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ORIGINAL PAPER

Hybrid rye performance under natural drought stress in Europe

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Abstract Several rye growing regions of Central Europe suffered from severe drought stress in the last decade. Rye is typically grown on sandy soils with low water-holding capacity in areas with low rainfall, thus drought-tolerant varieties are urgently needed. The main objective of our study was to evaluate the drought stress tolerance of rye hybrids using large-scaled field experiments. Two biparental populations (Pop-A, Pop-B) each consisting of 220 $F_{2:4}$ lines from the Petkus gene pool and their parents were evaluated for grain yield testcross performance under irrigated (*I*) and rainfed (*R*) regime in six environments. We observed for most environments severe drought stress leading to an average grain yield reduction of 23.8 % for rainfed compared to irrigated regime in drought stress environments. A decomposition of the variance revealed significant ($P < 0.01$) genotypic and genotype × environment interaction variances but only a minor effect of drought stress on the ranking of the genotypes with regard to grain yield. In conclusion, separate breeding programs for drought-tolerant genotypes are not superior to the currently practiced selection under rainfed conditions without irrigation in hybrid rye breeding in Central Europe.

Introduction

Drought is a major environmental limitation of agricultural production worldwide (Ceccarelli et al. 2007). Caused by the global climate change, also regions belonging to the humid climate zone suffer from a periodical water shortness that cannot be predicted by long-term forecast systems. Within recent years, Central Europe experienced rainless periods in spring and early summer (April to June), a time when the yield potential of winter rye is largely determined. In 2011, for example, spring was one of the driest since 1893 (DWD 2011) and April in 2007, 2009, 2010, and 2011 were among the driest in the last 20 years in Germany. Hence, selection of drought-tolerant germplasm is needed.

Rye (*Secale cereale* L.) is a major crop in Germany, Poland, Russia, Belarus, and Ukraine grown on a total of 4.0 million hectares in 2010 (FAOSTAT 2011). In Germany, 3.6 million tons of rye were produced per year during 2010–2011 with an average grain yield of 5.2 t ha^{-1}. About 60 % of the rye growing acreage in Germany is devoted to hybrid cultivars. Main rye growing areas are located in regions with sandy, infertile soils with low-pH value and less rainfall. Sandy soils possess a low water-retaining capability. Therefore, rye suffers from drought stress although the crop itself is rather tolerant to abiotic stress factors (Hoffmann 2008). In 2010 and 2011, for example, rye grown in Lower Saxony, one of the main rye growing areas in Germany, suffered from an average yield reduction ranging from 14 to 27 % compared to the

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mean of both previous years (LSV 2011). These data illustrate the need of selection of drought-tolerant germplasm. Because water stress is not predictable and occurs only in some years, the final aim of breeders in Central Europe is to develop genotypes that are superior under drought, but also have high grain yield under non-stress conditions.

When a genotype yields significantly higher than another under severe drought stress it is relatively more drought tolerant (Blum 2005). Drought tolerance is a quantitative trait and is considered to be complex from the genomic point of view (Blum 2011). Unfortunately, most adaptations to drought limit yield performance under normal conditions, e.g., by a fast physiological development, reduced assimilation of carbon dioxide or additional energy requirements for osmotic adjustment (Turner 1979). Consequently, crop adaptation must reflect a balance among escape, avoidance and tolerance while maintaining adequate productivity (Blum 2011). Nothing is known, however, on the physiological mechanisms of drought tolerance in rye to our knowledge.

In applied hybrid rye breeding programs, thousands of progenies have to be tested for their combining ability for agronomic important traits (Tomerius et al. 2008). Therefore, it is of high importance for breeders whether a large-scale screening method is feasible for selection of drought-tolerant genotypes in the field (Mitra 2001). To address this question, we have grown two segregating populations with each of 220 testcross progeny and their parents across six environments under irrigated and rainfed regimes. Our objectives were to (1) partition total variance into its most important components under rainfed and irrigated conditions with special regard to genotype × irrigation interaction and (2) evaluate the relative efficiency of indirect selection under irrigated conditions for genotypes adapted to drought.

