Chapter 24
Hybrid Breeding in Wheat

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Abstract Despite promising superior performance, hybrid wheat currently occupies only a niche sector in commercial wheat production. However, with the recent development of practicable hybrid seed production systems, a switch from line to hybrid breeding in wheat seems realistic. Here, we discuss what consequence this may have for wheat breeding programs and provide suggestions on how quantitative genetic analysis can contribute to design optimal selection strategies.

Status Quo of Wheat Hybrid Breeding

Hybrid cultivars with improve yield and other favorable agronomic traits are widely used in plant production. For wheat, one of the most important staple crops, commercial hybrid breeding and seed production is still restricted to a niche sector in comparison to other cereals like maize or rice (Longin et al. 2012; Whitford et al. 2013). Currently, there is a limited number of wheat hybrid cultivars based on chemical hybridization agents (CHAs, gametocytes) registered for the European market (Hybridwheat 2013). In China and India, hybrid wheat is produced based on cytoplasmic male sterility (CMS) systems or photoperiodic sensitivity sterility systems (Longin et al. 2012). Major practical limitations for a more widespread use of hybrid wheat are seed production capacities and costs, but progress has been made to improve the availability and economic competitiveness of hybrid wheat (reviewed by Kempe and Gils 2011; Whitford et al. 2013). Eventually, economically successful broad implementation of hybrid wheat will need the combination of a practicable

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low cost hybrid seed production system, high performance in traits of interest such as grain yield and yield stability and an efficient breeding scheme for further improvement (Longin et al. 2012).

Hybridization Systems in Wheat

Hybrid seed production requires the enforcement of an efficient cross-pollination between wheat inbred lines that overcomes the naturally autogamous pollination mode of wheat. This is practically achieved by planting male-sterile maternal plants with good pollen recipient properties in close proximity to paternal plants with good pollen shedding properties. Thus, effective male-sterility of the maternal plants is a general requirement that can be based on different mechanisms.

Some major efforts have been made to deploy cytoplasmic male sterility (CMS) for hybrid wheat breeding. While CMS is functional in other important cereals such as rice and rye, it has turned out to be difficult to develop, complex to maintain and marginally reliable for wheat. Although sterility-inducing cytoplasms were identified (e. g. from *Triticum timopheevii*), reliable restorer genes are not yet available for wheat (Angus 2001) and CMS systems are often sensitive to environmental factors, in particular to temperature and photoperiod (Kaul 1988; Murai et al. 2008). Thus, no wheat CMS system with more than regional application is currently available for hybrid seed production.

Rather, contemporary commercial hybrid wheat production is mainly based on the in-field application of CHA preventing the formation of viable pollen on the maternal crossing partner (Cisar and Cooper 2002). On a production site, the intended maternal line is planted in strips alternating with strips of the intended pollen donor lines and maternal plants are sprayed with CHA, while treatment of paternal plants is strictly avoided. Hybrid seeds are then harvested from the pollinated mother plants to give rise to F_1 progeny that then displays the heterosis (hybrid vigor) effect (Kempe and Gils 2011). The plant growth regulator Croisor®100 (Sintofen, former Dupont-Hybrinova, Saaten Union Recherche, France) is currently the only CHA for wheat registered in Europe for commercial production (Hybridwheat 2013). Although modern CHAs are in principle functional for a broad spectrum of genotypes and display relatively low phytotoxicity in wheat, they still have limitations such as compromised seed set on treated plants (Adugna et al. 2004) or variation in field-efficiency depending on the weather conditions at the time of application.

Alternatively, the exploitation of transgene technologies may be promising for the establishment of hybrid wheat production systems (Kempe and Gils 2011; Whitford et al. 2013). As an example, a recessive split-gene transgene system was suggested that utilizes complimentary fragments of barnase to induce male-sterility in maternal plants with simultaneously retaining pollen fertility and thus grain yield in the resulting F_1 hybrids (Gils et al. 2008; Kempe et al. 2009). Functional barnase formation in the tapetum layer of anthers and corresponding male-sterility should exclusively be effective in heterozygous plants, which can eventually serve as the mother plants in the hybrid cross. With both barnase gene fragments located on allelic chromosomal positions and thus "linked in repulsion", hybrid F_1 plants inherit only one of the barnase fragments and, as a result, remain fully fertile (Kempe and Gils 2011).

Moreover, the modification of the naturally closed inflorescence structure of wheat adapted to self-pollination to a more open structure allowing more efficient pollen reception as well as shedding will be an important breeding objective (Whitford et al. 2013). With these recent developments in hybrid seed production in mind, it seems now timely to devote some thought on how to develop optimal parental combinations for highest yield and quality improvements in wheat hybrid breeding.

