered to be stable. Values for EVS should be low for traits such as resistance to pests and diseases, and quality parameters. The ecovalence (EVD) calculated according to Wricke (1962) measures the contribution of a genotype to the genotype x environment interactions. A low EVD value indicates that the genotype reacts dynamically to changing environmental conditions (dynamic concept).

4.4 Results and Discussion

4.4.1 Grain Yield

Grain Dry Matter Yield and Yield Components at Marginal Sites (BE, SH, ZH)

The factors site and cultivar affected grain yield significantly, and site x cultivar interactions were significant (Table 4 3). Average grain yield was lowest at BE (2.2 Mg ha^{-1}), where the previous crop was potatoes, and higher at SH (2.6 Mg ha^{-1}) and ZH (2.8 Mg ha^{-1}). Wheat followed legume crops in the rotation at these two sites. Despite the application of slurry at SH, yield was slightly higher at ZH due to generally lower soil fertility at SH, as indicated by a low C_{org} content (Table 4 1). While soil P and K were sufficiently available at SH, there was hardly any Nmin detectable in the spring when plants are N-demanding. Grain yields at the marginal sites were lower than in the bio-dynamic systems of the DOK trial on loess, in which the grain yields were 3.7 Mg ha^{-1} (BIODYN 1) and 4.2 Mg ha^{-1} in 2007 (BIODYN 2) (Hildermann et al., 2009).

Averaged across the marginal sites, yield hardly differed among the cultivars, except for the low yielding old cv Probus. When calculated for each site separately, differences among cultivars were significant at BE and SH, but not at the higher yielding site ZH. Grain yield at BE ranged from 1.9 Mg ha^{-1} (cv Titlis) to 2.5 Mg ha^{-1} (cvs Scaro and Sandomir), whereas at SH, it ranged from 2.4 (cvs Probus and Sandomir) to 2.8 Mg ha^{-1} (CCP). This is in line with studies of Triboi et al. (2006), who found only small differences for wheat grain yields under non-limiting conditions, whereas Reid et al. (2009) observed slightly greater ranges among different wheat genotypes for measured parameters under conventional versus organic growing conditions.

The greatest differences in yield components were observed at the SH site, which was characterized by low number of ears m^{-2}, higher TKW (45 g versus 42 g) and higher harvest index (Table 4 3), but lower grain crude protein compared to the other two sites (Table 4 4). At the lowest yielding site BE, the total biomass at harvest was almost identical to the biomass obtained at SH. This biomass, however, could not be realized in grain yield, as reflected by the low HI.

Across the three sites, plant height of cultivars decreased from the old cv Probus (120 cm) to the conventionally bred cv Caphorn (71 cm). Plant height in the organically bred cultivars ranged between 95 cm (cv Scaro) and 116 cm (cv Sandomir) (data not shown). These reductions in plant height, especially of conventionally bred cultivars, resulted in lower straw yields and therefore higher HI, which is in line with the studies of Guarda et al. (2004) and Brancourt-Hulmel et al. (2005). HI ranged from 0.32 of the old cv Probus to 0.45 of the conventionally bred cv Caphorn. Across all sites, the highest TKW was achieved by cv Titlis (46 g); the lowest weights were measured for cvs Sandomir (40 g), Caphorn (41 g) and the CCP (41 g).

Effect of Breeding Categories on Grain Yield at the Marginal Sites (BE, SH, ZH)

Significant site x breeding category interactions were observed for the marginal sites. Calculated across the marginal sites, there was a significant increase in grain yield of the organically bred cultivars. In particular at BE, the site with the overall lowest yields, the organically bred cultivars achieved 14% higher yields than the conventionally bred and the old cultivars. This is remarkable in that only one of the organic cultivars (cv Scaro) was selected under these environmental conditions, whereas CCP and cv Sandomir were selected under different climatic conditions in north-eastern Germany and England. In close agreement with our results, Murphy et al. (2007) found that direct selection under organic conditions was particularly effective for yield improvement at marginal sites. The old cv Probus generally had the lowest yield. At BE and SH, the organically bred cvs Sandomir, Scaro and CCP had the highest yields, whereas at ZH the conventionally bred cv Antonius had the highest yield. These results are similar to those obtained in a previous cultivar test on loess (Hildermann et al., 2009).

There is an ongoing debate on whether cultivars for organic farming should be directly selected under organic conditions, or whether indirect selection would also result in suitable cultivars. In addition to the work of Murphy et al. (2007), Reid et al. (2009) showed that direct selection for grain yield under organic conditions resulted in higher yields than indirect selection under conventional conditions. Moreover, Burger et al., (2008) found strong genotype x system-interactions for maize yield under organic and conventional conditions, suggesting that genotypes should also be directly selected under the target conditions. The superiority of target site selection for low input conditions was demonstrated for wheat by Brancourt-Hulmel et al. (2005) and for barley by Ceccarelli (1996). In agreement with our study on marginal sites, Le Gouis et al. (2000) found significant genotype x system interactions comparing old and modern wheat cultivars in low and high N environments. Austin et al. (1980), however, found that modern cultivars yielded similarly well in both environments.

	Grain yield (GY)				Straw yield (SY)				Thousand kernel weight (TKW)				Harvest Index (HI)			
	Mg (DM) ha^{-1}				Mg (DM) ha^{-1}				g							
	All sites	BE	SH	ZH	All sites	BE	SH	ZH	All sites	BE	SH	ZH	All sites	BE	SH	ZH
Cultivar	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)
Mont Calme 245	2.5 a	2.3 ab	2.5 bcd	2.8 a	4.8 a	4.7 a	4.2 a	5.5 ab	45 b	43 b	47 a	44 b	0.35 f	0.33 cd	0.37 de	0.34 e
Probus	2.3 b	1.9 d	2.4 cd	2.7 a	4.7 a	4.4 abc	4.0 ab	5.9 a	43 cd	40 d	46 ab	43 bc	0.33 g	0.30 d	0.37 e	0.31 f
Scaro	2.6 a	2.5 a	2.6 abcd	2.8 a	4.2 cd	4.1 bc	3.8 b	4.6 c	42 d	40 cd	45 b	41 cd	0.39 bc	0.38 b	0.40 c	0.38 b
Sandomir	2.6 a	2.5 a	2.4 cd	2.9 a	4.6 ab	4.6 ab	3.9 ab	5.5 ab	40 e	39 d	42 d	40 de	0.36 ef	0.35 bc	0.38 d	0.34 de
CCP	2.6 a	2.2 abc	2.8 a	2.8 a	4.0 d	3.8 c	3.7 b	4.6 c	41 e	40 cd	44 c	39 e	0.39 b	0.37 b	0.43 b	0.38 bc
Titlis	2.4 ab	1.9 cd	2.6 abcd	2.8 a	4.3 bcd	4.1 bc	3.8 b	5.0 bc	46 a	47 a	45 b	45 a	0.36 de	0.32 d	0.40 c	0.36 cde
Antonius	2.6 a	2.3 ab	2.6 abcd	3.0 a	4.4 abc	4.2 abc	3.8 b	5.3 ab	44 bc	42 bc	46 ab	43 b	0.37 cd	0.35 bc	0.40 c	0.36 bcd
Caphorn	2.5 ab	2.0 bcd	2.7 abcd	2.8 a	3.1 e	2.8 d	2.9 c	3.5 d	41 e	42 b	41 d	40 e	0.45 a	0.42 a	0.48 a	0.45 a
Site	(n = 64)				(n = 64)				(n = 64)				(n = 64)			
BE	2.2 c				4.1 b				42 b				0.35 c			
SH	2.6 b				3.8 c				45 a				0.40 a			
ZH	2.8 a				4.9 a				42 b				0.37 b			
Breeding category																
OLD (n = 48)	2.4 b	2.1 b	2.4 b	2.8 a	4.8 a	4.6 a	4.1 a	5.7 a	44 a	43 a	0.34 c	0.31 b	0.34 c	0.31 b	0.37 c	0.37 a
ORG (n = 72)	2.6 a	2.4 a	2.6 a	2.8 a	4.3 b	4.2 a	3.8 b	4.9 b	41 b	40 b	0.38 b	0.36 a	0.38 b	0.36 a	0.40 b	0.33 b
CONV (n = 72)	2.5 ab	2.1 b	2.6 a	2.9 a	3.9 c	3.7 b	3.5 c	4.6 b	44 a	43 a	0.39 a	0.36 a	0.39 a	0.36 a	0.43 a	0.39 a
ANOVA																
Site *P* value (d.f. = 2)	< 0.0001				< 0.0001				< 0.0001				< 0.0001			
Cultivar *P* value (d.f. = 7)	< 0.0001	0.01	< 0.0001	n.s.	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Site x Cultivar *P* value (d.f. = 14)	< 0.0001				0.0022				< 0.0001							
BC *P* value (d.f. = 2)	0.0037	0.0001	0.0043	n.s.	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.00	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Site X BC *P* value (d.f. = 4)	0.006				n.s.				< 0.0001				n.s.			

d.f. degree of freedom

Table 4 3 Yield (DM) of grain and straw, thousand kernel weight and harvest index of eight winter wheat cultivars at three sites (BE, SH, ZH). ANOVA results and interactions of the different models are shown. Means, different letters indicate significant differences based on Tukey-Kramer test.

Comparison of Grain Yield on Marginal (BE, SH, ZH) versus Fertile Sites (BIODYN 1, BIODYN 2)

Grain yield was significantly affected by the highly differing sites and cultivars. It consistently increased from 2.2 Mg ha^{-1} at the marginal site BE to 4.3 Mg ha^{-1} in the BIODYN 2 system of the DOK trial (Figure 4 2). Across all five sites, the old cv Probus had the lowest grain yields (2.8 Mg ha^{-1}), whereas the conventionally bred cv Antonius (3.4 Mg ha^{-1}) had the highest grain yields. In contrast to the results at the marginal sites, across all five organic sites the organically bred cultivars were not superior with respect to grain yield compared to the three modern cultivars derived from conventional breeding programs. An optimal cultivar should show a dynamic yield response to the given site conditions, which would be expressed in our study by a consistent yield increase from BE to BIODYN 2. The low ecovalence (EVD) of cvs Mont Calme 245 (0.01), Scaro (0.02) and CCP (0.02) represent such a dynamic response. EVD was high for cvs Probus (0.07) and Sandomir (0.08), whereas cv Probus had extraordinary low yields in BIODYN 2. Cv Sandomir yielded equally high as cv Scaro at the sandy site BE, but had relatively low yields at the other four sites. Cv Sandomir was derived from an organic breeding program conducted on sandy and very marginal soils in north-eastern Germany. It might therefore be optimal for marginal soils, but it is not recommended for more fertile loess soils. Cv Titlis and Caphorn increased in yield from BE to BIODYN 1, but yielded at the same level in the BIODYN 2 system, therefore revealing high ecovalence values of 0.04 and 0.06, respectively.

4.4.2 Baking Quality

Baking Quality at the Marginal Sites (BE, SH, ZH)

Individual baking quality parameters (grain crude protein content (GCP), Zeleny value (ZV) and gluten index (GI)) and the resulting baking quality index (BQI) were significantly affected by sites and cultivars, and cultivar x site interactions were significant (Table 4 4). BQI was highest at the low yielding site BE (68), and lower at the SH (64) site and the high yielding site ZH (58). At the BE site, low yields along with small grain size lead to high GCP; however, high total gluten content and GI resulted in a high BQI. Despite higher GCP at the ZH site, BQI was higher at the SH site due to high gluten content and GI, which had a greater influence on the final bread making quality than GCP. Yield was highly variable at the BE site. In contrast, BQI was more consistent (35-80) at this site, whereas there was a better differentiation among cultivars at the SH (23-74) and ZH (24-74) sites. The old cvs Mont Calme 245 and Probus exemplify the success in the Swiss wheat quality breeding program. While the older cv Mont Calme 245 had an insufficient BQI, cv Probus along with the organically bred cv Scaro and the conventionally bred cv Antonius exhibited the highest BQIs. Along with cv Mont Calme 245, cv Titlis and the CCP generally achieved low BQIs at these three marginal organic sites.

Effect of Breeding Categories on Baking Quality at the Marginal Sites (BE, SH, ZH)

Three out of the eight cultivars achieved similarly high values, one out of each breeding category. The conventionally bred cv Antonius (77) achieved the highest BQI, followed by the organically bred cv Scaro (75) and the old cv Probus (75). Similarly, there was one cultivar with extraordinary low BQI among each breeding group (cv Mont Calme 245 (27), CCP (52) and cv Titlis (63)). We observed an increase of BQI from the old to the modern cultivars, which is in line with the findings of Guarda et al. (2004). These results were mainly due to the extraordinary low values of the old cv Mont Calme 245. Across the marginal sites, no significant differences between the organically and conventionally bred cultivars were observed for the general BQI, even though there were slight differences among the individual parameters. While Zeleny value and GI were similar, the old and the conventionally bred cultivars had higher GCPs than the organically bred cultivars, although they had smaller grains (Table 4 4).

