

Aus der
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Differences in yield performance and yield stability between hybrids and inbred lines of wheat, barley, and triticale

Dissertation
zur Erlangung des Grades eines Doktors
der Agrarwissenschaften

vorgelegt
der Fakultät Agrarwissenschaften
von

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2015

Die vorliegende Arbeit wurde am 04.02.2015 von der Fakultät Agrarwissenschaften der Universität Hohenheim als "Dissertation zur Erlangung des Grades eines Doktors der Agrarwissenschaften" angenommen.

Tag der mündlichen Prüfung: 07.04.2015

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1. General Introduction

Beginnings of hybrid breeding

Increased trait values of crossbred off-spring, termed “hybrid vigor” or “heterosis”, were observed and described as early as in the 18th century. Joseph Gottlieb Kölreuter, born in Sulz am Neckar, was probably the first modern scientist describing hybrid vigor in interspecific crosses in several genera, e.g. in *Dianthus* L., *Mirabilis* L., *Verbascum* L., *Nicotiana* L. (Kölreuter 1766 as cited in Zirkle 1952). The economic breakthrough of hybrids in modern agriculture took place much later in the maize growing areas of the United States of America, beginning in the 1930s (Crow 1998). While in 1935 less than 10% of maize grown in Iowa were hybrids, in 1939 more than 90% were hybrids. According to Crow (1998), probably the most important reason for the rapid spread of hybrids was that, compared to open pollinated varieties used at that time, they were more resistant to drought in the dust bowl period from 1934 to 1936. The use of hybrid varieties was coupled with a sustainable yield increase in the following years.

Stimulated by the success of hybrid maize and other events, such as the observation of cytoplasmic male sterility, the interest in hybrid wheat (*Triticum aestivum* L.) came up (Wilson and Driscoll 1983). Similarly, hybrid barley (*Hordeum vulgare* L.) gained the interest of scientists following the description of the first male sterile character in barley in 1940 (Ramage 1983). Research on hybrid breeding in triticale (\times *Triticosecale* Wittmack) started in the 1980s, much later than in wheat and barley (Nalepa 1990 as cited in Longin et al. 2012). Despite intensive research work over several decades, neither hybrid wheat nor hybrid barley or hybrid triticale could be established for a wide commercial use comparable to hybrid maize (Longin et al. 2012).

Prerequisites of hybrid breeding

From today's perspective, the reasons for the limited cultivation of hybrid wheat, hybrid barley and hybrid triticale were the not or not completely fulfilled prerequisites for successful hybrid breeding. The successful market launch of hybrids would require a cost-effective system to produce hybrid seeds as well as an economically significant level of heterosis (Gowda et al. 2010). In addition, the long-term success of hybrids requires a higher or at least equal selection gain per time unit in hybrid breeding compared to line breeding (Longin et al. 2012).

Different systems for hybrid seed production have been suggested and explained in detail (for review see, Wilson and Driscoll 1983, Whitford et al. 2013). Nowadays working hybridization systems are available for all three crops, which are commercially used to a limited extent (Longin et al. 2012). In Europe, two hybridization systems are currently relevant. The first system uses chemical hybridizing agents (CHA) and the second cytoplasmic male sterility (CMS). Both systems have advantages and disadvantages and a detailed description and discussion can be reviewed elsewhere (e.g. Whitford et al. 2013). Investigations on the expected selection gain of hybrid versus line breeding were also conducted (Longin et al. 2012), but reliable predictions are difficult due to multiple influencing factors, which in addition may change over time.

Yield performance of hybrids

The amount of heterosis has been well studied in wheat. Based on CMS as well as on CHA wheat hybrids were developed and evaluated with their parents in reliable yield trials across environments (Merfert et al. 1987, Borghi et al. 1988, Barbosa-Neto et al. 1996, Oury et al. 2000, Corbellini et al. 2002). Heterosis was on average around 10%. There were no severe differences in the amount of heterosis finally achieved with CMS-based and CHA-based hybrids. Only the development of the CMS-based hybrids needed much more time (Merfert et al. 1988).

In barley, results of earlier studies have to be interpreted with care, since they were usually based on small plots with reduced seed density and/or in fewer than three environments, i.e. year-by-location combinations (e.g. Suneson and Riddle 1944, Severson and Rasmusson 1968, Eckhoff and Ramage 1989). Estimates of heterosis of more than 20% (Suneson and Riddle 1944) may therefore not be confirmed, when evaluation for grain yield would be based on ordinary yield plots across multiple environments. It was speculated that heterosis in barley might be considerably higher than in wheat and triticale, since barley is diploid whereas wheat and triticale are hexaploid. Oettler et al. (2005) speculated that the lower heterosis in hexaploid triticale and hexaploid wheat compared to diploid rye (*Secale cereal* L.) might be a reason of the “fixed” heterosis in allopolyploid inbred lines due to epistatic interaction between genes of the different genomes.

Contrasting results about the magnitude of heterosis in triticale were reported. For CHA-based triticale hybrids, heterosis was with around 10% comparable to results in wheat (Oettler et al. 2005, Fischer et al. 2010). But the CMS-based triticale hybrids investigated by Gowda et al. (2013) showed only around 2% heterosis for grain yield.

In summary, the findings in wheat were constant and further research might only be necessary to verify, if the earlier findings agree with results of present germplasm and specific growing regions. For barley, however, a profound evaluation of hybrids and lines in ordinary yield trials across representative environments is urgently required to verify, whether the amount of heterosis is substantially higher than in wheat and triticale or not. The contrasting findings in triticale require further research to obtain reliable estimates of heterosis and detect the reasons for the large differences.

Yield stability of hybrids

Increased yield stability was frequently attributed to hybrids in addition to the higher absolute yields compared to inbred lines (e.g. Longin et al. 2012). As already mentioned, Crow (1998) named the higher drought resistance of hybrids, which can be interpreted as higher yield stability, as a decisive factor for the rapid success of hybrid maize. It is assumed, that hybrids can better buffer variable environmental conditions including abiotic stress compared to lines, since hybrids possess two different alleles at a loci whereas lines possess only one (personnel communication H. Friedrich Utz, University of Hohenheim, 2014). In hybrids of out-crossing crops Léon (1994) reported, based on literature review, a higher yield stability of hybrids compared to inbred lines, although not for self-pollinating crops. He mentioned that in the most

reviewed studies of self-pollinating crops hybrids were tested in a single row. Therefore his conclusions should be interpreted with care.

Yield stability of hybrids is an important argument for hybrid breeding. The average yield advantage of hybrids, compared to their parental inbred lines, was relatively low in experimental studies with approximately 10%. Compared with the better parent and/or outstanding line varieties, the yield advantage becomes smaller (e.g. Oettler et al. 2005, Gowda et al. 2010). At the same time the production of certified seeds for hybrids is more expensive and the development of hybrid varieties requires higher investments. Therefore, additional benefits such as higher yield stability may help to justify the higher investments in breeding hybrid instead of line varieties. The predicted climate change is another reason for the interest in yield stability of hybrids. If the frequency of weather extremes will increase, the importance of abiotic stress resistances, high vigor and buffering capacity as well as good adaptability will gain importance.

Assessment of yield stability

Assessment of buffering capacity or yield stability, however, is difficult for various reasons. Multiple traits, such as resistances to diseases, nitrogen use efficiency, ability for tillering, frost and drought tolerance can contribute to the complex trait “yield stability” (Piepho 1992). Their relevance and contribution depend on the specific environments (Fig. 1). Since it is difficult or even impossible to combine them to the trait “yield stability”, it is reasonable to use a biometrical model, where stability is described by an individual parameter (Piepho 1992).

