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ORIGINAL PAPER

Long-term perspective of hybrid versus line breeding in wheat based on quantitative genetic theory

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Abstract

Key message **The predicted future yield potential of hybrids was competitive with lines in the near future, but on a long term the competitiveness of hybrids depends on a number of factors.**

Abstract The change from line to hybrid breeding in autogamous crops is a recent controversial discussion among scientists and breeders. Our objectives were to employ wheat as a model to: (1) deliver a theoretical framework for the comparison of the selection gain of hybrid versus line breeding; (2) elaborate key parameters affecting selection gain in this comparison; (3) and evaluate the potential to modify these parameters in applied breeding programs. We developed a prediction model for future yield potential in both breeding methods as the sum of the population mean and the expected selection gain. The expected selection gain was smaller in hybrid than in line breeding and depended strongly on the hybrid seed production costs and the genetic variance available in hybrid versus line breeding. Owing to heterosis, the predicted future yield potential of hybrids was competitive with lines in the near future. On a long term, however, the competitiveness of hybrid compared to line breeding is questionable and depends on a number of factors. However, market specifications and political reasons might justify the current high interest in hybrid wheat breeding.

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Introduction

Hybrid breeding is a remarkable success story in several allogamous crop species. The main advantages of hybrid as compared to line varieties are increased trait values due to the exploitation of heterosis (Shull 1908), larger yield stability especially in marginal environments (Hallauer et al. 1988), the ease of stacking dominant major genes (Edwards 2001), and a larger return of investment for seed companies due to the built-in plant variety protection by inbreeding depression (Edwards 2001). The decision to start a hybrid breeding program depends on the competitiveness of hybrid versus lines varieties (Oettler et al. 2005). A major prerequisite is a stable yield surplus of hybrids to justify their higher seed production costs. Two recent studies based on a large number of hybrids evaluated across a high number of test locations reported a 1.00–1.86 t per ha yield advantage of the best hybrid compared to the highest yielding line variety (Gowda et al. 2012; Longin et al. 2013). Thus, hybrids appear to be a competitive alternative to line varieties in wheat.

The long-term competitiveness of hybrid versus line breeding, however, depends largely on the expected selection gain of both methods (Longin et al. 2012). Selection gain is strongly affected by variance components and a prerequisite for the estimation of the selection gain are therefore robust estimates of the amount of variance due to genotype and genotype-by-location interaction for line as compared to hybrid breeding. Moreover, detailed knowledge of the correlation between line per se and hybrid performance is required to optimize hybrid breeding schemes (Longin et al. 2007). For wheat, valuable estimates of these parameters were recently published (Gowda et al. 2012; Longin et al. 2013). This motivated us to compare line versus hybrid breeding in wheat based on a model study combining heterosis with the expected selection gain. Our objectives were to: (1) deliver a theoretical framework for the comparison of the selection gain of hybrid versus line breeding; (2) elaborate key parameters affecting selection gain in this comparison; (3) and evaluate the potential to modify these parameters in applied breeding programs.

Materials and methods

Line and hybrid breeding were compared assuming breeding schemes based on doubled haploid (DH) lines, which were preselected for traits with high heritability, i.e., disease resistances, plant height, flowering time, but not for yield. A number of N_1 DH lines are then evaluated for grain yield in yield trials in 2 years for line per se and hybrid performance, respectively. We further assume that the production of the DH lines requires 3 years and consequently the line breeding scheme has a total length of 5 years (Y_L) to finish one breeding cycle. In hybrid breeding, 1 year for testcross seed production by a chemical hybridization agent is required before yield testing extending the hybrid breeding scheme to 6 years (Y_H).

For the comparison of breeding methods, Schnell and Utz (1975) developed the 'usefulness' concept (for details see Bernardo 2002). Briefly, the usefulness combines information of the population mean and the genetic variance in that population both prerequisites to maximize the gain from selection. Adopting this usefulness concept, we compared hybrid versus line breeding by the predicted future yield potential (PFYP), which for line breeding is

$$\mathrm{PFYP}_L = \mu_L + {}^{\Delta G_L}\!/_{Y_L} \tag{1}$$

and for hybrid breeding

$$\mathrm{PFYP}_H = \mu_H + {}^{\Delta G_H}\!/_{Y_H} = \mu_H + {}^{\Delta G_L}\!/_{Y_L} \times {}^{\mathrm{Eff}}\!/_{100}, \tag{2}$$

