



## Relationship between leaf stages and epistasis for resistance to *Stagonospora nodorum* in durum wheat

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### Abstract

Ten varieties and eight generations (2F1, 2F2, 2B1 and 2B2) of durum wheat derived from two crosses were evaluated for resistance to natural infection by *Stagonospora nodorum* blotch (SNB) at the 2-3 and 6-7 leaf stages at two sites over two years. There were significant differences in the incidence of SNB between leaf stages in most of the wheat varieties, with resistance being most evident at the 6-7 leaf stage. Separate analyses of the mean values for each generation showed that the genetic mechanism of defense against the pathogen depended upon the leaf stage. At the 2-3 leaf stage, only additive and dominance effects were implicated in the control of SNB for the two crosses at the two sites and for the two replications. For the 6-7 leaf stage, inheritance was more complicated and an epistatic effect was involved. Narrow-sense heritability values (range: 0.63-0.67) were consistent between crosses and leaf stages. These findings indicate a lack of resistance to SNB at the 2-3 leaf stage whereas resistance was observed at the 6-7 leaf stage and involved the genetic mechanisms of plant defense such as epistasis.

*Key words:* adaptability, inheritance, leaf stage, *Stagonospora nodorum* blotch.

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### Introduction

Durum wheat (*Triticum turgidum* L. var. *durum*) is a tetraploid species widely cultivated in the Mediterranean Basin, Canada, USA, Argentina and India (Blanco *et al.*, 1998). 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). Information regarding the nature and magnitude of genetic effects prevailing in the breeding material is necessary in order to choose the breeding procedure that best exploits the genetic potential of different plant traits in a crop.

*Stagonospora nodorum* blotch (SNB), an important pathogen of wheat and related cereals, causes leaf and glume blotch in all major growing areas (Peter *et al.*, 2006; Friesen *et al.*, 2008). Resistance to SNB is particularly important in wheat breeding programs because of the detrimental effect of this biotic stress on plant growth and subsequent yields and grain quality (Eyal, 1981; King *et al.*, 1983; Eyal *et al.*, 1987). Several authors have shown that resistance to the leaf and head phases may be under separate genetic control (Bostwick *et al.*, 1993; Hu *et al.*, 1996;

Wicki *et al.*, 1999). Several independent genes that regulate glume and flag leaf resistance have been identified (Fried and Meister, 1987; Aguilar *et al.*, 2005), although single genes have been identified in some *Triticum* accessions (Parlevliet, 1977; Ma and Hughes, 1995; Murphy *et al.*, 2000; Feng *et al.*, 2004). Disease resistance is often highly correlated with late-maturing, tall cultivars (Scott, 1973; Eyal, 1981; Trottet and Merrien, 1982; Aguilar *et al.*, 2005). Inheritance of SNB has been the subject of intensive studies at different vegetative stages: *e.g.* 2-3 leaf (Chu *et al.*, 2008; Oliver *et al.*, 2008), 4 leaf (Kim *et al.*, 2004) and heading (Fried and Meister, 1987) stages. The objective of this study was to determine the mode of inheritance of SNB at the 2-3 and 6-7 leaf stages in durum wheat varieties.

### Materials and Methods

#### Plant material

Eighteen populations of durum wheat were evaluated for resistance to natural infection by SNB at two Tunisian sites (Tunis and El Kef) during two successive agricultural seasons (2008-2009 and 2009-2010). These populations consisted of ten varieties (Inrat 69, Swabaa Eljija, Chili, Derbassi, Biskri, Khair, Om Rabiaa, Maâli, Razzek and Karim 80) and eight generations (2F1, 2F2, 2B1 and 2B2)

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derived from two crosses: Swabaa Elijia (Pr) x Karim 80 (Ps) and Chili (Pr) x Karim 80 (Ps). A randomized complete block design was used for the experiment.

**Evaluation of resistance to SNB**

Resistance to SNB at the 2-3 and 6-7 leaf stages was assessed based on the percentage of leaf area affected, with each leaf being assigned to one of the following categories: 0, 1, 5, 10, 25, 50, 75 and 100% of the area affected (Eyal *et al.*, 1987). For each plant, the percentage of affected area for all leaves was averaged for each stage. The number of plants evaluated varied depending on the generation and was greater in generations with greater segregation, such as F2, B1 and B2.