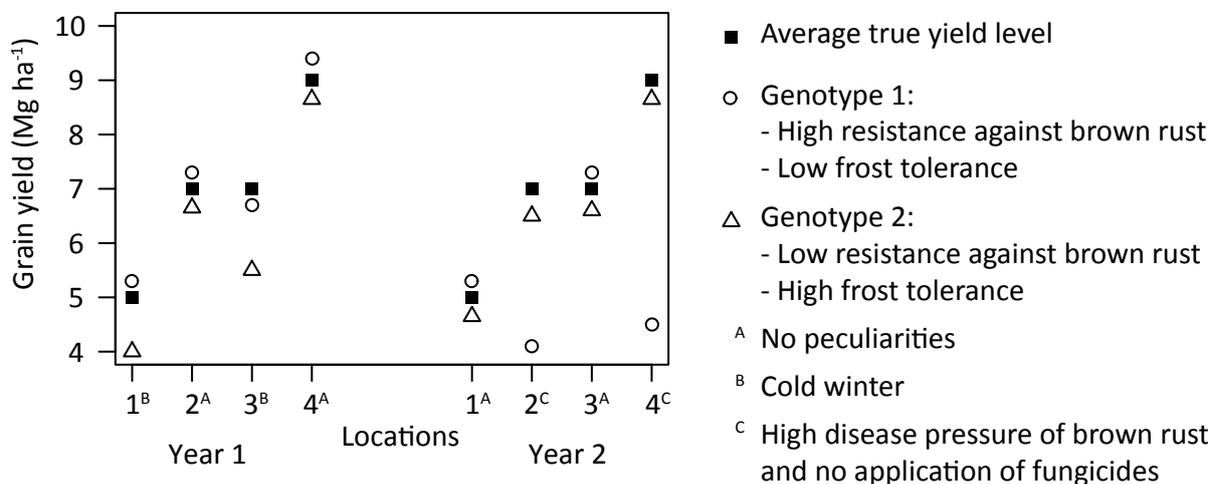


Figure 1 Exemplary description of the influence of agronomic traits on yield stability. In year 1 genotype 1 is stable and genotype 2 unstable, but in year 2, where a different agronomic trait is decisive for yield stability, genotype 2 is stable and genotype 1 is unstable.

With this approach, however, the next challenge arises: There were many different stability parameters suggested which have to be interpreted differently (for review see Lin et al. 1986, Becker and Léon 1988, Piepho 1998). Several studies compared different stability parameters in experimental datasets (e.g. Becker 1981, Piepho and Lotito 1992). They found stability parameters, which were very similar, but they also observed independent stability measures. This suggested that a genotype might be stable according to one stability parameter,

but unstable according to another one. Becker and Léon (1988) described two concepts of stability, the static and the dynamic concept. According to the static concept a stable genotype should have a minimum variation in yield across environments (Fig. 2). In the dynamic concept, a stable genotype should have only linear deviations from the yield levels at the individual environments.

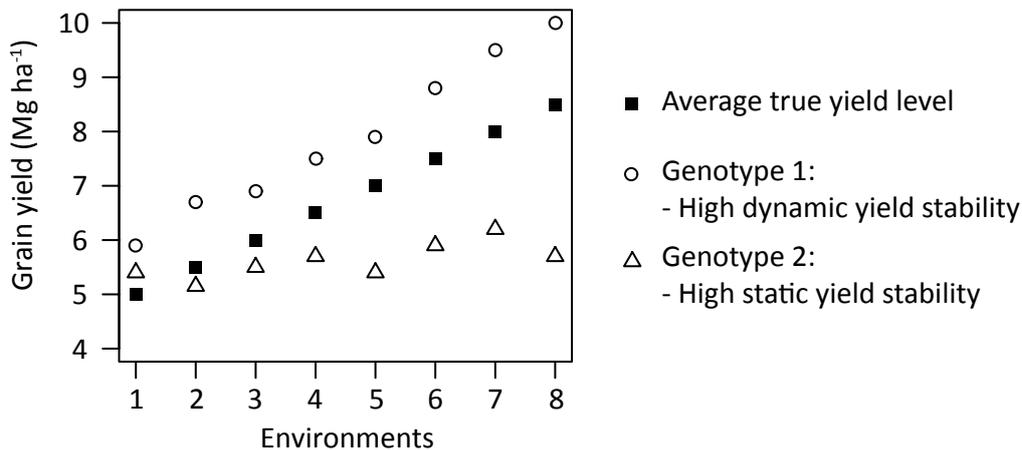


Figure 2 Exemplary description of dynamic and static yield stability.

The major constraint in the static concept is that stability is frequently associated with low yield (Becker and Léon 1988). The reason for this is, that the chance is higher that a wheat genotype possesses a constantly low performance, e.g. 5 Mg ha⁻¹ across marginal and fertile environments, than that a wheat genotype yields 9 Mg ha⁻¹ across all environments including dry locations (Fig. 3). In the dynamic concept, this problem is solved, but the estimation of the yield level becomes a new issue. Usually the yield level is determined by the average yield either of a group of genotypes, e.g. several check varieties, or of all genotypes included in the experiment. In this way, genotypes that have similar fluctuation in yield as the group or as the majority are stable, but genotypes which react differently e.g. due to novel resistance genes, are unstable (Fig. 4, compare Francis and Kannenberg 1978). It was suggested to determine the yield level of an environment by independent measures like rainfall, temperature, and soil fertility (Eberhart and Russell 1966). But the high number of relevant factors and their complex interactions will probably prevent their use for precise prediction of the yield level. Summed up, a genotypes' stability can differ depending on (1) the set of environments, (2) the definition of stability and statistical analysis, and (3) other genotypes included in the analysis.

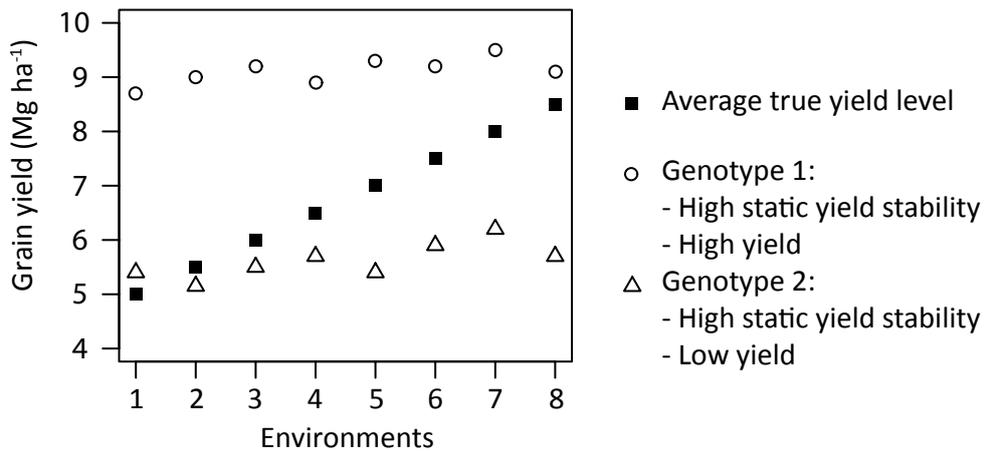


Figure 3 Exemplary description of a genotype with high static yield stability and at the same time high yield and of another genotype with high static yield stability and at the same time low yield.

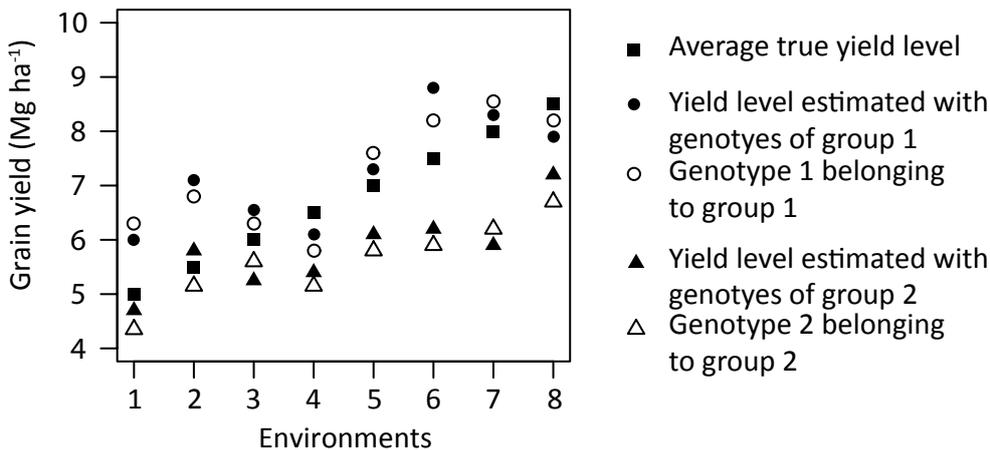


Figure 4 Exemplary description of two genotypes belonging to different groups, which react differently to changing environmental conditions. Dynamic yield stability depended strongly on the definition of the yield level. When the yield level is estimated with genotypes of group 1, genotype 1 will be stable and genotype 2 unstable. But when the yield level is estimated with genotypes of group 2, the opposite will be true.

