

Original Research Article

Gene effects of resistance to *Septoria tritici* in durum wheat under three water stress level

Running title: Relationship between gene effects and water stress level in resistance to *septoria tritici* in durum

Abstract

Gene effects and narrow-sense heritability estimates for components of resistance to *Septoria tritici* Blotch assessed under three water stress levels were evaluated using two populations derived from crossing partial-resistant durum wheat inbred lines Agili and Jneh Kottifa and susceptible inbred lines Karim 80 and Razzek by the generation means analysis. Populations included the resistant parents, susceptible parents, F₁ and F₂ generations and backcrossed BC₁Pr and BC₁Ps generations. The presence of an epistatic effect was dependent upon water stress level. In the absence of water stress, only additive and dominance effects were induced for the two populations and the two isolates. Therefore, in the presence of water stress levels, the variation of generation means was adequately explained by additive, dominance and digenic epistatic effects for the two populations. The variation in the mode of the gene effect of STB resistance inheritance with water stress level complicated the procedure of incorporating genes of resistance in agronomically acceptable cultivars. In the absence of water stress, selection would be simpler, because only additive and dominance effects were implicated. However, the genetic mechanism will not be stable when the plant experiences water stress. For cultivars designed for exploitation in a wide range of environmental conditions, selection under water stress is suggested for the stability of resistance to STB. Narrow-sense heritability estimates were consistent between combinations of crosses–isolates–water stress levels and ranged from 51 to 72 %.

Keywords: durum wheat, **efficient selection**, gene effects, stability, water stress

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1. Introduction

Septoria tritici Blotch (STB) caused by the ascomycete *Mycosphaerella graminicola* (Fuckel) J. Schröt in Cohn.(anamorph: *Septoria tritici* Roberge in Desmaz), is an important disease in many areas where wheat is grown (Shipton et al., 1971; King et al., 1983; Eyal et al., 1987). It can cause considerable yield losses of up to 50_% in the wheat growing areas with severe infections (Eyal and Levy, 1987). In Tunisia, durum wheat is the primary cultivated crop and occupies more than half of the area dedicated to cereal crops (Bnejdi and El Gazzah, 2008), with biotic and abiotic stresses the major factors seriously severely affecting crop production. Resistance to STB is of great high relevance in wheat breeding; and is quantitatively inherited and controlled by multiple genes (Schnurbusch et al., 2003; Uphaus et al., 2007; Kelm et al., 2011). Both additive and dominance effects (Van Ginkel and Scharen, 1987) play an importanta significant role in the expression of resistance, and epistasis also has a substantial effect (Bnejdi et al., 2011b).The environmental problem caused by continuous use of chemicals for control makes breeding for resistance to STB an essential component in controlling managing this important foliar disease of wheat. The genetic architecture of complex traits consists of not only the action of genes in single loci, but also the inter-locus interactions and gene × environment interactions. The complexity of the genetic architecture can be largely mainly attributed to epistasis, which plays a significant role in heterosis, inbreeding depression, adaptation, reproductive isolation and speciation (Yang and Zhu, 2005). The efficiency of any methodology of selection is associated with the unbiased estimates of the additive genetic effect (Viana, 2000).The lack of empirical work on epistasis, in part, reflects the difficulty in in the quantification of epistasis (Whitlock et al., 1995; Fenster et al., 1997). Nonetheless, many studies that attempt to identify the genetic basis of quantitative traits ignore the possibility that loci interact (Carlborg and Haley, 2004), as well as the effects of environment on the expression of gene effects and their interactions with the

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genetic background. It is important to note that most models of inheritance are simplifications of complex genetic phenomena. Epistasis is a significant component in the inheritance of quantitative characters, and geneticists must face the reality of complex genetic systems. A better understanding of the relative importance of water stress in genetic components of resistance to STB would potentially lead to the more efficient development of resistant varieties and deployment of germplasm resources. Therefore, the objective of the present research was to evaluate the role of water stress in the variation of gene effects in resistance to STB in durum wheat.