Materials and Methods

Plant material

Three parental elite inbred lines (Lo90-N, Lo115-N, Lo117-N) from the Petkus gene pool were chosen for this study due to their divergent efficiency under drought conditions. Lo115 showed in previous breeding trials a good performance under conditions of low rainfall, whereas Lo90 and Lo117 had lower performance than Lo115 (Wilde, personal communication, 2009). Two segregating populations, each consisting of 220 $F_{2:4}$ lines were generated by crossing the three parental lines as follows: Pop-A consisted of Lo115-NxLo90-N and Pop-B of Lo115-NxLo117-N. Parents belong to the Petkus gene pool (seed parent) and possessed normal cytoplasma (N). Randomly sampled 220 $F_{2:4}$ lines of both Pop-A and Pop-B, respectively, were crossed to an unrelated cytoplasmic-male sterile (CMS) tester of the Petkus gene pool. Thus, the testcrosses consisted only of non-restorer materials (Petkus × Petkus), which required the supply of external pollen for fertilization. All plant materials used in this study were kindly supplied by KWS LOCHOW GmbH, Bergen, Germany.

Field experiments and irrigation system

Field experiments were conducted in the years 2010 and 2011 at three locations: (1) Wohlde, Germany, latitude 52.8°N, longitude 10.0°E, 80 m above sea level, loamy sand soil texture; (2) Petkus, Germany, latitude 51.6°N, longitude 13.2°E, 130 m above sea level, loamy sand soil texture; and (3) Walewice, Poland, latitude 52.6°N, longitude 19.4°E, 184 m above sea level, heavy loamy soil texture. The six location × year combinations were referred to as environments in the following.

The two populations with 220 testcross progenies were evaluated with their parents (repeated 9 times) and arranged according to an incomplete 24 × 10 lattice design with two randomized replications. Plot size ranged from 5 to 6 m^2 with a seeding rate ranging from 150 to 200 kernels m^{-2}. Mineral fertilizer, herbicides and fungicides were applied following local standards to warrant high grain yield. To avoid lodging, growth regulators were applied three times. Final aim was to exclude abiotic and biotic stresses other than drought as far as possible. As external pollen source for providing fertilization, a pollen-shedding rye population was grown in the alleys and in stripes in a regularly distance of ten plots through the whole experiment.

All genotypes were evaluated under irrigated and rainfed water regimes. For each genotype, plots of both water regimes were placed with the narrow side opposite to each other to reduce effects due to soil differences (Supplementary material 1). Between water regimes, 2–2.5 m wide alleys were established. Water was applied by a drip irrigation system with five drip lines per plot to ensure a uniform irrigation in each plot depending on the particular local conditions (Supplementary material 2). The aim was to supply an optimal water regime considering the natural rainfall. For adjusting irrigation, we collected data on evapotranspiration for the German locations from the nearest stations of the German weather service (DWD) and used the recommendations of the Agrometeorological Survey of the DWD after delivering our site-specific data. For the Polish location Walewice, irrigation level was determined by experience. Plots were combine-harvested and grain yield was adjusted to a moisture concentration of 140 g H_2O kg^{-1}.

Statistical analyses

A two step procedure proposed by Möhring and Piepho (2009) was used for data analysis. In a first step, analysis of variance (Cochran and Cox 1957) was performed separately for each regime, environment and population. Outlier tests were performed following Anscombe and Tukey (1963). Best linear unbiased estimates (BLUEs) of each genotype from each environment and water regime were used with their squared error variance as weighting factor in a second step to estimate variance components (Möhring and Piepho 2009) using following statistical model:

$$Y_{ij} = \mu + G_i + E_j + e_{ij}$$

where Y_{ij} denote the BLUE for the ith genotype in the jth environment, μ was an intercept term, G_i was the genetic effect of the ith genotype, E_j the effect of the jth environment. Please note that the variance of e_{ij} reflects the sum of variance components due to genotype × environment interaction effects and single environmental residuals divided by the number of replications. Variance components were determined by the restricted maximum likelihood (REML) method assuming a random model using PROC MIXED of software package SAS (SAS 2008).

Analysis of variance was also carried out across irrigated (I) and rainfed (R) regime for each environment separately based on the following statistical model:

$$Y_{iklm} = \mu + G_i + I_k + (GI)_{ik} + R_{lk} + B_{klm} + e_{iklm}$$

where Y_{iklm} denote the phenotypic observation for the ith genotype with kth treatment (irrigation or rainfed) in the mth incomplete block of the lth replication, μ was an intercept term, G_i was the genetic effect of the ith genotype, I_k the effect of the kth treatment, $(GI)_{ik}$ the interaction effect, R_{lk} was the effect of the lth replication with treatment k, B_{klm} the effect of the mth incomplete block of the lth replication with treatment k, and e_{iklm} the residual. Genotype and genotype × irrigation interaction were treated as random.