In marginal environments the stability of genotypes is particularly urgent. Genotypes should be able to buffer unsuitable growing conditions such as soil compaction, waterlogging, drought, heat, and low temperatures. But for experiments, usually fertile and homogenous fields are selected to reduce errors arising from e.g. locally varying supply of nutrients or water. It was frequently observed, that experiments under stress had a low heritability (e.g. Weber et al. 2012, Hübner et al. 2013), which means that the differentiation between genotypes was less precise. Therefore the number of replications has to be increased. Additionally or alternatively statistical methods may be used, which correct for the spatial heterogeneity.

Repeatability of stability parameters is the basic requirement for their use in variety description and selection. In general, earlier studies reported a lower repeatability of yield stability parameters as of yield (Pham and Kang 1988, Léon and Becker 1988, Jalaluddin and

Harrison 1993, Kumar et al. 1998, Sneller et al. 1997). Furthermore, results on yield stability parameters were partially not consistent across other data sets. Becker (1987) and Piepho (1998) described for some stability measures, that their intrinsic properties give reason for their imprecise estimation. The difficulty to assess some stability measures precisely led some researchers to conclude that the respective measures were only meaningful in a specific set of environments (Pham and Kang 1988) or even non-genetic (Lin and Binns 1991). Against this background, it is crucial not only to provide estimates of stability parameters, but also some information about their validity, e.g. by significance tests or heritability.

Current status of research on yield stability of hybrid wheat, barley, and triticale

In wheat, several studies from North America investigated the yield stability of hybrids and lines in plot-based multi-environment trials (Peterson et al. 1997; Bruns and Peterson 1998; Koemel et al. 2004). Compared to lines, however, none of these studies reported an increased yield stability of hybrids, and therefore confirmed the result of Léon (1994). In France, Oury et al. (2000) compared yield stability of hybrids and lines based on a different stability parameter and reported a significantly higher yield stability of the wheat hybrids. Therefore, review of literature requires a detailed understanding of the different factors, which may influence yield stability. In barley and triticale no earlier study with plot-based multi-environment trials was focused on yield stability of hybrid versus lines. Therefore, for the comparison of hybrids and lines with respect to yield stability further research is required for all three crops.

Objectives

The overall objective of the present thesis was to investigate differences in yield performance and yield stability between lines and hybrids of wheat, barley, and triticale using plot-based yield trials across multiple environments.

The specific objectives were to:

- (1) investigate optimal strategies to analyze field trials with low heritability due to spatial varying drought stress,
- (2) assess the amount of heterosis for grain yield in barley,
- (3) examine the potential to predict yield performance of barley hybrids based on midparent values or general combining ability (GCA) effects,
- (4) investigate dynamic yield stability of the group of hybrids versus the group of lines in the self-pollinating cereals wheat, barley, and triticale,
- (5) examine the required number of test environments to precisely estimate yield stability of individual barley genotypes,
- (6) compare grain yield performance, static and dynamic yield stability of six-rowed hybrids, six-rowed lines and two-rowed lines of barley,
- (7) study the association of various agronomic traits with yield performance and static and dynamic yield stability in barley,
- (8) investigate, which biometrical model is suitable to compare dynamic yield stability of hybrids and lines,
- (9) examine, whether CMS-based triticale hybrids possess a higher grain yield performance and higher dynamic yield stability compared to inbred lines, and
- (10) study optimal strategies to predict yield performance and dynamic yield stability of triticale hybrids.

2. Visual scorings of drought stress intensity as covariates for improved variety trial analysis

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Journal of Agronomy and Crop Science 199.5 (2013): 321–330

The original publication is available at
<http://onlinelibrary.wiley.com/>

Abstract. Drought stress may cause that spatial soil differences become more evident and reduce heritability in variety trials. At two locations of a winter triticale (*×Triticosecale* Wittmack) trial the field heterogeneity was increased and as a result heritability was reduced. The four remaining locations were not affected by severe drought stress. At Willstätt the intensity of drought stress was visually scored based on the habitus and curled and wizened leaves at two dates in May. At Issoudun, the overall impression of a plot, which might have depended partially on the drought stress, was visually scored once. It was investigated if the impact of the high field heterogeneity can be reduced by usage of (1) incomplete blocks, (2) row and/or column effects, (3) the visual scorings as covariates in an analysis of covariance (ANCOVA), or (4) modeling a spatial covariance between adjacent plots. In addition it was investigated, if the visual scorings fulfill the requirements of an independent covariate; this means, if they were independent from the genotypic effects and linearly associated with the response (grain yield). The different models were compared based on AIC and phenotypic correlation between the genotypic estimates obtained from the model under investigation in a drought stress location with genotype means obtained from the analysis of the remaining locations. In Willstätt, neither incomplete blocks nor row or column effects were suitable to correct for the spatial trend. But the first and second visual scorings fulfilled the requirements of an ANCOVA and increased heritability from 0.03 to 0.50 and 0.60, respectively. Also spatial models were able to increase heritability up to 0.50. In Issoudun, incomplete block effects and row effects corrected for most of the field heterogeneity. The visual scoring was not independent from the genotype and could therefore not be used. The usage of spatial models did not lead to a substantial further improvement after incomplete block or row effects were added. It could be concluded, that covariates, which measure confounding factors such as spatial varying drought stress, can be used in an ANCOVA to obtain more precise genotypic estimates from variety trials.

3. Hybrid breeding in barley*

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Crop Science 53.9 (2013): 819–824

The original publication is available at
<https://www.crops.org/>

Abstract. Yield trials of six-rowed winter barley (*Hordeum vulgare* L.) hybrids and lines conducted at five locations in Western and Central Europe between 2009 and 2011 were used to study the extent of heterosis and the possibility to predict the hybrid performance with midparent values or general combining ability (GCA) effects. In total, 124 hybrids, their 27 male and 38 female parental inbred lines, nine line and seven hybrid varieties were evaluated for grain yield. On average hybrids were tested in 4.3 environments, i.e. year-by-location combination, males in 6.5 environments, females in 6.4 environments and checks in 5.3 environments. In a two-stage analysis, genotypic estimates of grain yield, GCA effects, and variance components were calculated. Midparent heterosis was 11.3% on average and ranged between 0.7% and 19.9%. Better-parent heterosis was slightly lower with a mean of 9.2% and a range from -1.7% to 18.3%. Commercial heterosis, i.e. the difference between the hybrid yield and the yield of the best commercial line included in the study was 2.7% on average and ranged between -5.2% and 7.6%. Estimates of heterosis demonstrated the potential of hybrid breeding in barley. Hybrid performance could be predicted based on midparent values and based on GCA effects ($P < 0.001$), but the accuracy was low with a correlation coefficient of 0.46 and 0.38, respectively. Therefore alternative approaches for hybrid prediction should be investigated.

* This paper is an extended and improved version of the Master thesis from Jonathan Mühleisen.

4. Yield stability of hybrids versus lines in wheat, barley, and triticale

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Theoretical and Applied Genetics 127.2 (2014): 309–316

The original publication is available at
<http://link.springer.com/>

Abstract. Hybrids are assumed to be more yield stable as inbred lines, but earlier results of autogamous cereals were contrasting. Yield stability of wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and triticale (\times *Triticosecale* Wittmack) hybrids and lines was investigated in multi-location yield trials. The wheat trial comprised 1606 hybrids and 143 lines, the barley trial 41 single-cross hybrids, 15 three-way hybrids and 36 lines, the triticale trial 80 hybrids and 50 lines. Each genotype was tested in up to five contrasting location in Western and/or Central Europe. Stability variance was estimated for the group of hybrids and lines and in the barley experiment additionally for the group of three-way hybrids. For all three crops, hybrids were significantly ($P < 0.05$) more stable compared to inbred lines. In barley, the three-way hybrid were significantly ($P < 0.05$) more stable than inbred lines, but their superiority in stability compared to single-cross hybrids was not significant ($P > 0.05$). The improved yield stability of hybrids could be considered as a major step forward, to prepared arable crops for the predicted climate change and the associated fluctuation in weather conditions.

