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Generation mean analysis to estimate genetic parameters of some traits for rice–weed competitiveness

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Weeds are the most widespread biotic production constraint of rice in Africa and one of the major factors limiting grain yield. An efficient breeding strategy could be particularly important for improving weed management in sub-Saharan Africa (SSA) because most smallholder rice farmers use few external inputs. To understand rice weed competitiveness, experiments on reciprocal interspecific crosses derived from FKR19 (*Oryza sativa*) and CG20 (*Oryza glaberrima*) were carried out to estimate gene effects and heritability of traits: plant height at five leaves, plant height 30 days after transplanting, plant height at maturity, number of tillers at 30 and 60 DAT, number of fertile tillers, width of leaves at 80 DAT and at maturity, and length of leaves at 80 DAT and at maturity for rice–weed competitiveness. Six generations – P₁, P₂, F₁, F₂, BC₁F₁ and BC₂F₁ – were raised and subjected to generation mean analysis. The lowest heterosis of F₁ was obtained in both crosses (CG20/FKR19 and FKR19/CG20), except for plant height at 30 days after transplanting and leaf width at maturity in the CG20/FKR19 cross. The majority of traits displayed higher dominance gene effects (H_{5_L}, H₃₀ and L₈₀ for CG20/FKR19; W_{mat} and L_{mat} for FKR19/CG20) than additive gene effects; the latter were slight and non-significant for the majority of traits. Duplicate epistasis was observed for the number of tillers 30 days after transplanting and leaf length at maturity and plant height at maturity. Additive genetic variance values were higher in CG20/FKR19, revealing that the CG20 variety can be used as a donor parent. Plant height at maturity, length of leaves at 80 DAT and at maturity showed high narrow-sense heritability ($h_n^2 > 0.70$), influencing weed competitiveness.

Key words: Additive, dominance, heritability, rice, variance components, weed competitiveness.

INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most important crops in the world. It is the fifth most important cereal in Africa in terms of area harvested, and fourth in terms of production (FAO, 2008). In sub-Saharan Africa (SSA),

80% of rice is produced by smallholder farmers (WARDA, 2004, personal communication). Weeds are the most widespread biotic production constraint of rice in Africa and one of the major factors limiting grain yield (Halidou

et al., 2006). Screening assessments have revealed a selection of rice varieties that provide a superior level of weed competitiveness in African production systems. These include IG10 (Johnson et al., 1998; Fofana and Rauber, 2000), CG14 (Dingkuhn et al., 1998; Jones et al., 1996) and CG20 (Jones et al., 1996; Sarla and Mallikarjuna, 2005; Moukoumbi et al., 2011). Understanding the dynamics of crop genetic resources facilitates access to the diversity of traits – including weed competitiveness – that can be exploited. An efficient breeding strategy could be particularly important for improving weed management in SSA because most smallholder rice farmers use few external inputs (Rodenburg and Johnson, 2009).

The choice of an effective rice breeding approach to select for a particular characteristic depends substantially on the knowledge of the genetic system controlling these characteristics (Azizi et al., 2006). The value of each parameter depends on a combination of its genotypic effects and environmental effects. Genotypic variance can be divided into genetic additive variance (V_A), dominance (V_D), interactive additive–dominance (V_{AD}) and environmental (V_E) components. Determining these components contributes to a better understanding of the action of genes involved in the expression of the trait (Wolf and Hallauer, 1997). Generation mean analysis (Mather and Jinks, 1971) or scaling tests have been widely used for genetic analysis (Fall, 1994; Kearsey and Pooni, 1996; Möhring and Piepho, 2010). This approach was used in the present research to estimate genetic parameters such as additive gene effects, dominance gene effects and narrow-sense heritability. This leads to an understanding of the inheritance of traits and the nature of the epistatic gene effects (Fall, 1994).