Advantages of Hybrids in Comparison to Lines

In several outcrossing crop plant species, hybrid varieties have already largely replaced population varieties (Coors and Pandey 1999). The major benefits of hybrids compared to population varieties are increased yields due to an optimal exploitation of heterosis, higher biotic and abiotic stress resistance, and enhanced yield stability (Hallauer et al. 1988). In wheat as an autogamous species, the amount of midparent heterosis for grain yield is less pronounced, and commercial heterosis, the contrast between hybrids and the best commercially available line variety, is lower in comparison to outcrossing cereal species such as maize (Longin et al. 2012). Concerning yield stability, Léon (1994) concluded that for autogamous crops, findings in hybrids versus lines are contrasting, ranging from higher yield stability of hybrids (Borghi et al. 1988; Oury et al. 2000; Oettler et al. 2005; Gowda et al. 2010) to no differences (Borghi and Perenzin 1990; Peterson et al. 1997; Bruns and Peterson 1998; Koemel et al. 2004).

Recent large scale-phenotyping activities involving extended collections of inbred lines and hybrids, however, revealed a positive commercial heterosis for grain yield in hybrid winter wheat adapted to Central Europe (Gowda et al. 2012; Longin et al. 2013). Thus, a change from line to hybrid varieties has the potential to break the yield barriers in wheat breeding. Using a broad base of data from multi-location field trials, Mühleisen et al. (2013) also re-evaluated grain yield stability in wheat, triticale, and barley hybrids in comparison to lines. The authors observed consistently higher yield stability for hybrids in all three autogamous crops (Fig. 24.1). Moreover, the lack of consistencies of results on yield stability of hybrids versus lines in previous studies is most likely owing to an unbalanced definition of the environmental index caused by exploiting exclusively data from inbred lines but not from hybrids. Thus, in summary, current experimental studies clearly underline the advantages of hybrids in comparison to inbred lines in terms of higher yield and yield stability. Due to the expected climate change with more extreme weather conditions, such improved robustness of performance will become even more important in the future.

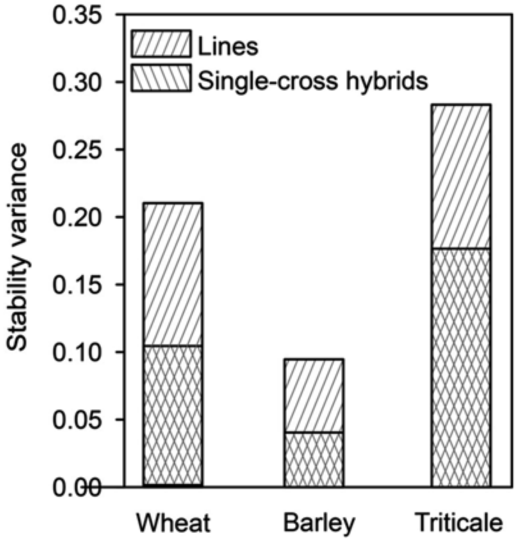

Fig. 24.1 Yield stability measured based on the stability variance of wheat, barley, and triticale single-cross hybrids (descending hatching) versus lines (ascending hatching) based on the data published by Mühleisen et al. (2013). Low values of stability variance correspond to high yield stability

Beyond improved grain yield and yield stability, hybrid wheat also outperforms inbred lines in sturdiness to abiotic and biotic stress. Longin et al. (2013) observed a positive midparent (albeit negative better parent) heterosis for frost tolerance as well as resistance against leaf rust, stripe rust, septoria tritici blotch, and powdery mildew for hybrid winter wheat. In two companion genome-wide mapping studies, Zhao et al. (2013a) and Gowda et al. (2013) investigated the degrees of dominance of putative QTL underlying the above outlined abiotic and biotic stress resistances. For most QTL with large effect on the genotypic variation, the degree of dominance was in the range of partial dominance. Thus, if particular traits are in focus, superior genotypes should carry resistance QTL in the homozygous state, favoring breeding of lines instead of hybrids. However, if pyramiding of multiple relevant QTL is desired, hybrid breeding will offer far more flexibility to combine favorable partially dominant alleles originating from either maternal or paternal inbred lines. This advantage of hybrids is illustrated by calculating a stress susceptibility index combining data on frost tolerance and resistance to leaf rust, stripe rust, septoria tritici blotch, and powdery mildew for an extended set of winter wheat inbred lines and hybrids derived from them (Fig. 24.2). Hybrids show overall lower stress susceptibility than related inbred lines, which might also be contribute the higher yield stability observed for hybrids as mentioned above (Mühleisen et al. 2013).

