

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

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Abstract

Key message We present experimental data for wheat, barley, and triticale suggesting that hybrids manifest on average higher yield stability than inbred lines.

Abstract Yield stability is assumed to be higher for hybrids than for inbred lines, but experimental data proving this hypothesis is scarce for autogamous cereals. We used multi-location grain yield trials and compared the yield stability of hybrids versus lines for wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and triticale (\times *Triticosecale* Wittmack). Our study comprised three phenotypic data sets of 1,749 wheat, 96 barley, and 130 triticale genotypes, which were evaluated for grain yield in up to five contrasting locations. Yield stability of the group of hybrids was compared with that of the group of inbred lines estimating the stability variance. For all three crops we observed a significantly ($P < 0.05$) higher yield stability of hybrids compared to lines. The enhanced yield stability of hybrids as compared to lines represents a major

step forward, facilitating coping with the increasing abiotic stress expected from the predicted climate change.

Introduction

In recent years, hybrid breeding in the autogamous cereals wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and triticale (\times *Triticosecale* Wittmack) has been of increasing interest. General advantages of hybrid compared to line varieties are higher yields due to maximum exploitation of heterosis, the possibility of combining dominant genes, and high returns of investments for breeding companies due to higher seed prices and higher sales of certified seeds (Longin et al. 2012). A further frequently claimed advantage is higher yield stability of hybrids compared to inbred lines (e.g., Longin et al. 2012).

Becker and Leon (1988) suggested grouping the measures of yield stability into static and dynamic approaches. Static measures define a genotype as yield stable if the performance does not change across environments. The major drawback of the static concept is that genotypes are preferred which make no use of favorable environmental conditions in terms of enhanced yield. This aspect is taken into account in the dynamic concept where genotypes are considered as stable if they show only marginal deviations from the general response of genotypes to growing conditions.

Several reviews were published discussing in detail the advantages and disadvantages of the different dynamic measures for yield stability (Lin et al. 1986; Becker and Leon 1988; Piepho 1998). One popular measure of dynamic yield stability estimates the variance of genotype-by-environment interactions specific for every genotype (Becker and Leon 1988). Implementations have been suggested by

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Wricke (1962; denoted as ecovalence) and Shukla (1972; denoted as stability variance). Alternatively, the regression of the genotypic performance on environmental yield levels has been suggested to describe the dynamic yield stability (Finlay and Wilkinson 1963). The variance of deviations from the linear regression (Eberhart and Russell 1966) is considered as measure of yield stability and is closely related to the ecovalence and stability variance (Becker 1981; Pham and Kang 1988; Piepho and Lotito 1992).

Summarizing the results of several experimental studies, Léon (1994) concluded that in outcrossing species, the yield stability of hybrids is higher than that of lines. For autogamous crops such as wheat, barley, and triticale the results are contrasting, ranging from higher yield stability of hybrids versus lines (Borghini et al. 1988; Oury et al. 2000; Oettler et al. 2005; Gowda et al. 2010; Mühleisen et al. 2013a) to no differences in yield stability (Borghini and Perenzin 1990; Peterson et al. 1997; Bruns and Peterson 1998; Koemel et al. 2004). It is important to note that comparison across studies has to be interpreted carefully because different approaches have been applied to quantify yield stability. Furthermore, the minimum number of locations needed to assess yield stability of single genotypes is high with empirical estimates suggesting using data of at least ten locations (Becker 1987). Alternatively, groups of lines and hybrids can be contrasted leading to a reduced number of locations needed to assess yield stability (e.g., Rowe and Andrew 1964; Léon 1994).

We re-analyzed three published data sets of wheat, barley, and triticale to investigate the yield stability of hybrids versus lines. All experiments comprised a large number of hybrids and lines evaluated for grain yield performance in multi-location field trials. We arranged genotypes into genotypic groups and estimated stability variance specific for each group.

Materials and methods

Our study is based on phenotypic data from three published experiments, where hybrids and inbred lines were evaluated for grain yield in multi-location field trials. The first data set comprised 1,749 winter wheat genotypes phenotyped in 2012 at five locations (Longin et al. 2013). The second experiment included data from 96 six-rowed winter barley hybrids and inbred lines evaluated in 2011 at five locations (Mühleisen et al. 2013a). The third experiment comprised data from 130 winter triticale hybrids and inbred lines tested in 2011 at five locations (Mühleisen et al. 2013b).