	Grain crude protein content (GCP)				Zeleny value (ZV)				Gluten Index (GI)				Baking quality index (BQI)			
	g kg^{-1}				ml											
	All sites	**BE**	**SH**	**ZH**	**All sites**	**BE**	**SH**	**ZH**	**All sites**	**BE**	**SH**	**ZH**	**All sites**	**BE**	**SH**	**ZH**
Cultivar	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)
Mont Calme 245	103.4 c	110.9 bc	96.1 cd	103.1 b	23 e	27 f	21 e	19 d	19 d	31 e	14 d	11 f	27 e	35 d	23 f	24 e
Probus	112.1 a	116.3 b	108.0 a	112.1 a	60 b	67 abc	53 b	60 ab	86 b	88 ab	87 bc	82 bc	75 a	80 a	76 a	70 ab
Scaro	103.7 c	108.4 cd	99.3 bcd	103.5 b	65 a	69 a	62 a	63 a	96 a	96 a	97 a	95 a	75 a	79 a	76 a	71 ab
Sandomir	107.2 bc	108.4 cd	102.6 ab	110.4 a	57 c	61 d	52 b	58 b	80 b	77 bc	88 bc	76 cd	66 bc	68 b	70 bc	61 c
CCP	96.7 d	102.6 d	89.0 ef	98.6 b	40 d	43 e	36 d	40 c	73 c	67 cd	87 c	66 de	52 d	53 c	58 e	44 d
Titlis	113.3 a	134.4 a	93.1 de	112.5 a	59 bc	64 cd	54 b	60 ab	71 c	60 d	94 ab	58 e	63 c	69 b	68 cd	51 d
Antonius	109.3 ab	112.7 bc	100.5 bc	114.6 a	57 bc	65 bc	47 c	60 ab	94 a	94 a	96 a	91 ab	77 a	82 a	74 ab	74 a
Caphorn	97.0 d	110.9 bc	83.2 f	97.0 b	58 bc	68 ab	51 bc	57 b	97 a	95 a	99 a	97 a	70 b	80 a	64 d	66 bc
Standort	(n = 64)				(n = 64)				(n = 64)				(n = 64)			
BE	113.1 a				58 a				76 b				68 a			
SH	96.5 c				47 c				83 a				64 b			
ZH	106.5 b				52 b				72 c				58 c			
Breeding category																
OLD (n = 48)	107.8 a	113.6 a	102.0 a	107.6 a	41 b	47 b	37 b	40 b	52 b	60 b	51 b	47 b	51 b	57 b	49 b	47 b
ORG (n = 72)	102.5 b	106.5 b	97.0 ab	104.2 a	54 a	58 a	50 a	54 a	83 a	80 a	91 a	79 a	64 a	67 b	68 a	59 ab
CONV (n = 72)	106.5 a	119.3 a	92.3 b	108.0 a	58 a	66 a	51 a	59 a	87 a	83 a	96 a	82 a	70 a	77 a	69 a	64 a
ANOVA																
Site																
P value (d.f. = 2)	< 0.0001				< 0.0001				< 0.0001				< 0.0001			
Cultivar																
P value (d.f. = 7)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Site x Cultivar																
P value (d.f. = 14)	< 0.0001				< 0.0001				< 0.0001				< 0.0001			
BC																
P value (d.f. = 2)	0.053	< 0.0001	0.0009	n.s.	< 0.0001	0.0002	0.0007	< 0.0001	< 0.0001	0.0026	< 0.0001	< 0.0001	< 0.0001	0.0005	0.0003	0.006
Site X BC																
P value (d.f. = 4)	0.003				n.s.				n.s.				n.s.			

d.f. degree of freedom

Table 4 4 Grain crude protein content, Zeleny value, gluten index and a calculated baking quality index of eight winter wheat cultivars at three sites (BE, SH, ZH). ANOVA results and interactions of the different models are shown. Means, different letters indicate significant differences based on Tukey-Kramer test.

Comparison of Baking Quality on Marginal (BE, SH, ZH) versus Fertile Sites (BIODYN 1 and BIODYN 2)

Results for baking quality are discussed for the gluten index (GI) example, as it is one of the most important parameters determining quality. Baking quality parameters should be stable in changing environments. In contrast to grain yield and total gluten content (data not shown), GI did not show a general increase from marginal to fertile sites. At the higher yielding sites ZH and BIODYN 2 and at the low yielding site BE, GI was highly variable among cultivars, whereas GI was generally high for all cultivars except for the oldest cv Mont Calme 245 (Figure 4 1). At the BE and ZH sites, where relatively high GCP was observed (Table 4 4), and the more fertile BIODYN 2 site, the cvs Sandomir, CCP and Titlis exhibited low GIs compared to the SH and BIODYN 1 sites, indicating a shift in the gluten composition towards higher portions of weak gluten. Therefore, these cultivars do not guarantee a stable baking quality under organic farming conditions, as indicated by the variable GI. On the other hand, cultivars such as Scaro, Antonius and Caphorn showed high GI stability across all 5 environments, as indicated by the low environmental variance (EVS)

(Table 4 7), and are therefore better suited for high quality bread wheat production.

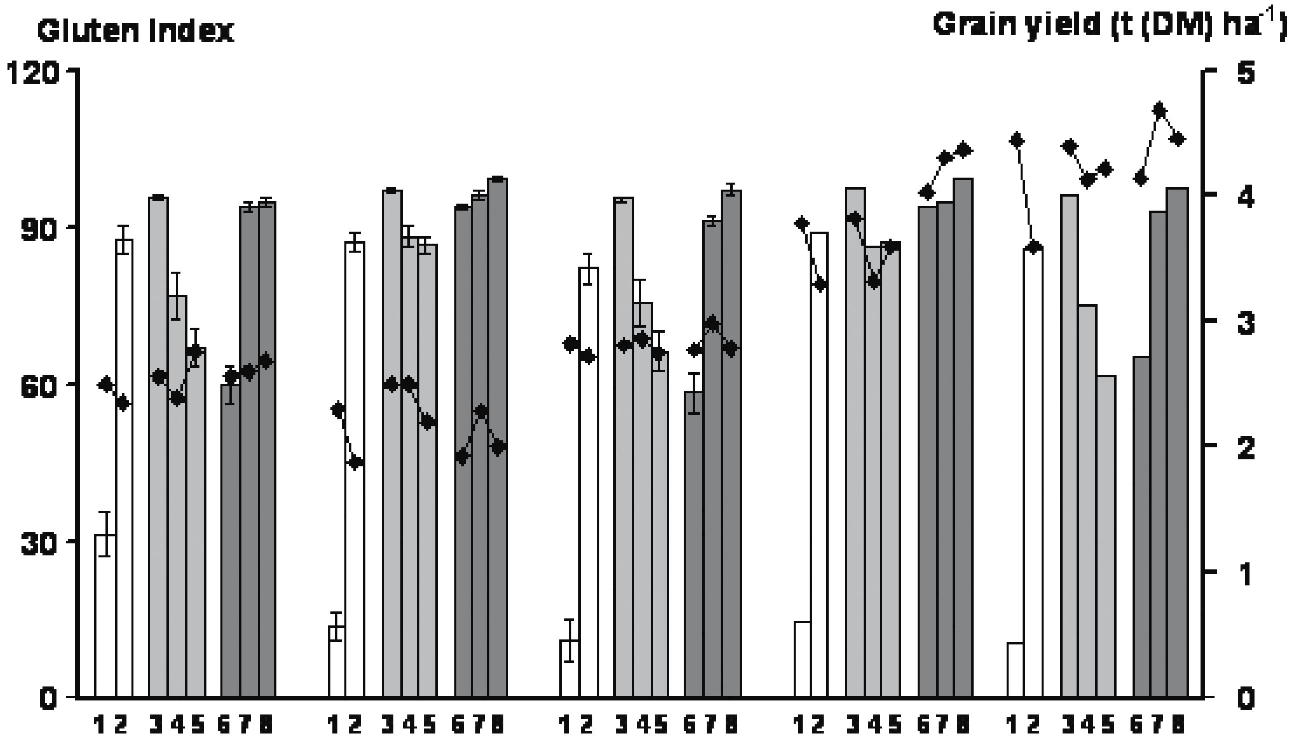

Figure 4 1 Gluten Index (bars) and grain DM yield (dots) of eight winter wheat cultivars at five sites (means; n = 4; bars represent SEM; due to pooled samples in BIODYN 1 and BIODYN 2, no SEM can be calculated). 1: Mont Calme 245, 2: Probus, 3: Scaro, 4: Sandomir, 5: CCP, 6: Titlis, 7: Antonius, 8: Caphorn

4.4.3 Nutrient Use Efficiency

Nutrient Use Efficiency at the Marginal Sites (BE, SH, ZH)

Sites and cultivars affected all parameters related to N and P use efficiency, and site x cultivar interactions were significant for all parameters except for N-Fl, P-S and PUtE (Table 4 5 and Table 4 6). As the increase in plant biomass causes a dilution effect, N-Fl, N-S, P-Fl and P-S were significantly lowest at the high yielding site ZH. N-Fl and N-S were highest at the poor yielding site BE. P-Fl and P-S were highest at the SH site, probably due to high soil-P contents. However, P-Fl was not translocated efficiently into the grain at the SH site, as indicated by the significantly lower P-G value at that site compared to the ZH and BE sites. The high TKW at the SH site also contributed to a lower P-G (dilution effect).

The efficiency parameters NUtE and PUtE reflect the ability of the plant to transform N and P from plant tissue into grain yield. Under the marginal conditions of the bio-dynamic farms, NUtE was significantly lower at the BE site (34.2 kg (DM) kg^{-1} N) than at the SH (43.5 kg (DM) kg^{-1} N) and ZH (43.3 kg (DM) kg^{-1} N) sites. The extraordinarily nutrient limited conditions at the BE site were not conducive to high NUtE. Similar results were obtained under Nordic conditions by Muurinen et al. (2006), who measured an average NUtE of 26 – 42 kg (DM) kg^{-1} N) of spring wheat in an experiment in which no N was applied. Foulkes et al. (Foulkes et al., 1998) found a 15% higher NUtE in unfertilized than in fertilized environments. PUtE was significantly higher at ZH (170.2 kg (DM) kg^{-1} P) than at BE (126.1 kg (DM) kg^{-1} P) and at SH (123.8 kg (DM) kg^{-1} P). Under fertile conditions, nutrient use efficiency usually decreases with increasing nutrient input (Guarda et al., 2004; Hildermann et al., 2009); however, other factors might also have limited the grain yield at the BE site, resulting in low NUtE and PUtE. Across all sites, the old cv Mont Calme 245 had the highest NUtE and PUtE, whereas the lowest values were measured for cv Caphorn.

Effect of Breeding Categories on Nutrient Use Efficiency at the Marginal Sites (BE, SH, ZH)

Breeding categories affected all parameters related to N use efficiency (NUE). Due to the lower plant height, N-Fl and N-S in the conventionally bred cultivars were higher than in the organically bred and the old cultivars. N-G in the organically bred cultivars was significantly lower compared to N-G in the conventional and old cultivars. This might be due to the higher yields of the organic cultivars and the negative correlation between grain yield and N-G. Generally, a decrease in N-G in modern cultivars was observed by Guarda et al. (2004) and Hildermann et al. (in revision).

No differences in N-Gup between the breeding categories were observed when calculated across marginal sites; however, N-Tup in the conventionally bred cultivars (66 kg ha^{-1}) and the organically bred cultivars (65 kg ha^{-1}) was significantly higher than N-Tup in the old cultivars (59 kg ha^{-1}). The observed improvement of N-Tup in modern cultivars is in line with other studies comparing old and modern wheat cultivars (Calderini et al., 1995; Foulkes et al., 1998; Guarda et al., 2004; Sylvester-Bradley and Kindred, 2009). Across the marginal sites, NUtE ranged from 34 kg DM kg N^{-1} in the conventionally bred cv Caphorn to 45 kg DM kg^{-1} N in the old cv Probus. NUtE in the conventionally bred cultivars (38 kg DM kg^{-1} N) was significantly lower under these marginal conditions than NUtE in the old and organically bred cultivars (42 kg DM kg^{-1} N). There is some controversy regarding the improvement of NUE in modern wheat cultivars. Several studies (Calderini et al., 1995; Brancourt-Hulmel et al., 2003; Guarda et al., 2004; Muurinen et al., 2006) found increased NUE in modern cultivars, whereas Foulkes et al. (1998) could not observe any differences under unfertilized vs. fertilized conditions. The organically bred cv Sandomir seemed to be well-adapted to conditions at the marginal sites. At these three marginal sites, the lowest N-Fl was measured for this tall growing cultivar (77 g kg^{-1}), and the highest N-Fl was measured for the short, semi-dwarf cv Caphorn (98 g kg^{-1}). At harvest, cv Sandomir achieved medium to high N-G (180 g kg^{-1} at SH and 194 g kg^{-1} at BE), whereas cv Caphorn achieved one of the lowest N-Gs (171 g kg^{-1}), although it had low TKW. Cv Sandomir exhibited a high NUtE (43 kg DM kg^{-1} N) in spite of having the lowest shoot-N, indicating an efficient N-translocation into the grain. This finding is similar to that of Le Gouis et al. (2000), who observed old cultivars but also some modern cultivars having high NUE under unfertilized conditions.

In contrast to the results for N, the breeding categories only affected P-S and PUtE but not P-Fl and P-G. Similar to N-S, the conventionally bred cultivars had the highest P-S concentrations (Table 4 6). PUtE in the conventionally bred cultivars (121 kg DM kg^{-1} P) was significantly lower than in the organically bred (139 kg DM kg^{-1} P and the old ones (124 kg DM kg^{-1} P). This was due to the extremely high PUtE of the old cv Mont Calme 245 (213 kg DM kg^{-1} P). Again the organically bred cv Sandomir exhibited high P-G and high PUtE (148 kg DM kg^{-1} P, despite a relatively low P-Fl. In contrast to our results, Calderini et al. (1995) found higher PUtE in modern than in old cultivars. The results show that a high total biomass due to tall plants (represented by the old and organically bred cultivars) does not necessarily reduce grain yield, but can result in plants translocating N and P efficiently into the grain.