Similar as described above, we estimated the variance components across environments and across water regimes ($I + R$) for each population with the following linear model:

$$Y_{ijklm} = \mu + G_i + E_j + I_k + (EI)_{jk} + (GE)_{ij} + (GI)_{ik} + (GEI)_{ijk} + R_{jkl} + B_{jklm} + e_{ijklm}$$

where Y_{ijklm} denotes the phenotypic performance for the ith genotype in jth environment with the kth treatment (irrigation or rainfed) in the mth incomplete block of the lth replication, μ was an intercept term, G_i the genetic effect of the ith genotype, E_j the effect of jth environment, I_k the effect of the kth treatment, $(EI)_{jk}$, $(GE)_{ij}$, $(GI)_{ik}$ and $(GEI)_{ijk}$ the interaction effects, R_{jkl} the effect of the lth replicate at jth environment with kth treatment, B_{jklm} the effect of the mth incomplete block of the lth replication with kth treatment at jth environment, and e_{ijklm} the residual. Genotype and all interactions with genotype were treated as random. Heritability (h^2) was estimated on a progeny mean basis as described by Hallauer and Miranda (1981):

$$h^2 = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{G\times E}^2}{\mathrm{Env}} + \frac{\sigma_e^2}{\mathrm{rep}\times\mathrm{Env}}}$$

where, σ_G^2, $\sigma_{G\times E}^2$ and σ_e^2 refer to the genotypic, genotype × environment interaction and error variances, and Env and rep indicate the number of environments and replications, respectively.

Simple phenotypic correlation coefficients (r_P) were calculated between irrigated and rainfed regime. Coefficients of genotypic correlation (r_G) were calculated based on the procedure described by Mode and Robinson (1959) and the analysis was performed with PLABSTAT computer program (Utz 2010). Genotype × environment interaction was analyzed by applying principal coordinate analysis (PCoA) based on grain yield data and performed by using the SAS (2008).

The relative efficiency (RE) of indirect selection under irrigated (I) regime compared with direct selection under rainfed (R) conditions can be predicted assuming equal selection intensities in both water regimes as proposed by Falconer and Mackay (1996):

$$\mathrm{RE} = \frac{h_R \times r_G}{h_I}$$

where h is the square root of heritability and r_G the genotypic correlation between the performance at both water regimes. If RE = 1, direct and indirect selection are predicted to be equally different, values >1 indicated that direct selection for drought at $I + R$ would be more efficient than indirect selection at R.

Results

Striking less rainfall compared to long-term average precipitation occurred during critical phases of plant development (Fig. 1; Supplementary material 2). Total sums of precipitation were between 14 and 89 % lower compared to long-term average precipitation in April and June 2010 and April, May, and June 2011 with the exception of Wohlde in the latter month. Additionally, average daily temperatures were higher compared to long-term average daily temperature in most instances.

In 2011, grain yield of entries in the irrigated regime was in Wohlde high throughout and similar high in the other