Breeding weed-competitive cultivars requires an easily used protocol for selection under weed regimes. Competitiveness is an interaction between members of the same population for limited quantities of the same essential resource. The weed competitiveness of a crop has two components: weed tolerance, the ability to maintain high yields despite weed competition; and weed-suppressive ability, the ability to reduce weed growth (Jannink et al., 2000). Rice–weed competitiveness is controlled by a mixture of qualitative and quantitative genes (Azizi et al., 2006), but there are few existing studies that assess its genetic effects. However, some previous studies of the genetic effects of wheat–weed competitiveness have shown that it is possible to combine high grain yield with high competitiveness in a single genotype (Gibson and Fischer, 2004). Applying this approach to rice has the potential to generate new knowledge about the nature and magnitude of gene effects and their contribution to the control of rice–weed competitive traits, and to assist

in formulating an efficient breeding program. In addition, main rice characteristics were reported to be associated with weed competitiveness include plant height (Caton et al., 2003); higher tiller number (Fisher et al., 2001); droopy leaves (Dingkuhn et al., 1999); high biomass accumulation at the early stage (Ni et al., 2000); high leaf area index and high specific leaf area (Dingkuhn et al., 1999) during vegetative growth stage.

The present research investigated genetic effects and heritability in reciprocal interspecific crosses for weed-competitiveness. It measured ten main quantitative traits: plant height at five leaves (H_{5L}), plant height 30 days after transplanting (DAT) (H_{30}), plant height at maturity (H_{mat}), number of tillers at 30 DAT (T_{30}) and 60 DAT (T_{60}), number of fertile tillers (T_{fert}), width of leaves at 80 DAT (W_{80}) and at maturity (W_{mat}), and length of leaves at 80 DAT (L_{80}) and at maturity (L_{mat}).

MATERIALS AND METHODS

Experiments were conducted for a preliminary germplasm screening (Moukoumbi et al., 2011) and selected CG20 (*Oryza glaberrima*) as tolerant variety and FKR19 (*O. sativa*) as susceptible parent. F_1 seeds and their parents were planted to generate second filial generations (F_2), BC_1F_1 (CG20/2*FKR19 and FKR19/*2CG20) and BC_2F_1 (CG20/3*FKR19 and FKR19/*3CG20) backcross generations according to the reciprocal interspecific crosses. The populations BC_1F_1 and BC_2F_2 were developed using hand pollination. The experiment was conducted at the Africa Rice Center in Benin (6°25'N, 2°19'E and 15 m altitude) during the 2009/2010 wet season. Six generations derived from two crosses were transplanted in a randomized block design in three replications. Each generation was transplanted on 1.5 m long plot with spacing of 0.20 m between and within rows. For the F_1 , BC_1F_1 and BC_2F_1 generations, the number of plants per block varied according to plant material availability: 15 F_1 , 200 F_2 , 39 BC_1F_1 and 38 BC_2F_1 with CG20 as female and FKR19 as male; 14 F_1 , 137 F_2 , 29 BC_1F_1 and 32 BC_2F_1 for a reciprocal cross (FKR19/CG20); CG20 and FKR19 plants. Fertilizers were applied at the rate of 200 kg ha⁻¹ of NPK₁₅₋₁₅₋₁₅ (vegetative stage) and 50 kg ha⁻¹ urea (reproductive stage). Ten quantitative agro-morphological data were collected at the appropriate growth stage, following the Standard Evaluation System for rice (INGER–IRRI, 1996) and descriptors for rice (*Oryza* spp.) from Biodiversity International–IRRI–AfricaRice (2007).

A formula explaining gene effects, first proposed by Mather and Jinks (1971), then by Kearsey and Pooni (1996) and finally by Möhring and Piepho (2010), was used: $\mu_i = m + [a]x_{i1} + [d]x_{i2} + [aa]x_{i1}^2 + [dd]x_{i2}^2 + [ad]x_{i1}x_{i2}$, where μ = mean of each generation, m = phenotypic mean of both parents, $[a]$ = additive gene effect, $[d]$ = gene effect of residual dominance, $[aa]$, $[dd]$ and $[ad]$ = epistatic (interaction between loci), and x_{i1} and x_{i2} = assigned coefficients for each generation (Table 1). The type of epistasis was determined only when the dominance effect $[d]$ was significant and when these effects had the same sign, the epistasis was complementary while the different sign indicated duplicate epistasis (Dvojković et al., 2010).

Following Möhring and Piepho (2010), an ANOVA mixed model was applied to estimate mean values, standards errors and to test

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Table 1. Linear models for means, genetic variances and total within-plot variance of six generations for generation mean analysis using the additive–dominance model of Kearsley and Pooni (1996).