	Shoot N (N-FI)				Straw N (N-S)				Grain N (N-G)				N-utilization efficiency (NUtE)			
	g N kg^{-1}				g N kg^{-1}				g N kg^{-1}				kg DM kg^{-1} N-Tup			
	All sites	BE	SH	ZH	All sites	BE	SH	ZH	All sites	BE	SH	ZH	All sites	BE	SH	ZH
Cultivar	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)
Mont Calme 245	7.9 cd	8.4 b	8.4 bc	6.9 bc	2.0 d	2.3 de	2.1 b	1.5 e	18.1 c	19.4 bc	16.9 cd	18.1 b	45.4 a	39.8 ab	47.4 a	49.2 a
Probus	8.4 bc	8.8 b	8.9 abc	7.7 bc	2.4 c	2.9 bcd	2.3 b	2.0 cde	19.7 a	20.4 b	18.9 a	19.7 a	38.3 c	32.3 cd	40.3 b	42.4 cd
Scaro	8.2 bcd	8.8 b	7.9 c	8.0 b	2.3 cd	2.6 cd	2.4 b	1.8 cde	18.2 c	19.0 cd	17.4 bcd	18.2 b	43.1 ab	38.8 ab	43.2 ab	47.3 ab
Sandomir	7.7 d	8.2 b	8.3 bc	6.5 c	1.9 d	1.8 e	2.3 b	1.7 de	18.8 bc	19.1 cd	18.0 ab	19.4 a	43.8 a	43.3 a	42.8 ab	45.3 abc
CCP	8.7 b	9.2 b	9.0 ab	7.9 b	3.0 b	3.4 b	2.9 a	2.6 b	17.0 d	18.0 d	15.6 ef	17.3 b	39.5 c	32.7 cd	43.0 ab	42.7 bc
Titlis	8.2 bcd	9.2 b	8.4 bc	7.1 bc	2.6 c	3.2 bc	2.3 b	2.3 bc	19.9 a	23.6 a	16.3 de	19.7 a	38.3 c	27.4 de	46.5 a	40.8 cd
Antonius	8.3 bcd	8.4 b	8.8 abc	7.7 bc	2.4 c	2.8 bcd	2.3 b	2.2 bcd	19.2 ab	19.8 bc	17.6 bcd	20.1 a	40.1 bc	35.0 bc	44.1 ab	41.3 cd
Caphorn	9.8 a	10.5 a	9.7 a	9.2 a	3.6 a	4.1 a	3.3 a	3.3 a	17.1 d	19.6 bc	14.6 f	17.0 b	34.3 d	24.4 e	40.9 b	37.7 d
Standort	(n = 64)				(n = 64)				(n = 64)				(n = 64)			
SH	8.7 a				2.5 b				16.9 c				43.5 a			
ZH	7.6 b				2.2 c				18.7 b				43.3 a			
BE	8.9 a				2.9 a				19.9 a				34.2 b			
Breeding category																
OLD (n = 48)	8.2 b	8.6 a	8.6 ab	7.3 a	2.2 b	2.6 b	2.2 b	1.8 b	18.9 a	19.9 a	17.9 a	18.9 a	41.9 a	36.0 a	43.8 a	45.8 a
ORG (n = 72)	8.2 b	8.8 a	8.4 b	7.5 a	2.4 b	2.6 b	2.5 ab	2.0 b	18.0 b	18.7 b	17.0 ab	18.3 a	42.1 a	38.3 a	43.0 a	45.1 a
CONV (n = 72)	8.8 a	9.3 a	9.0 a	8.0 a	2.9 a	3.3 a	2.6 a	2.6 a	18.7 a	21.0 a	16.2 b	19.0 a	37.6 b	29.0 b	43.8 a	39.9 b
ANOVA																
Site *P* value (d.f. = 2)	< 0.0001				< 0.0001				< 0.0001				< 0.0001			
Cultivar *P* value (d.f. = 7)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.0001	< 0.0001
Site x Cultivar *P* value (d.f. = 14)	n.s.				0.001				< 0.0001				< 0.0001			
BC *P* value (d.f. = 2)	0.0011	0.04	n.s.	n.s.	< 0.0001	0.0004	0.02	< 0.0001	0.0007	< 0.0001	0.001	n.s.	< 0.0001	0.001	n.s.	< 0.0001
Site X BC *P* value (d.f. = 4)	n.s.				n.s.				< 0.0001				< 0.0001			

d.f. degree of freedom

Table 4 5 Shoot, straw and grain N concentration and nitrogen utilization efficiency (NUtE) of eight winter wheat cultivars at three sites (BE, SH, ZH). ANOVA results and interactions of the different models are shown. Means, different letters indicate significant differences based on Tukey-Kramer test

	Shoot P (P-FI)				Straw P (P-S)				Grain P (P-G)				P-utilization efficiency (PUtE)			
	g P kg^{-1}				kg P kg^{-1}				kg P kg^{-1}				kg DM kg^{-1} P-Tup			
	All sites	**BE**	**SH**	**ZH**	**All sites**	**BE**	**SH**	**ZH**	**All sites**	**BE**	**SH**	**ZH**	**All sites**	**BE**	**SH**	**ZH**
Cultivar	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)	(n = 24)	(n = 8)	(n = 8)	(n = 8)
Mont Calme 245	3.7 bc	3.6 bc	4.5 a	2.9 bc	0.9 c	0.7 d	1.6 bcd	0.5 c	2.9 e	3.1 d	2.7 f	2.9 e	212.7 a	130.8 bc	165.8 a	268.6 a
Probus	3.3 d	2.9 d	4.2 a	2.7 cd	0.4 d	0.3 e	0.7 e	0.3 d	6.1 a	5.6 a	6.3 a	6.5 a	129.6 c	202.7 a	119.0 bc	139.8 d
Scaro	3.6 bcd	3.6 c	4.2 a	3.0 abc	1.3 b	1.2 b	2.1 ab	0.8 b	4.7 b	4.7 b	4.6 b	4.7 bc	132.4 bc	126.9 bc	104.8 c	166.4 bc
Sandomir	3.5 cd	3.5 c	4.5 a	2.6 cd	0.9 c	0.9 c	1.5 cd	0.5 c	4.8 b	5.0 ab	4.7 b	4.8 b	148.4 b	146.0 b	122.3 bc	177.2 b
CCP	4.1 a	4.1 a	4.9 a	3.3 ab	1.3 b	1.3 ab	2.0 abcd	0.9 ab	3.6 d	3.9 c	3.1 ef	3.7 d	135.3 bc	114.0 bc	119.1 bc	173.2 b
Titlis	3.3 cd	3.4 c	4.1 a	2.4 d	1.2 b	1.4 ab	1.5 d	0.8 b	4.6 b	5.2 ab	3.8 cd	5.0 b	129.1 c	98.3 cd	139.4 ab	149.8 cd
Antonius	3.9 ab	4.1 ab	4.7 a	3.1 abc	1.3 b	1.4 ab	1.8 abcd	1.0 a	4.7 b	4.6 b	4.3 bc	5.0 b	130.3 bc	120.9 bc	125.0 bc	145.8 cd
Caphorn	4.2 a	4.3 a	4.8 a	3.5 a	1.6 a	1.7 a	2.3 a	1.0 a	4.3 c	5.1 ab	3.5 de	4.2 cd	102.4 d	72.7 d	95.7 c	139.1 d
Standort	(n = 64)				(n = 64)				(n = 64)				(n = 64)			
SH	4.5 a				1.6 a				4.1 b				123.8 b			
ZH	2.9 c				0.7 c				4.6 a				170.2 a			
BE	3.7 b				1.0 b				4.6 a				126.1 b			
Breeding category																
OLD (n = 48)	3.5 a	3.3 b	4.3 a	2.8 a	0.6 c	0.5 c	1.1 b	0.4 c	4.3 a	4.4 a	4.5 a	4.7 a	169.1 a	167.1 a	140.8 a	199.8 a
ORG (n = 72)	3.7 a	3.7 a	4.5 a	3.0 a	1.1 b	1.2 b	1.9 a	0.7 b	4.4 a	4.5 a	4.1 a	4.4 a	138.6 b	129.1 b	115.4 b	172.3 a
CONV (n = 72)	3.8 a	3.9 a	4.5 a	2.9 a	1.4 a	1.5 a	1.8 a	0.9 a	4.5 a	5.0 a	3.9 a	4.7 a	121.3 c	97.3 c	122.3 ab	144.9 b
Site *P* value (d.f. = 2)	< 0.0001				< 0.0001				< 0.0001				< 0.0001			
Cultivar *P* value (d.f. = 7)	< 0.0001	< 0.0001	n.s.	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Site x Cultivar *P* value (d.f. = 14)	n.s				< 0.0001				< 0.0001				< 0.0001			
BC *P* value (d.f. = 2)	n.s	0.0002	n.s.	n.s.	< 0.0001	< 0.0001	< 0.0001	n.s.	n.s.	n.s.	n.s.	n.s.	< 0.0001	< 0.0001	0.0123	< 0.0001
Site X BC *P* value (d.f. = 4)	n.s.				0.000				0.018				0.007			

d.f. degree of freedom

Table 4 6 Shoot, straw and grain P concentration and phosphorus utilization efficiency (PUtE) of eight winter wheat cultivars at three sites (BE, SH, ZH). ANOVA results and interactions of the different models are shown. Means, different letters indicate significant differences based on Tukey-Kramer test

Comparison of Nutrient Use Efficiency at Marginal (BE, SH, ZH) versus Fertile Sites (BIODYN 1 and BIODYN 2)

In contrast to the results at the marginal sites, NUtE was affected only by sites and not by cultivars across all tested environments. However, site x cultivar interactions were statistically significant ($p < 0.01$). As was shown before for grain yield, NUtE generally increased from marginal to fertile sites (Figure 4 2). This is in line with the findings of Guarda et al. (2004), but in contrast to those of Le Gouis et al. (2000). Differences among cultivars were more pronounced at the marginal sites than at the fertile DOK sites, where only cv Probus showed exceptionally low values. Cultivars with high NUtE are needed for growing under nutrient-limited organic conditions, especially on marginal sites. In contrast, cultivars with a strong reaction to nutrient input are less suitable for such sites. The ecovalence (EVD) of cvs Scaro (6.50) Mont Calme 245 (4.51), CCP (0.65) and Antonius (2.87) was low, whereas it was high for cv Caphorn (43.13) and Sandomir (27.37). While cv Sandomir had a high ecovalence due to high NUtE, especially under marginal conditions, NUtE of cv Caphorn was lowest at the BE site and highest at the BIODYN 2 site, indicating a dependency on higher nutrient availability and fertile soil conditions.

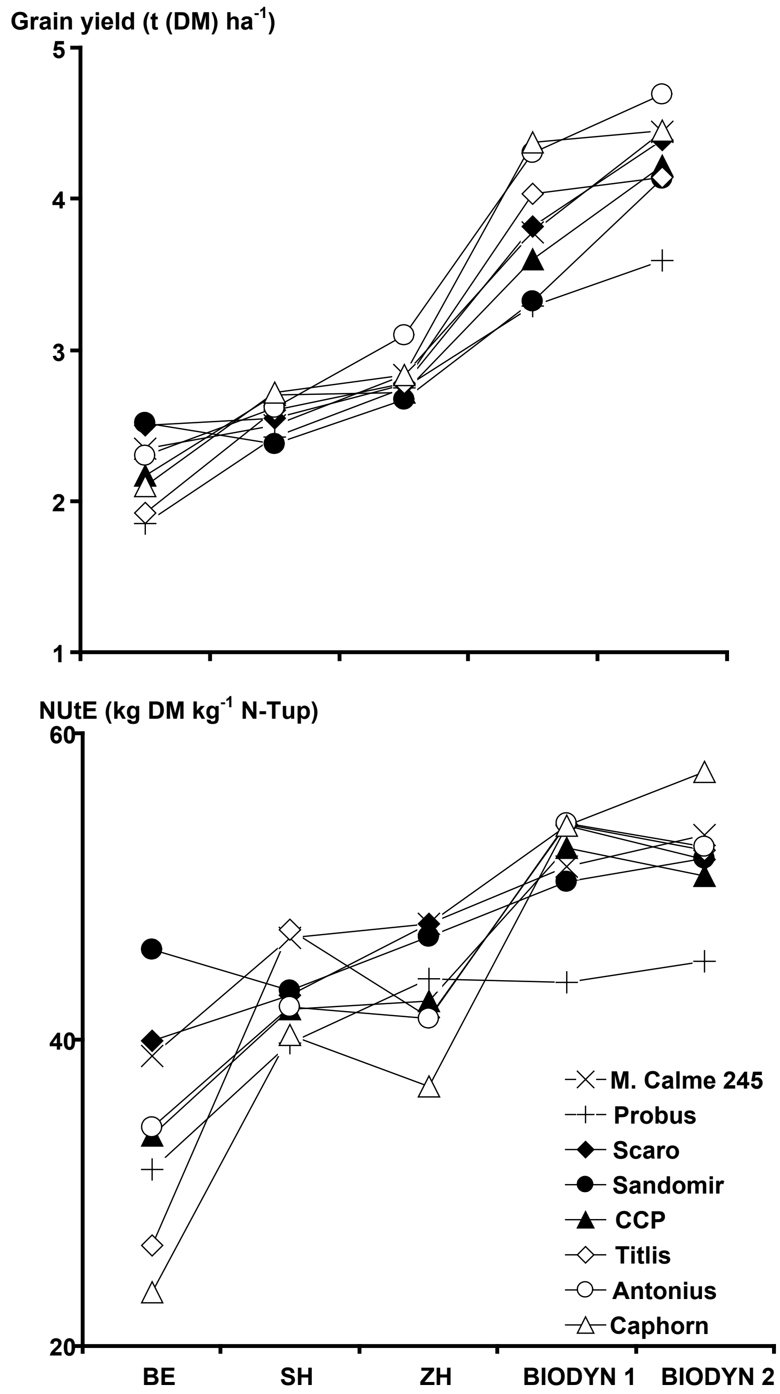

Figure 4 2 Grain DM yield (a) and N-utilization efficiency (NUtE) (b) of eight winter wheat cultivars tested at five organically managed sites (means, n = 4)

Sustainable agricultural systems combined with nutrient use-efficient cultivars that provide high and stable yields are necessary prerequisites for coping with future resource scarcity and the increasing demand for food. The genotypic influence was greater than the environmental influence, as indicated by high to medium values for broad sense heritability (h^2) (Table 4 7) in our study for traits such as thousand kernel weight (92.11%), harvest index (91.73%), gluten index (97.88%) and grain yield (73.68%). In contrast, h^2 was very low for N-utilization efficiency (NUtE) (45.48%), reflecting large environmental effects and genotype x environment interactions for this complex trait and implying the need to observe this trait in different types of environments. Our results are in agreement with studies on NUE of maize (Presterl et al., 2003) and confirm the hypothesis of Brancourt-Hulmel et al. (2003) and Sylvester-Bradley and Kindred (2009) that cultivars bred under high input conditions might loose nutrient use efficiency.