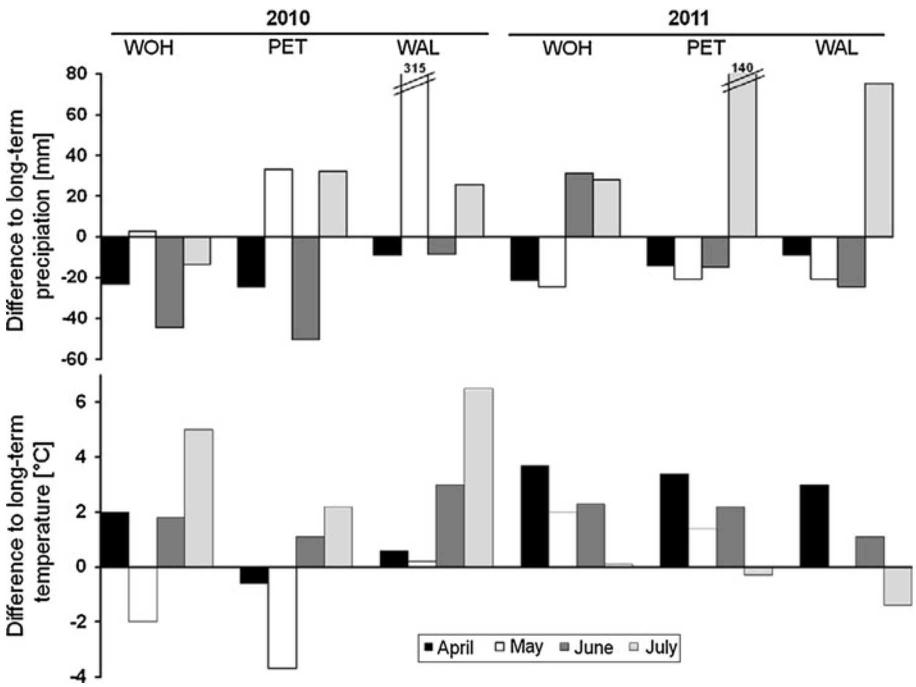

Fig. 1 Difference between long-term average precipitation and total sum of precipitation, and long-term average daily temperature and average daily temperature of Wohlde (WOH), Petkus (PET) and Walewice (WAL) from April to July in 2010 and 2011 (WOH and PET: long-term average from 1981 to 2010; *WAL* long-term average from 1967 to 2010)

locations for both populations (Table 1). Only in 2010, entries in Petkus and Walewice yielded considerably less than in Wohlde. Grain yield reduction between irrigated and rainfed regimes ranged from 1.9 to 29.6 % and from 2 to 40.5 % for Pop-A and Pop-B, respectively (Table 1). Differences between both water regimes were significant ($P < 0.05$) for five environments in Pop-A and four environments in Pop-B. We denoted these environments in the following as "drought environments". Only Walewice 2010 (Pop-A, Pop-B) and Petkus 2010 (Pop-B) showed no significant differences between both water regimes.

Principal coordinate analysis revealed no clustering of irrigated and rainfed regimes (Supplementary material 3). Obviously, both water regimes of Walewice 2010 and 2011 were separated from each other and the German environments.

The analyses of individual environments revealed genotypic variances (σ_G^2) of grain yield significantly ($P < 0.05$) larger than zero in all but one environment (Wohlde in 2011) for both water regimes (Supplementary material 4). Genotypic variances were significantly ($P < 0.01$) larger from zero also for the comparison of the irrigated and rainfed regime ($I + R$), whereas genotype × irrigation interaction variances ($\sigma_{G \times I}^2$) being significantly ($P < 0.1$) larger than zero only in three environments for Pop-A and four environments for Pop-B (Table 1).

The partitioning of variance from the combined analysis across drought environments with significant genotype × irrigation interaction ($\sigma_{G \times I}^2$) revealed that genotypic and genotype × environment interaction ($\sigma_{G \times E}^2$) variances were of higher relative importance in the

Table 1 Mean values for grain yield (t ha^{-1}) of irrigated (*I*) and rainfed (*R*) water regime, their mean differences (Δ*I*, in %), and significance of Δ*I* and genotype × irrigation (*G* × *I*) interaction for Pop-A and Pop-B evaluated at three locations in 2010 and 2011

Year Location	Pop-A				Pop-B			
	I	*R*	Δ*I* (%)[a]	Significance *G* × *I*[b]	*I*	*R*	Δ*I* (%)[a]	Significance of *G* × *I*[b]
2010								
Wohlde	8.15	5.91	27.5**	*	7.52	5.46	27.4**	+
Petkus	5.20	4.97	4.4*		5.11	4.93	3.5	
Walewice	5.38	5.28	1.9		5.08	4.98	2.0	
2011								
Wohlde	9.91	7.30	26.3**		9.78	5.82	40.5**	**
Petkus	8.79	6.19	29.6**	+	9.20	6.07	34.0**	*
Walewice	9.25	8.29	10.4**	**	8.36	7.18	14.1**	**
Progeny mean	7.78	6.32	18.8		7.51	5.74	23.6	
Parental mean	7.87	6.88	12.6		8.77	5.51	37.2	

+, *,** Significance at the 0.1, 0.05 and 0.01 probability level, respectively

[a] Difference = $(I - R)/I \times 100$

[b] For details, please refer to Supplemental material 4

irrigated than in the rainfed regime for both populations (Table 2; Supplementary material 5). Error variances were relatively more important under drought stress. Accordingly, heritability estimates were considerably higher for the irrigated than for the rainfed regime (0.6–0.7 vs. 0.4–0.5). Significant ($P < 0.05$) variances due to interactions between genotypes and water regime ($\sigma^2_{G\times I}$) were observed in both populations. The estimate of $\sigma^2_{G\times I}$, however, was of low relevance compared to $\sigma^2_{G\times E}$. The three-way interaction variance between genotypes, environments, and water regimes ($\sigma^2_{G\times E\times I}$) was significantly ($P < 0.05$) larger than zero and of similar size compared to $\sigma^2_{G\times I}$.