5. Exploitation of yield stability in barley

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Theoretical and Applied Genetics 127.9 (2014): 1949–1962

The original publication is available at
<http://link.springer.com/>

Abstract. Yield stability and the associated abiotic stress tolerance is expected to become more important for field crops due to the predicted climate change. The objectives of the study were to (1) investigate the required dimensioning of field trials for precise assessment of the yield stability of individual winter barley (*Hordeum vulgare* L.) genotypes, (2) examine differences in yield performance and yield stability among six-rowed hybrids, six-rowed lines, and two-rowed lines, (3) assess the relationship between various agronomic traits and yield as well as yield stability. Five series of three-year registration trials, with each 4 or 5 six-rowed hybrids, 40 to 46 six-rowed inbred lines, and 42 to 49 two-rowed inbred lines, were used to assess yield and yield stability. The genotypes were tested in 10 to 45 environments, i.e. year-by-location combinations in Germany. We found, that the minimum number of test environment required for a precise assessment varied strongly between series. Finally, we concluded that at least 40 environments should be used. In contrast, yield performance could be reliably described based on less than ten environments in all five series. The high demand on test intensity for precise assessment of yield stability exceeds the capacity of normal barley breeding programs and is therefore not possible. Agronomic traits could not be used for indirect improvement of yield stability, since no agronomic trait showed a constant association with yield stability. We found, that hybrids tend to combine high dynamic yield stability with high grain yield. Considered as a group, neither six-rowed inbred lines nor two-rowed inbred lines combined both features. Therefore we concluded that hybrid breeding may be a promising way to improve yield stability in barley.

6. Yield performance and stability of CMS-based triticales hybrids

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Theoretical and Applied Genetics 128.2 (2015):291–301

The original publication is available at
<http://link.springer.com/>

Abstract. Hybrids are expected to possess an increased vigor causing high yield performance coupled with increased yield stability. Our objectives were to (1) assess the optimum choice of the biometrical model to compare yield stability of hybrids versus lines in triticales (*×Triticosecale* Wittmack), (2) investigate if hybrids are superior in grain yield performance and yield stability, and (3) examine possible strategies to predict yield stability of hybrids. The present study comprised 141 triticales genotypes which were evaluated in plot-based yield trials in up to 20 environments. The genotypes can be grouped in 13 female and 7 male parental inbred lines, their 91 factorial hybrids and 30 commercial line varieties or advanced breeding lines. Each hybrid was produced by open pollination of the male sterile female parental line with the surrounding male parental line. Male sterility of the female lines was ensured through a cytoplasmic male sterility (CMS)-inducing cytoplasm originating from *Triticum timopheevii* Zhuk. We found, that the magnitude of stability variance of lines and hybrids depended strongly on the choice of the biometrical model. The addition of a group-by-environment interaction term was suitable to obtain a proper comparison among groups. Hybrid showed a marginal yield advantage compared to their parents of 3% ranging from -15.0% to 11.5%. Better parent heterosis was considerable lower with an average of -4.2% and no hybrid outyielded the best inbred line. Hybrids showed on average lower yield stability as their parents and as commercial lines. Midparent values and general combining ability (GCA)-predicted values could be used to predict hybrid performance in grain yield. But stability variance of hybrids could only be predicted with GCA-predicted values. We speculated, that problems associated with the currently used CMS system, such as negative effects of CMS cytoplasm or incomplete restoration of male fertility in the hybrids might be the reason for the poor hybrid yields. Therefore, a detailed study investigating the reasons for the low heterosis is of paramount importance. A special focus should be set on possible yield penalties of the CMS cytoplasm or insufficient restoration depending on environmental conditions or the genetic background of the female.

7. General Discussion

Prospect of hybrid wheat

Reliable estimation of heterosis for grain yield and yield stability requires that hybrids, their parents, and reference varieties trace back to adapted and up-to-date genetic material. Evaluation of genotypes for grain yield should take place across locations and years within the target region. Growing conditions within plots should be similar to commercial fields, which requires yield plots and commercial seeding rate. Therefore sufficient amounts of hybrid seed are required for reliable evaluation of hybrids.

Production of hybrid seeds

Production of hybrid seed in self-pollinating crops requires a system that prevents the natural self-pollination of the seed parent, but allows its pollination by the pollen parent (Longin et al. 2012). In wheat, male sterility can be induced by CMS (Whitford et al. 2013). The usage of the CMS-system requires longstanding breeding work to introduce CMS-cytoplasm and restorer genes into adapted germplasm. Completely male sterile CMS-lines have to be developed, which can serve as female parents of the hybrids as well as male restorer lines, which are able to restore male fertility of the hybrids completely. Male sterility as well as restoration of male sterility have to be stable across environments.

Beside the CMS-system, male sterility in wheat can also be induced by CHA (Whitford et al. 2013). In crossing blocks the seed parent is sprayed with the CHA, but the neighboring pollen parent is not sprayed. If the CHA works properly and causes complete male sterility, and if the pollen parent sheds sufficient amounts of pollen at the right time, commercial quantities of hybrid seed can easily be produced without years of preliminary work.

Hybrid performance of wheat

Walter Merfert, hybrid wheat breeder at the Institute of Cereal Research Bernburg-Hadmersleben (Institut für Getreideforschung Bernburg-Hadmersleben) in the German Democratic Republic (GDR) succeeded in the development of adapted CMS-based hybrids. For 17 outstanding hybrids he reported an average midparent heterosis of 9%, ranging from 0% to 15% (Merfert et al. 1987). With respect to the commercial competitiveness, Merfert et al. (1988) reported a commercial heterosis of 3% based on a five year average. He expressed the expectation, that commercial heterosis could be increased by the usage of improved restorer lines and genetic divergent CMS-lines. The wheat hybrids developed by Walter Merfert were the result of around 20 years of systematical hybrid breeding. The introduction of the CMS into adapted inbred lines started in 1965 (Merfert et al. 1988) and the commercial competitive hybrids were available in the mid to late 1980s. Hence, the development of CMS-based hybrids in wheat required a long start-up period.

In contrast to the CMS-based hybrids, CHA-based hybrids can be produced directly from present breeding germplasm. Observed problems are the limited amount of fertile pollen spread by the male parent and a relatively narrow time window in which the male and female parent have to flower (Longin et al. 2012), which hampers the production of arbitrary hybrid combinations. Nevertheless, CHA-based wheat hybrids have been produced in multiple countries and hybrid yield was compared with the yield of parental inbred lines or other adapted inbred lines in ordinary yield trials across environments (e.g. Bruns and Peterson 1998, Oury 2000, Corbellini et al. 2002, Koemel et al. 2004, Gowda et al. 2010, Longin et al. 2013). The amount of midparent heterosis for grain yield fluctuated widely. In Italy, e.g. Corbellini et al. (2002) observed a mid-parent heterosis of 3.5% on average in one data set, but in another data set a midparent heterosis of 15% on average was observed. In North America, the average yield advantage of hybrids compared to lines was around 10% (Bruns and Peterson 1998, Koemel et al. 2004). In France, Oury et al. (2000) reported an average mid-parent heterosis of around 10% and Longin et al. (2013) observed 10.7% mid-parent heterosis on average in Germany. Summed up, it is reasonable to expect an average midparent heterosis of 10% for grain yield in wheat. Compared to the better parent or outstanding inbred lines, however, the yield advantage will be smaller (Longin et al. 2013).

Several studies from North America investigated the dynamic yield stability of hybrids and lines (Peterson et al. 1997; Bruns and Peterson 1998; Koemel et al. 2004) with the deviation variance of the regression approach of Eberhart and Russell (1966). But none of these studies reported an increased yield stability of hybrids compared to lines. In France, Oury et al. (2000) compared yield stability of hybrids and lines based on Wricke's (1962) ecovalence and reported a significantly higher yield stability of the wheat hybrids.

Based on theoretical considerations, it is expected that dynamic yield stability favors genotypes which are yielding similar as the majority of genotypes across environments (see general introduction, compare Francis and Kannenberg 1978). For the deviation variance, a dynamic stability measure, Mühleisen et al. (2014a) demonstrated that depending on the definition of the environmental index results can be contrasting. Mühleisen et al. (2015) investigated several approaches to compare the stability variance of genotypic groups and found that the simple modeling of a group-specific stability variance was not suitable for a reasonable comparison. They suggested that the addition of a group-by-environment interaction effect leads to more appropriate results.

Assessment of dynamic yield stability in terms of deviation variance of the regression approach (Eberhart and Russell 1966) depended strongly on the definition of the environmental index (Mühleisen et al. 2014a). Peterson et al. (1997) as well as Bruns and Peterson (1998) used the average yield of inbred line entries as environmental index. The definition of the environmental index based only on yields of inbred lines is problematic, if hybrids and lines react differently to growing conditions. In this case, regression lines would be closer to line yields than to hybrid yields. As a result, deviation variances of lines would be underestimated and deviation variances of hybrids overestimated. Koemel et al. (2004) used two long-term checks for estimation of the environmental index, but did not mention, whether the checks were lines or hybrids. Assuming both were lines, all three studies from North America would favor inbred lines

due to the unsuitable definition of the environmental index. Therefore, their conclusion, that hybrids possessed no higher dynamic yield stability than inbred lines might be revised, if the environmental index would be defined as the mean of the mean of lines and the mean of the hybrids.