where μ is the respective mean of the breeding populations (Table 1), ΔG the respective selection gains, and Eff the relative efficiency of hybrid versus line breeding. Eff was defined based on the selection gain formula of Cochran (1951) as

$$\mathrm{Eff} = 100\,\%\frac{\Delta G_H/Y_H}{\Delta G_L/Y_L} = 100\,\%\frac{i_H h_H \sigma_{G_H} Y_L}{i_L h_L \sigma_{G_L} Y_H}, \tag{3}$$

where i is the selection intensity, h the square root of the heritability and σ_G the square root of the genetic variance in line and hybrid breeding, respectively. It must be noted, that in recurrent hybrid breeding only the variance due to general combining ability (GCA) can be exploited, while the variance due to specific combining ability (SCA) acts as a masking variance (for details see Longin et al. 2007). The selection intensity is a function of $\alpha =$ (number of selected lines)/(number of tested lines) and the heritability was defined as $h^2 = \sigma_G^2/(\sigma_G^2 + \frac{\sigma^2_{G\times\mathrm{Loc}}}{L} + \frac{\sigma^2_{\mathrm{error}}}{L})$ (cf. Longin et al. 2006), where $\sigma^2_{G\times\mathrm{Loc}}$ and $\sigma^2_{\mathrm{error}}$ were the variances due to genotype × location interaction and residual error, respectively, and L the number of test locations used to screen the N_1 DH lines. We set the number of replications per location to one, which refers to their optimum allocation for fixed budgets (cf. Becker 1993). This is due to the much larger impact of increased L on the heritability compared with increased number of replications (cf. Becker 1993).

Table 1 Input variables underlying this study based on experimental data for grain yield (t per ha; Longin et al. 2013)

	Line breeding	Hybrid breeding
σ^2_G	0.141	0.057
$\sigma^2_{G\times\mathrm{Loc}}$	0.223	0.119
$\sigma^2_{\mathrm{error}}$	0.244	0.244
μ	9.70	10.70
No. of years	5	6

σ^2_G, genetic variance; $\sigma^2_{G\times\mathrm{Loc}}$, variance due to genotype × location interaction; $\sigma^2_{\mathrm{error}}$, variance due to residual error; no. of years, number of years required in the breeding scheme to finish one breeding cycle

Variance components (Table 1) were taken from a vast experimental study comprising 1,604 hybrids and their 135 parental lines phenotyped for grain yield in 11 German locations (for details see Longin et al. 2013). With these estimates, Eq. 3 can be simplified to

$$\mathrm{Eff} = 100\,\%\frac{i_H h_H \sigma_{G_H} Y_L}{i_L h_L \sigma_{G_L} Y_H} = 53\,\%\frac{i_H h_H}{i_L h_L} \tag{4}$$

indicating the superiority of line compared to hybrid breeding as long as selection intensities and heritabilities are similar in both breeding schemes.

We further investigated whether an increased budget for hybrid breeding can compensate for this lower efficiency. To this end, we defined a basic scenario for line breeding with $i_L = 2.67$ resulting from an $\alpha = 10/1000 = 1/100$, $h_L^2 = 0.64$ resulting from the variance components of Table 1, and $L = 6$, which is a number of locations often used in line breeding programs. Eff was then calculated by stepwise increasing L to twice the number of test locations by $L = 6 + 0.4x$ and stepwise increasing the selection intensity to twice the number of tested individuals, i.e., decreasing α by $\alpha = {}^{1}\!/_{(100+50y)}$. Testcross seed production is one of the most expensive steps in hybrid wheat breeding. The production of enough seed for testing one hybrid combination in multi-location yield trials across 2 years costs about four times the costs for one yield