2. Materials and methods

2.1 Plant materials

Parental lines were selected depending on their differential reactions to STB. The partially resistant parents (Pr) were Agili and Jneh Kottifa, and susceptible parents (Ps) were Karim 80 and Razzek. F₁ and F₂ generations and BC₁Pr and BC₁Ps backcross generations from the crosses of Karim 80 × Agili and Razzek × Jneh Kottifa were used in this study. Plants were grown in a randomized complete block design with two replications. Two seeds of each genotype were sown in 1-L pots containing loam substrate with three water stress levels (LS0, LS1 and LS2 representing respectively 100%, 70% and 50% of field capacity and placed in a growth chamber at 20 ± 2 °C with a 12-h photoperiod. Pots were weighed, and water was added to bring the pots to the required saturation, if the water level was more than 10% below the required level.

2.2 Pathogen production and disease evaluation

Two isolates (ISTB1 and ISTB2) of STB were collected from infected durum wheat plants from the northwest of Tunisia. Conidia of each isolate were streaked on PDA (39 g of potato dextrose agar per 1 L) Petri plates. Then the plates were placed in the growth chamber at 20 ±

81 | 2 °C with a 12-h photoperiod. When the edge of the pink colony began to darken, the conidia
82 | were ready to harvest. A conidial suspension was prepared using equal quantities of the two
83 | isolates, filtered through two layers of cheesecloth and adjusted to 10⁶ conidia mL⁻¹ using a
84 | haemocytometer. Plants (two-leaf stage) were inoculated evenly by spraying the fungal
85 | conidia suspensions (40 mL/100 plants) onto leaves with an atomizer. After inoculation, the
86 | plants were covered with black polyethylene film for 72 h; and 21 days later the disease
87 | symptoms were assessed.

88 | Disease ratings of all leaves of each plant were recorded on a 1–9 scale, based on the
89 | infection response (amount of necrosis and chlorosis) and on density of pycnidia (Zhang et
90 | al., 1999). The scale was defined as follows: (1) no visible symptoms, and the leaves
91 | remained green and healthy; (2) a few chlorotic lesions were present, and the infection site
92 | was a tan-coloured spot; (3) extensive chlorotic lesions were present, lesions occasionally had
93 | necrosis at the infection; (4) extensive chlorotic lesions merged with each other, and
94 | individual lesions were identified by initial infection sites, and necrosis and chlorosis both
95 | existed on the leaf; (5) lesions were fully merged, and more than half of the leaf was
96 | desiccated by necrosis; (6) the entire leaf was desiccated, and water-soaked lesions occupied
97 | the entire leaf; (7) a few pycnidia were visible on the infected sites, and < 30% of the leaf
98 | was occupied by pycnidia-covered lesions that remain dry and green; (8) pycnidia occupied
99 | 50–70% of the leaf, and infected sites were dry yet still green; and (9) the entire leaf was
100 | covered by pycnidial lesions, and the leaf was dry yet still green. The number of plants
101 | evaluated varied depending on the generation and was greater in generations with greater
102 | segregation, such as F₂, BC₁Pr, and BC₁Ps.

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104 | 2.3 Statistical analyses

105 | Prior to Before analysis, transforming the data by log, square root, arc-sine, and arc-sine of
106 | the square root of the variable had no effect on data distribution or in removing epistatic

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107 effects. Analysis of variance by population, stress level and isolate using general linear model
108 (GLM) procedures (SAS, 1990) indicated that the replication and generation $\times$ replication
109 effects were not significant. Therefore, generation means analysis was conducted without
110 adjusting data for replication.

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2.3.1 Gene effects

113 Generation means analysis was determined separately for each combination of cross-isolate-
114 water stress level as follows: Weighted least squares regression analyses were used to solve
115 for mid-parent [m] pooled additive [d], pooled dominance [h] and pooled digenic epistatic
116 ([i], [l] and [j]) genetic effects, following the models and assumptions described in Mather
117 and Jinks (1982). A simple additive-dominance genetic model contains only the
118 m, d and h effects was tested first, using the joint scaling test described in Rowe and
119 Alexander (1980). Adequacy of the genetic model was assessed using a chi-square goodness-
120 of-fit statistic derived from deviations from this model. If statistically significant at $p < 0.05$,
121 the genetic models containing digenic epistatic effects were then tested until the chi-square
122 statistic was non-significant.