		M. Calme 245	Probus	Scaro	Sandomir	CCP	Titlis	Antonius	Caphorn	h^2 (%)
Grain yield	Mean	3.18	2.78	3.21	3.01	3.08	3.1	3.4	3.29	
	EVS	0.01	0.04	0.02	0.07	0.02	0.04	0.01	0.04	73.68
	EVD	0.01	0.07	0.02	0.08	0.02	0.04	0.04	0.06	
Thousand kernel weigth	Mean	44.27	41.93	42.13	39.56	40.69	44.47	42.93	39.81	
	EVS	0.44	1.79	1.23	0.39	0.60	3.48	0.34	4.20	92.11
	EVD	0.33	1.49	0.94	0.36	0.47	2.68	0.28	3.17	
Harvest Index	Mean	0.35	0.33	0.4	0.36	0.4	0.37	0.39	0.46	
	EVS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	97.75
	EVD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
Nitrogen harvest index	Mean	0.84	0.78	0.81	0.86	0.71	0.79	0.81	0.64	
	EVS	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	91.73
	EVD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	
Zeleny value	Mean	20.75	58.75	60.6	55.35	37	55.4	54	54.85	
	EVS	7.67	7.89	7.73	2.01	2.37	3.42	10.07	1.72	99.02
	EVD	10.16	6.10	5.80	6.60	5.05	2.79	16.26	11.47	
Gluten Index	Mean	17.13	85.41	97.56	87.49	79.31	81.19	96	97.66	
	EVS	125.48	26.17	0.35	26.27	15.22	61.90	2.87	6.65	97.88
	EVD	145.70	50.64	15.78	31.75	65.23	186.00	8.14	17.12	
Grain crude protein content	Mean	10.05	10.84	9.86	9.93	9.35	10.44	10.37	9.06	
	EVS	0.03	0.01	0.03	0.54	0.05	0.39	0.22	0.25	76.82
	EVD	0.06	0.20	0.17	0.40	0.24	1.07	0.18	0.41	
Grain nitrogen concentration	Mean	17.63	19.02	17.3	17.91	16.4	18.31	18.19	16.21	
	EVS	0.20	0.03	0.09	0.40	0.09	0.61	0.67	0.76	77.87
	EVD	1.33	2.03	1.96	2.80	2.17	1.17	1.61	0.29	
Total nitrogen uptake	Mean	66.17	67.73	67.62	62.66	69.11	69.99	75.13	79.99	
	EVS	4.04	13.02	10.04	12.83	17.04	28.95	20.49	68.91	83.00
	EVD	11.95	9.86	12.32	10.63	14.35	22.16	16.54	77.07	
Nitrogen utilization efficiency	Mean	47.55	40.82	47.23	47.58	44.31	44.33	44.91	42.42	
	EVS	2.80	5.46	0.81	1.32	8.18	7.08	4.72	14.06	45.48
	EVD	2.87	43.13	0.65	4.51	11.42	27.37	6.50	21.19	
Grain phosphorus concentration	Mean	2.6	5.1	4.05	4.24	3.16	3.94	3.98	3.82	
	EVS	0.02	0.55	0.03	0.03	0.04	0.12	0.08	0.30	92.00
	EVD	0.21	0.65	0.06	0.04	0.10	0.12	0.11	0.24	
Total phosphorus uptake	Mean	11.58	16.33	17.52	15.33	15.91	16.05	18.57	21.66	
	EVS	1.32	1.82	2.35	0.23	1.54	4.37	2.94	6.64	88.75
	EVD	4.27	1.40	2.01	1.81	2.00	3.95	2.53	14.63	
Phosphorus utilization efficiency	Mean	293.89	193.33	200.02	210.23	221.29	211.29	202.18	183.07	
	EVS	432.02	38.48	96.24	186.98	258.59	447.30	72.34	111.47	93.40
	EVD	613.46	194.44	284.09	541.02	485.97	335.79	77.75	165.55	

Table 4 7 Means, environmental variance (EVS), ecovalence (EVD) and heritability (h2) of selected parameters of eight winter wheat cultivars calculated across five sites (BE, SH, ZH, BIODYN 1, BIODYN 2, CONMIN)

4.4.4 Effect of Seed Origin on Selected Parameters at the Marginal Sites (BE, SH, ZH)

The origin of the seeds (conventional vs organic seeds) affected only a few of the measured parameters at the three marginal sites (Table 4 8). Due to the abundance of common wheat bunt spores, all of the seed was treated with Tillecur, which may have diminished some of the potential effects. Straw yield, N-G and consequently N-Sup, N-Gup, N-Tup and P-Tup in the conventional seeds was higher than in the organic seeds. TKW of the organic seeds that were used for the experiment had been lower than that of the conventional seeds (Hildermann et al., 2009) resulting in increased plant growth and higher straw yields in 2008 in the DOK trial. In line with our results, Carr et al. (2006) found no effects of seed lots on grain yield and TKW, nor on N-G when comparing conventional and organic winter wheat seed lots. In contrast, Müller (2009) found lower TKW, grain yield and N-G in organically propagated barley seeds compared to conventional seed lots.

	Straw yield (Mg (DM) ha^{-1})			Grain N (N-G) (g kg^{-1})			Grain N uptake (N-Gup) (kg ha^{-1})			Straw N uptake (N-Sup) (kg ha^{-1})			Total N uptake (N-Tup) (kg ha^{-1})			Total P uptake (P-Tup) (kg ha^{-1})		
	CONMIN	BIODYN		CONMIN	BIODYN		CONMIN	BIODYN		CONMIN	BIODYN		CONMIN	BIODYN		CONMIN	BIODYN	
All sites (n = 96)	4.3	4.2	*	18.6	18.4	*	47.1	45.3	*	15.7	14.4	*	65.5	62.0	**	19.8	18.8	*
SH (n = 32)	3.9	3.7	**	17.0	16.9	-	43.8	42.2	*	15.4	14.5	-	60.2	57.7	*	10.7	10.0	-
ZH (n = 32)	5.1	4.8	*	18.7	18.7	-	53.3	51.5	-	11.6	11.3	-	67.1	64.6	-	17.5	17.1	-
BE (n = 32)	4.1	4.1	-	20.1	19.6	*	44.4	42.3	*	21.6	18.1	*	69.2	63.7	**	19.9	18.5	*

* significant effect of seed P < 0.05
** significant effect of seed P < 0.01
' - no significant effect of seed

Table 4 8 Parameters significantly affected by seed origin (CONMIN vs BIODYN) tested at the three marginal sites (BE, SH, ZH) (means)

4.4.5 AMF-Root Colonization at the Marginal Sites (BE, SH, ZH)

The sites but not the cultivars affected AMF-root colonization (AMF-RC) measured at flowering stage at the three marginal sites in 2008 (data not presented). AMF-root colonization was similarly high at the SH (39.8%) and BE (38.6%) sites and significantly lower at the higher yielding ZH (31.8%) site. Among cultivars, AMF-root colonization ranged from 35.2% (cv Probus) to 39.1% (CCP), but these differences were not statistically significant. This is in line with results of the previous study at the more fertile DOK trial in 2007 as described in Hildermann et al. (in revision) and Friedel et al. (2008). We did not observe a correlation between AMF-root colonization and P-Fl, P-S and P-G or final grain yield at any of the three marginal sites (BE, SH, ZH), whereas Hildermann et al. (in revision) reported a significant correlation between AMF-RC and shoot-P content in system BIODYN 2 of the DOK trial in 2007. In contrast, Hetrick et al. (1996) found a contribution of AMF to P-uptake in wheat in a pot study.

4.5 Conclusion

In this study, we tested cultivars derived from different breeding programs and assessed their suitability for organic farming. Comparing cultivars derived from organic and conventional breeding programs, at marginal organic sites the organically bred cultivars achieved higher grain yield and nutrient use efficiency for N and P combined with a good baking quality. However, these findings were not confirmed at more fertile organic sites. Our results stress the importance of observing both the absolute yield amount and the stability across environments, as there were cultivars with high yields but low stability and vice versa. Cultivars suitable for organic farming should achieve high grain yields, nutrient use efficiency and baking quality, but should also be stable in heterogeneous environments. An example of such a cultivar is the organically bred cv Scaro. For successful selection, cultivar screening should therefore be conducted in multi-location trials covering a wide range of environmental conditions.

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5 GENERAL DISCUSSION

In this chapter, an introductory part provides general remarks on the strength and limits of the experiments of this thesis followed by a combined analysis across the seven test environments. The main findings of the study are summarized and structured along the individual objectives. Based on these specific results, the overall aim of the thesis, the need of specific breeding programs for organic farming is discussed in detail. Socio-economic aspects of plant breeding are closing the chapter.

5.1 General Remarks on the Strengths and Limits of the Study

This thesis presents the results of two one-year cultivar tests conducted in 2007 and 2008. Cultivar tests heavily rely on the selected cultivars and on the experimental sites. Climatic conditions during the growing season also contribute to plant performance and affect the results. The DOK study comparing organic and conventional farming systems in 2007 together with the on-farm study at three organically managed farms in different geographical areas in 2008 allowed the analyses of a total of seven sites in highly differing environments and two different years. The main focus of the study was to observe the performance of different cultivars derived from organic and conventional breeding programs and old cultivars under organic conditions (BIODYN 1 and BIODYN 2 of the DOK trial and ZH, SH and BE in the on-farm trials). Furthermore, one conventionally managed site (CONMIN) and one unfertilized control (NOFERT) of the DOK trial were included in the study. To compare the suitability of cultivars for organic farming, cultivars are usually tested on organic and conventional farms. In such an experimental design, however, field properties may differ due to spatial variations of soils and micro-climate. The DOK trial offers the unique opportunity to conduct cultivar tests under organic and conventional conditions at a homogenous site under identical soil and climatic conditions. This is a promising novel methodological approach for research questions on the genetic adaption using long-term field trials. In order to use this opportunity, the cultivar experiment in the DOK trial will be repeated for two more years. However, these replications have to fit into the DOK crop rotation (Chapter 2.3.1) and were therefore not within the scope of this thesis, because no wheat was grown in the DOK trial in 2008. The number of cultivars ranged between eight and ten in each experiment, which is at the lower limit for a cultivar test. However, spatial limitations due to the size of the DOK plots prevented inclusion of more cultivars. The experimental lay-out of one DOK-plot is given in the Annex (Figure 0 3).

The choice of intrinsic organically bred cultivars adapted to Swiss growing conditions is still limited, especially if the selected cultivars should represent different organic breeding programs. The selection of the organically bred cultivars in this study comprised cultivars of three organic breeding programs in Switzerland, Germany and the United Kingdom. The cvs Scaro and Sandomir are derived from classical pedigree breeding schemes. The composite cross population demonstrates moreover a different methodological approach in breeding for organic farming.

Most cultivar tests published are narrowed to a few parameters. Among those, grain yield is the most common one. The advantage of this study is not only the broad spectrum of environments but also the broad spectrum of assessed parameters. This broad-based design may therefore compensate for the limitations of two one year trials. It would have been advantageous to include an on-farm conventionally managed site under marginal soil conditions to better balance the ratio between organic and conventional sites. This would have allowed to calculate the genotypic correlation between traits assessed under organic and conventional farming, which is needed for the quantification of breeding grains of direct versus indirect selection (Harrer and Utz, 1990) (see also Chapter 5.5).

Conducting mycorrhizal research under field conditions is difficult and challenging. To exactly determine AMF-contribution to nutrient uptake and plant growth, AMF effectiveness has to be assessed, which requires a non-mycorrhizal control. Due to the ubiquity of AMF in most ecosystems, the establishment of such a control in field trials is challenging. Usually it is done by soil fumigation. However, soil fumigation causes heavy disturbances of the soil life as it is also detrimental to other fungi, not only to AMF, and thus the method is therefore highly controversial (Johnson et al., 1997; Kahiluoto et al., 2001). The setting of the studies, within the DOK trial and on organically managed farms would not have allowed for including a fumigated non-mycorrhizal control as the guidelines and regulations of organic farming do not allow for applying fungicides.