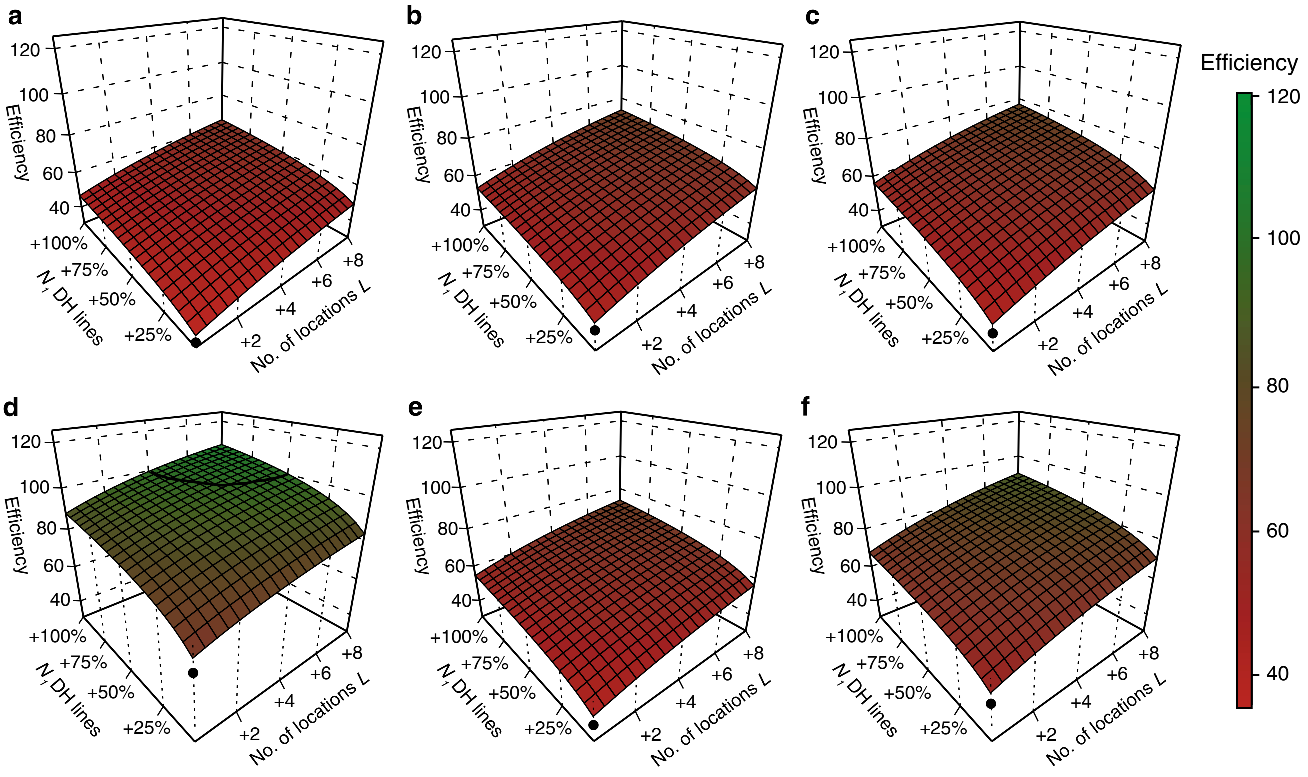

Fig. 1 **a** Efficiency of hybrid versus line breeding for similar budget (*filled circle*) and for a higher budget in hybrid breeding which is spent to increase the number of test locations L (increased heritability) or the number of DH lines N_1 (increased selection intensity). **b** Scenario assuming no costs for testcross seed production (Eff_{cost}). **c** Scenario assuming the same length of breeding scheme for lines and hybrids ($\text{Eff}_{\text{rapid}}$). **d** Scenario assuming a doubled genetic variance for hybrid breeding ($\text{Eff}_{\text{highvar}}$). **e** Scenario assuming a genetic variance for hybrid breeding increased from 0.057 to 0.067. **f** Optimistic scenario for hybrids combining assumptions of **c** and **e** with testcross seed productions amounting to three yield plots (cost = 3; Eff_{opt})

plot (cost = 4; V. Lein, pers. Comm.). Thus, we adjusted α for the hybrids to $\alpha = {}^{\text{cost}}/_{(100+50y)}$.