Wheat experiment

The wheat experiment included 1,604 experimental single-cross hybrids of winter wheat (*Triticum aestivum* L.), their 15 male parental lines, their 120 female parental lines (Fig. 1), 2 hybrid varieties (*As de Coeur*, *Hystar*), and 8

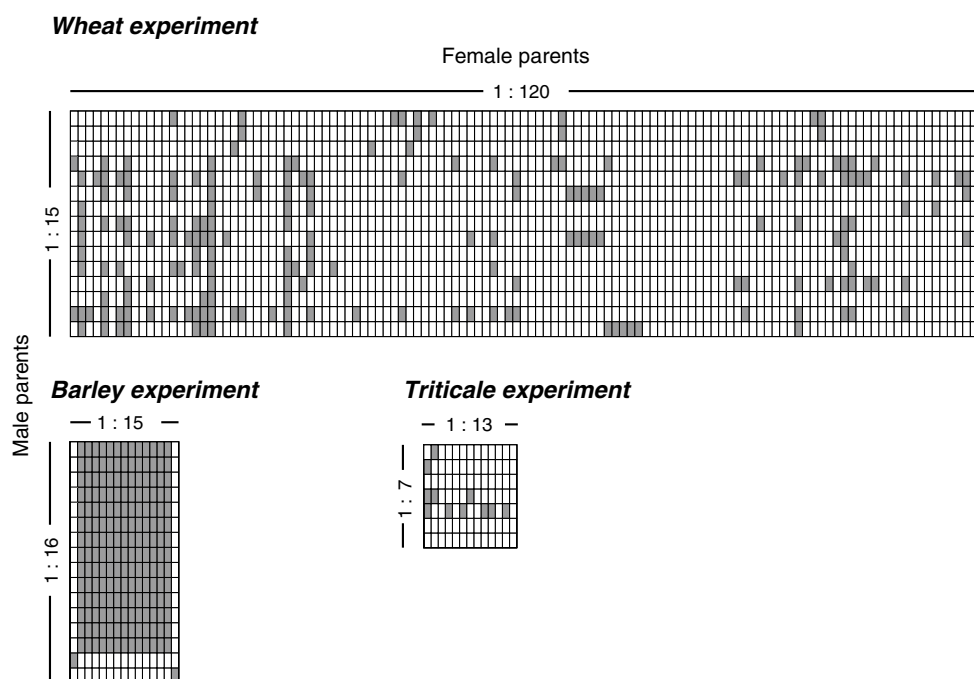


Fig. 1 Crossing scheme of female and male parents used to produce the experimental hybrids for the wheat, barley, and triticale experiments (white boxes indicate the presence of hybrids; gray boxes indicate the absence of hybrids)

line varieties (*Colonia, Genius, JB Asano, Julius, Kredo, Tabasco, Tobak, Tuerkis*). Hybrids were produced in the following way: the female parents were emasculated by chemical hybridizing agents (CHAs) and pollinated with surrounding male lines, which were not sprayed with CHAs. In 2011/2012, all genotypes were tested in partially replicated field trials at five locations in Germany (Table 1). At each location, three separate trials were performed. The experimental design of the trials was a partially replicated alpha design. Parents and 29 % of the experimental hybrids were replicated two times, but the remaining hybrids were not replicated (Longin et al. 2013). The two hybrid and eight line varieties were replicated two times in each of the three separate trials to connect the trials. In February 2012, winter crops were affected by severe frost damage in Germany. In the wheat experiment, plots of several genotypes at multiple locations were thinned out up to loss of all plants due to frost damage. We treated those plots as missing values. For that reason, genotypes were tested on average at around four locations. Plot size ranged across locations between 5 and 7.4 m², and row distance between 12 and 15 cm. The number of rows was either 8 or 10, and seed density ranged between 230 and 290 seeds m⁻². There was no difference in seed density between hybrids and lines.

Barley experiment

The experiment comprised 41 experimental single-cross hybrids, 15 experimental three-way hybrids, 15 female