Mean parameter			Variance parameter			
Generations	[a] (coefficient x_{i1})	[d] (coefficient x_{i2})	σ_a^2	σ_d^2	σ_{ad}	$V_{(fijk)} = V_{(gijk + eijk)}$
P ₁	1	0	0	0	0	$\sigma_1^2 = \sigma_e^2$
P ₂	-1	0	0	0	0	$\sigma_1^2 = \sigma_e^2$
F ₁	0	1	0	0	0	$\sigma_1^2 = \sigma_e^2$
F ₂	0	0.5	1	1	0	$\sigma_2^2 = \sigma_e^2 + \sigma_a^2 + \sigma_d^2$
BC ₁ F ₁	0.5	0.5	0.5	1	-1	$\sigma_3^2 = \sigma_e^2 + 1/2(\sigma_a^2) + \sigma_d^2 - \sigma_{ad}$
BC ₂ F ₁	-0.5	0.5	0.5	1	1	$\sigma_4^2 = \sigma_e^2 + 1/2(\sigma_a^2) + \sigma_d^2 + \sigma_{ad}$

[a] : additive effect ; [d] : dominance effect ; [ad] : interaction between loci = epistasis; x_{i1} et x_{i2} coefficients affected to each generation ; $V_{(fijk)}$: Phenotypic variance ; $V_{(gijk)}$: genotypic variance ; $V_{(eijk)}$: Environmental variance ; i =generation ; j =Block number and k =plant number tested

homogeneity of the genetic components of variance (V_A , V_E , V_{AD} and V_E) and genetic effects (additive, dominance and additive \times dominance). A lack of fit test was added to check the adequacy of the model for estimating genetic effects. In addition, a Wald f-test, based on the mixed model and equivalent to the joint scaling test proposed by Mather and Jinks (1971), was used to confirm the model.

The variance components were determined following two formulae: $V_P = V_G + V_E$, where V_P = phenotypic variance, V_G = genotypic variance, and V_E = environmental variance; and: $V_G = V_A + V_D + V_{AD}$, where V_A = additive variance, V_D = dominant variance, and V_{AD} = epistasis. V_D and V_{AD} values were set to zero when estimated variance turned out to be negative. Broad-sense heritability was estimated using $h^2_b = V_G/(V_G + V_E)$ and narrow sense heritability using $h^2_n = V_A/(V_G + V_E)$. All statistical analysis was carried out using SAS 9.1 (2003) software.

RESULTS

Mean values and their standard errors for the ten traits of the two crosses are presented in Table 2a and b. The parents used in the reciprocal interspecific cross showed significant difference ($P \leq 0.0001$) with all traits except for H_{30} . The mean values of the ten traits for the F_1 generation derived from the CG20/FKR19 cross were lower than the mean values for either parent, except for the trait W_{mat} , where it was higher than the mean value of both parents. The mean values for the traits L_{80} and L_{mat} were the highest when FKR19 was the female parent. Of the F_1 generation derived from the FKR19/CG20 cross, the mean value was also generally lower than the mean value for either parent, except for H_{30} where it was greater than the donor parent, and for the trait W_{mat} , where it was greater than both parents. The mean values of the second filial generation F_2 derived from the CG20/FKR19 cross were better than the parental lines for the traits H_{mat} , W_{mat} and L_{80} . In addition, with the second cross (FKR19/CG20), the values obtained with H_{mat} (donor parent) and W_{mat} were higher than their parents.

The differences between generations obtained were analyzed using generation mean analysis following the additive–dominance model, and all tests were found to be

significant at 0.05. Dominance gene effects (Table 3) were found to be more important for H_{mat} , T_{30} , T_{60} , T_{fert} , W_{80} , W_{mat} and L_{mat} in the CG20/FKR19 cross, and for H_{5L} , H_{30} , H_{mat} , T_{30} , T_{60} , T_{fert} , W_{80} and L_{80} in the FKR19/CG20 cross. Superdominance and epistatic gene effects were predominant in controlling inheritance with the CG20/FKR19 cross for five traits: H_{mat} , T_{30} , T_{60} , T_{fert} and W_{80} . In addition, the negative values of the dominance gene effect were found for H_{30} , H_{mat} and L_{mat} in the reciprocal cross, and for W_{80} in the FKR19/CG20 cross. In the CG20/FKR19 cross, additive gene effects were significant and important for H_{30} , H_{mat} , T_{30} and L_{mat} . In the FKR19/CG20 cross, additive gene effects were also significant but moderate for H_{30} , H_{mat} , W_{80} , L_{80} and L_{mat} .