Furthermore, we evaluated different scenarios for hybrid breeding. The standard scenario was defined using the variance components of Table 1, cost = 4, and $Y_H = 6$ ($\text{Eff}_{\text{stand}}$). Alternatively, we calculated Eff by assuming: (1) no extra costs for hybrid seed production with cost = 1 (Eff_{cost}); (2) the same length of the breeding scheme for line and hybrid breeding with $Y_L = Y_H = 5$ ($\text{Eff}_{\text{rapid}}$); (3) a doubled genetic variance for hybrids with $\sigma^2_{GH} = 0.115$ ($\text{Eff}_{\text{highvar}}$); and (4) an optimistic scenario for hybrids combining cost = 3, $Y_H = 5$ with $\sigma^2_{GH} = 0.067$ (Eff_{opt}). All analyses were performed with the statistical software R (R Development Core Team 2011).

Results

The long-term competitiveness of hybrid versus line breeding was investigated in two steps. First, we evaluated the efficiency of recurrent selection by comparing the expected selection gains in both breeding schemes. For the standard scenario based on the estimates given in Table 1 and assuming a similar budget for both breeding methods, the efficiency of hybrid versus line breeding was low with $\text{Eff}_{\text{stand}} = 32.5\ \%$ (Fig. 1a). This efficiency was increased by a stronger selection intensity, i.e., the use of additional DH lines (N_1), or a higher number of test locations (L) in hybrid breeding. For instance, doubling the number of DH lines ($N_1 + 100\ \%$) for a constant number of test locations $L = 6$ led to an $\text{Eff}_{\text{stand}} = 46.6\ \%$. Similarly, the use of eight additional test locations for screening the initial $N_1 = 1{,}000$ DH lines led to $\text{Eff}_{\text{stand}} = 49.4\ \%$. The combination of $N_1 + 100\ \%$ and $L + 8$ led to $\text{Eff}_{\text{stand}} = 63.9\ \%$. Similar trends were observed for the other scenarios of hybrid breeding (Eff_{cost}, Eff_{year}, $\text{Eff}_{\text{highvar}}$, and Eff_{opt}; Fig. 1).

The number of years required to finish the hybrid breeding cycle (Y_H), the testcross seed production costs (cost) as well as the genetic variance available for hybrid breeding (σ^2_{GH}) had a strong impact on the efficiency of hybrid versus line breeding (Fig. 1). Reducing the testcross seed production costs by factor four led to an increased efficiency of $\text{Eff}_{\text{cost}} \geq 40\ \%$ (Fig. 1b). A similar effect on the efficiency was observed for the reduction of the length of the breeding cycle of hybrids to the same length as in line breeding $Y_H = Y_L = 5$ (Fig. 1c; $\mathrm{Eff}_{\mathrm{rapid}}$). The by far largest effect on the efficiency of hybrid versus line breeding was observed for the amount of genetic variance available for hybrid breeding ($\sigma^2_{G_H}$). A doubled $\sigma^2_{G_H}$ resulted in an $\mathrm{Eff}_{\mathrm{highvar}}$ which was about twice as high as $\mathrm{Eff}_{\mathrm{stand}}$, ranging 61.8–107.0 % (Fig. 1d).

In order to evaluate the long-term effects of this efficiency derived from the comparison of hybrid versus line breeding, we considered heterosis and projected the PFYP of varieties derived from line and hybrid breeding over the next 30 years. PFYP was higher for hybrid than for line breeding in the near future (Fig. 2), but line breeding caught up with a speed depending strictly on the efficiency (Eff) described above. For instance, assuming an Eff = 40 % and a heterosis of 10 %, i.e., $\mu_H = 10.7$ t per ha compared to $\mu_L = 9.7$ t per ha (Table 1), PFYP of line breeding became rapidly better than hybrid breeding and the two projections intersected after 11 years. In contrast, PFYP of hybrids remained higher than PFYP of lines throughout the next 30 years assuming an Eff = 80 %. The advantage of hybrids over lines in PFYP was further increased assuming a heterosis of 15 %, i.e., $\mu_H = 11.2$ t per ha compared to $\mu_L = 9.7$ t per ha.