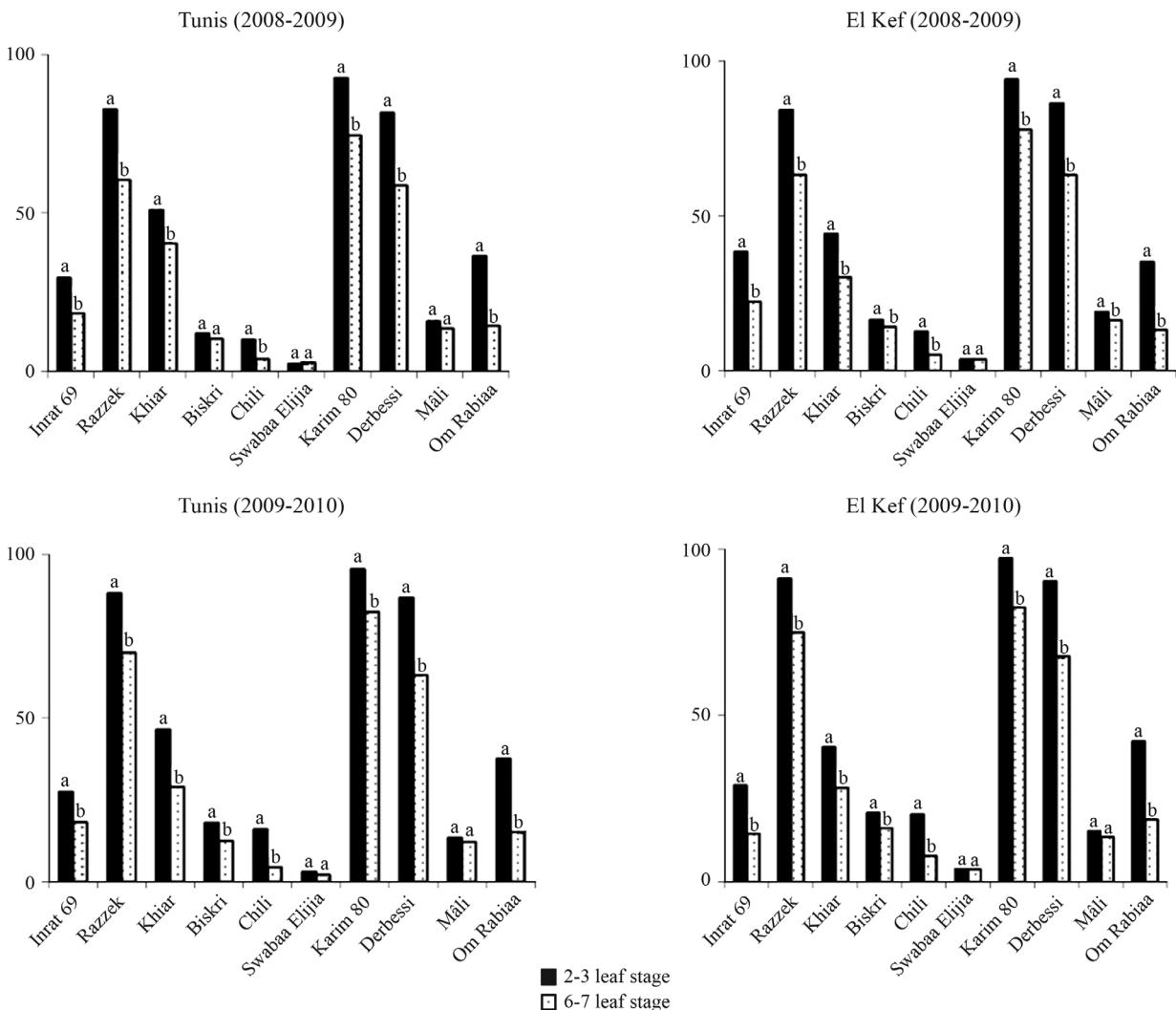
**Statistical analyses**

Analysis of variance using general linear model (GLM) procedures (SAS Institute, 1990) indicated that replication and site effects were significant. Therefore, the

means for each generation were analyzed separately by site and replication.

*Best-model:* The means of different generations were analyzed by a joint scaling test as described by Rowe and Alexander (1980) using the weighted least squares method (Mather and Jinks, 1982; Kearsey and Pooni, 1996; Lynch and Walsh, 1998). The observed generation means were used to estimate the parameters of a model consisting only of mean (m), additive (a) and dominance (d) genetic effects. The adequacy of this genetic model was assessed using a chi-square goodness-of-fit statistic derived from deviations from this model. When the additive-dominance model was insufficient, a six-parameter model was applied. The significance of each parameter was determined by a *t*-test.