Phenotypic correlation between rainfed and irrigated regime was significant ($P < 0.01$) for both populations (Pop-A: 0.55, Pop-B: 0.58; Fig. 2). In comparison, coefficients of genotypic correlation were considerably higher (Pop-A: 0.86, Pop-B: 0.84). Accordingly, some progeny yielded above the population mean in both water regimes simultaneously. Indirect selection for drought tolerance under irrigated regime was predicted to be equally or more efficient than direct selection in the $I + R$ regime (RE = 1.1 in Pop-A and 0.99 in Pop-B).

Discussion

Measuring drought stress under field conditions

Grain yield evaluated in drought stress environments is a common criterion to judge the drought tolerance of crops (Mitra 2001; Li et al. 2011). One option to induce drought stress in Central Europe consists in the use of rain-out shelters. Experiments based on rain-out shelters enables well defined drought stress conditions but are cost and labor intensive and often limited in space. The latter is in particular of relevance for plant breeding research where several hundreds of genotypes have to be evaluated. As an alternative to rain-out shelters in this study natural occurring drought stress was used to evaluate the drought stress tolerance of two populations each with 220 testcross progenies. We assessed the magnitude of naturally occurring drought stress by contrasting the rainfed regime with an irrigated regime. The two water regimes were separated by 2.0–2.5 m wide alleys in order to reduce influence of water drift between irrigated and rainfed plots (Supplemental material 1).

A crucial prerequisite for selecting drought tolerance in field tests is, of course, a reduced rainfall in the period

Table 2 Estimation of variance components ($\times 10^{-2}$, genotypic, σ^2_G; genotypic × environment interaction, $\sigma^2_{G\times E}$; pooled error, σ^2_e; genotype × irrigation interaction, $\sigma^2_{G\times I}$; genotype × environment × irrigation interaction, $\sigma^2_{G\times E\times I}$), and heritabilities ($h^2$) for grain yield for irrigated (I), rainfed (R) and across irrigated and rainfed ($I + R$) water regimes, and significances for the difference between I and R (ΔI) and environment × irrigation interaction (EI) across three drought environments for Pop-A, and four drought environments for Pop-B with significant $G \times I$

Population	I				R				$I + R$						
	σ^2_G	$\sigma^2_{G\times E}$	σ^2_e	h^2	σ^2_G	$\sigma^2_{G\times E}$	σ^2_e	h^2	ΔI^a	EI^a	σ^2_G	$\sigma^2_{G\times E}$	$\sigma^2_{G\times I}$	$\sigma^2_{G\times E\times I}$	σ^2_e
Pop-A	5.17**	4.88**	9.56	0.62	3.54**	6.06**	21.96	0.38	**	**	3.82**	4.28**	0.88*	0.92+	15.18
Pop-B	6.35**	6.39**	9.29	0.70	3.87**	5.61**	19.30	0.50	**	**	4.38**	4.32**	0.98*	1.72**	13.89