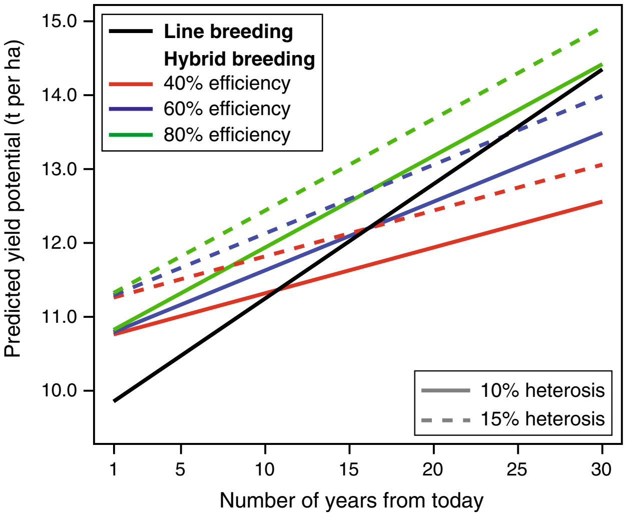

Fig. 2 Predicted future yield potential of varieties delivered by line breeding and hybrid breeding assuming an efficiency of hybrid breeding of 40, 60 or 80 % compared with line breeding

Discussion

One of the currently intensively discussed questions in wheat breeding companies is whether to invest in hybrid breeding. This is due to several reasons, mainly the low yield increase in the last years and the very high rate of farm-saved seed (Longin et al. 2012). Our aim was therefore to deliver a model framework to judge the long-term potential of hybrid versus line breeding in wheat. Breeding companies largely vary in size (e.g., budget, lab facilities, field trial management), status regarding hybrid breeding technologies (e.g., seed production system, availability of males) and marketing structures across countries. To account for this diversity, we employed a simple one-stage selection model (Eq. 4) and present our results in a way enabling breeders to identify their scenario themselves.

Prediction model and economic framework

Based on the usefulness concept (Schnell and Utz 1975), we developed a prediction model for future yield potential (PFYP) in both breeding methods as the sum of the population mean and the expected selection gain. This selection gain defines the potential recurrent improvement of the new varieties. Moreover, as hybrids in wheat are currently developed by crossing the top inbred lines from line breeding, the average heterosis is reflected by the difference in population means between line and hybrid breeding.

We first determined PFYP for standard scenarios in hybrid and line breeding. For line breeding, we defined an overall scenario which is not modified anymore in order to standardize our approach. We assumed that in line breeding approximately $N_1 = 1{,}000$ DH lines are available for first yield testing and that the ten best performing of these lines will enter preregistration trials (E. Ebmeyer; V. Lein; pers. Comm.). Furthermore, we assumed that these lines are tested in six locations resulting in an $h^2 = 0.64$ for grain yield based on the variance components of Table 1.

For the standard hybrid scheme, we assumed that one hybrid seed production by a chemical hybridization agent delivers enough seed for multi-location yield trials across 2 years. Thus, the hybrid breeding scheme requires 1 year longer ($Y_H = 6$) than the line scheme ($Y_L = 5$) to finish one breeding cycle. This kind of breeding scheme is common practice in the current market leading companies for hybrid wheat with hybrid seed production costs amounting to fourfold the cost of one yield plot (cost = 4; V. Lein; pers. Comm).

This standard hybrid breeding scheme was then modified in order to elaborate key parameters for the maximization of selection gain in hybrid breeding. These key parameters were: (1) the number of years required to finish a breeding cycle (Y); (2) the costs for hybrid seed production (cost) and (3) the variance components in line versus hybrid breeding. Estimates of variance components were taken from the largest ever published hybrid wheat experiment comprising 1,604 hybrids and their 135 parental elite lines tested for grain yield in field trials at 11 German locations (Table 1; Longin et al. 2013).

Major factors affecting the efficiency of hybrid versus line breeding

Our results showed that hybrids have a currently predicted yield advantage of about 10 % over lines (Fig. 2). Although this seems quite high, the higher seed production costs of hybrids diminish this yield advantage. Furthermore, this advantage decreases constantly with a speed directly depending on the relative selection gain in both methods (Eff). For instance, assuming a low Eff = 40 %, line breeding will already outperform hybrid breeding in about 10 years. In contrast, assuming Eff = 80 %, lines will not reach the predicted yield potential of hybrids within the next 30 years. Consequently, factors influencing this efficiency are of utmost importance and warrant a closer examination.