The analysis of the gene effects revealed that additive and dominance effects were involved in the inheritance of most traits. Dominance gene effects were non-significant and negative in the CG20/FKR19 cross for H_{5L} , H_{30} and L_{80} , and in the FKR19/CG20 cross for W_{mat} and L_{mat} . The additive–dominance model used cannot explain the variation between generations, which may be the result of the complexity of the mechanisms of genetic control of these traits. The dominance gene effects on H_{mat} , T_{30} , T_{60} , T_{fert} and W_{80} (CG20/FKR19 and FKR19/CG20), L_{mat} and W_{mat} (CG20/FKR19) and H_{5L} , W_{mat} and L_{mat} (FKR19/CG20) were significant. In this case, the variation in generation revealed a digenic epistatic model between generations.

V_E component values were higher for all traits analyzed, with the exception of W_{80} and L_{80} in both crosses. Estimated V_A component values were highest for all analyzed traits except for H_{30} and T_{fert} in the CG20/FKR19 cross and H_{5L} and W_{80} in the FKR19/CG20 cross. In accordance with the results shown in Table 4a and b, estimated values of broad-sense heritability (h^2_b) ranged from 0 (W_{80}) to 0.86 (H_{5L}) in FKR19/CG20, and from 0.23 (T_{30}) to 0.86 (H_{mat}) in CG20/FKR19. For narrow-sense heritability (h^2_n), the highest estimated value was 0.79 (H_{mat} and L_{80}) in CG20/FKR19, while the range in FKR19/CG20 was 0.72

Table 2a. Generation means and standard errors for ten quantitative traits using CG20 and FKR19 as female and donor parents.

Generations	Traits (Mean ± SE)									
	H _{5_L}	H ₃₀	H _{mat}	T ₃₀	T ₆₀	T _{fert}	W ₈₀	W _{mat}	L ₈₀	L _{mat}
P ₁ : CG20	30.40±1.04 ^{ab}	53.13±1.12 ^a	135.40±1.72 ^a	17.32±1.23 ^a	37.10±1.99 ^a	32.48±1.78 ^a	1.51±0.03 ^b	0.82±0.06 ^c	41.81±0.89 ^{ab}	43.73±0.85 ^a
P ₂ : FKR19	27.37±1.01 ^{ab}	57.20±1.08 ^a	118.12±1.65 ^b	14.9±1.18 ^a	38.22±1.91 ^a	36.62±1.71 ^a	1.67±0.03 ^a	0.93±0.05 ^{bc}	42.44±0.85 ^{ab}	39.57±0.82 ^{ab}
F ₁ : CG20/FKR19	26.93±1.64 ^{ab}	53.93±1.76 ^a	95.66±2.70 ^c	5.37±0.65 ^c	20.2±3.12 ^b	11.53±2.79 ^d	1.18±0.05 ^c	1.11±0.08 ^{ab}	38.36±1.39 ^{ab}	29.96±1.34 ^c
F ₂ :CG20/FKR19 (<i>self pollinisation</i>)	26.67±0.61 ^b	52.96±0.92 ^a	133.72±2.35 ^a	10.56±0.45 ^b	24.26±0.8 ^b	20.88±0.87 ^{bc}	1.26±0.02 ^c	1.17±0.01 ^a	42.95±1.03 ^{ab}	42.20±0.98 ^{ab}
BC ₁ F ₁ : CG20/2*FKR19	28.20±1.13 ^{ab}	54.96±1.53 ^a	108±2.25 ^{bc}	6.31±0.82 ^c	18.20±1.37 ^b	16.68±1.22 ^{cd}	1.18±0.02 ^c	1.10±0.02 ^{ab}	44.61±1.61 ^a	44.16±1.18 ^a
BC ₂ F ₁ : CG20/3*FKR19	32.12±1.44 ^a	55.87±3.63 ^a	105.16±6.68 ^{bc}	5.37±0.65 ^c	21±2.18 ^b	26.62±3.83 ^b	1.13±0.06 ^c	1.12±0.05 ^{ab}	36.65±1.50 ^b	37.13±1.28 ^b

Table 2b. Generation means and standard errors for ten quantitative traits using FKR19 and CG20 as female and donor parents.