Oury et al. (2000) used the ecovalence (Wricke 1962) for estimation of stability variance. In their experiment, however, the number of hybrids slightly exceeded the number of lines, which may cause hybrids to be favored (compare Introduction). Mühleisen et al. (2014a) reported higher dynamic yield stability of hybrids but had not fitted a group-by-environment interaction effect as recommend by Mühleisen et al. (2015). The reanalysis of the experiments described in Mühleisen et al. (2014a), however, suggested that yield stability of hybrids was indeed higher than that of inbred lines (see Appendix). Nevertheless further research seems necessary due to differences between studies and the strong influence of the analysis.

Summarized, hybrid wheat showed an increased yield potential and most probably also higher dynamic yield stability. Further research should focus on the development of CMS-based hybrids, since in mixed plantings hybrid seed production is much cheaper (Longin et al. 2012). Beside verification of the higher dynamic yield stability of hybrids, it would be interesting to know, whether relative and/or absolute heterosis is higher in marginal environment. The evaluation of genotypes under stress conditions, however, might require particular care in statistical analysis (Mühleisen et al. 2013b).

Prospect of hybrid barley

Production of hybrid seeds

In contrast to wheat, public studies on CHA-hybrid barley are not known by the author. Previous investigations were mainly based on small amounts of hybrid seeds produced by hand emasculatation of the seed parent or by recessive inherited genetic male sterility. Hand emasculatations of course were only possible for small experiments. The usage of recessive inherited genetic male sterility was made difficult by the complicated maintenance of the sterile seed parent (for review of proposed methods see Ramage 1983).

The only genetic male sterility, which was used to produce hybrid seeds in a commercial scale, was maintained by balanced tertiary trisomic (BBT) lines (Ramage 1983). The BBT system finally failed, since the BBT lines were adapted to Arizona, and transfer to Montana, England, Sweden, and Eastern Germany failed. In Arizona, the BBT-based hybrids had 15% to 20% higher yields under high yielding conditions than inbred varieties. But short-strawed lodging-resistant inbred cultivars, which entered the market some years later had the same yield advantage compared to older, taller inbred varieties and replaced the hybrids completely.

In 1979, Hannu Ahokas, scientist at the University of Helsinki, described a cytoplasmic male sterility and a corresponding reliable single restorer gene (Ahokas 1979). The cytoplasmic male sterility originates from a wild barley (*Hordeum spontaneum* K. Koch) strain collected in

Israel and was detected in the F₂ generation of a cross between cultivated barley (*Hordeum vulgare* L.) and the wild barley strain, in which the wild barley strain was the seed parent. Paul Bury, barley breeder in the United Kingdom, started hybrid breeding in barley based on the CMS-system in 1994, and developed adapted male and female parental lines in the following years (Longin et al. 2012). In this way six-rowed winter barley hybrids as well as parental lines suitable for multi-location evaluation for grain yield became available.

Yield performance of hybrid barley

Syngenta Seeds, currently the only company with released hybrid barley varieties, evaluated experimental hybrids and parental lines together with released hybrid and line varieties for grain yield in field trials at multiple locations and years. From the scientific point of view, these trials had the shortcoming that the first replicate was not randomized. Breeders frequently want to see genotypes in the same order across locations and therefore they do not randomize the first replicate. However, the author expects that the missing randomization of the first replicate did not substantially affect the final result. The Federal Plant Variety office (Bundessortenamt, Hannover) evaluates variety candidates three years before final decision about their registration. For several years, the registration trials also include hybrids beside inbred lines. Yield trials from Syngenta as well as from the federal plant variety office were used to investigate differences in yield performance between hybrids and lines (Mühleisen et al. 2013a, Mühleisen et al. 2014b).

In the trials of Syngenta, Mühleisen et al. (2013a) found an average midparent heterosis of 11.3%, ranging from 0.7% to 19.9%. Better-parent heterosis was slightly lower with a mean of 9.2% and ranged from -1.7% to 18.3%. Commercial heterosis was again lower with a mean of 2.7% and a range between -5.2% and 7.6%. It has to be noted that the highest yielding variety in the trial “Pelican” was probably not the highest yielding inbred strain. A fair economical comparison would require the comparison of hybrid and line varieties released in the same year or experimental hybrids and lines in a comparable stage of the breeding programs. The registration trials, analyzed by Mühleisen et al. (2014b), were therefore suitable to investigate the economical competitiveness of hybrids. We found, that on average hybrids were higher yielding than the inbred lines, but individual high-yielding inbred lines could compete with the best hybrids and partially even surpassed the best hybrids.

Three main conclusions could be drawn based on these results. First, positive heterosis for grain yield in barley existed. Second, hybrids could compete with the best inbred lines but had no constant yield advantage on average. Third, heterosis in diploid barley was not substantially higher as in hexaploid wheat hybrids, indicating that the “fixed” heterosis in allopolyploid inbred lines is not as relevant as suspected by Oettler (2005).

Comparison with earlier studies on hybrid barley

Heterosis in barley was partially estimated to be very high. Probably for the first time, Immer (1941) investigated heterosis for grain yield in barley. He reported, based on spaced plantings, an average yield increase of 27% in yield per plant. Suneson (1962) reported results of a two year experiment, where in each year three hybrids were evaluated, and expected 30% to 50% higher

yields of hybrids compared to their better parent. Many comparable studies were conducted leading to questionable results from today's perspective. Severson and Rasmusson (1968) provided evidence that the amount of heterosis depended on the plant density. They found a non-significant average midparent heterosis of 3.2% at the commercial seeding rate and up to 22.5% significant average midparent heterosis when seeding rate was reduced. The hybrid with the highest heterosis even had 47.5% mid-parent heterosis at the widest spacing. These results indicated that estimates of heterosis had validity only for the described growing conditions and the reliability of conclusions on the amount of heterosis in commercial fields depended strictly on the experimental conditions.

Very few reliable reports about heterosis in barley could be found. One is the already mentioned statement in Ramage (1983), that commercial grown barley hybrids had 15% to 20% higher yields than tall inbred varieties under high-yielding conditions in Arizona. But short inbred lines were developed, which had the same yield advantage. In addition, Matchett and Cantu (1977) reported the experiences of the Northrup King Company (Woodland, California) with hybrid barley during eight years. They used the BBT system for hybrid seed production and evaluated hybrids and inbred lines at multiple locations in yield trials. Yield of the highest yielding hybrids was mostly not significantly higher than yield of the highest yielding inbred line. Furthermore, they failed to introduce the BBT system into their germplasm. For those reasons they terminated the hybrid program.

Yield stability of hybrid barley

Dynamic yield stability of hybrid barley was investigated based on groups and based on individual genotypes (Appendix, Mühleisen et al. 2014a, Mühleisen et al. 2014b). Precise assessment of yield stability of individual genotypes is difficult, since the heritability of the dynamic yield stability parameters was low (Becker 1987, Mühleisen et al. 2014b) and reliable estimation, i.e. heritability of 0.5 or larger, requires that genotypes are evaluated in at least 40 environments. In contrast, the comparison of groups instead of individual genotypes enables detecting significant differences between groups also in data sets comprising only a few test environments (Mühleisen et al. 2014a). The reason for this is, that a group of many genotypes evaluated in a given set of environments results in a larger sample of genotype-by-environment interaction effects than an individual genotype evaluated in the same environments.

The comparison of groups revealed that hybrids in breeding trials where they were tested together with their parents, had a significantly higher dynamic yield stability (Appendix, Mühleisen et al. 2014a). In registration trials, hybrids mostly showed a significantly higher dynamic yield stability compared to six- and two-rowed inbred and on average higher yields compared to six- and two-rowed inbred lines (Appendix, Mühleisen et al. 2014b). Dynamic yield stability and yield performance of individual genotypes revealed that hybrids combined high yield performance with high yield stability (Mühleisen et al. 2014b).

The low heritability of dynamic yield stability hampers selection for yield stability. Indirect selection by means of agronomic traits, such as plant height or disease resistances was not possible, since there was no constant association between any agronomic trait and yield stability

(Mühleisen et al. 2014b). Since hybrids combined yield and yield stability on average better than six- or two-rowed inbred lines, the switch from line to hybrid breeding seems the most suitable way for sustainable increase of dynamic yield stability and yield.