A higher budget is available in hybrid than in line breeding

For the standard scenario of hybrid breeding, the relative selection gain of hybrids was low compared to lines with $\text{Eff}_{\text{stand}} = 32.5$ % (Fig. 1a). However, this efficiency can be increased by investing a higher budget in hybrid than in line breeding. For instance, the use of additional DH lines or test locations in hybrid breeding increased the $\text{Eff}_{\text{stand}}$ up to 63.9 % under the standard scenario. Although this represents a doubling of Eff, it must be noted that this increase in Eff is not linearly proportional to the increase in the required budget (Fig. 1). This can be explained by the asymptotic slope of the selection intensity and heritability with increasing number of test candidates and locations (cf. Becker 1993).

Nevertheless, using hybrids instead of lines, breeding companies would certainly ensure a higher return of investment due to a strong reduction of farm-saved seed. Consequently, a higher budget would be available for research and development (R&D). By contrast, with the current rate of farm-saved seed it appears impossible to maintain the R&D budget currently available for line breeding. Thus, the standard scenario with $\text{Eff}_{\text{stand}} = 32.5$ % underestimates the potential of hybrid breeding. The above shown non-linear efficiency increase by investing in higher numbers of lines or test locations requires, however, the evaluation of alternative parameters to increase Eff.

Costs of hybrid seed production and breeding cycle duration

One major topic for R&D in hybrid wheat breeding is to improve the efficiency of hybrid seed production (for a detailed review see Kempe and Gils 2011; Longin et al. 2012). Currently, only one sterility system—chemical hybridization agent Croisor®100 (sintofen; former Dupont-Hybrinova, Saaten Union Recherche, France)—is available in the market. Furthermore, the limited amount and spread of pollen of most elite lines complicates hybrid seed production (Langer et al. 2014). Consequently, large amounts of male lines have to be planted per seed production area and a relative low yield of seeds is harvested on females maximizing costs of hybrid seed production.

The reduction of hybrid seed production costs had a large influence on Eff. Currently, the production of seed for one-test hybrid amounts to four times the costs of one yield plot. Assuming strongly reduced costs for hybrid seed of only a quarter, increased Eff to $\text{Eff}_{\text{cost}} \geq 40$ % (Fig. 1b). Having reduced hybrid seed production costs, the saved money could be invested into increased numbers of lines and locations further increasing Eff_{cost}. While the reduction of seed production costs by four might be unrealistic for the near future, the current intensive and synergistic research approaches across public and private institutes bear the potential to substantially ameliorate this disadvantage of hybrids.

A similar increase in Eff could be realized by shortening the hybrid breeding scheme to the same length as the line breeding scheme ($Y_H = Y_L = 5$, $\text{Eff}_{\text{rapid}} \geq 40$ %; Fig. 1c). This is feasible by changing the hybrid breeding scheme towards a breeding scheme combining line per se with testcross performance. That means that the N_1 lines are tested in year four for their line per se performance with parallel hybrid seed production. Only the hybrid combination of the best of these lines will then be tested in the fifth year. For maize, a combined scheme like this maximized the selection gain for GCA as long as the correlation of line per se and testcross performance was >0.7 (Longin et al. 2007). For wheat, this correlation was estimated to be 0.77 (Longin et al. 2013), but as seed production costs are much higher in wheat than in maize the potential of this combined breeding scheme requires further research. Collectively, our results underline the necessity to improve the efficiency of hybrid seed production in wheat.

Genetic variance in line versus hybrid breeding

The amount of genetic variance available for long-term hybrid breeding $\sigma^2_{G_H}$ was the most crucial factor in the comparison of line and hybrid breeding (Fig. 1d). Doubling $\sigma^2_{G_H}$ approximately doubled the efficiency to $\text{Eff}_{\text{highvar}} \geq 62$ % (Fig. 1d). Furthermore, an increase in the number of N_1 lines or L test locations led to a higher increase of $\text{Eff}_{\text{highvar}}$ compared to the other scenarios ($\text{Eff}_{\text{standard}}$, Eff_{cost}, $\text{Eff}_{\text{rapid}}$; Fig. 1). This can be explained by the formula for the selection gain (Eq. 3), where $\sigma^2_{G_H}$ enters as variable itself and additionally via the heritability.