+, *,** Significant at the 0.1, 0.05 and 0.01 probability level, respectively

[a] Fixed effect

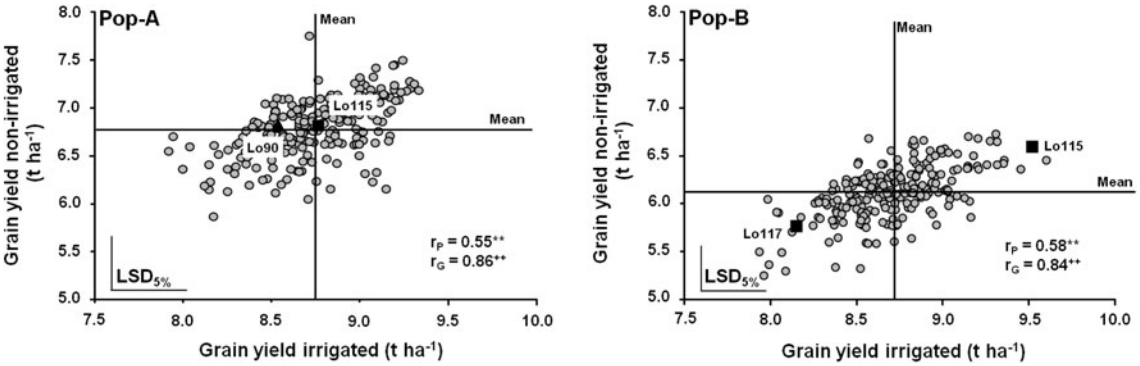

Fig. 2 Association between grain yield of the irrigated versus rainfed regime for 220 testcross progenies and their parents (Lo90, Lo115, Lo117) averaged across three drought environments for Pop-A and four drought environments for Pop-B with significant genotype × irrigation interaction variance

critical for grain yield formation, which ranges for rye from April to June. At least in 2 months in the period from April to June, rainfall was sharply reduced in several environments of our field trials (Fig. 1). The reduced rainfall resulted for several environments in drought stress reflected by a significantly lower average grain yield under rainfed compared to irrigated conditions (Table 1). We defined those environments exhibiting a significant difference between rainfed and irrigated conditions (ΔI) as "drought environments". For selection purposes, only environments that show additionally a significant genotype × irrigation interaction ($G \times I$) are valuable (Table 1). Therefore, we addressed in our survey three types of environments: (1) all environments together, (2) drought environments, and (3) drought environments with $G \times I$. This is the first report on field-induced drought stress in winter rye.

Intensity of drought stress

Drought stress occurred in this experiment in the rainfed variant at most environments as concluded from significant yield reductions between rainfed and irrigated regime ranging from 2 to 40.5 % (Table 1). Differences were lower in environments with heavy loam soils (2–14 %) in both years as could have been expected. Data from Wohlde 2010 + 2011 and Petkus 2011 illustrate a severe drought stress for Central European conditions.

In our study, five (Pop-A) and four (Pop-B) drought environments occurred (Table 1). Additionally, we observed in three (Pop-A) and four (Pop-B) drought environments genotype × irrigation interaction variances significantly larger than zero. Consequently, for a stress-tolerant crop like rye (Hoffmann 2008), we observed a remarkably high drought stress caused by lower rainfall in concordance with higher temperatures.

Genetic and environmental variances

The principal coordinate analysis of the environments revealed absence of clustering of the two water regimes, irrigated and rainfed (Supplementary material 3). Instead, single environments were aggregating. Dodig et al. (2008) reported similar results for 100 winter wheat cultivars and landraces from Serbia. The Polish environments Walewice were clearly separated from the North German locations in both years (Supplemental Material 3). This illustrates the different soil and weather conditions in Walewice compared to Wohlde and Petkus resulting in high interaction variances of genotypes × environments. The variances of genotypes × environments were of similar size than genotypic variances in the irrigated regime and across both water regimes, but considerably higher in the rainfed regime (Table 2). The same was observed for error variances resulting in considerably lower heritabilities in stressed compared to non-stressed environments as reported in previous studies (for review see Golabadi et al. 2011). Causes for higher error variances in rainfed regime are inhomogeneous soil textures with differences on small spatial scales, soil trends within a field (Whitmore and Whalley 2009), and consequently, highly varying water availability across the field. Concomitant with differences in soil water content is also a different availability of plant nutrients further enhancing error variances. The lighter the soil, the more pronounced are these non-genetic effects. We tried to counterbalance them by growing irrigated and rainfed plots of one genotype opposite to each other, by high nitrogen and water input and by using an incomplete block design, but obviously even this was not sufficient to reduce the plot error. Additionally, every environment very likely suffered from a different kind of drought stress because the period and intensity of drought was highly variable (Mitra 2001). This is indicated by significant genotype × environment × irrigation interaction variances. At individual environments on contrast, in particular Wohlde 2010 and Walewice 2011 (Pop-A), Wohlde 2011 and Walewice 2011 (Pop-B), genotype × irrigation variance had a much higher relevance compared to genotypic variance than in the combined analyses (Supplementary Material 4). Dodig et al. (2008) also reported that genotype × environment effects are much higher than genotype × irrigation effects in wheat. Nevertheless, lower heritability estimates considerably reduce selection gain for stress tolerance. Obviously, more test environments have to be used when selecting under abiotic stress situations than on irrigated water regimes.