Therefore, most research is done in pot studies; however, results are not directly transferable to field conditions as pot studies are conducted under strictly controlled conditions in greenhouses or climate chambers in limited soil compartments and display just a simplification of the complexity of field conditions. Results of a meta-analysis on legumes revealed that there was growth response of legume crops to AM fungi in pot studies, however, here was no yield response in field trials (Kaschuk et al., 2010). To obtain information on the AMF symbiosis, AMF-RC was measured in this study. It is known, that there is no linear correlation between AMF-RC and AMF-effectiveness. Therefore, the results based on AMF-RC have to be carefully interpreted. Nevertheless, Hetrick et al. (1992) proposed AMF-RC in field studies as a potential activity indicator of AMF symbiosis as it is a necessary precondition for the plant to benefit from the symbiosis.

5.2 Combined Analysis across the Seven Environments

To illustrate differences and similarities between the seven test environments and the selected cultivars, a redundancy analysis was calculated on grain yield and yield components, baking quality, nutrient use efficiency parameters and AMF (Figure 5 1). The statistical procedure followed the description given in Chapter 2.3.7. The aim of a redundancy analysis, a method of multivariate statistic, is to achieve an ordination of a set of data caused by a gradient, for example the nutrient status of the soil. This redundancy analysis was carried out including data of all seven test environments. Methods of multivariate statistic mainly help visualizing complex data and are a valuable tool in addition to the more detailed analysis of variance for single parameters.

Similar to the results obtained for the redundancy analysis conducted in the DOK systems only (Chapter 2.4.4), the influence of the systems / environments (65%) clearly exceeded the influence of the cultivars (17.5%) demonstrated by the short length of the cultivars' vectors. While the DOK study had revealed a slight affinity between the conventionally bred cultivars and the conventional system and between some old and organically bred cultivars and the organic systems, no such affinities could be shown across all seven environments. An affinity is indicated by the same vector direction of the respective cultivars and systems and may be interpreted as a hint of a better performance of these cultivars in the respective systems.

In the analysis across all seven environments, the first axis was mainly determined by the specific soil conditions and clearly separated the DOK systems (NOFERT, BIODYN 1 and BIODYN 2, CONMIN) at the fertile loess soil from the three marginal on-farm sites (BE, SH, ZH) on sandy soils. Although the marginal sites were highly heterogenic with respect to site management, soil and climatic conditions, they formed a separate group as they were less fertile. This is mainly reflected by the much lower grain yields at these sites when compared to the DOK systems. Due to higher soil-P and soil-K, site SH is slightly separated from sites BE and ZH. Thereby it has to be considered that these P- and K- reserves originate from the intensive conventional management before the farm was converted to organic farming.

The CONMIN system of the DOK trial was clearly segregated from all other test environments. This system together with the unfertilized control NOFERT was responsible for the second axis of the graph that clearly reflects the different levels of nutrient input. Parameters related to yield and yield components (grain and straw yield, N- and P-uptake parameters, HI and NHI) were grouped next to the conventional CONMIN system whereas the efficiency parameters N-utilization efficiency (NUtE) and P-utilization efficiency (PUtE) were grouped next to the organic BIODYN 1 and BIODYN 2 systems (Figure 5 1).

Generally, the test environments can be classified into marginal sites with currently low nutrient input (BE, SH, ZH), fertile soils with low nutrient input (NOFERT, BIODYN 1 and BIODYN 2) and fertile soils with high nutrient input (CONMIN). The diversity in soil type and climatic conditions resulted in large productivity differences at the seven environments and may have contributed to the genotype x environment interactions that are described in detail in Chapter 5.5.

5.3 Genotypic Correlations among Traits

Beside the decision in which environment selection should take place, the potential genotypic correlations between different traits have to be considered. Genotypic correlations provide information on whether it is possible to improve two traits simultaneously. Most important are the correlations between grain yield and baking quality and between grain yield and nutrient use efficiency. Across the seven test sites, grain yield and N-utilization efficiency and grain yield and P-utilization efficiency were not correlated (Table 0 1). This means that it is possible to breed for nutrient use efficiency without losses in yield. However, there was a negative correlation between NUtE and PUtE and Zeleny value and between NUtE and gluten index. Zeleny value and gluten index represent two major baking quality parameters. These negative correlations indicate that it is difficult to breed for improved nutrient use efficiency without a negative impact on baking quality. NUtE and PUtE were strongly correlated, implying that it is possible to breed indirectly for a higher PUtE by breeding for a higher NUtE.

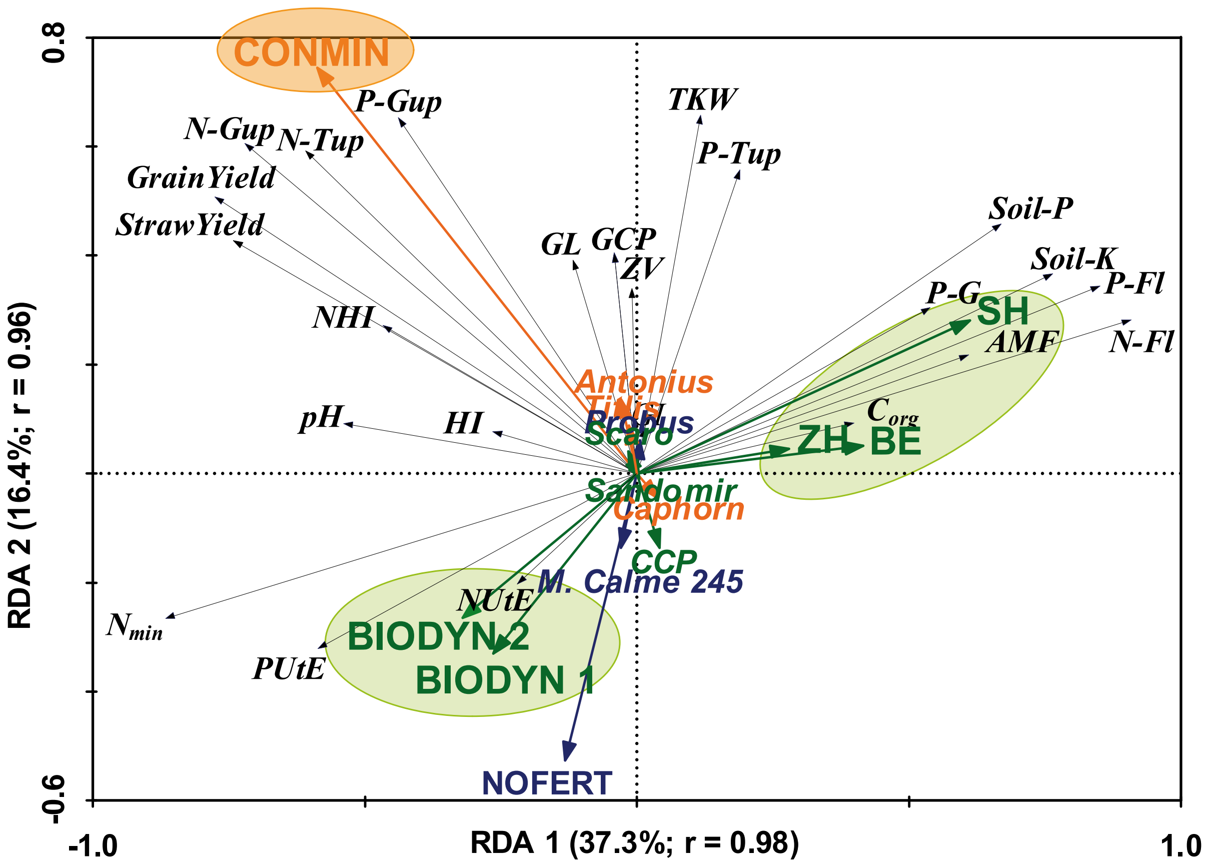

Figure 5 1 Constrained ordination axis of first two canonical axis as determined by redundancy analysis of seven test environments and eight cultivars on grain yield and yield components, baking quality, nutrient use efficiency parameters and AMF-root colonization. Vector directions indicate the maximum variation due to corresponding factor; vector lengths indicate the strength of the correlation.

Parameter	Symbol	Component	Symbol
N mineral soil	N_{min}	Gluten content	GL
Soil Phosphorous content	Soil-P	Gluten Index	GI
Soil Potassium content	Soil-K	Grain crude protein	GCP
Soil organic carbon	C_{org}	Harvest Index	HI
		N-Harvest Index	NHI
Shoot N at flowering	N-Fl	Thousand kernel weight	TKW
Grain N uptake	N-Gup	Zeleny value	ZV
Total N uptake	N-Tup		
Nitrogen utilization efficiency	NUtE	Arbuscular mycorrhizal fungi	AMF
Shoot P at flowering	P-Fl		
Grain P	P-G		
Grain P uptake	P-Gup		
Total P uptake	P-Tup		
Phosphorus utilization efficiency	PUtE		

5.4 Main Findings

Objective 1: To compare yield, baking quality and nutrient use efficiency of modern winter wheat cultivars derived from organic and conventional breeding programs as well as old cultivars **in organic and conventional systems of the DOK long-term system comparison trial** at a fertile site (Chapter 2 and 3).

Significant effects of wheat cultivars and farming systems on yield, baking quality parameters and nutrient use efficiency were observed for the organic and conventional farming systems of the DOK trial. However, the expected genotype x environment interactions were not detected.

The conventionally bred cultivars achieved the highest grain yields in the conventional system, whereas the organically bred cultivars could not outperform the conventionally bred cultivars under organic conditions. A much higher yield improvement of the modern compared to the old cultivars was realized in the conventional system than in the organic system, indicating that breeding for grain yield improvement was successful for conventional high input but not for organic low input farming. The protein and the total gluten content dropped in relation to the year of release of the cultivars. Despite lower protein contents, there was an increase of Zeleny value and Gluten index with the year of release, implying an improvement of technological baking quality in the modern cultivars. The sustainability of organic farming systems was shown by the higher nutrient use efficiency of N and P in the organic systems BIODYN 1 and BIODYN 2 than in the conventional system CONMIN. Among the cultivars, nutrient use efficiency parameters for N increased with the year of release; however, similarly to the results obtained for grain yield, the organically bred cultivars showed no improved nutrient use efficiency in the organic systems compared to the conventionally bred cultivars.

Objective 2: To compare yield, baking quality and nutrient use efficiency of modern winter wheat cultivars derived from organic and conventional breeding programs as well as old cultivars **at three organically managed on-farm trials at marginal sites** (Chapter 4).

A trend towards higher yields of the organically bred cultivars were detected at the three marginal on-farm sites. Remarkably, this difference was statistically significant at the lowest yielding site BE, where the organically bred cultivars achieved 14% higher yields. Significant genotype x environment interactions were detected for almost all traits.

Grain yield was significantly affected by the highly differing sites and generally much lower than in the DOK study. Averaged across the marginal sites, grain yield hardly differed among cultivars, except for the low yielding old cv Probus. However, when calculated for each site separately, differences among cultivars were significant at BE and SH, but not at the higher yielding site ZH. Similar to the results obtained in the DOK trial, baking quality (here calculated by a baking quality index) increased from old to modern cultivars; however, no significant difference was found between the organically and conventionally bred cultivars. Averaged across cultivars, nutrient use efficiency was higher at the slightly fertilized sites in SH and at also ZH, the site with the highest Corg content compared to the site BE. This emphasizes the importance of fertilization management under organic conditions, which can improve or decrease nutrient use efficiency. In contrast to the results obtained in the DOK trial, N-utilization efficiency of the organically bred cultivars was higher than N-utilization efficiency of the conventionally bred cultivars under the marginal conditions.

Objective 3: To analyse phenotypic stability of modern winter wheat cultivars derived from organic and conventional breeding programs as well as old cultivars for grain yield, baking quality, nutrient use efficiency **across marginal and fertile organic sites** (Chapter 4).

For organic farming, cultivars should achieve high grain yields, nutrient use efficiency and baking quality but should also be stable in heterogeneous environments. In this study, the organically bred cv Scaro showed such a performance. However, no general trend of higher stability of all organically bred cultivars was observed.

Related to grain yield, a cultivar suitable for organic farming should respond dynamically to the given environmental conditions. Such a dynamic behaviour would be expressed by a consistent grain yield increase from the marginal sites to the fertile DOK sites. Among the organically bred cultivars, cv Scaro and the composite cross population (CCP) revealed such a dynamic increase but not cv Sandomir. Among the conventionally bred cultivars, only cv Antonius achieved such an increase. In contrast, for baking quality, a genotype should achieve stable values across a wide range of environments. Among the organically bred cultivars, only cv Scaro exhibited high stability of gluten index, an indicator for bred making quality but not cv Sandomir and the CCP. Among the conventionally bred cultivars the cvs Antonius and Caphorn exhibited high stability of gluten index.

Among the parameters calculated for nutrient use efficiency, the nutrient utilization efficiency (grain yield / total N uptake) was observed exemplarily across all seven test environments. Cultivars with high nutrient utilization efficiency are needed to obtain stable crops yield under nutrient-limited organic conditions, especially on marginal sites. In contrast, cultivars with a strong reaction to nutrient input are less suitable for such sites. There were clear differences for the phenotypic stability of nutrient utilization efficiency among the tested cultivars, however, these differences were not related to organic and conventional breeding programs.

Objective 4: To assess **AMF-root colonization** (AMF-RC) of modern winter wheat cultivars derived from organic and conventional breeding programs as well as old cultivars and the correlation between of AMF-root colonization and nutrient concentrations in shoots and in grain and straw at harvest, nutrient uptake and grain yield under field conditions (Chapter 3.4.4 and 4).