In summary, hybrid barley showed a yield advantage compared to midparent performance of around 10% (Mühleisen et al. 2013a), but the highest yielding inbred lines were still competitive with the barley hybrids (Mühleisen et al. 2014b). Dynamic yield stability of hybrids was higher than or equal compared to inbred lines (Mühleisen et al. 2014a; Mühleisen et al. 2014b). Nevertheless, further efforts are required to develop barley hybrids with a significant and sustainable yield advantage over the best inbred lines. Possibly, development of genetic divergent males and females, as suggested by Merfert et al. (1988), can help to increase heterosis. This conjecture is supported by an empirical study of Fischer et al. (2010), where heterosis of CHA-based triticale hybrids increased when parental inbred lines were divided into suitable heterotic groups. Maybe the application of nitrogen fertilizer, fungicides, and growth regulators should be different for hybrids and lines in order to compare the differences in yield performance, since Syngenta Seeds GmbH recommends a hybrid-optimized crop management. Published studies on this aspect, however, are not available.

Prospect of hybrid triticale

In triticale, CHA- and CMS-based hybrids were evaluated (Oettler et al. 2005, Fischer et al. 2010, Gowda et al. 2013). In contrast to wheat, substantial differences in the amount of midparent heterosis between CHA- and CMS-based hybrids were observed.

Performance of CHA-based hybrids

Oettler et al. (2005) investigated 209 hybrids in 2002 at six German locations and Fischer et al. (2010) 210 hybrids in 2006 at five German locations. In both studies, hybrids were produced using a CHA. Midparent heterosis was comparable to the results observed in wheat and barley with 10.3% and 8.6%, respectively. Yield stability of hybrids was not explicitly examined, but the genotype-by-environment interaction variance was lower for hybrids than for lines (Oettler et al. 2005) and indicated that hybrids possess a higher dynamic yield stability.

Performance of CMS-based hybrids

The first CMS-based triticale hybrids showed a drastic reduction in midparent heterosis compared to the CHA-based hybrids and had only around 2% midparent heterosis (Gowda et al. 2013). In individual trials it can happen, that heterosis is unexpectedly low. Therefore the low heterosis of CMS-based triticale hybrids should be verified. Mühleisen et al. (2015) investigated 91 hybrids, their parental lines and additional commercial inbred lines in up to 20 environments. They observed an average midparent heterosis of 3.0% across environments. At the individual environments average midparent heterosis ranged between -4.6% and 7.2%. Therefore heterosis in CMS-based hybrids of triticale seemed to be lower indeed than in CHA-based triticale.

The CMS-inducing cytoplasm originated from *Triticum timopheevii* Zhuk. (personal communication Sigrid Weissmann, Saatzucht Dr. Hege, 2014) like the CMS cytoplasm used by Merfert et al. (1988). Despite the fact that the breeding of CMS-based triticale hybrids already started in 1994 (personnel communication Sigrid Weissmann, Saatzucht Dr. Hege, 2014), almost 20 years later hybrids showed a midparent heterosis of only 3%, whereas Merfert et al. (1987) achieved in a comparable time frame approximately 9% midparent heterosis.

The reasons for the markedly different results in triticale are unknown. Negative effects of the CMS cytoplasm were not observed in the field, but problems of the complete restoration of male fertility in the hybrid were known (Mühleisen et al. 2015). The male parents were selected for restoration of one female across multiple environments, but not for restoration of several females. From CMS-based wheat hybrids it is known that restoration can also depend on the genetic background of the female parent (Wilson and Driscoll 1983). Therefore incomplete restoration might be one reason.

The comparison with the CHA-based hybrid indicated that the reason for the low heterosis is probably associated with constraints or disadvantages of the CMS system. Therefore, a detailed research of the used CMS system, including possible negative effects of the CMS cytoplasm on grain yield and the aspect of environment and genetic background depending restoration, is urgently required.

Up to now, it cannot be said that the CMS system is the reason of the low heterosis for sure. Hans Peter Maurer, triticale breeder at the State Plant Breeding Institute of the University of Hohenheim, suspected that the high selection pressure in the development of restorer and especially maintainer lines caused unfavorable hybrid combinations (personnel communication, 2014). Normally one would expect that midparent heterosis should not be affected by the strong selection pressure, but only the commercial heterosis. It cannot be excluded, ruled out, that the specific hybrid combination would also have a low yield, when the hybrid would have a normal cytoplasm. Therefore, in addition it might be required to compare CMS-based hybrids with CHA-based hybrids possessing the same nuclear genome. The hybrids with normal cytoplasm can be easily produced by applying a CHA on the maintainer line but not on the surrounding male restorer line.

With regard to dynamic yield stability, hybrids were not as stable as inbred lines (Mühleisen et al. 2015). Compared with female parents and commercial lines dynamic yield stability of hybrids was even significantly lower. In summary, CHA-based triticale hybrids showed similar advantages as wheat and barley hybrids, but CMS-based triticale hybrids had only a marginal midparent heterosis without a general hybrid advantage in yield stability.

Relevance of dynamic stability

In the present thesis the author focused on dynamic yield stability described by parameters widely used in stability analysis (Becker and Léon 1988). As outlined in the introduction, dynamic yield stability depends strongly on the genotypes included in the analysis and is not necessarily

related with increased stress tolerance or higher adaptability to varying growing conditions. The author is not aware of any study investigating, whether vigorous and stress tolerant genotypes can be identified by dynamic stability, or if high dynamic yield stability represent an economic advantage for breeders or farmers. The higher dynamic yield stability of wheat and barley hybrids can therefore not be regarded as proof of increased stress resistance or high yield performance of hybrids in marginal environments. The author considers research on the relevance of dynamic yield stability necessary as well as the direct assessment of yield performance of hybrids under adverse growing conditions.

Conclusions

Hybrids of wheat, barley, and triticale generally showed increased yield and increased dynamic yield stability compared to inbred lines. This general advantage should not be regarded as sufficient to recommend breeding and cultivating hybrid instead of inbred varieties. Heterosis for grain yield might be slightly overestimated in ordinary field trials, since hybrids are by tendency taller and may therefore have a competitive advantage. Therefore further comparisons of hybrids and inbred lines in yield trials should consider this aspect in the experimental layout. Additional research is required to increase the economical competitiveness in all three crops, to identify and eliminate the reasons for poor performance of CMS-based triticale hybrids and to investigate the suitability of dynamic yield stability measures to identify vigorous and stress tolerant genotypes.

8. Appendix

Corrections of group-specific stability estimates in Mühleisen et al. (2014a) and Mühleisen et al (2014b).

The group comparison for the wheat, barley, and triticale experiment described in Mühleisen et al. (2014a) as well as for the five series of winter barley registration trials described in Mühleisen et al. (2014b) was done without consideration of the group-by-environment interaction effect. Mühleisen et al. (2015) found that this may cause a bias. Therefore, in addition the author of the present thesis reanalyzed the data of Mühleisen et al. (2014a) and Mühleisen et al. (2014b) with the three approaches described in Mühleisen et al. (2015). Stability analysis of the wheat, barley, and triticale experiment in Mühleisen et al. (2014a) was based on plot data and not on location means. Therefore it was in addition required to consider the design effects in the models of the approaches described in Mühleisen et al. (2015). The models for the plot data are subsequently described. For the mean data the author refers to the description in Mühleisen et al. (2015).

In the first approach the data were split into sub data sets each comprising only the data of one group. The plot data of Mühleisen et al. (2014a) were then analyzed with the following model:

$$y_{ijkl} = \mu + g_i + u_j + (gu)_{ij} + t_{jk} + r_{jkl} + \varepsilon_{ijkl},$$

where y_{ijkl} is the yield of the i th genotype in the j th location within the k th trial, within the l th replicate. The effect μ denotes the intercept and g_i the effect of the i th genotype, u_j the effect of the j th location, $(gu)_{ij}$ the genotype-by-location interaction effect of the i th genotype and j th location, t_{jk} the effect of the k th trial within the j th location, r_{jkl} the effect of the l th replicate within the k th trial and the j th location, and ε_{ijkl} is the error corresponding to y_{ijkl} . The intercept and genotypic main effects were assumed to be fixed. The other effects were assumed to be random with independent normal distribution, zero mean and variance σ_u^2 , σ_{gu}^2 , σ_r^2 , and σ_ε^2 , where σ_u^2 is the location variance, σ_t^2 the trial variance, σ_r^2 the replicate variance, σ_{gu}^2 the genotype-by-location interaction variance (i.e. stability variance), and σ_ε^2 the residual variance. The author did not fit incomplete block effects, since the split of the data set into subsets caused many missing values in the incomplete block structure of individual subsets. The stability variance (σ_{gu}^2) estimated in the dataset of a specific group is the stability variance of that group.