parental lines, 16 male parental lines (Fig. 1), 4 hybrid varieties (*Hobbit, SY Leoo, Volume, Galation*), and 5 line varieties (*Cervoise, Escadre, Lomerit, Pelican, Souleyka*) of six-rowed winter barley (*Hordeum vulgare* L.). The single-cross hybrids were produced by open pollination of a female line that is male sterile due to cytoplasmic male sterility (CMS) with the surrounding male restorer line. For the three-way hybrids, the female parent was a male sterile single-cross hybrid. All hybrids and parental lines belonged to the European barley breeding program of Syngenta Seeds Ltd, Cambridge, UK. All genotypes were tested in field trials 2010/2011 at five locations (Table 1). Due to limited seed availability or country-specific adaptation, some genotypes were not tested at all locations. For that reason, single-cross hybrids were tested on average only at 4.5 locations, three-way hybrids on average at 4.9 locations, and lines on average at 4.6 locations. At each location, two separate trials were laid out in a 7 × 7 lattice with two replicates. The trials were connected by common genotypes. Plot size ranged across locations between 7.6 and 15.0 m², row distance between 15 and 18 cm, and number of rows between 7 and 10. Seed density ranged for hybrids between 200 and 225 seeds m⁻² across locations and for lines between 275 and 325 seeds m⁻².

Triticale experiment

In total, 80 experimental single-cross hybrids and 50 lines of winter triticale (×*Triticosecale* Wittmack) were tested at five locations in 2010/2011 (Table 1). The lines comprised

Table 1 Description of the locations used in the wheat, barley, and triticale experiment

Location	Year	Soil type	Mean grain yield (Mg ha ⁻¹)	Date of heading	Repeatability
Wheat experiment					
Böhnshausen	2012	Sandy loam	10.89	2 June	0.58
Hadmersleben	2012	Silt loam	11.14	23 May	0.41
Harzhof	2012	Sandy loam	12.41	31 May	0.53
Hohenheim	2012	Sandy loam	9.81	24 May	0.50
Seligenstadt	2012	Silty clay loam	11.31	26 May	0.52
Barley experiment					
Andelu	2011	Silt	8.01	2 May	0.88
Bad Salzuflen	2011	Loam	8.38	12 May	0.91
Buzancais	2011	Clay	6.01	25 April	0.77
Horncastle	2011	Sandy loam	8.57	17 May	0.77
Spickendorf	2011	Loam	7.57	13 May	0.79
Triticale experiment					
Stuttgart	2011	Silt loam	9.85	13 May	0.81
Issoudun	2011	Loamy sand	5.12	4 May	0.72
St. Johann	2011	Sandy loam	7.57	24 May	0.92
Ranzin	2011	Sandy loam	8.63	25 May	0.86
Weimar	2011	Loam	8.25	21 May	0.92

16 Central European triticale varieties (*Agostino*, *Agrano*, *Amarillo 105*, *Benetto*, *Cando*, *Cosinus*, *Grenado*, *Korpus*, *Madilo*, *Moderato*, *Sequenz*, *SW Talentro*, *Tarzan*, *Ticino*, *Tulus*, and *Vuka*), 14 lines in registration, 13 female parental lines, and 7 male parental lines (Fig. 1). Two female parental lines were not tested at Issoudun. The single-cross hybrids were produced with the use of CMS in the same way as in the barley experiment. Genotypes were evaluated in one trial at each location. The experimental design was an alpha design with block size 10 and two replicates. Plot size ranged between 5 and 11.2 m², row distance between 13.2 and 18 cm, and row number between 6 and 9. Seed density was the same for hybrids and lines. In Ranzin, seed density was 250 seeds m⁻², and at the other locations 280 seeds m⁻².

Statistical analysis

For analysis of all experiments, the genotypes were divided into genotypic groups based on their level of heterozygosity and heterogeneity. For the wheat and triticale experiment, the genotypic groups were lines and single-cross hybrids. In the barley experiment, there was an additional genotypic group consisting of three-way hybrids. For each genotypic group, a separate variance for genotype-by-location interactions was assumed. The statistical model for the analysis can be described with the following mixed model:

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

where y_{ijklm} is the yield of the i th genotype in the j th location within the k th trial, within the l th replicate within the m th incomplete block, and ε_{ijklm} is the error corresponding to y_{ijklm} . 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, b_{jklm} the effect of the m th incomplete block within the l th replicate, the k th trial and the j th location, and ε_{ijklm} the error corresponding to y_{ijklm} . The intercept and genotypic main effects were assumed to be fixed. The other effects were assumed to be random with independent distribution, zero mean, and variance σ_u^2 , $\sigma_{gu(q)}^2$, σ_t^2 , σ_r^2 , σ_b^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_b^2 the incomplete block variance, $\sigma_{gu(q)}^2$ the genotype-by-location interaction variance of the q th genotypic group (henceforth denoted as stability variance), and σ_ε^2 the residual variance. The stability variance can be interpreted analogously to the stability variance described by Shukla (1972) with the difference that the above-described stability variance is specific for genotypic groups, whereas Shukla's stability variance is specific for individual genotypes. For the triticale experiment, where only one trial per location was

performed, the trial effect was dropped. Variance components were estimated using restricted maximum likelihood (REML). Significance of differences between stability variances of the genotypic groups were tested with a likelihood ratio test, where the reduced model assumes a common stability variance for the two groups under comparison, but the full model a separate one for each.