AMF-RC differed significantly between the seven sites and was significantly higher under organic than under conventional conditions. AMF-RC did not differ among the wheat cultivars. The results of the two experiments gave no evidence for the hypothesis that the capacity of wheat for AMF-RC might be lost during breeding for high input conditions.

For the organic nutrient limited systems and sites, a positive correlation between AMF-RC and nutrient concentrations had been expected, while for the conventional high input systems, no or even negative correlations had been expected. In one organically managed system (BIODYN 2) and in the unfertilized control (NOFERT) a positive correlation between AMF-RC and shoot P concentration at tillering was measured. No such correlation was obtained in the conventional system. These results slightly indicate that higher AMF-RC might contribute to shoot P supply under organic conditions. However, the measured effect of the AMF-wheat symbiosis was only observed in early growth stages and was not reflected in improved P-uptake or grain yield at harvest. Moreover, no correlation was obtained at the bio-dynamically managed on-farm sites. A negative correlation between AMF-RC and shoot Mn concentration at tillering and flowering was found in the unfertilized control NOFERT in the DOK trial. No correlations were obtained between AMF-RC and Zn concentrations. Beside a slightly negative correlation in system BIODYN 2 with grain P uptake and in system NOFERT with Mn uptake, no correlations were obtained between AMF-RC and nutrient uptake and grain yield.

5.5 Do the Results Indicate the Need for Specific Organic Breeding Programs?

If direct selection in the target environment is more efficient, specific breeding programs should be carried out in the target environment. Such an analysis usually requires the parameters broad sense heritability, the genotypic correlation between traits assessed at the different test environments and the genotype x environment interactions (Becker, 1993). The analysis is conducted within several steps of decision. The scientific analysis whether direct selection in the target environments (e.g. organic farming) is more efficient than indirect selection (e.g. conventional farming) is outlined for low input breeding for maize by Harrer and Utz (1990) and Presterl et al. (2003) and for organic farming for maize by Burger et al. (2008). Unfortunately it was not possible to calculate reliable estimates of the genetic correlation for traits assessed in CONMIN vs BIODYN 1 and BIODYN 2 as data of only one location and one experimental year were available. Due to the positive correlation between the genotypic correlation coefficient and the genotype x environment interactions (Presterl et al., 2003), the genotypic correlation coefficient was substituted by the genotype x environment interactions in this analysis.

The procedure therefore had to be adapted and finally comprised three steps:

Step 1: Assessing broad sense heritability of the organic and conventional systems of the DOK trial.

Step 2: Assessing the genotype x environment interactions.

Step 3: Comparing the variance components of the cultivars and the variance components of the genotype x environment interactions.

Step 1: Assessing broad sense heritability of the organic and conventional systems of the DOK trial.

Broad sense heritability describes the ratio of the genotypic variance solely to the total phenotypic variance including genotypic and environmental impacts. The heritability value is indicative for the success of selection and breeding gains in the given environment. It is assumed that heritability values are higher under conventional conditions than under organic conditions due to more controlled conditions in conventional systems. A high heritability implies a minor environmental impact and a trait which is highly stable across environments. If heritability differs strongly between test environments, it is recommended to select indirectly in the environment with the higher heritability scores. If heritability is similar between test environments, the variance components of the cultivars and the variance components of the genotype x environment interactions between test environments have to be assessed.

The design of the study allowed for comparing the heritabilities in diverse organic environments, differing in plot size but also in tillage, fertilization and weed management or precrops (systems BIODYN 1 and BIODYN 2 versus sites BE, SH, ZH). It also allowed for comparing the heritabilities of organic versus conventional farming systems under homogenous site conditions (BIODYN 1 and BIODYN 2 versus CONMIN). Heritability values (h^2) calculated for the most traits except for grain yield were very similar for all seven test environments including organic and conventional environments (Table 5 1). These results are in line with other studies on maize, where similar heritability values were found for grain yield under low compared to high N conditions (Presterl et al., 2003) and under conventional compared to organic systems (Lorenzana and Bernardo, 2008). Direct comparison of heritability values between organic and conventional systems was only possible for the DOK trial. Here, the organic system BIODYN 2 revealed lower heritability especially for grain yield, which might be related to inhomogeneity in the field and therefore higher error variance. It might not necessarily be related to the organic farming system since heritability values for the organic system BIODYN 1 were in the same range than those for the conventional system CONMIN. Also heritability values obtained at the marginal sites were comparable to those obtained in the DOK systems. The results of this study on wheat show that it was possible to assess the genotypic value of the cultivar with the same precision under organic farming without herbicide and pesticide usage as under the more controlled conventional system.

	NOFERT	BE	SH	ZH	BIODYN 1	BIODYN 2	CONMIN
				h^2			
Grain yield	50.9	86.9	65.3	50.1	81.3	26.0	83.5
Thousand kernel weight	87.6	89.7	97.4	93.5	84.9	84.9	81.3
Harvest Index	90.3	95.9	99.0	98.1	90.4	74.3	93.3
N-Harvest Index	66.5	92.8	92.7	95.2	89.0	64.2	-*
Zeleny value	97.5	99.5	98.7	99.4	96.9	97.4	97.7
Gluten Index	-*	97.0	99.6	97.8	-*	-*	-*
Grain N concentration	-*	94.1	92.0	91.5	88.7	86.4	84.5
N-Total uptake	44.7	82.6	75.3	87.2	51.6	-	-*
N utilization efficiency	-*	93.8	58.4	88.3	91.1	76.3	83.1
Grain P concentration	77.1	95.1	95.0	95.4	86.7	82.8	71.5
P-Total uptake	65.8	81.0	90.7	95.7	-*	49.7	56.5
P utilization efficiency	85.3	90.9	88.1	96.7	-*	80.1	59.9

-* could not be calculated due to missing values

Table 5 1: Heritability (h^2) of selected parameters in seven test environments

Step 2: Assessing the Genotype x Environment Interactions

Tested in the organic and conventional systems of the DOK trial, the cultivars reacted similarly to the given environmental conditions: no significant genotype x environment interactions appeared (Chapter 2 and 3). However, significant genotype x environment interactions were detected among the three marginal sites (Chapter 4). Here, cross-over reactions revealed a better performance of the organically bred than the conventionally bred cultivars under poor organic conditions (site BE) for grain yield and NUtE and PUtE in contrast to the results obtained at sites ZH and SH. When calculated across all seven test environments, significant interactions were found for parameters of main interest such as grain yield, N-harvest index, gluten index, grain N-concentration and NUtE and PUtE. No significant interactions were obtained for harvest index and N-total uptake (Table 5 2). The significant interactions here imply that there are differences in genotype ranking between the test environments, although this was not found between conventional and organic systems in the DOK trial in 2007. From a breeder's point of view, significant genotype x environment interactions indicate different genotype ranking in the tested environments and strongly support the need of multi-location trials representing the most typical growing conditions.

Parameter	Variance components of cultivars	Variance components of the genotype x environment interactions	Level of significance of the genotype x environment interactions
Grain yield	0.048	0.035	***
Thousand kernel weight	3.65	0.921	***
Harvest Index	0.002	0.000	n.s.
N-Harvest Index	0.003	0.001	***
Zeleny value	204.45	5.053	***
Gluten Index	694.68	293.82	***
Grain N concentration	0.759	0.600	***
N-Total uptake	20.20	-3.990	n.s.
N utilization efficiency	2.27	10.45	***
Grain P concentration	0.367	0.153	***
P-Total uptake	5.34	2.62	***
P utilization efficiency	1033.16	227.31	***

n.s.: not significant

Values significant at * P < 0.05, ** P < 0.01, *** P < 0.001

Table 5 2: Variance components of cultivars and genotype x environment interactions, p-values and level of significance of a two-way ANOVA across seven sites and eight cultivars of selected parameters

Step 3: Comparing the Variance Components of the Cultivars and the Variance Components of the Genotype x Environment Interactions.

The variance components quantify the cultivar effect and the genotype x cultivar interaction. If the genotype x environment interaction is smaller than the genotypic influence, a few test environments would be sufficient for the reliable evaluation of the genotypic value of a cultivar. In such a case, the variance components of the cultivars are greater than the variance components of the genotype x environment interactions. If the environmental influence strongly exceeds the influence of the cultivar this would not directly emphasize the need of specific breeding programs. However, this would at least emphasize that multi-environment tests are compulsory. In such a case, the variance components of cultivars are equal to or smaller than the variance components of the genotype x environment interactions.

For thousand kernel weight, Zeleny value, gluten index, total N-uptake and P-utilization efficiency, larger variance components of the cultivars than of genotype x environment interactions were observed. For these parameters, selecting in only a few sites would be sufficient (Table 5 2). Equal or smaller variance components of cultivars than of genotype x environment interactions were observed for grain yield, harvest index, N-harvest index, grain N-concentration, N-utilization efficiency and total P-uptake. For these parameters it would be required to conduct multi-location tests or even establish specific breeding programs. The results reveal that no general conclusion can be drawn, comprising all parameters measured in this study as they react quite differently. It might therefore be necessary to decide on the parameters of major interest such as grain yield, gluten index as an indicator for baking quality and N-utilization efficiency. While highly heritable traits like the thousand kernel weight can be selected equally efficiently in conventional and organic conditions, N-utilization efficiency must be selected in the target environment.

To sum up, for the limited number of cultivars that could be tested in this study under organic and conventional conditions, it can not be directly concluded that completely separate breeding programs were inevitable for organic cultivation. However, results from this study strongly indicate the need of organic selection environments at least in later generations of wheat breeding when selection for grain yield takes place. Firstly, significant genotype x environment interactions were observed across all seven test environments for important traits indicating different ranking of the cultivars in the test environments. Secondly, for parameters of major interest such as grain yield, harvest index and N-utilization efficiency, the variance components of the cultivars were smaller than the variance components of the genotype x environment interactions. The findings underline the need for multi-environmental testing for the reliable assessment of the genotypic value for these traits.

5.6 Socio-Economic Aspects of Plant Breeding

This thesis tried to answer the question of the need of organic breeding programs from an agronomical point of view. For the sake of completeness, it should be mentioned that there are other aspects in this context such as the economical or legal situation or the concentration of market power in the seed industry that should be taken into account. Some aspects will be briefly discussed in this chapter.

5.6.1 Economical Aspects of Organic Plant Breeding

The norms for organic production and processing are not just product oriented. In fact, the values of organic agriculture are oriented on the process of farming. Organic farming worldwide is based on the principles of health, ecology, fairness and care described in detail by the International Federation of Organic Agriculture Movement (IFOAM, 2006) and in Europe moreover based on the EU Council Regulation (EC) No 834/2007 on organic production and labelling of organic products (http://eur-lex.europa.eu). These guidelines demand as a general principle, that all seeds and plant material have to be certified organic. Moreover, the production of propagating material has to comply with the principles of organic agriculture. However, there are only few organic breeding programs and a few released cultivars because of a lack of incentives to invest in such programs. An important reason might be the high investment costs of minimum 60.000 Euros annually for at least 10 – 12 years for the development of a new cultivar and the still small area of organic farming (Willing, 2007). For the return of the investment, a wheat cultivar must be produced on 20.000 ha at minimum (Niggli, 2002; Osman, 2007). Based on this calculation, in Germany there would be a potential for four cultivars and in France and Austria there would be a potential of only one cultivar. In Switzerland, organic wheat was produced only on 2000 ha in 2006. As a consequence, cultivars developed especially for organic farming would have to be grown across huge geographical and climatic areas. However, this is in conflict with the major objective of organic breeding, which is the development of locally adapted cultivars. The European Consortium for Organic plant breeding (www.ecopb.org) recently discussed new strategies and different models for financing organic breeding (ECO-PB, 2007). Looking at currently successful models, organic breeding might be financed in future times by a mixture of public financial support, project-oriented research funding, private donors and partnerships between breeders and private enterprises. Financial support is e.g. given in German-speaking countries since 1998 by the Future Farming Foundation (Zukunftsstiftung Landwirtschaft; www.saatgutfonds.de) (Willing, 2007). A promising model of a partnership between a breeder and a private enterprise is demonstrated by the SATIVA-Model of the Getreidezüchtung Peter Kunz (GZPK) in cooperation with the COOP supermarket. COOP produces bread out of cultivars from GZPK in its own bakeries and sells them under the trademark "SATIVA" in the COOP shops (Niggli, 2002; Osman, 2007). The cereal processing company ErdmannHAUSER supports organic breeding with a certain amount of money per product, which is explicitly labelled as a special benefit on the products (www.erdmannhauser.de). The GZPK is moreover funded by a network of about 250 private donors.

5.6.2 Does the Current Legal Situation Restrict Organic Plant Breeding?

The current legal system for plant breeding, seed propagation and distribution consists of a huge set of national and international guidelines, conventions, directives and regulations. To have a cultivar approved, it needs to conform to the criteria of the "International Union for the Protection of New Varieties of Plants (UPOV)" (1991). The cultivar must be clearly distinguishable from other cultivars of commercial knowledge, be novel in terms of commercialization, be sufficiently homogenous and stable. The UPOV guideline is granting sui generi intellectual property rights, which serve as a tool to provide royalties for a newly developed cultivar and hold the exclusive right for propagation and marketing. The breeders' authorization however is not needed for the use of the cultivar as an initial source of variation for the purpose of creating novel cultivars by other breeders. This so-called "breeder's exception" is a central feature in the UPOV convention (Le Buanec, 2006). In addition, the Swiss and European seed law allows only the commercial distribution of listed cultivars that have passed the VCU test on the Value of Cultivation and Use. In this test the cultivars are tested for three years at many locations and must outperform the standard cultivars. This evaluation is up till now conduced in most countries under high input conditions and strongly focused on yield. The regulations provide and promote an effective system of plant cultivar protection with the ultimate aim of encouraging the development of new cultivars. However, it does not fit with the organic system as it is aiming on large-scale cultivars with a broad adaptation to large geographical areas with the intention to serve huge markets (Lammerts van Bueren et al., 1999; Borgen, 2009). The current criteria of novelty, distinctiveness, uniformity and stability as well as the higher benchmark of cultivar approval should be replaced by a set that is wider and more flexible (van den Dool, 2009). For example Leskien and Flitner (1997) proposed to replace uniformity and stability by "identifiability". This means that a typical combination of few characteristics may be sufficient to identify a plant cultivar.