Experimental estimates of $\sigma^2_{G_H}$ in wheat are rare, but indicate roughly a halved genetic variance as compared to line breeding (Gowda et al. 2012; Longin et al. 2012). This is astonishing as the substantial magnitude of SCA variance observed in these studies points towards the presence of significant dominance effects for which a relative genetic variance compared to line breeding higher than 0.5 is expected (Longin et al. 2012). The presence of epistasis which largely inflates the genetic variance of line breeding might be one theoretical explanation. In addition, practical reasons might also have contributed to the low $\sigma^2_{G_H}$. Compared to line breeding, very limited efforts have been made for hybrids in wheat. For instance, only few lines were yet screened for GCA performance. Furthermore, combination of lines into test hybrids and new crosses for systematic hybrid breeding was mainly driven by logistical constraints like open flowering males and not based on GCA estimates. With an improved hybrid seed production system, we can consequently expect an increase in $\sigma^2_{G_H}$ in the future by systematic hybrid breeding and selection for GCA but the extent of this increase cannot be predicted. Nevertheless, an increase of $\sigma^2_{G_H}$ from 0.057 (Table 1; $\mathrm{Eff}_{\mathrm{stand}}$) to 0.067 resulted in a curve similar to that of $\mathrm{Eff}_{\mathrm{rapid}}$ (Fig. 1e) emphasizing that already a small increase of $\sigma^2_{G_H}$ has a large impact on Eff.

In conclusion, there are several factors that can be manipulated by breeders which strongly influence Eff. While the amount of $\sigma^2_{G_H}$ has the by far largest effect on Eff, breeders can only partly influence it. By contrast, the hybrid seed production costs are a further important factor for Eff which deserves to be intensively improved by further research. While it currently seems unrealistic to improve Eff > 100 % a value considerably higher than $\mathrm{Eff}_{\mathrm{stand}} = 32.5$ % should be feasible. For instance, the assumption of $\sigma^2_{G_H} = 0.067$, cost = 3 and $Y_H = 5$, resulted in an $\mathrm{Eff}_{\mathrm{opt}}$ ~53 % (Fig. 1f). Taking the potential of a higher budget in hybrid than in line breeding into account as discussed above, an efficiency of about 70 % appears feasible.

The extent of heterosis

Owing to heterosis, the hybrids have a head start in PFYP which is systematically reduced by the higher Eff of line breeding (Fig. 2). For instance, assuming an Eff = 60 % and a heterosis of 10 %, the PFYP of lines reached that of hybrids after 16 years (Fig. 2). Even a moderate increase in heterosis from 10 to 15 % already delays this time point to 25 years emphasizing the importance of heterosis for the comparison of hybrid versus line breeding.

The development of heterotic groups in wheat bears the potential to increase heterosis, but the required change in allele frequencies needs a long-term commitment (Longin et al. 2012). In maize and barley heterosis was considerably larger under stress conditions than under high-yielding conditions (Hallauer et al. 1988; Duvick et al. 2004; Mühleisen et al. 2013). Consequently, the predicted climate change and the increased necessity to grow wheat on poorer soils in more marginal environments may lead to a higher heterosis in wheat which would in turn benefit hybrid breeding.

Hybrid wheat: to breed or not to breed?

Based on current estimates regarding variance components and costs for hybrid seed production, line breeding seems to be a competitive method for future wheat breeding. However, improvements in hybrid seed production and a more intensive screening and selection for lines with high GCA holds the potential to improve the efficiency of hybrid breeding. In addition, several parameters with a large potential to increase the relative efficiency of hybrids are difficult to predict and were therefore not considered in this model framework. For instance, hybrids are known from other crops to be extremely high performing which can potentially facilitate the market launch of wheat hybrids. In addition, the use of specific traits in wheat (GM and non-GM) will become more and more important in the future and hybrids present the perfect protection system against illegal dissemination. Finally, the development of heterotic groups will increase the competitiveness of hybrid breeding as: (1) the substantial amount of SCA variance detected in current elite material (Longin et al. 2013) will be reduced thereby improving the prediction accuracy of untested hybrids and (2) the stacking of major genes with dominant gene action is facilitated (Gowda et al. 2013; Zhao et al. 2014; Miedaner et al. 2013). In conclusion, while hybrids currently outperform line varieties in wheat, the long-term success of a hybrid breeding program depends on a number of parameters. Consequently, the decision whether or not to embark on hybrid breeding cannot be answered in general but must be decided on a case-by-case basis for each individual breeder.

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

Ethical standard The authors declare that the experiments comply with the current laws of Germany.