Beside the described advantages of hybrid versus line varieties in terms of yield, yield stability and biotic as well as abiotic stress resistance, it is pivotal to point out that the recurrent selection gain in hybrid breeding is at least as high in hybrid as compared to line breeding. The expected recurrent selection gain depends on quantitative genetic parameters such as the ratio of additive variance which can be exploited in hybrid versus line breeding. Besides quantitative genetic parameters,

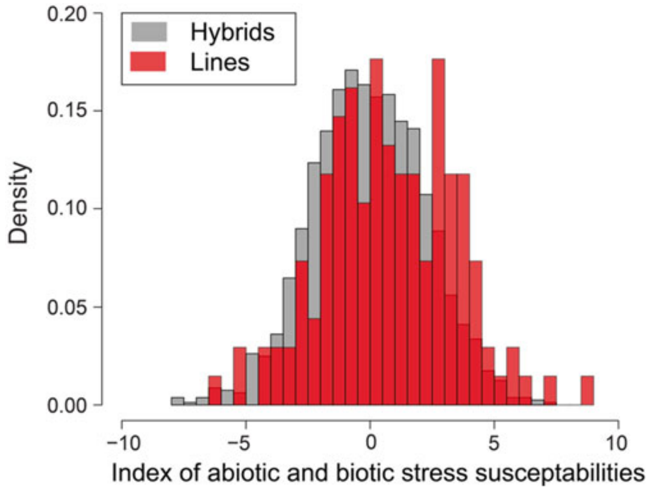

Fig. 24.2 Distribution of 1.604 wheat hybrids (*grey*) and 135 parental lines (*red*) for a stress susceptibility index combining frost tolerance and resistance to leaf rust, stripe rust, septoria tritici blotch, and powdery mildew. Calculation was done assuming equal weight based on data published by Longin et al. (2013)

the economic framework such as the return in investment is pivotal to determine the selection gain of line versus hybrid breeding. Longin et al. (2012) performed a first rough theoretical comparison of the expected selection gain for line versus hybrid breeding under the simplifying assumption of an equal budget. The model calculations indicate that if the dominance effect is substantial, hybrid breeding can result in a competitive selection gain as compared to line breeding (Longin et al. 2012, 2014). These theoretical considerations are corroborated by one study comparing hybrid versus line breeding using experimental data of official variety tests in hard winter wheat across 20 years in the U.S. (Koemel et al. 2004). The authors observed a higher selection gain across time for hybrids compared to line breeding. These findings are very stimulating but further experimental data are needed to substantiate the long-term selection gain for hybrid versus line breeding in autogamous cereals.

Prediction of Hybrid Wheat Performance

In a traditional wheat breeding program, several thousand inbred lines are produced every year. Superior genotypes are efficiently identified by applying multi-stage selection programs. Selection of superior hybrids, however, is afflicted by the vast number of potential single-cross combinations among available elite parental lines (Zhao et al. 2013a). Consequently, field evaluation of all potential hybrid combinations is unfeasible, leading to a strong demand for hybrid prediction approaches.

For complex traits such as grain yield, midparent performance is only moderately associated with hybrid performance (Longin et al. 2012). Predicting hybrid performance based on general combining ability (GCA) effects of their parents is accurate in situations with predominance of variance due to GCA (σ^2_{GCA}) versus variance due to specific combining ability (SCA) effects (σ^2_{SCA}). A recent large scale experimental study in wheat revealed that σ^2_{SCA} is quite substantial for grain yield in wheat (Longin et al. 2013), which suggests that field testing of single-cross combinations is needed at least in the final stages of a selection program. Therefore, robust methods to predict hybrid wheat performance are urgently required.

The potential of genomic selection to predict hybrid wheat performance has been investigated for grain yield with a small factorial mating design comprising 90 hybrids fingerprinted with a 9k SNP array (Zhao et al. 2013b). The results of this cross validation study point towards a high potential of genomic selection to predict hybrid wheat performance. This finding was further substantiated in further studies predicting hybrid wheat performance with genomic selection focusing on several agronomic traits (Miedaner et al. 2013; Zhao et al. 2013a, 2014). Further empirical data analyses are needed, however, to finally judge the prospects of genomic selection models for predicting hybrid wheat performance.

Upcoming Challenges for Wheat Hybrid Breeding

In conclusion, the most urgent challenges for wheat hybrid breeding will be (i) development of a stable hybridization system to reduce the costs of hybrid seed production compared to the use of CHA, (ii) identification of the genetic architecture of pollination capability for knowledge-based improvement of cross-pollination among elite lines, (iii) optimum design of hybrid wheat breeding programs including dimensioning of multi-stage selection programs including genome wide prediction approaches and (iv) development of heterotic pools in wheat.

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