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2.3.2 Heritability

125 Homogeneity of variances of non-segregating generations was tested using Bartlett's test
126 (Bartlett, 1937), and when the variances were heterogeneous, the environmental variance
127 (V_E) was replaced by an adequate number of separate parameters and pooled to produce a
128 single environmental variance. Additive, dominance and environmental variance components
129 were estimated using the maximum likelihood method with the observed variance of the six
130 basic generations being used as the initial weights [$df/(2 \times S^2)$] until the chi-squared test value
131 reached a minimum (Lynch and Walsh, 1998). Narrow-sense heritability was calculated as
132 follows: $h^2_n = V_A/(V_A + V_D + V_E)$. Where V_A is the additive genetic component of variance,

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133 V_D the dominance genetic component of variance and V_E the environmental variance
134 (Kearsey and Pooni, 1996).

135 3. Results

136 Comparison of means using Duncan's multiple range test ($\alpha = 0.05$), indicated significant
137 differences between generations in all combinations of cross-isolate-water stress level. As
138 expected, the two parental lines in each cross were consistently different for the three
139 experimental water levels (Table I).

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140 The results of generation means analysis revealed that in the absence of water stress (LS0),
141 the three-parameter model was sufficient to explain the genetic variation of generation means
142 of resistance to STB in the four combinations of cross-isolate and the probability of
143 goodness-of-fit varied from 34 to 89%. Additive (d) type effect was significant, negative and
144 more pronounced than dominance (h) type effect. However, in the presence of water stress
145 (LS1 and LS2) the additive-dominance model did not adequately fit for all combinations, and
146 so the digenic epistatic model was applied and found appropriate. The probability of
147 goodness-of-fit of these models ranged from 27 to 99%. In the majority of cases, dominance
148 (h), additive $\times$ additive (i) and dominance $\times$ dominance (l) types' effects (when significant)
149 contributed more in to the control of resistance than additive effects. In all cases additive and
150 dominance effects (when significant) were negative. The additive $\times$ dominance (j) effect was
151 significant only in the cross Karim 80 $\times$ Agili with isolate ISTB1, where the additive $\times$
152 additive (i) effect was not significant (Table II).

153 Variance components were estimates and used to calculate narrow-sense heritability (h^2_n) for
154 both crosses and isolate-water stress level combinations. For all cases, the additive variance
155 effect was significant and ranged from 2.15 to 11.45 in the cross Karim 80 $\times$ Agili, and from
156 3.45 to 7.33 in the cross Razzek $\times$ Jneh Kottifa. The dominance variance effect was smaller
157 than the additive variance and ranged from 0.8 to 4.13 in the cross Karim 80 $\times$ Agili, and

158 from 0.55 to 2.86 in cross Razzek × Jneh Kottifa. Environmental variance estimates were
159 smaller than additive and dominance variances estimates and ranged from 0.36 to 1.12 in the
160 two crosses. Under the three levels of water stress, h^2_n was consistent between crosses and
161 isolates with a range from 51 to 72% (Table III).

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163 4. Discussion

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164 Significant differences were observed among generation means for resistance to STB in all
165 combinations of cross-isolate-water stress level. This indicates that the magnitude of
166 differences in the two populations was sufficient for selecting genotypes to improve
167 resistance to STB in presence and absence of water stress. Plant genetic adaptability is of
168 primary importance in many aspects of genetic research and is a special particular priority in
169 the study of the main major crops grown in a wide range of environments. Therefore, the
170 variation of inheritance of quantitative traits with environmental conditions has infrequently
171 been infrequently studied considered and there is little knowledge on this topic. Recently
172 Bnejdi et al. (2011a) reported that inheritance of resistance to salt on durum wheat at
173 germination stage was dependent upon salt stress level. The variation of gene effects with
174 water stress levels indicated that the mechanism of genetic control was not stable and was
175 dependent upon environmental conditions. In the absence of water stress (LS0), only additive
176 and dominance effects were implicated in the genetic control of resistance to STB. Therefore,
177 both additive and non-additive (i.e., dominance and epistasis) effects were induced under by
178 water stress levels (LS1 and LS2). The results from our experiments indicate that epistasis
179 contributed consistently and substantially in resistance to STB under water stress. The
180 Significance of epistatic effects were was reported for resistance to yellowberry in durum
181 wheat (Bnejdi and El Gazzah, 2008), for resistance to *Phytophthora nicotianae* in pepper
182 (Bnejdi et al., 2009) and for resistance *Puccinia coronata* in oats (Bnejdi et al., 2010).