In the second approach the data set was not split and the genotype-by-location interaction variance (i.e. stability variance) was assumed to be heterogeneous for groups, i.e. the variance of $(gu)_{ij}$ was $\sigma_{gu(t)}^2$, where t is the group index.

In the third approach group-by-environment interaction effects were added:

$$y_{ijkl} = \mu + g_i + u_j + (au)_{ij} + (gu)_{ij} + t_{jk} + r_{jkl} + \varepsilon_{ijkl},$$

where $(au)_{ij}$ denoted the group-by-environment interaction effect of the i th group with the j th environment. Group-by-environment interaction effects were assumed to be random with independent normal distribution, zero mean and variance σ_{au}^2 .

In the first approach, the estimation of group-specific stability variance depended solely on the genotypes of the respective group. Therefore, these estimates can be regarded as independent estimates and other estimates should be rated based on them. In the wheat, barley, and triticale experiment as well as in the five series of barley registration trials the third, approach including the group-by-environment interaction effect resulted without exception in stability variances closer to those of the first approach (Tables 1 and 2). In contrast, when the group-by-environment interaction effect was not considered, the resulting stability variances partially were markedly different from those of the first approach. Therefore the author concludes that the group-by-environment interaction effect is required when genotype-by-environment interaction variances of several groups are estimated, just as the group main effect is needed, when genotypic variances of several groups are of interest.

Despite the high influence of the chosen model, the comparison between the second approach and the third approach revealed, that the final conclusions of Mühleisen et al. (2014a) and of Mühleisen et al. (2014b) remained largely unchanged. In the wheat and barley experiment, hybrids maintained a significantly lower stability variance, i.e. higher yield stability, compared to the inbred lines (Table 1). In the triticale experiment, however, stability variance of hybrids remained smaller, but the difference became non-significant. Honesty compels the author to mention that in a two-stage analysis of the wheat experiment, the stability variance of hybrid became slightly larger than stability variance of lines (results not shown). The small difference, however, was not significant ($P > 0.05$). Within the very limited time, the author was not able to figure out the reason for this notable difference between one- and two-stage analyses and therefore this issue will not be further discussed. In the barley registration trials, the superiority of hybrids in yield stability was pronounced even more, when the analysis was done with the third approach instead of the second approach (Table 2).

Table 1 Stability variance of single-cross hybrids (Hybrids) and inbred lines (Lines) of winter wheat, winter barley, and winter triticale genotypes as well as of three-way hybrids (Hybrids³) of winter barley evaluated for grain yield (Mg ha^{-1}) in multi-location trials in Germany and partially also in France and the UK. Stability variances within one experiment and the same row with no common letter were significantly different ($P < 0.05$).

Experiment	Wheat		Barley		Triticale	
	Hybrids	Lines	Hybrids	Hybrids ³	Hybrids	Lines
Approach 1	0.11	0.17	0.02	0.01	0.14	0.15
Approach 2	0.10 ^A	0.21 ^B	0.04 ^A	0.01 ^A	0.18 ^A	0.28 ^B
Approach 3	0.10 ^A	0.19 ^B	0.03 ^B	0.00 ^A	0.16 ^A	0.20 ^A
Approach 4	0.10 ^A	0.19 ^B	0.03 ^B	0.00 ^A	0.16 ^A	0.20 ^A
Approach 4*	0.10	0.21	0.06	0.05	0.33	0.20

Table 2 Stability variance of six-rowed hybrid (6RH), six-rowed lines (6RL) and two-rowed lined (2RL) of winter barley genotypes evaluated for grain yield (Mg ha^{-1}) in five series of multi-environment trials in Germany. Stability variances within one series and the same row with no common letter were significantly different ($P < 0.05$).

Series	2006 to 2008		2006 to 2008		2006 to 2008		2006 to 2008	
	6RH	6RL	6RH	6RL	6RH	2RL	6RH	2RL
Approach 1	0.11	0.21	0.17	0.13	0.34	0.22	0.09	0.20
Approach 2	0.22 ^{AB}	0.28 ^B	0.20 ^A	0.32 ^{AB}	0.42 ^B	0.25 ^A	0.13 ^A	0.23 ^B
Approach 3	0.11 ^A	0.21 ^C	0.17 ^B	0.16 ^A	0.34 ^B	0.22 ^A	0.09 ^A	0.20 ^B
Approach 4	0.11 ^A	0.21 ^C	0.17 ^B	0.14 ^A	0.34 ^B	0.22 ^A	0.09 ^A	0.20 ^B
Approach 4*	0.14	0.22	0.33	0.33	0.46	0.28	0.10	0.20

9. References

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10. Summary

Hybrids of wheat, barley, and triticale are expected to possess higher yield performance and yield stability compared to inbred lines. Assessment of yield performance as well as yield stability requires the evaluation of genotypes in plot-based yield trials across multiple environments. Evaluation of genotypes under stress conditions can be associated with increased field heterogeneity, which may result in imprecise estimates of genotypic values. The assessment of yield stability requires intensive testing in many environments, and it would be interesting to know how many test environments are required to reliably estimate yield stability.

The key objectives of the present thesis were to (1) investigate optimal strategies to analyze field trials with high error variance due to spatially varying drought stress, (2) identify the required number of test environments to precisely estimate yield stability of individual barley genotypes, and (3) examine yield performance and yield stability of wheat, barley, and triticale hybrids and lines.

Drought stress at two locations of a winter triticale trial caused increased field heterogeneity, resulting in lower heritabilities compared to the four non-stress locations. It was found that heritability could be increased by modeling incomplete block and row effects, by using visual scorings of drought stress intensity as covariates in an analysis of covariance, and by modeling a spatial covariance between adjacent plots. The most suitable model can be identified using the Akaike Information Criterion. In addition, it has to be ensured that the covariate is independent from genotypic effects and that it is linearly related with the response variable.

Dynamic yield stability of genotypes was frequently found to depend strongly on the specific set of test environments. When the genotypes were evaluated in different environments, e.g. in the following year, the ranking in yield stability could be different. This would result in a low heritability. Theoretical assumptions and empirical studies showed that heritability can be increased when the number of test environments is increased. Five series of barley registration trials with a reduced number of 16 to 27 genotypes evaluated in 39 to 45 environments were used to investigate the relationship between magnitude of heritability of yield stability and number of test environments. Based on a cross-validation approach, it was found, that at least 40 test environments should be used to obtain a heritability of 0.5. Magnitude of heritability, however, varied strongly within and between series. Therefore, depending on the respective set of environments and genotypes, more or less test environments can be needed.

Yield performance of wheat hybrids produced using chemical hybridizing agents (CHA) or cytoplasmic male sterility (CMS) was well investigated in other studies reporting around 10% midparent heterosis for grain yield. In the present thesis, CMS-based barley hybrids were compared with parental inbred lines and unrelated commercial inbred lines in breeding and registration trials. Midparent heterosis was around 10%. The comparison with commercial inbred lines in the registration trials revealed that hybrids could compete with and partially surpass outstanding inbred lines. Triticale hybrids, produced using CMS, were evaluated for grain yield at up to 20 environments with their parents and commercial inbred lines. Midparent

heterosis amounted to 3% and no hybrid outyielded the best inbred line. The low yield performance of triticales hybrids is probably associated with CMS-system, since CHA-based triticales hybrids showed a midparent heterosis around 10% in early studies, which is comparable to the midparent heterosis found in wheat and barley.

Yield stability of CHA-based wheat as well as CMS-based hybrids of barley and triticales was compared with yield stability of parental and commercial inbred lines on group level. The wheat and barley hybrids showed on average significantly higher dynamic yield stability compared to inbred lines, but the triticales hybrids did not. In the barley registration trials, hybrids had the highest dynamic yield stability on average. The CMS-based triticales hybrids, however, showed on average significantly lower dynamic yield stability as their female parents and the commercial inbred lines across 20 environments.