In addition, individual locations were analyzed separately to describe the environmental diversity in more detail. The used model is a sub-model of the model described above and can be written in the following way:

$$y_{iklm} = \mu + g_i + t_k + r_{kl} + b_{klm} + \varepsilon_{iklm}.$$

The model differs from the above model only in dropping the location main effects and corresponding interactions. For triticale, the trial effect was dropped from the model because there was only one trial at each location. The best linear unbiased estimators (BLUEs) of genotypes were computed. The mean of all genotypic BLUEs was used as the location mean. For estimation of the genotypic variance (σ_g^2), the model was fitted assuming random genotypic effects. Broad-sense heritability of an individual location, henceforth denoted as repeatability, was calculated with the following formula (Piepho and Möhring 2007):

$$\text{repeatability} = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\overline{vd}}{2}},$$

where \overline{vd} is the mean variance of a difference of two adjusted genotype means (BLUEs).

Statistical analyses were performed using the software package ASReml-R 3.0 (Butler et al. 2009).

Weather data

Data of temperature (°C), precipitation (mm), global radiation (kJ cm⁻²), and soil moisture in percentage of usable field capacity were provided by the German Meteorological Service (Deutscher Wetterdienst) from a nearby weather station. Soil moisture in percentage of usable field capacity was calculated for the soil layer 0–60 cm assumed sandy loam soil texture and growth of winter wheat on the soil. This parameter, however, could be only provided for the German locations. For the location Horncastle in the UK, the German Meteorological Service was not able to provide suitable data. Therefore, we used temperature and precipitation data provided by the local cooperation partner (Syngenta Seeds Ltd).

Results

The locations of all three experiments, where the genotypes were evaluated, were diverse with respect to the

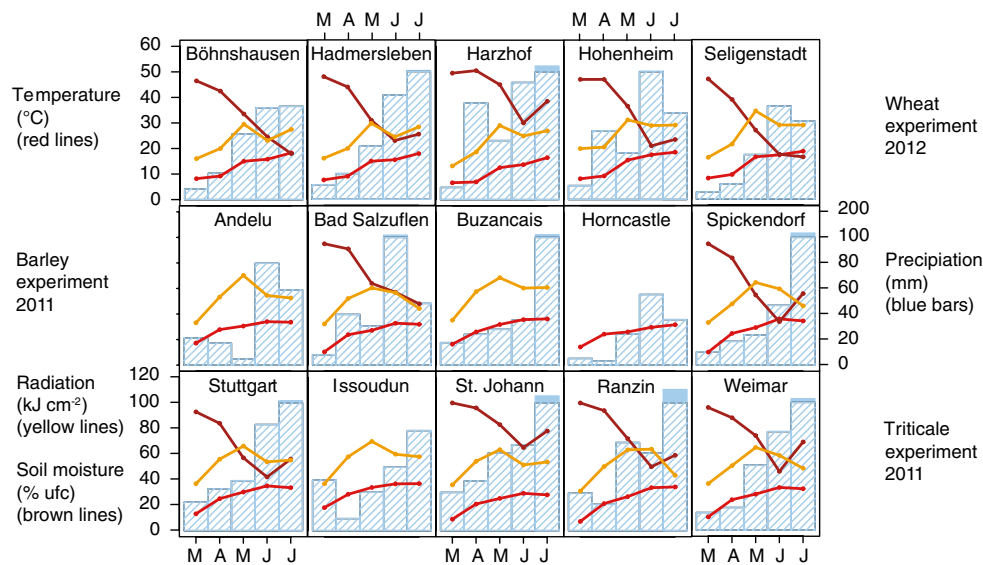


Fig. 2 Monthly average temperature (°C), precipitation total (mm), global radiation total (kJ cm⁻²), and average soil moisture in % of usable field capacity (ufc) for the months March (M), April (A), May (M), June (J), and July (J) in 15 European environments

temperature, precipitation, soil moisture, and global radiation profiles (Fig. 2). The differences among locations were especially pronounced in the year 2011, where some locations were affected by drought stress during flowering time, while water stress was low in the remaining locations. In addition to the differences in the weather conditions, locations varied also with respect to the soil type and earliness of the genotypes (Table 1). The variation in environmental conditions was reflected by large differences in average grain yield observed for the single locations. For wheat and barley, the differences between the lowest and highest yielding location were 2.6 Mg ha⁻¹. For triticale, the difference was even more pronounced and amounted to 4.7 Mg ha⁻¹.