Covariation between irrigated and rainfed regime

For analyzing the ranking of genotypes according to drought stress only drought environments with significant genotype × irrigation interaction variance were used. Despite this strict procedure, genotype × irrigation interaction variances were smaller in the combined analysis compared to the genotypic variances (Table 2). The three-way interaction variance ($\sigma^2_{G\times E\times I}$) also includes a genotype × irrigation interaction component, but this cannot be exploited by the breeder. Obviously, testcrosses differed not substantially in drought tolerance leading to genotypic correlations between both water regimes of 0.86 and 0.84 for Pop-A and Pop-B, respectively. Taking into account the different heritabilities in both water regimes, Harrer and Utz (1990) concluded that indirect improvement of genotypes under optimal conditions will be superior to direct selection under suboptimal conditions when genotypic correlation is higher than 0.6. Our prediction of relative efficiency according to Falconer and Mackay (1996) affirmed this for Pop-A. For Pop-B a combined improvement would be similarly efficient (Presterl et al. 2003). In accordance to our findings Dodig et al. (2008) concluded that grain yield under irrigated conditions was positively correlated with grain yield under drought stress conditions in sheltered plots among 100 wheat lines with, on average, 37.5 % yield reduction. Because indirect selection under irrigated regime implies the chance to discard high-yielding genotypes under a rainfed regime (see Fig. 2), a combined evaluation ($I + R$ water regimes) might be recommendable at least in an advanced breeding step (Ceccarelli et al. 1998). This would increase yield stability under a maximum array of environments. Generally, target areas for hybrid rye programs are geographically more widespread and diverse than market areas for other cereals. Hybrid rye breeders are, thus, highly interested in similar diverse testing environments including drought stress.

Lack of substantial crossover interaction between irrigated and rainfed regime

This study was performed within one heterotic group and data are valuable for improving the Petkus gene pool via recurrent selection. Selection based on a minimum yield decrease under drought stress relative to the irrigated regime would, however, result in reduced yield under both, stress and non-stress conditions (data not shown) as previously reported for wheat (Dodig et al. 2008).

The lack of substantial crossover interaction (Table 2) might indicate that (1) the stress was still not severe enough, (2) a restricted genetic variation within the two populations for drought stress tolerance occurred (Blum 2005), or (3) an effective selection against genotypes highly susceptible to drought stress in previous breeding stages was already performed (Weber et al. 2012). Considering that the target environments of our germplasm is Central Europe, the observed grain yield reduction of 24 % averaged across drought environments was high for this region. Our results are substantiated by data of Blum (1996, 2005) who reported that yield potential of a genotype has a large effect on yield under moderate drought stress conditions. However, grain yield level on both, I and R water regimes was high compared to the yield level achieved in practical agriculture on sandy soils. Drought stress increased therefore to some extent owing to the use of high agronomical input. According to quantitative-genetic theory, additive genotypic variance exploited in segregating populations from randomly drawn parental lines is about half the additive variance within the total gene pool. Consequently, a restricted genetic variation within the two populations for drought stress tolerance is unlikely. Therefore, we consider selection towards abiotic stress tolerance of hybrid rye prior to this study as the most probable reason for less crossover interaction, because (1) the parental elite lines were already highly selected for combining ability for grain yield across several testers and multiple environments (Wilde, personal communication, 2012) and (2) rye breeders routinely test their elite material for yield performance always on some locations with light, shallow soil under rainfed conditions to select for high nutrient and water use efficiency. Although such yield performance tests were not specifically designed for selecting stress tolerance they can gradually increase this complex trait on the long term.

Conclusions

Drought stress in Central Europe occurs at present irregularly and, therefore, genotypes are needed that perform well in both, stressed and high-yielding non-stressed environments. Progenies that perform above average under drought stress as well as in irrigated plots were already available in the crossing populations. To improve drought tolerance of hybrid rye, breeders should (1) include stress environments, i.e., rainfed environments on light soil, into their field trial system and (2) test advanced candidate lines under both water regimes to confirm their above average performance under drought stress. If these precautions are taken into account separate breeding programs in the Petkus gene pool are not required at present in hybrid rye breeding.