Generations	Traits (Mean ± SE)									
	H _{5_L}	H ₃₀	H _{mat}	T ₃₀	T ₆₀	T _{fert}	W ₈₀	W _{mat}	L ₈₀	L _{mat}
P ₁ : FKR19	27.38±0.89 ^{ab}	57.1±0.95 ^a	118.25±1.62 ^b	14.90±1.23 ^{ab}	38.23±1.87 ^a	36.63±1.69 ^a	1.67±0.03 ^a	0.93±0.05 ^{bc}	42.44±0.92 ^b	39.57±0.82 ^b
P ₂ : CG20	30.41±0.93 ^{ab}	53.13±0.99 ^a	135.40±1.68 ^a	17.32±1.23 ^a	37.11±1.95 ^a	32.49±1.76 ^a	1.51±0.03 ^b	0.85±0.05 ^c	41.81±0.95 ^b	43.79±0.85 ^{ab}
F ₁ : FKR19/CG20	25.14±1.51 ^{ab}	55.71±1.61 ^a	111.41±2.74 ^{bc}	8.36±2.01 ^{cd}	11.79±3.17 ^c	13.70±2.86 ^b	1.22±0.05 ^c	1.17±0.08 ^{ab}	42.48±1.55 ^b	41.29±1.38 ^b
F ₂ : FKR19/CG20 (<i>self pollinisation</i>)	24.31±1.06 ^b	53.07±2.21 ^a	137.03±4.03 ^a	10.35±0.84 ^{bc}	22.35±1.42 ^b	19.54±1.35 ^b	1.28±0.03 ^c	1.15±0.03 ^{ab}	41.36±1.86 ^b	39.02±1.58 ^b
BC ₁ F ₁ : FKR19/2*CG20	31.25±3.26 ^a	54.37±4.7 ^a	103±4.91 ^c	4.38±0.82 ^d	13.38±1.13 ^c	10.88±1.05 ^b	1.26±0.08 ^c	1.22±0.06 ^{ab}	41.31±1.57 ^b	38.56±1.97 ^b
BC ₂ F ₁ : FKR19/3*CG20	29.45±3.67 ^{ab}	51.27±2.12 ^a	107.81±4.91 ^{bc}	3.45±0.47 ^d	20.18±2.39 ^{bc}	17.55±1.85 ^b	1.34±0.03 ^c	1.34±0.05 ^a	50.16±2.10 ^a	47.88±2.63 ^a

(H_{mat}).

DISCUSSION

The variations depended on the cross and on the associated trait. Variation in the generation means did not, in most cases, fit a simple epistatic model, as also reported by Dvojković et al. (2010). This indicates that improvement in the traits studied would be more difficult to achieve in comparison

with simpler models of inheritance such as additive–dominance and digenic epistatic models, which are considered best from a breeder's point-of-view. These results are in accordance with the literature, and were validated through genetic analysis of the ten traits following the technique reported by Möhring and Piepho (2010).

The unexpectedly low F₁ values obtained could be explained by the regression of heterosis reported by Lefort-Busson (1985), personal communication who mentions that the dispersion

of alleles from the parents can occur when a cross is carried out between two genetically opposed parents, such as a rice–weed competitive variety and rice–weed non-competitive variety. On the other hand, the moderate heterosis values obtained suggest the genetic gain in the performance of some traits, but this depends on the cross carried out. In addition, maternal effect might explain some of the disparities between the crosses for T₃₀, T₆₀, T_{fert}, L₈₀ and L_{mat}. For the first and second backcrosses and reciprocal

Table 3. Estimation of gene effects for quantitative traits with standard errors and p-value of lack of fit (m = constant; a = additive gene effects; d = dominance gene effects and ad: epistasis; * = significant at 0.05; ** = significant at 0.01-0.001; *** = significant at 0.0001; ns = non-significant at 0.05).