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183 The moderate to **high h^2_n** values indicate that genetic effects were larger than environmental
 184 effects. A similar result was reported by Bastam et al. (2010). The general stability of h^2_n
 185 noted between water stresses levels indicated that resistance to STB **was not under separate**
 186 **genetic control. However, a genetic interaction was evident only when plants were cultivated**
 187 under water stress. Wolf et al. (2000) reported that epistasis contributes to a variety of
 188 evolutionary phenomena, including adaptation, **outbreeding depression, heterosis,** the
 189 evolution of sex, reproductive isolation, founder effects and hybrid zone dynamics.
 190 Breeding for resistance to STB in the absence of water stress is simple and efficient. In fact,
 191 the **absence lack** of epistatic effects and the preponderance of additive (**d**) compared to
 192 dominance (**h**) type effects facilitates the fixation of favourable genes of resistance in the
 193 productive cultivars desired. In the presence of water stress, the breeding for resistance to
 194 STB is complicated by the presence of epistasis. So, the fixation of genes of resistance and
 195 suitable interactions such as additive $\times$ additive (i) type effects requires an appropriate
 196 schema of selection. Evolution research has established that the assembly and maintenance of
 197 favourable epistatic combinations adapted **for to a specific particular** environment is a **major**
 198 **primary** mechanism of adaptation in various plant species (Allard, 1996).

199 5. **Conclusion**

200 Our results suggest that inheritance of resistance to STB in durum wheat depended upon
 201 water stress level. Thus, for the improvement of resistance of cultivars designed for
 202 exploitation in a wide range of environmental water stress, the choice of the environment in
 203 which the selection is made is **very importantcritical**. Indeed, in the presence of water stress
 204 the genetic interactions are solicited and are considered by breeders. However, in the absence
 205 of water stress, genetic interactions are not induced and not **considered found** in the
 206 procedure of selection. Thus, the stability of selected cultivars in different environmental
 207 conditions is not guaranteed. **To conclude, the higher estimates of h^2_n indicated that genetic**

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effects were larger than environmental effects. Therefore, breeding **of for** resistance to STB requires an adequate choice of **the** parent. Also, the **choice selection** of environmental conditions in which the genetic components of resistance are incorporated in agronomically acceptable cultivars is suggested for the efficiency of any breeding strategy.

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Table I. Leaf means scores $\pm$ SE for two isolates of STB (ISTB1 and ISTB2) in parents and offspring populations from two crosses (Karim 80 $\times$ Agili and Razzek $\times$ Jneh Kottifa) assessed at three water stress levels (LS0, LS1 and LS2 representing respectively 100%, 70% and 50% of field capacity).