References

Becker H (1993) Pflanzenzüchtung (in German). Verlag Eugen Ulmer, Stuttgart, pp 129–132

Bernardo R (2002) Breeding for quantitative traits in plants. Stemma Press, Woodbury, pp 110–120

Cochran WG (1951) Improvement by means of selection. In: Proceedings of 2nd Berkeley symposium mathematical statistics and probability, pp 449–470

Duvick DN, Smith JSC, Cooper M (2004) Long-term selection in a commercial hybrid maize breeding program. In: Janick J (ed) Plant breeding reviews, vol 24, part 2. Long term selection: crops, animals, and bacteria. Wiley, New York, pp 109–151

Edwards IB (2001) Origin of cultivated wheat. In: Bonjean AP, Angus WJ (eds) The world wheat book-a history of wheat breeding, vol 1. Lavoisier Publishing, Paris, pp 1019–1045

Gowda M, Longin CFH, Lein V, Reif JC (2012) Relevance of specific versus general combining ability in winter wheat. Crop Sci 52:2494–2500

Gowda M, Zhao Y, Würschum T, Longin CFH, Miedaner T, Ebmeyer E, Schachschneider R, Kazman E, Schacht J, Martinant JP, Mette MF, Reif JC (2013) Relatedness severely impacts accuracy of marker-assisted selection for disease resistance in hybrid wheat. Heredity 2013:1–10. doi:10.1038/hdy.2013.139

Hallauer AR, Russell WA, Lamkey KR (1988) Corn breeding. In: Sprague GF, Dudley JW (eds) Corn and corn improvement, 3rd edn. AgronMonogr18 ASA, CSSA, SSSA, Madison, pp 469–565

Kempe K, Gils M (2011) Pollination control technologies for hybrid breeding. Mol. Breed 27:417–437

Langer S, Longin CFH, Würschum T (2014) Phenotypic evaluation of floral traits with relevance for hybrid breeding in wheat (*Triticum aestivum* L.). Plant Breed. doi:10.111/pbr12192

Longin CFH, Utz HF, Reif JC, Schipprack W, Melchinger AE (2006) Hybrid maize breeding with doubled haploids. I. One-stage versus two-stage selection for testcross performance. Theor Appl Genet 112:903–912

Longin CFH, Utz HF, Melchinger AE, Reif JC (2007) Hybrid maize breeding with doubled haploids. II. Optimum type and number of testers in two-stage selection for general combining ability. Theor Appl Genet 114:393–402

Longin CFH, Mühleisen J, Maurer HP, Zhang H, Gowda M, Reif JC (2012) Hybrid breeding in autogamous cereals. Theor Appl Genet 125:1087–1096

Longin CFH, Gowda M, Mühleisen J, Ebmeyer E, Kazman E, Schachschneider R, Schacht J, Zhao Y, Reif JC (2013) Hybrid breeding in wheat: heterosis, relevance of general and specific combining ability effects and consequences for optimum breeding strategies. Theor Appl Genet 126:2791–2801

Miedaner T, Zhao Y, Gowda M, Longin CFH, Korzun V, Ebmeyer E, Kazman E, Reif JC (2013) Genetic architecture of resistance to *Septoria tritici* blotch in European wheat. BMC Genomics 14:858

Mühleisen J, Maurer HP, Stiewe G, Bury P, Reif JC (2013) Hybrid breeding in barley. Crop Sci 53(3):819–824

Oettler G, Tams SH, Utz HF, Bauer E, Melchinger AE (2005) Prospects for hybrid breeding in winter triticale: I. Heterosis and combining ability for agronomic traits in European elite germplasm. Crop Sci 45:1476–1482

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.r-project.org

Schnell FW, Utz HF(1975) F1-Leistung und Elternwahl in der Züchtung von Selbstbefruchtern (In German). In: Bericht über die Arbeitstagung der Vereinigung österreichischer Pflanzenzüchter. BAL Gumpenstein, Gumpenstein, Austria, pp 243–248

Shull GH (1908) The composition of a field of maize. Am Breed Assoc Rep 4:296–301

Zhao Y, Mette MF, Gowda M, Longin CFH, Reif JC (2014) Bridging the gap between marker-assisted and genomic selection of heading time and plant height in hybrid wheat. Heredity 2014:1–8. doi:10.1038/hdy.2014.1