In conclusion, hybrids of wheat and barley possessed an increased yield potential as well as an enhanced dynamic yield stability. In contrast, the CMS-based triticales hybrids showed only marginal yield advantages coupled with low dynamic yield stability. Further research is required to increase economical competitiveness of hybrids in all three crops, to identify and eliminate the reasons for poor performance of CMS-based triticales hybrids and to investigate the suitability of dynamic yield stability measures to identify vigorous and stress tolerant genotypes.

11. Zusammenfassung

Es wird erwartet, dass Weizen-, Gerste- und Triticalehybriden eine höhere Ertragsleistung und Ertragsstabilität als die jeweiligen Inzuchtlinien besitzen. Die Erfassung der Ertragsleistung sowie der Ertragsstabilität erfordert eine Prüfung in Ertragsparzellen über mehrere Umwelten. Bei Ertragsprüfungen unter Stressbedingungen kann die Feldheterogenität erhöht sein, was zu ungenauen genotypischen Schätzwerten führen kann. Die Erfassung der Ertragsstabilität erfordert, dass die Genotypen in vielen Umwelten geprüft werden. Es wäre interessant zu wissen, wie viele Prüfumwelten benötigt werden, um genaue genotypische Schätzwerte für die Ertragsstabilität zu erhalten.

Die wichtigsten Ziele der vorliegenden Arbeit waren (1) optimale Strategien für die Auswertung von Feldversuchen, die eine niedrige Heritabilität aufgrund von räumlich variierenden Trockenstress haben, zu untersuchen, (2) die benötigte Anzahl Prüfumwelten für eine genaue Schätzung der Ertragsstabilität einzelner Gerstegenotypen zu ermitteln und (3) die Ertragsleistung und Ertragsstabilität bei Hybriden und Linien von Weizen, Gerste und Triticale zu untersuchen.

An zwei Orten eines Wintertriticaleversuchs verursachte Trockenstress eine erhöhte Feldheterogenität, was zu niedrigeren Heritabilitäten im Vergleich zu den vier Orten ohne Stress führte. Es wurde festgestellt, dass die Heritabilität erhöht werden kann, wenn im Modell unvollständige Bockeffekte und Reiheneffekte berücksichtigt werden, visuelle Boniturnoten der Trockenstressintensität als Kovariablen in einer Kovarianzanalyse verwendet werden und räumliche Kovarianzen zwischen benachbarten Parzellen modelliert werden.

Es wurde festgestellt, dass die dynamische Ertragsstabilität von Genotypen stark von der spezifischen Gruppe an Prüfumwelten abhängt. Wenn die Genotypen in anderen Umwelten geprüft werden, z.B. im darauffolgenden Jahr, ist die Reihenfolge in der Ertragsstabilität anders. Das spiegelt sich in einer niedrigen Heritabilität wieder. Theoretische Annahmen und empirische Untersuchungen zeigen, dass die Heritabilität erhöht werden kann, wenn die Anzahl Prüfumwelten erhöht wird. Fünf Zulassungsversuchsserien der Gerste mit einer reduzierten Zahl von 16 bis 27 Genotypen, die in 39 bis 45 Umwelten geprüft worden sind, wurden verwendet, um die Beziehung zwischen der Höhe der Heritabilität und der Anzahl Prüfumwelten zu untersuchen. Basierend auf einem Kreuzvalidierungsansatz wurde festgestellt, dass mindestens 40 Prüfumwelten verwendet werden sollten, um eine Heritabilität von 0,5 zu erhalten. Die Höhe der Heritabilität schwankt allerdings stark - sowohl innerhalb der Serien als auch zwischen den Serien. Daher können in Abhängigkeit der jeweiligen Umwelten und Genotypen mehr oder weniger Prüfumwelten benötigt werden.

Die Ertragsleistung von Weizenhybriden, die mit Hilfe von Gametoziden oder der zytoplasmatisch-männlichen Sterilität (englisch cytoplasmatic male sterility, CMS) produziert worden sind, wurde in anderen Studien ausführlich untersucht. Für Kornertrag wurde eine Midparentheterosis von ungefähr 10% gefunden. In der vorliegenden Arbeit wurden CMS-basierte Gerstehybriden mit elterlichen Inzuchtlinien und unverwandten kommerziellen Inzuchtlinien in Züchtungsversuchen und Zulassungsversuchen. Die Heterosis lag bei

ungefähr 10%. Der Vergleich mit kommerziellen Inzuchtlinien in den Zulassungsversuchen zeigte, dass die Hybriden mit den besten Inzuchtlinien konkurrieren und diese auch teilweise übertreffen können. CMS-basierte Triticalehybriden wurden in bis zu 20 Umwelten mit ihren Eltern und kommerziellen Inzuchtlinien auf Kornertragsleistung geprüft. Die Heterosis betrug 3% und keine Hybride übertraf die beste Inzuchtlinie im Ertrag. Die schwache Ertragsleistung der Triticalehybriden hängt vermutlich mit dem CMS-System zusammen, da Gametozid-basierte Triticalehybriden in früheren Studien eine Heterosis um die 10% gezeigt haben, was vergleichbar ist mit der Heterosis, die bei Weizen und Gerste gefunden wurde.

Die Ertragsstabilität von Gametozid-basierten Weizenhybriden sowie CMS-basierten Gerste- und Triticalehybriden wurde mit der Ertragsstabilität der Elterlinien und anderen kommerziellen Inzuchtlinien auf Gruppenebene verglichen. Die Weizen- und Gerstehybriden zeigten im Gegensatz zu Triticalehybriden im Schnitt eine signifikant höhere dynamische Ertragsstabilität als die Inzuchtlinien. In den Zulassungsversuchen der Gerste hatten die Hybriden im Schnitt die höchste dynamische Ertragsstabilität. Allerdings zeigten die CMS-basierten Triticalehybriden über 20 Umwelten eine signifikant niedrigere dynamische Ertragsstabilität als ihre Mutterlinien und als die kommerziellen Inzuchtlinien.

Zusammengefasst betrachtet besitzen Weizen und Gerstehybriden ein erhöhtes Ertragspotential sowie eine erhöhte dynamische Ertragsstabilität. CMS-basierte Triticalehybriden zeigten nur marginale Ertragsvorteile verbunden mit einer niedrigen Ertragsstabilität. Weitere Forschung ist nötig, um die wirtschaftliche Konkurrenzfähigkeit der Hybriden in allen drei Kulturarten zu verbessern, um die Gründe der schwachen Leistung der CMS-basierten Triticalehybriden zu identifizieren und eliminieren und um die Eignung dynamischer Stabilitätsmaße für die Identifizierung wüchsiger und stresstoleranter Genotypen zu untersuchen.

13. Acknowledgments

I would like to thank Prof. Dr. Jochen C. Reif and Prof. Dr. Hans-Peter Piepho that they supervised and supported me during writing my doctoral thesis. Their support comprised, among other things, statistical explanations, linguistic corrections and improvements, structuring contents and improving comprehensibility as well as references to appropriate literature. In discussions and written or verbal contact new aspects and ideas could be developed and/or communicated.

Prof. Dr. Jochen C. Reif already supported me during my Bachelor thesis and continued his support during my Master study and thesis and finally during my doctoral thesis. He was not only an excellent supervisor, who brought me forward professionally as well as methodically, but also a very friendly person and it was pleasant for me to work with him.

Prof. Dr. Hans Peter Piepho was lecturer of several statistical courses and I benefited greatly from his lectures and scripts. Also his and his staffs' statistical consultancy helped me to understand and apply statistical procedures.

Sincere thanks to Prof. Dr. H. Friedrich Utz for his statistical consultancy, helpful discussions, and references to relevant literature. I also want to thank Dr. Hans Peter Maurer and his assistants for organizing and conducting the field trials. Furthermore I thank Dr. Hans Peter Maurer for his support in using the statistical software R as well as for discussions about hybrid breeding in triticale.

Many thanks go to Joachim Lipsius for linguistic corrections and improvements of my doctoral thesis.

Further thanks go to numerous members of the University of Hohenheim who made my stay in Hohenheim pleasant and supported me in my work. It would go beyond the scope of these acknowledgements to name all persons and their specific contribution.

My work was supported by BMELV/BLE within the „Züchtung von Triticalesorten für extreme Umwelten – eine Frage des Sortentyps?“ project (Grant ID: 2814502410) and by BMBF within the HYWHEAT project (Grant ID: FKZ0315945D). I thank the German government as well as the German taxpayers for providing the funds.

14. Curriculum vitae

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