Traits	Parameter (Mean ± SE) using CG20 and FKR19 as female and donor parents				Lack of fit (α=0.05)
	m	a	d	ad	
H _{5_L}	28.89± 0.72**	-1.51± 0.72 ^{ns}	-4.44± 1.89 ^{ns}	24.84± 6.43*	0.07
H ₃₀	55.16± 0.77*	2.03± 0.77**	-4.39± 2.41 ^{ns}	7.55± 15.07 ^{ns}	0.50
H _{mat}	126.76± 1.19**	-8.64± 1.19***	13.92± 5.27***	-96.96± 28.44***	0.01
T ₃₀	16.11± 0.85**	-1.21± 0.85**	-11.09± 1.93***	-18.34± 3.61***	0.68
T ₆₀	37.66± 1.38**	0.55± 1.38 ^{ns}	-26.79± 3.28***	-14.18± 9.84***	0.04
T _{fert}	34.55± 1.23**	2.06± 1.23 ^{ns}	-27.33± 3.03***	18.81± 15.93*	0.04
W _{_80}	1.59± 0.02*	0.08± 0.02 ^{ns}	-0.66± 0.07***	-0.66± 0.28***	0.02
W _{_mat}	0.89± 0.04**	0.05± 0.04 ^{ns}	0.59± 0.08***	-0.32± 0.23 ^{ns}	0.01
L _{_80}	42.12± 0.61**	0.31± 0.61 ^{ns}	1.65± 2.40 ^{ns}	-25.86± 7.41 ^{ns}	0.01
L _{_mat}	41.68± 0.59**	-2.11± 0.59**	1.05± 2.3***	16.06± 6.58**	0.01

Traits	Parameters (Mean ± SE) using FKR19 and CG20 as female and donor parents				Lack of fit (α=0.05)
	m	a	d	ad	
H _{5_L}	28.89± 0.64**	-1.51± 0.64 ^{ns}	-9.16± 2.49*	-17.55± 15.34 ^{ns}	0.04
H ₃₀	55.16± 0.68**	2.03± 0.68**	-4.18± 4.63*	3.15± 12.36 ^{ns}	0.10
H _{mat}	126.76± 1.17*	-1.21± 0.85***	-11.53± 2.41***	118.16± 25.53 ^{ns}	0.01
T ₃₀	16.11± 0.85**	0.55± 1.35 ^{ns}	-30.64± 3.93**	29.99± 4.24**	0.01
T ₆₀	37.66± 1.35**	-8.64± 1.17 ^{ns}	12.54± 8.39**	7.54± 11.47 ^{ns}	0.01
T _{fert}	34.55± 1.23*	2.06± 1.22 ^{ns}	-30.03± 3.64***	3.83± 9.50***	0.01
W _{_80}	1.59± 0.02*	0.08± 0.02***	-0.61± 0.08***	-0.37± 0.21 ^{ns}	0.04
W _{_mat}	0.89± 0.03*	0.04± 0.03 ^{ns}	0.52± 0.10 ^{ns}	-0.84± 0.26**	0.01
L _{_80}	42.12± 0.66**	0.31± 0.66*	-1.62± 3.41***	-36.02± 10.59 ^{ns}	0.07
L _{_mat}	41.68± 0.59*	-2.10± 0.59***	-5.32± 3.39 ^{ns}	-31.21± 12.36*	0.19

Table 4a. Estimation of genetic variance component and heritability for ten quantitative traits using CG20 and FKR19 as female and donor parents.

Parameter	Traits (Mean ± SE)									
	H _{5_L}	H ₃₀	H _{mat}	T ₃₀	T ₆₀	T _{fert}	W _{_80}	W _{_mat}	L _{_80}	L _{_mat}
V _E	40.43	46.71	109.76	56.43	146.64	117.49	0.05	0.11	29.38	27.31
V _A	18.37	0	644.76	16.55	61.15	0	0.07	0.02	109.39	135.74
V _D	0	44.45	0	0	0	0	0	0	0	0
V _{AD}	0	18.72	60.37	0	0	37.16	0.01	0	0	0
V _G	18.37	63.18	705.13	16.55	61.15	37.17	0.07	0.03	109.40	135.74
V _P	58.80	109.90	814.89	72.98	207.79	154.65	0.12	0.14	138.78	163.05
h ² _b	0.312	0.57	0.86	0.23	0.29	0.24	0.59	0.18	0.80	0.83
h ² _n	0.21	0	0.79	0.22	0.28	0	0.56	0.18	0.79	0.72

backcrosses, the differences found come from the parent's contribution during the crosses.

These results indicate that improving these traits would be difficult, as reported by Dvojkočić et al. (2010) in their genetic analysis for yield and yield traits associated for two winter wheat crosses. The present research showed a preponderance of dominance gene effects over additive gene effects in the expression of the ten traits (7/10 in CG20/FKR19 and 8/10 in FKR19/CG20), as already

reported by Akhtar and Muhammad (2006), Fethi and El Mohamed (2010) and Hasib et al. (2002) regarding tillering ability and plant height. Highly significant dominance gene effects could explain the phenomenon of great dominance indicated by Akhtar and Muhammad (2006), resulting from the strong accumulation of dominant genes from parents of all generations, and indicating that the parents were dispersing genes (Dhanda and Sethi, 1996; Fethi and El Mohamed, 2010).