*Heritability:* Homogeneity of the variances of non-segregating generations was tested using Bartlett's test (Bartlett, 1937). When the variances were heterogeneous, the environmental variance was replaced by an adequate



**Figure 1** - Mean leaf area (%) damaged by SNB at two leaf stages in ten varieties of durum wheat evaluated at two sites (El Kef and Tunis) during two growing seasons (2008-2009 and 2009-2010).

number of separate parameters and pooled to produce a single environmental variance. Additive, dominance and environmental variance components were estimated using the maximum likelihood method with the observed variance of the six basic generations (Pr, Ps, F1, F2, B1 and B2) as the initial weights ( $df/2 \times S^2$ ) (Lynch and Walsh, 1998). Narrow-sense heritability ( $h^2_n$ ) was calculated as:  $h^2_n = VA/(VA + VD + VE)$ , where VA is the additive genetic component of variance, VD is the dominance or non-additive genetic component of variance, and VE is the environmental variance (Kearsey and Pooni, 1996).

## Results

The incidence of SNB varied with the leaf developmental stage and, for most varieties, was more important at the 2-3 leaf stage than at the 6-7 leaf stage (Figure 1). For the varieties Beskri, Maâli and Swabaa Eljia there was no significant difference in the resistance between the leaf stages. There were differences in the resistance to SNB be-

tween genotypes during the two seasons and at the two sites. The varieties Swabaa Eljia and Chili were more tolerant than the other varieties. The varieties Inrat-69, Om Rabiaa and Maâli were moderately resistant, while Khiar, Derbessi, Razzek and Karim 80 were very susceptible.

For the two crosses, significant differences among generations were detected in all environments and at the two stages of growth. As expected, the parental lines were consistently different and the means for Pr and Ps in each cross and leaf stage tended to be extreme whereas the means for B1 and B2 tended to be close to those of their respective recurrent parents (Table 1). Estimates of the different types of gene effects in the individual crosses clearly illustrated this variation. At the 2-3 leaf stage, the variation among generation means for resistance to SNB was sufficiently explained by a simple additive-dominance model for the two crosses and the combination site - year (Table 2). The P-values ranged from 0.38 to 0.93 for the cross Razzek x Swabaa Eljia and from 0.93 to 0.99 for Karim 80

**Table 1** - Mean percentage of leaf area ( $\pm$  standard error) damaged by SNB at two leaf stages in two crosses evaluated at two sites (El Kef and Tunis) during two growing seasons (2008-2009 and 2009-2010).