The repeatabilities of the grain yield tests were high for the barley and triticale experiments (Table 1). In the wheat experiment, repeatabilities were lower, since the trials were only partially replicated. Repeatability values ranged from 0.41 to 0.58 for the wheat experiment, from 0.77 to 0.91 for the barley experiment, and from 0.72 to 0.92 for the triticale trials.

For the wheat, barley, and triticale experiments, we found an increased yield stability of hybrids compared to lines, as illustrated by lower stability variances (Fig. 3). Likelihood ratio tests revealed that stability variance of lines and single-cross hybrids were significantly different for the wheat experiment ($P < 0.001$), barley experiment ($P = 0.013$), and triticale experiment ($P = 0.020$). In the barley experiment, stability variances of lines and three-way hybrids were significantly different ($P < 0.001$), and for the stability variances of single-cross and three-way hybrids we found a slightly significant difference ($P = 0.094$).

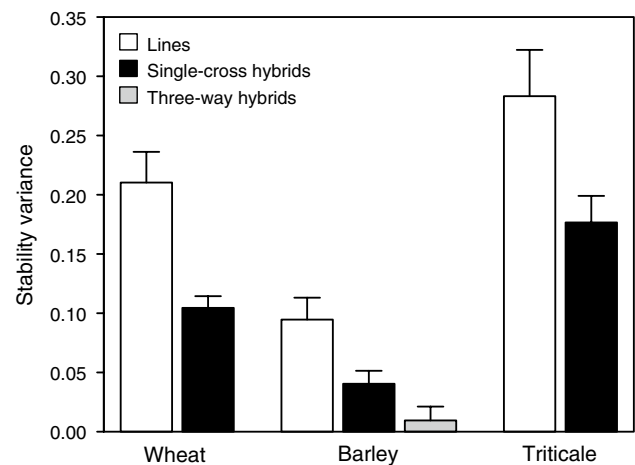


Fig. 3 Stability variances and corresponding standard errors of wheat, barley, and triticale lines, single-cross hybrids, and three-way hybrids evaluated for grain yield (Mg ha⁻¹) in multi-location field trials

Discussion

Hybrids showed higher yield stability than lines

Diverse environments are crucial to assess yield stability with high accuracy. The locations used for all three experiments varied widely with respect to the growing conditions and geographic regions despite being part of the target mega-environment of the varieties (Table 1; Fig. 2). In the barley and triticale experiment, for instance, subgroups of locations were affected by low precipitation, high temperature, and intensive radiation (Fig. 2). The stress conditions

occurring in the subgroups of environments did not lead to a severe decrease in the repeatability of the grain yield estimates of the affected single locations (Table 1) as observed in a previous study in rye (Hübner et al. 2013). Therefore, we concluded that the set of environments offers great potential to investigate yield stability for the three autogamous crops, wheat, barley, and triticale.

Previous studies emphasized the need to test genotypes in a high number of environments (Becker 1987; Cole et al. 2009) to precisely determine the yield stability of single genotypes. Piepho (1998) recommended, based on theoretical considerations, 50 to 200 environments to estimate yield stability. Becker (1987) proposed 10 to 15 environments, which are substantially less than those suggested by Piepho (1998), but still at an order of magnitude hard to meet if large numbers of genotypes are tested. The considerations of Piepho (1998) and Becker (1987) were focused on the comparison of individual genotypes. If, on the contrary, only groups of genotypes are compared, as in the study of Rowe and Andrew (1964), fewer environments are required to precisely contrast the yield stability compared to studies focusing on the yield stability of single genotypes. This is because a group of a larger number of genotypes yields a large sample of genotype–environment effects, so that the corresponding variance can be estimated with better precision than for individual genotypes. Consequently, the use of diverse environments and the comparison of groups rather than individual genotypes meant that, despite a relatively small number of environments, we were able to establish substantially and significantly ($P < 0.05$) higher yield stability of the hybrids compared to the lines across all three crops (Fig. 3).