Additionally to the plant breeders' rights, both utility patents as well as plant patents exist, mainly in the US. In the European Union, the European Patent Convention rules that "European patents shall not be granted in respect to plant or animal cultivars or essential biological processes for the production of plants or animals" (EPO, 2007). However, with the promulgation of a new European Directive on the Protection of Biotechnological Inventions in 1998, biotechnological innovations involving plants became patentable (Le Buanec, 2006).

5.6.3 Consolidation and Monopolization in the Global Seed Industry

The commercial seed industry has undergone tremendous consolidation in the last 40 years. This development started in the US with the introduction of hybrids, particularly maize hybrids. In the 1980s, agro-chemical companies that were mainly active in biotechnology research began to acquire seed companies. In the 1990s, globally acting multi-national giant firms were built up by acquiring or merging with competing firms. Nowadays, the sale of seed has globally become dominated by a few companies among which Monsanto, Novartis (now Syngenta), Du Pont, Astra-Zeneca, Dow-Agroscience and Aventis are the largest ones (Srinivasan, 2003; Howard, 2009). All of them are heavily involved in the utilization of genetic modification. The top four seed firms control 56% of the global proprietary seed market (ETC, 2008). Meanwhile, there is a high degree of concentration in the ownership of plant cultivar rights for the six major crops (wheat, maize, soybean, potato, perennial ryegrass, oilseed rape) mainly in the developed world. The top 10 companies worldwide share for these six crops the plant cultivar protection certificates from a little over 40% in wheat to 70% in rapeseed and maize. This was shown in a study conducted on data of 30 UPOV member-countries (Srinivasan, 2003). This development was associated with a reduction of seed lines. In order to retain sovereignty of food production it is essential that farmers have the ability and means to breed and propagate their own seed and to produce food without relying on giant, globally acting companies. This concentration of power is fundamentally incompatible with sustainable farming systems.

6 CONCLUSION AND OUTLOOK

The main hypothesis of this thesis was that cultivars bred under organic conditions would perform better under organic conditions than conventionally bred cultivars. This hypothesis was confirmed at the three marginal organically managed sites. However this hypothesis was not confirmed at the more fertile organically managed DOK sites. There were cultivars achieving high grain yields, good baking quality or high nutrient use efficiency under organic conditions but this was irrespective of the breeding program they were derived from. As there was genetic variation in the measured parameters among the cultivars, cultivars for further breeding and also for growing in organic farming should be carefully selected for nutrient limited conditions.

Large variance of the genotype x environment interactions were observed across the seven environments; among those important agronomic traits such as grain yield, harvest index and especially N use efficiency parameters. Based on this study it is concluded that screening and selection for these traits should not only be performed under organic farming but at many different types of organic farms representing the predominant practice of cultivation.

This study gave no clear evidence for the hypothesis that the capacity of wheat for AMF-RC was lost during breeding for high input conditions or that the functionality of the AMF-wheat symbiosis was essential for improved nutrient uptake under organic farming. However, this can not be conclusively assessed by observing solely AMF-root colonization and such a limited number of cultivars. Other parameters, such as AMF-hyphae length should be observed additionally. Moreover, a non-mycorrhizal control is needed to measure AMF-response. The old cultivars bred before 1950 and as such before the green revolution were included in the study as a reference for selection under low input conditions. However, maintenance of these cultivars was conducted under "actual" soil nutrient conditions. Molecular studies on AMF-diversity of a larger set of cultivars grown under low input conditions could shed more light on the coevolution of wheat and AMF during breeding programs.

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Abbreviations

DOK	Bio-Dynamic, Organic, Konventionell (conventional)
BIODYN 1 / D1	Bio-dynamic farming system, low level of fertilization
BIODYN 2 / D2	Bio-dynamic farming system, high level of fertilization
CONMIN / M	Conventional farming system
NOFERT/ N	Unfertilized control
D	Bio-dynamic
O	Bio-organic
K	Conventional farming with manure
BE	Bio-dynamically managed site at Vielbringen-Worb, Canton Bern
SH	Bio-dynamically managed site at Rheinau, Canton Zurich
ZH	Bio-dynamically managed site at Fehraltorf, Canton Zurich
ART	Agroscope Reckenholz-Tänikon Research Station
CIMMYT	International Maize and Wheat Improvement Centre
ECO-PB	European Consortium for Organic plant breeding
FiBL	Research Institute of Organic Agriculture
GZPK	Getreidezüchtung Peter Kunz
IFOAM	International Federation of Organic Agriculture Movement
UPOV	Union for the Protection of New Varieties of Plants
AT	Austria
CH	Switzerland
DE	Germany
EU	European Union
FR	France
UK	United Kingdom
US	United States
BFCA	Breeding for conventional agriculture
BFOA	Breeding programs for organic agriculture
OPB	Organic plant breeding
Cv	Cultivar
Cvs	Cultivars
CCP	Composite Cross Population
AM	Arbuscular mycorrhiza
AMF	Arbuscular mycorrhizal fungi
AMF-RC	Root colonization with arbuscular mycorrhizal fungi
C	Carbon
Ca	Calcium
Cl	Chloride
C_{org}	Organic carbon
K	Potassium
Mn	Manganese
N	Nitrogen
Nmin	Nitrogen mineral soil
P	Phosphorus
Zn	Zinc
DM	Dry matter
EVD	Ecovalence
EVS	Environmental variability
FN	Falling number
GCP	Grain crude protein
GI	Wet gluten Index
Gtot	Wet gluten total
GY	Grain yield
h2	Heritability
ha	Hectare
HI	Harvest index
LU	Livestock units
NHI	Nitrogen harvest index
ZV	Zeleny value
Navf	N available fertilizer
Ntav	Total available N
Ntf	N total fertilizer
N-Ti	Shoot N at tillering
N-Fl	Shoot N at flowering
N-S	Straw N
N-G	Grain N
N-Gup	Grain N uptake
N-Sup	Straw N uptake
N-Tup	Total N uptake
NUpE	Nitrogen uptake efficiency
NUtE	Nitrogen utilization efficiency
Nit-UE	Nitrogen use efficiency for grain yield
P-Ti	Shoot P at tillering
P-Fl	Shoot P at flowering
P-S	Straw P
P-G	Grain P
P-Gup	Grain P uptake
P-Sup	Straw P uptake
P-Tup	Total P uptake
PUtE	Phosphorus utilization efficiency
Mn-Tup	Total Mn uptake
Zn-Tup	Total Zn uptake
ANOVA	Analysis of variance
d.f.	Degree of freedom
LSD	Least significant difference
p	Probability
RDA	Redundancy analysis
SEM	Standard error of means

Annex

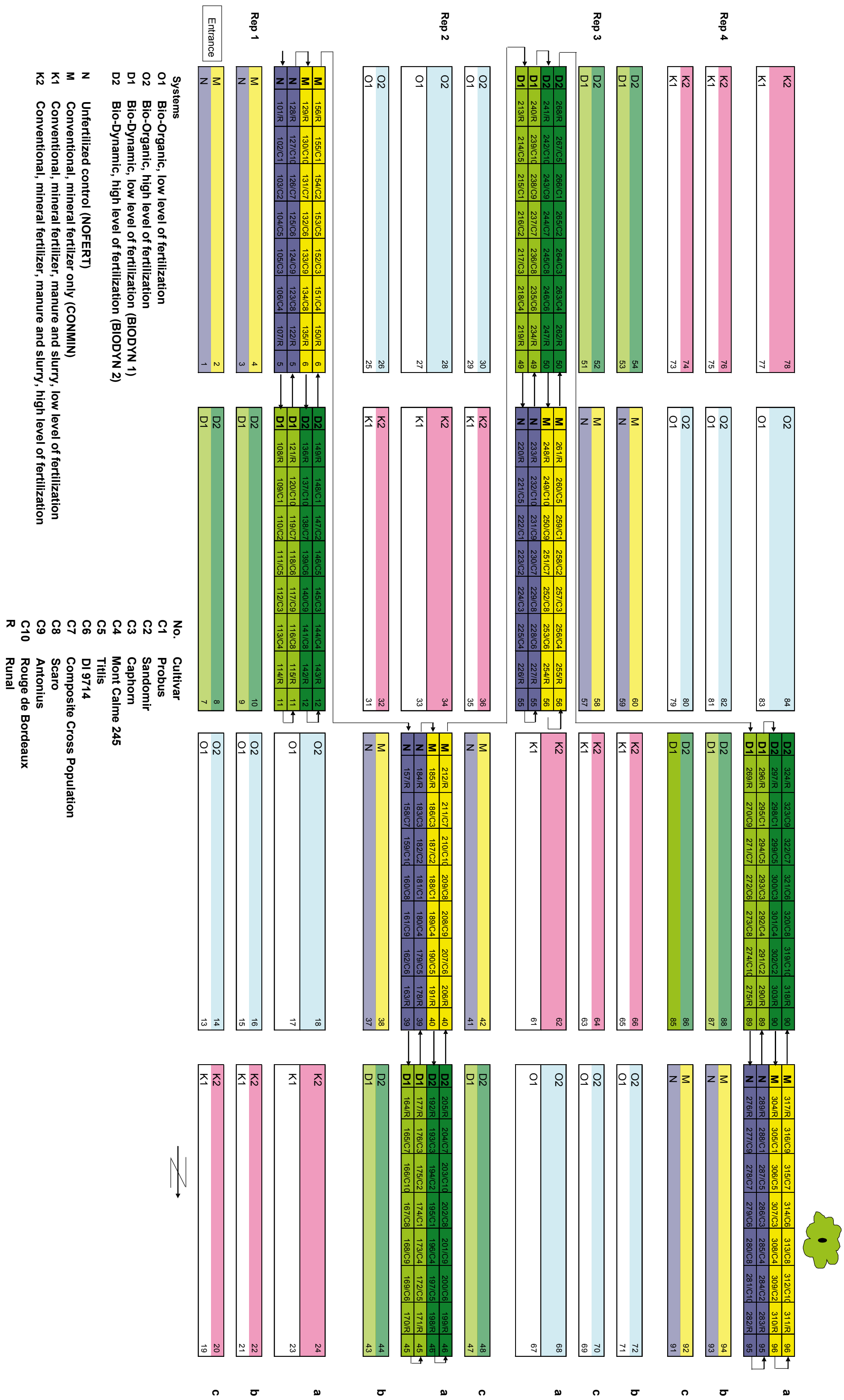
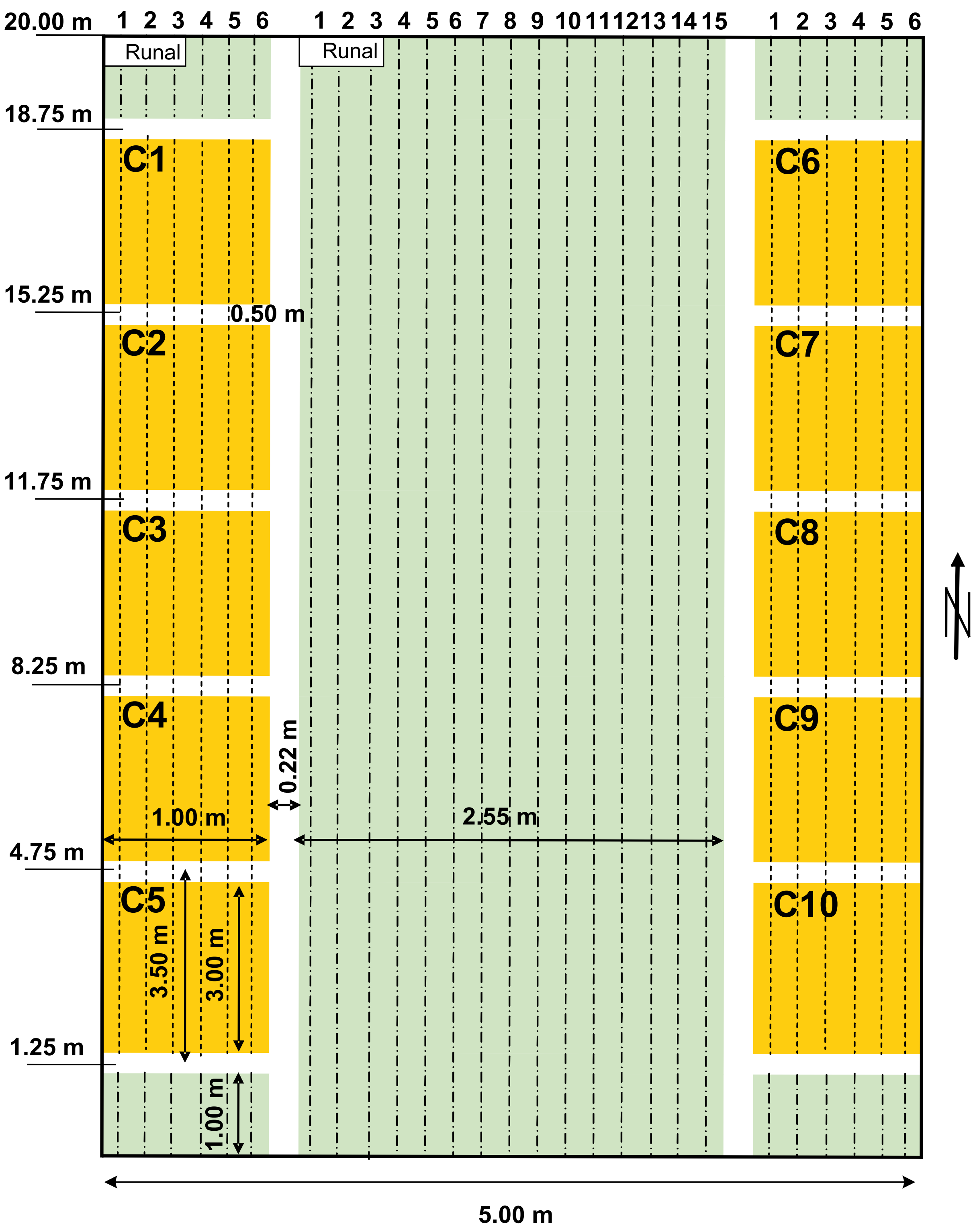