Cross	Water stress level/isolate	Population					
		Ps(20) ^y	BC1Ps(30)	F1(20)	F2(50)	BC1Pr(30)	Pr(20)
Karim 80 (Ps) $\times$ Agili (Pr)	LS0/ISTB1	3.84 $\pm$ 1.35a	3.90 $\pm$ 2.14a	3.00 $\pm$ 1.43ab	3.42 $\pm$ 2.65a	2.1 $\pm$ 1.19bc	1.44 $\pm$ 0.53c
	LS1/ISTB1	6.10 $\pm$ 2.39a	6.00 $\pm$ 1.84a	4.46 $\pm$ 1.30bc	5.06 $\pm$ 2.27b	3.76 $\pm$ 1.48c	2.55 $\pm$ 0.61d
	LS2/ISTB1	7.05 $\pm$ 0.64a	6.58 $\pm$ 2.62ab	4.5 $\pm$ 1.09c	5.93 $\pm$ 2.19b	4.34 $\pm$ 1.09c	3.90 $\pm$ 0.62c
	LS0/ISTB2	4.07 $\pm$ 1.36a	3.87 $\pm$ 1.82a	2.90 $\pm$ 1.37b	3.19 $\pm$ 2.26ab	1.91 $\pm$ 1.04c	1.22 $\pm$ 0.38c
	LS1/ISTB2	6.42 $\pm$ 0.45a	5.82 $\pm$ 1.65ab	4.58 $\pm$ 0.64c	5.14 $\pm$ 1.88bc	3.44 $\pm$ 0.87d	2.47 $\pm$ 0.18e
	LS2/ISTB2	7.08 $\pm$ 0.64a	5.99 $\pm$ 2.13b	5.06 $\pm$ 1.54c	5.95 $\pm$ 2.13b	4.21 $\pm$ 0.98c	3.23 $\pm$ 0.60d
Razzek (Ps) $\times$ Jneh Kottifa (Pr)	LS0/ISTB1	4.43 $\pm$ 0.76a	4.04 $\pm$ 1.68a	2.98 $\pm$ 1.33b	2.83 $\pm$ 1.99b	2.18 $\pm$ 1.72b	1.48 $\pm$ 0.45c
	LS1/ISTB1	6.90 $\pm$ 0.43a	6.22 $\pm$ 2.34ab	4.86 $\pm$ 2.23cd	5.64 $\pm$ 2.78bc	4.06 $\pm$ 1.28de	3.65 $\pm$ 0.70e
	LS2/ISTB1	7.62 $\pm$ 0.75a	7.05 $\pm$ 2.56a	4.93 $\pm$ 1.43bc	5.86 $\pm$ 2.34b	5.41 $\pm$ 1.25b	4.02 $\pm$ 0.65c
	LS0/ISTB2	5.16 $\pm$ 0.82a	4.27 $\pm$ 1.41b	3.17 $\pm$ 0.96c	3.43 $\pm$ 1.83c	2.25 $\pm$ 1.18d	1.36 $\pm$ 0.31e
	LS1/ISTB2	7.03 $\pm$ 0.39a	5.77 $\pm$ 1.65b	4.93 $\pm$ 1.48c	5.18 $\pm$ 1.94bc	3.45 $\pm$ 0.71d	2.73 $\pm$ 0.14d
	LS2/ISTB2	7.77 $\pm$ 0.81a	6.28 $\pm$ 2.27b	5.18 $\pm$ 1.26c	5.92 $\pm$ 2.20bc	4.14 $\pm$ 1.01d	3.27 $\pm$ 0.50d

For each cross, means within a line, bearing different letters differ ($P < 0.05$)

^y Number of plants evaluated in each generation

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Table II. Estimates of additive, dominance and epistatic effects ($\pm$ SE) for resistance to two isolates of STB (ISTB1 and ISTB2) in two crosses (Karim 80 $\times$ Agili and Razzek $\times$ Jneh Kottifa) evaluated at three water stress levels (LS0, LS1 and LS2 representing respectively 100%, 70% and 50% of field capacity).

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C cross	water stress level/isolate	Best-fit model						P value
		m	d	h	i	l	j	
Karim 80 (Ps) $\times$ Agili (Pr)	LS0/ISTB1	2.7 $\pm$ 0.1**	-1.3 $\pm$ 0.1**	0.4 $\pm$ 0.3	----	----	----	0.34
	LS1/ISTB1	-5.1 $\pm$ 1.6**	-1.9 $\pm$ 0.2**	0.2 $\pm$ 3.8	-0.7 $\pm$ 0.1**	-0.9 $\pm$ 0.1**	----	0.31
	LS2/ISTB1	7.3 $\pm$ 0.6**	-1.5 $\pm$ 0.1**	-2.8 $\pm$ 0.7**	----	-1.8 $\pm$ 0.6**	-1.32 $\pm$ 0.9*	0.99
	LS0/ISTB2	2.9 $\pm$ 0.1**	-1.5 $\pm$ 0.1**	0.1 $\pm$ 0.2	----	----	----	0.73
	LS1/ISTB2	7.7 $\pm$ 1.8**	-1.6 $\pm$ 0.1**	-5.6 $\pm$ 3.1*	-2.5 $\pm$ 1.1*	2.7 $\pm$ 1.4*	----	0.29
	LS2/ISTB2	4.1 $\pm$ 1.6**	-1.7 $\pm$ 0.1**	6.0 $\pm$ 3.8*	1.6 $\pm$ 0.6**	-5.2 $\pm$ 2.3**	----	0.77
Razzek (Ps) $\times$ Jneh Kottifa (Pr)	LS0/ISTB1	2.7 $\pm$ 0.2**	-1.5 $\pm$ 0.2**	0.2 $\pm$ 0.3	----	----	----	0.42
	LS1/ISTB1	6.9 $\pm$ 1.3**	-2.0 $\pm$ 0.1**	-4.7 $\pm$ 2.8*	-2.4 $\pm$ 1.2**	2.38 $\pm$ 1.7*	----	0.27
	LS2/ISTB1	8.4 $\pm$ 1.4**	-1.9 $\pm$ 0.1**	-6.5 $\pm$ 3.2**	-3.3 $\pm$ 1.4**	3.14 $\pm$ 2.2*	----	0.73
	LS0/ISTB2	3.3 $\pm$ 0.1**	-1.2 $\pm$ 0.1**	-0.04 $\pm$ 0.2	----	----	----	0.89
	LS1/ISTB2	7.4 $\pm$ 1.3**	-2.2 $\pm$ 0.1**	-6.2 $\pm$ 2.8**	-2.47 $\pm$ 1.3*	3.85 $\pm$ 1.7**	----	0.63
	LS2/ISTB2	8.2 $\pm$ 1.4**	-2.2 $\pm$ 0.1**	-6.2 $\pm$ 3.1**	-2.7 $\pm$ 1.4**	3.2 $\pm$ 2.0**	----	0.82