Comparison of the wheat experiment with previous results

In previous experiments, yield stability was either measured for groups of lines and hybrids (Borghi et al. 1988; Oury et al. 2000; Gowda et al. 2010) or based on individual genotypes (Borghi and Perenzin 1990; Peterson et al. 1997; Bruns and Peterson 1998; Oury et al. 2000; Koemel et al. 2004). For the latter, however, yield stability was also averaged across genotypes to determine the grain yield stability of the groups of lines and hybrids. This is comparable to the direct estimation of group-specific yield stability and, consequently, the comparison among the above-mentioned studies is reasonable.

Interestingly, previous reports always observed higher yield stability for hybrids than for lines when measuring the yield stability based on the stability variance (Borghi et al. 1988; Oury et al. 2000; Gowda et al. 2010). In contrast, studies using the regression approach suggested by Eberhart and Russell (1966) observed no differences between hybrids and lines in the variance of deviations from linear regression (Borghi and Perenzin 1990; Peterson

et al. 1997; Bruns and Peterson 1998; Koemel et al. 2004). This finding is surprising, because in empirical studies with different crops, the variance of deviations from regression was closely related to the stability variance (Becker 1981; Pham and Kang 1988; Piepho and Lotito 1992). This stimulated us to investigate the implementation of the regression approach in the studies of Borghi and Perenzin (1990), Peterson et al. (1997), Bruns and Peterson (1998), as well as Koemel et al. (2004) in more detail.

In the regression approach, grain yield of each genotype in the individual environments is regressed on an environmental index. The environmental index is defined as the average response of all genotypes in the particular environment. Therefore, the regression approach requires that all genotypes are tested in each environment. The crucial task is to determine the environmental index in experimental studies. Peterson et al. (1997) and Bruns and Peterson (1998) used the mean grain yield of lines as a measure of the environmental index. This definition of the environmental index considered only the response of lines, but not of hybrids. Assuming there were general differences in the response between hybrids and lines, deviations from linear regression will be overestimated for hybrids, but underestimated for lines. Re-analysis of the triticale experiment with the regression approach defining the environmental index as (1) the mean performance of the lines, (2) the mean performance of hybrids, (3) the overall mean, and (4) the mean of line mean and hybrid mean confirmed our suspicion (Supplementary Information). This shortcoming is also expected for the study of Borghi and Perenzin (1990), where the mean yield of a neighboring variety trial—most likely comprising solely inbred lines—was used as environmental index, and for the study of Koemel et al. (2004), where the mean yield of two checks—most likely inbred lines—was used. Hence, we consider the definition of the environmental index as the most likely reason that previous studies using the regression approach found no increased yield stability for hybrids as opposed to our findings. It would be of great interest to re-analyze the previous experiments estimating the environmental index as a mean of line mean and hybrid mean to investigate whether superiority in yield stability of wheat hybrids as compared to lines could be confirmed on an even broader basis.

Comparison of the barley and triticale experiment with previous results

In contrast to wheat, only a very limited number of studies investigated the yield stability of barley and triticale hybrids and lines. Mühleisen et al. (2013a) reported the first evaluation of barley hybrids and lines using grain yield trials conducted on a plot basis at multiple environments. The experimental design was highly unbalanced across

years and, therefore, we used a relatively orthogonal subset of the data published by Mühleisen et al. (2013a) to investigate the yield stability of hybrids versus lines. We additionally considered the yield data for three-way hybrids. We observed for the subset that yield stability was more pronounced for hybrids as compared to lines. This is in accordance with the unbalanced full data set suggesting that unbalanced data sets of breeding programs are also valuable to investigate the yield stability of hybrids and lines in barley. In addition, in the present study we found for the three-way hybrids higher yield stability compared to single-cross hybrids. Three-way hybrids combine heterozygosity with heterogeneity, which explains the higher yield stability in accordance with previous findings in allogamous crops (for review, see Smithson and Lenne 1996).

Oettler et al. (2005) reported grain yield data for 62 lines and their resulting 209 factorial single-cross hybrids. Their results also revealed a smaller genotype-by-location interaction variance for the group of hybrids than for the group of lines. Consequently, the higher yield stability observed for triticale hybrids as compared to lines in our study is also in accordance with previous findings.

Conclusions

Our findings clearly suggest that wheat, barley, and triticale hybrids are on average more yield stable than inbred lines. Consequently, switching from line to hybrid breeding allows tackling a broader target environment with one breeding program. The enhanced yield stability of hybrids as compared to lines represents a major step forward facilitating coping with the increasing abiotic stress expected from the predicted climate change. However, the results need to be confirmed by future studies, including several years and considering the different crop managements recommended for hybrids and lines.

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Conflict of interest The authors declare that they have no conflict of interest.

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