Figure 0 1 Experimental lay-out of the DOK trial in 2007 including the position of the cultivars



Winter wheat cultivars C1 - C10: row distance 16.66 cm

Area subplot brutto: 3.50 m^{-2}

Area subplot netto: 3.00 m^{-2}

Figure 0 2: Experimental lay-out of the cultivar test in 2007 in one DOK-plot

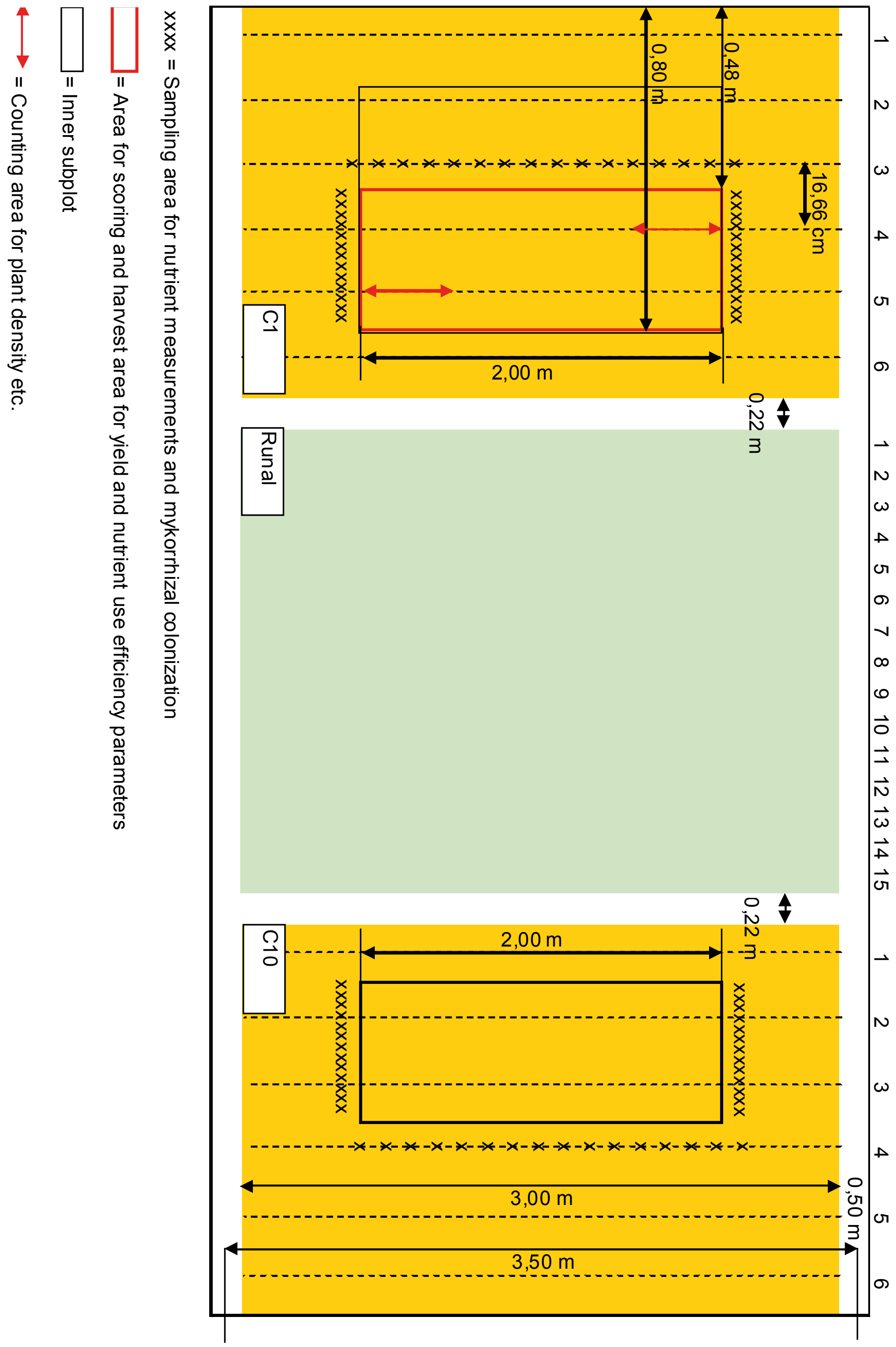


Figure 0 3 Experimental layout of the cultivar subplots in DOK trial in 2007

PNR Block-0	PNR Block-1	PNR Block-2	PNR Block-3	PNR Block-4	PNR Block-5	PNR Block-6	PNR Block-7	PNR Block-8
	Rep IV				Rep III			
81	01 Titlis (C05)	9 Sandomir (C02)	17 Titlis (C05)	25 Sandomir (C02)	33 Caphorn (C03)	41 Probus (C01)	49 Caphorn (C03)	57 Probus (C01)
82	02 Scaro (C08)	10 Antonius (C09)	18 Scaro (C08)	26 Antonius (C09)	34 CCP (C07)	42 Scaro (C08)	50 CCP (C07)	58 Scaro (C08)
83	03 Caphorn (C03)	11 CCP (C07)	19 Caphorn (C03)	27 CCP (C07)	35 Antonius (C09)	43 Sandomir (C02)	51 Antonius (C09)	59 Sandomir (C02)
84	04 MC 245 (C04)	12 Probus (C01)	20 MC 245 (C04)	28 Probus (C01)	36 MC 245 (C04)	44 Titlis (C05)	52 MC 245 (C04)	60 Titlis (C05)
85	05 Sandomir (C02)	13 Scaro (C08)	21 Sandomir (C02)	29 Scaro (C08)	37 Caphorn (C03)	45 Titlis (C05)	53 Caphorn (C03)	61 Titlis (C05)
86	06 Caphorn (C03)	14 Probus (C01)	22 Caphorn (C03)	30 Probus (C01)	38 Sandomir (C02)	46 MC 245 (C04)	54 Sandomir (C02)	62 MC 245 (C04)
87	07 CCP (C07)	15 MC 245 (C04)	23 CCP (C07)	31 MC 245 (C04)	39 CCP (C07)	47 Scaro (C08)	55 CCP (C07)	63 Scaro (C08)
88	08 Titlis (C05)	16 Antonius (C09)	24 Titlis (C05)	32 Antonius (C09)	40 Antonius (C09)	48 Probus (C01)	56 Antonius (C09)	64 Probus (C01)
	Rep I				Rep II			

1.50 m

2.75 m

22.00 m

Figure 0 4 Experimental lay-out of the on-farm cultivar tests in 2008 at organically managed sites

	Em^{-2}	GY	GCP	TKW	HI	NHI	ZV	Glu	GI	N-FI	N-G	N-Gup	N-Tup	NUtE	P-G	P-G	P-Gup	P-Tup	PUtE	AMF-FI
Em^{-2}	1.00	-0.27	0.46	0.24	-0.68	0.88 **	-0.17	0.64	-0.23	-0.89 **	0.47	0.13	-0.56	0.53	-0.4	0.11	0.14	-0.4	0.05	-0.29
GY	-0.40 +	1.00	-0.51	0.07	0.75 *	-0.24	0.06	-0.74 *	0.24	0.47	-0.5	0.74 *	0.80 *	0.44	0.67	-0.41	0.06	0.49	0.17	0.40
GCP	0.63 +	-0.50 +	1.00	0.57	-0.83* *	0.66	0.20	0.86 **	-0.13	-0.65	1.00 **	0.16	-0.25	-0.3	-0.82 *	0.52	0.34	-0.21	-0.14	-0.44
TKW	0.28	0.06	0.62 ++	1.00	-0.47	0.57	-0.31	0.53	-0.52	-0.63	0.48	0.49	0.10	0.18	-0.37	-0.27	-0.27	-0.35	0.45	-0.18
HI	-0.84 ++	0.82 ++	-0.89 ++	-0.49 +	1.00	-0.76 *	0.22	-0.99 **	0.50	0.87 **	'-0.81 *	0.14	0.69	0.10	0.76 *	-0.18	0.12	0.00	0.00	0.54
NHI	1.04 ++	-0.40 +	0.81 ++	0.63 ++	-0.83 ++	1.00	-0.11	0.76 *	-0.36	-0.91 **	0.69	0.35	-0.46	0.47	-0.58	0.08	0.04	-0.56	0.28	-0.46
ZV	-0.19	0.07	0.20	-0.32 +	0.22	-0.11	1.00	-0.18	0.91 **	0.29	0.23	0.16	0.29	-0.37	-0.36	0.85 **	0.93 **	0.71 *	-0.92 **	0.02
Glu	0.77 ++	-0.77 ++	0.95 ++	0.58 ++	-1.05 ++	0.93 ++	-0.20	1.00	-0.52	-0.83 *	0.80 *	-0.01	-0.65	0.00	-0.80 *	0.14	-0.16	-0.85 **	0.47	-0.37
GI	0.27	0.25	-0.11	-0.54 ++	0.51 ++	-0.40 +	0.92 ++	-0.56 ++	1.00	0.53	-0.08	0.13	0.41	-0.31	0.06	0.68	0.85 **	0.00	0.00	0.34
N-FI	-1.03 ++	0.64 ++	-0.85 ++	-0.66 ++	0.96 ++	-1.00 ++	0.31	-1.02 ++	0.60 ++	1.00	-0.68	-0.02	0.63	-0.19	0.53	-0.02	0.20	0.74 *	-0.31	0.21
N-G	0.64 ++	-0.50 +	1.00 ++	0.51 +	-0.86 ++	0.85 ++	0.24	0.88 ++	-0.06	-0.87 ++	1.00	0.16	-0.25	-0.3	-0.78 *	0.55	0.37	-0.18	-0.19	-0.5
N-Gup	0.09	0.76 ++	0.15	0.52 +	0.15	0.32	0.16	0.01	0.14	0.00	0.15	1.00	0.63	0.37	0.12	-0.2	0.25	0.00	0.13	-0.06
N-Tup	-0.76 ++	0.96 ++	-0.40 +	0.06	0.80 ++	-0.48+ +	0.30	-0.90 ++	0.48 +	0.72 ++	'-0.40 +	0.66 ++	1.00	-0.19	0.49	-0.16	0.27	0.71 *	-0.12	0.28
NUtE	0.77 ++	0.39	-0.17	0.34	0.07	0.43 +	-0.51 +	0.32	-0.49 +	-0.16	-0.17	0.49 +	0.03	1.00	0.25	-0.61	-0.35	-0.42	0.59	0.01
P-G	-0.44 +	0.85 ++	-0.98 ++	-0.42 +	0.82 ++	-0.63 ++	-0.40 +	-1.02 ++	0.07	0.58 ++	'-0.94 ++	0.18	0.55 +	0.52+ +	1.00	-0.59	-0.28	0.47	0.15	0.25
P-G	0.11	-0.48 +	0.55 ++	-0.31	-0.19	0.09	0.88 ++	0.16	0.72 ++	-0.04	0.57 ++	-0.27	-0.24	-0.95 ++	-0.63 ++	1.00	0.88 **	0.42	-0.86 **	-0.09
P-Gup	0.14	-0.01	0.39 +	-0.3	0.12	0.00	0.98 ++	-0.16	0.90 ++	0.24	0.42 +	0.19	0.26	-0.70 +	-0.26	0.89 ++	1.00	0.77 *	-0.91 **	-0.06
P-Tup	-0.50 +	0.55 ++	-0.26	-0.40 +	0.00	-0.58 ++	0.74 ++	-1.10 ++	0.00	0.86 ++	'-0.23	0.00	0.71 ++	-0.46 +	0.53 +	0.43 +	0.84 ++	1.00	-0.74 *	0.00
PUtE	0.04	0.18	-0.14	0.48 +	0.00	0.26	-0.96 ++	0.62 ++	0.00	-0.32	-0.2	0.17	-0.06	0.79 ++	0.21	-0.91 ++	-1.00 ++	-0.75 ++	1.00	-0.15
AMF-FI	-1.71	1.75	-2.11	-0.94	2.22	-1.79	0.07	-1.49	0.65 +	0.00	-4.03	0.00	2.05	1.00	1.42	-0.36	-0.28	0.00	0.00	1.00

Table 0 1 Phenotypic and genotypic correlation between traits calculated across seven test environments. Correlations above the diagonal represent values of the phenotypic correlation, while correlations below the diagonal represent values of the genotypic correlation. r values significant at $P < 0.05$, $P < 0.01$ or $P < 0.001$. Abbreviations are given on page 144

Curriculum Vitae

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List of Publications

Publications in peer-reviewed journals

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