m, d, h, i, l, j = mean, additive, dominance, additive $\times$ additive, dominance $\times$ dominance and additive $\times$ dominance genetic effects, respectively. P = probability of adequateness of the model. * $p < 0.05$ and ** $p < 0.01$ compared to zero.

347 **Table III.** Estimates of additive (V_A), dominance (V_D) and environmental variances (V_E) with $\pm$ SE and
 348 narrow-sense heritability (h^2_n) for resistance to two isolates of STB (ISTB1 and ISTB2) in two durum wheat
 349 crosses (Karim 80 $\times$ Agili and Razzek $\times$ Jneh Kottifa) assessed at three water stress levels.

Cross	Water stress level / isolate	V_E	V_A	V_D	$\chi^2 (3 df)$	h^2_n
Karim 80 (Ps) $\times$ Agili (Pr)	LS0/ISTB1	1.02 $\pm$ 0.18**	10.37 $\pm$ 3.00**	4.13 $\pm$ 1.65	ns	0.66
	LS1/ISTB1	1.12 $\pm$ 0.27**	5.16 $\pm$ 2.49**	0.80 $\pm$ 1.6**	ns	0.72
	LS2/ISTB1	0.76 $\pm$ 0.23**	6.63 $\pm$ 2.17**	2.37 $\pm$ 1.27**	ns	0.67
	LS0/ISTB2	0.53 $\pm$ 0.09**	2.15 $\pm$ 0.02**	1.49 $\pm$ 1.41	ns	0.51
	LS1/ISTB2	0.46 $\pm$ 0.20**	11.45 $\pm$ 3.30**	4.01 $\pm$ 1.82*	ns	0.71
	LS2/ISTB2	0.96 $\pm$ 0.25**	7.01 $\pm$ 2.52**	2.17 $\pm$ 1.51*	ns	0.69
Razzek (Ps) $\times$ Jneh Kottifa (Pr)	LS0/ISTB1???	0.85 $\pm$ 0.24**	7.33 $\pm$ 2.28**	2.86 $\pm$ 1.31	ns	0.66
	LS1/ISTB1	0.36 $\pm$ 0.19**	4.94 $\pm$ 1.69**	1.53 $\pm$ 1.03*	ns	0.72
	LS2/ISTB1	0.75 $\pm$ 0.22**	6.45 $\pm$ 2.05**	2.45 $\pm$ 1.2**	ns	0.66
	LS0/ISTB2	0.56 $\pm$ 0.21**	3.45 $\pm$ 1.62**	0.55 $\pm$ 1.05	ns	0.75
	LS1/ISTB2	0.44 $\pm$ 0.19**	5.94 $\pm$ 1.72**	2.40 $\pm$ 0.99**	ns	0.67
	LS2/ISTB2	0.79 $\pm$ 0.23**	6.98 $\pm$ 2.16**	2.72 $\pm$ 1.25**	ns	0.66

350 df = degrees of freedom, calculated as the number of generations minus the number of estimated variance parameters
 351 ns = non-significant. * p <0.05 and ** p <0.01 compared to zero.

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