Table 4b. Estimation of genetic variance components and heritability for ten quantitative traits using FKR19 and CG20 as female and donor parent.

Parameter	Traits (Mean ± SE)									
	H _{5_L}	H ₃₀	H _{mat}	T ₃₀	T ₆₀	T _{fert}	W ₈₀	W _{mat}	L ₈₀	L _{mat}
V _E	32.25	36.58	105.56	56.78	141.10	115.25	0.05	0.10	33.97	26.96
V _A	0	21.63	405.13	29.38	32.99	48.38	0	0.01	47.34	23.68
V _D	171.59	69.21	0	0	0	0	0	0	0	15.01
V _{AD}	31.60	0	45.21	0	26.34	14.44	0	0	10.43	22.50
V _G	203.19	90.85	450.34	29.38	59.34	62.82	0	0.01	57.77	61.19
V _P	235.44	127.43	555.90	86.17	200.44	178.08	0.04	0.10	91.74	88.15
h ² _b	0.86	0.71	0.81	0.34	0.29	0.35	0	0.01	0.62	0.69
h ² _n	0	0.16	0.72	0.31	0.16	0.27	0	0.01	0.51	0.26

On the other hand, genetic recombination during the crossing process could explain the significant negative dominance gene effects obtained in generations, with the high degree of dispersion of increasing alleles between parents contributing to a slight and non-significant additive gene effect.

In most cases the variation between generation means did not fit a simple epistatic model, but the additive–dominance model was accurate for the main gene effects for H_{mat}, T₃₀ and L_{mat} in the CG20/FKR19 cross and for H₃₀, H_{mat}, W₈₀ and, L₈₀ in the FKR19/CG20 cross. Epistatic affects following an additive–dominance interaction were more important with the CG20/FKR19 cross than with the FKR19/CG20 cross. Duplicate epistasis was observed for H_{mat}, T₃₀ and L_{mat} and means that the model was adequate for both crosses. However, a better explanation of this duplicate epistasis, offering greater precision on rice–weed competitiveness (Griffiths et al., 2006; Cuguen, 2010), could be obtained by estimating the substitution effects of additive–additive (aa), dominance–additive (da) and dominance–dominance (dd).

V_A was high, despite some variations noted in CG20/FKR19, revealing that the variety CG20 can be used as donor parent in a breeding strategy to develop a weed-competitive rice variety. The negative, nil and non-significant estimates obtained with V_D could be due to environmental variation, sampling errors and/or the fact that basic generations are inefficient for determining dominance variance (Dvojković et al., 2010). In addition, the inheritance of quantitative traits has been described as a ‘moving target’ (Lewis and John, 1999 cited by Benjdi and El Gazzah, 2010), since it is affected not only by the actions of multiple individual genes, but also by the interactions between genes and environmental factors. The estimates values of narrow-sense heritability were lower than broad-sense heritability and are in accordance with those reported by Robinson et al. (1949) who identified three levels of heritability, low (h²<0.2), moderate (0.2<h²<0.4) and high (h²>0.4). Reported estimates of heritability indicate that these agro-morphological traits influence the weed-competitiveness

of the variety. But for traits where estimates of heritability were low to moderate, further analysis of rice–weed competitiveness is needed, ensuring that the breeding population is wide and that selection for rice–weed competitiveness in later generations is exercised under controlled conditions (Saha and Amirul, 2008).

The initial expectations of this research were met and the study provided estimations of additive and dominance gene effects. Additive–dominance interaction effects enabled an explanation of the gene effects involved in the rice–weed competitiveness. The additive components of variance were higher with H_{mat}, T₃₀ and L_{mat}. Dominance gene effects were high and significant, and epistasis was more important than additive gene effects, which were slight and non-significant for the majority of traits. The contribution of environmental component variance in governing weed competitiveness cannot be elucidated without estimates of the other substitution effects such as additive–additive (aa), dominance–additive (ad) and dominance–dominance (dd). These could confirm the nature of epistasis and offer new opportunities for genetic improvement of rice–weed competitiveness.

Conflict of Interest

The authors have not declared any conflict of interest.

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