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References

Anscombe FJ, Tukey JW (1963) The examination and analysis of residuals. Technometrics 5:141–160

Blum A (1996) Crop responses to drought and the interpretation of adaptation. Plant Growth Regul 20:135–148

Blum A (2005) Drought resistance, water-use efficiency, and yield potential-Are they compatible, dissonant, or mutually exclusive? Aust J Agric Res 56:1159–1168

Blum A (2011) Drought resistance—is it really a complex trait? Funct Plant Biol 38:753–757

Ceccarelli S, Grando S, Impiglia A (1998) Choice of selection strategy in breeding barley for stress environments. Euphytica 103:307–318

Ceccarelli S, Grando S, Baum M (2007) Participatory plant breeding in water-limited environments. Exp Agric 43:411–435

Cochran WG, Cox GM (1957) Experimental designs. Wiley, New York

Dodig D, Zoric M, Knezevic D, King SR, Surlan-Momirovic G (2008) Genotype × environment interaction for wheat yield in different drought stress conditions and agronomic traits suitable for selection. Aust J Agric Res 59:536–545

DWD (Deutscher Wetterdienst) (2011) Drought conditions in Europe 2011 .http://www.dwd.de/bvbw/generator/DWDWWW/Content/Oeffentlichkeit/KU/KU2/KU23/rcc-cm/products/BesondereWetterereignisse/European/20110510__dryness2011__statement__for__WMO__en,templateId=raw,property=publicationFile.pdf/20110510_dryness2011_statement_for_WMO_en.pdf (see Supplementary material 6)

Falconer DS, Mackay TF (1996) Introduction to quantitative genetics, 4th edn. Longman Group Ltd, London

FAOSTAT (2011) Production. crops. http://faostat.fao.org/site/567/default.aspx#ancor. Accessed 22 Feb 2012

Golabadi M, Arzani A, Mirmohammadi Maibody SAM, Sayed Tabatabaei BE, Mohammadi SA (2011) Identification of microsatellite markers linked with yield components under drought stress at terminal growth stages in durum wheat. Euphytica 177:207–221

Hallauer AR, Miranda JB (1981) Quantitative genetics in maize breeding. Iowa State University Press, Ames

Harrer S, Utz HF (1990) A model study for breeding low-input varieties using maize as an example. (In German) pp. 9–20. *In* Bericht über die Arbeitstagung der “Arbeitsgemeinschaft der Saatzuchtleiter” im Rahmen der “Vereinigung österreichischer Pflanzenzüchter”. Bundesanstalt für alpenländische Landwirtschaft, Gumpenstein, Austria, November 20–22, 1990

Hoffmann B (2008) Alteration of drought tolerance of winter wheat caused by translocation of rye chromosome segment 1RS. Cereal Res Commun 36:269–278

Li P, Chen J, Wu P (2011) Agronomic characteristics and grain yield of 30 spring wheat genotypes under drought stress and non-stress conditions. Agron J 103:1619–1628

LSV (Landessortenversuche 2011) Ergebnisse der Landessortenversuche. Bericht zum Versuchswesen. Landwirtschaftskammer Niedersachsen, Germany

Mitra J (2001) Genetics and genetic improvement of drought resistance in crop plants. Curr Sci 80:758–763

Mode CJ, Robinson HF (1959) Pleiotropism and the genetic variance and covariance. Biometrics 15:518–537

Möhring J, Piepho HP (2009) Comparison of weighting methods in two-stage analysis of plant breeding trials. Crop Sci 49:1977–1988

Presterl T, Seitz G, Landbeck M, Thiemt EM, Schmidt W, Geiger HH (2003) Improving nitrogen-use efficiency in European maize: estimation of quantitative genetic parameters. Crop Sci 43:1259–1265

SAS Institute Inc (2008) SAS/STAT_9.2 User’s Guide. Cary, NC, USA

Tomerius A, Miedaner T, Geiger HH (2008) A model calculation approach towards the optimization of a standard scheme of seed-parent line development in hybrid rye breeding. Plant Breed 127:433–440

Turner NC (1979) Drought resistance and adaptation to water deficits in crop plants. In: Mussel H, Staples RC (eds) Stress physiology in crop plants. Wiley, New York, pp 181–194

Utz HF (2010) PLABSTAT. A computer program for statistical analysis of plant breeding experiments 3A. Institute of Plant Breeding, Seed Science and Population Genetics University of Hohenheim, Stuttgart

Weber VS, Melchinger AE, Magorokosho C, Makumbi D, Bänziger M, Atlin GN (2012) Efficiency of managed-stress screening of elite maize hybrids under drought and low nitrogen for yield under rainfed conditions in Southern Africa. Crop Sci 52:1011–1020

Whitmore AP, Whalley WR (2009) Physical effects of soil drying on roots and crop growth. J Exp Bot 60:2845–2857