Site (year)	Crosses	Razzak x Swabaa Eljia		Karim 80 x Chili	
		2-3 leaves	6-7 leaves	2-3 leaves	6-7 leaves
El Kef(2008-2009)	Ps(20)*	83.0 $\pm$ 16.9 <sup>a</sup>	60.5 $\pm$ 15.4 <sup>a</sup>	92.5 $\pm$ 8.5 <sup>a</sup>	74.5 $\pm$ 13.6 <sup>a</sup>
	B1(50)	63.7 $\pm$ 12.4 <sup>b</sup>	38.6 $\pm$ 18.5 <sup>b</sup>	69.2 $\pm$ 7.1 <sup>b</sup>	51.5 $\pm$ 16.1 <sup>b</sup>
	F1(20)	46.5 $\pm$ 11.3 <sup>c</sup>	20.5 $\pm$ 13.9 <sup>c</sup>	47.5 $\pm$ 4.7 <sup>c</sup>	17.8 $\pm$ 9.8 <sup>d</sup>
	F2(100)	46.5 $\pm$ 35.1 <sup>c</sup>	32.3 $\pm$ 27.5 <sup>b</sup>	47.5 $\pm$ 40.9 <sup>c</sup>	36.5 $\pm$ 34.1 <sup>c</sup>
	B2(50)	27.2 $\pm$ 9.0 <sup>c</sup>	16.2 $\pm$ 6.9 <sup>c</sup>	25.2 $\pm$ 4.1 <sup>d</sup>	17.1 $\pm$ 7.7 <sup>d</sup>
	Pr(20)	10.0 $\pm$ 7.3 <sup>c</sup>	4.0 $\pm$ 5.0 <sup>d</sup>	2.5 $\pm$ 4.4 <sup>e</sup>	3.0 $\pm$ 4.7 <sup>e</sup>
Tunis (2008-2009)	Ps(20)	88.5 $\pm$ 15.7 <sup>a</sup>	70.5 $\pm$ 15.4 <sup>a</sup>	95.5 $\pm$ 6.9 <sup>a</sup>	82.5 $\pm$ 13.6 <sup>a</sup>
	B1(50)	68.8 $\pm$ 13.8 <sup>b</sup>	50.3 $\pm$ 12.7 <sup>b</sup>	72.2 $\pm$ 5.2 <sup>b</sup>	38.5 $\pm$ 17.9 <sup>b</sup>
	F1(20)	52.3 $\pm$ 11.9 <sup>c</sup>	13.9 $\pm$ 15.3 <sup>cd</sup>	49.3 $\pm$ 4.5 <sup>c</sup>	16.3 $\pm$ 10.2 <sup>c</sup>
	F2(100)	54.4 $\pm$ 35.5 <sup>c</sup>	40.0 $\pm$ 3.3 <sup>c</sup>	49.3 $\pm$ 42.0 <sup>c</sup>	35.8 $\pm$ 35.4 <sup>b</sup>
	B2(50)	32.7 $\pm$ 11.2 <sup>d</sup>	18.1 $\pm$ 7.9 <sup>c</sup>	26.4 $\pm$ 4.6 <sup>d</sup>	16.2 $\pm$ 7.4 <sup>c</sup>
	Pr(20)	16 $\pm$ 11.4 <sup>e</sup>	4.5 $\pm$ 6.5 <sup>d</sup>	3.0 $\pm$ 6.2 <sup>e</sup>	2.0 $\pm$ 4.1 <sup>e</sup>
El Kef (2009-2010)	Ps(20)	86.3 $\pm$ 15.9 <sup>a</sup>	65.3 $\pm$ 15.4 <sup>a</sup>	78.0 $\pm$ 13.4 <sup>a</sup>	78.0 $\pm$ 13.4 <sup>a</sup>
	B1(50)	66.2 $\pm$ 13.3 <sup>b</sup>	43.3 $\pm$ 15.6 <sup>b</sup>	59.0 $\pm$ 11.1 <sup>b</sup>	37.4 $\pm$ 18.0 <sup>b</sup>
	F1(20)	49.4 $\pm$ 10.8 <sup>c</sup>	35.3 $\pm$ 9.2 <sup>b</sup>	40.9 $\pm$ 8.4 <sup>c</sup>	25.1 $\pm$ 18.0 <sup>b</sup>
	F2(100)	43.5 $\pm$ 30.3 <sup>c</sup>	35.3 $\pm$ 29.2 <sup>b</sup>	40.9 $\pm$ 34.8 <sup>c</sup>	33.4 $\pm$ 29.3 <sup>bc</sup>
	B2(50)	30.0 $\pm$ 9.5 <sup>d</sup>	17.0 $\pm$ 8.9 <sup>c</sup>	22.7 $\pm$ 7.2 <sup>d</sup>	11.3 $\pm$ 6.8 <sup>c</sup>
	Pr(20)	12.8 $\pm$ 9.7 <sup>e</sup>	5.3 $\pm$ 7.3 <sup>d</sup>	3.8 $\pm$ 6.7 <sup>e</sup>	3.8 $\pm$ 6.7 <sup>c</sup>
Tunis (2009-2010)	Ps(20)	91.0 $\pm$ 13.8 <sup>a</sup>	75.0 $\pm$ 15.6 <sup>a</sup>	97.3 $\pm$ 0.9 <sup>a</sup>	82.5 $\pm$ 14.0 <sup>a</sup>
	B1(50)	71.7 $\pm$ 12.5 <sup>b</sup>	39.1 $\pm$ 24.9 <sup>7b</sup>	73.9 $\pm$ 3.5 <sup>b</sup>	41.9 $\pm$ 19.2 <sup>b</sup>
	F1(20)	55.6 $\pm$ 11.3 <sup>c</sup>	25 $\pm$ 19.8 <sup>c</sup>	50.6 $\pm$ 0.9 <sup>c</sup>	20 $\pm$ 8.0 <sup>cd</sup>
	F2(100)	55.6 $\pm$ 34.2 <sup>c</sup>	41.4 $\pm$ 32.6 <sup>b</sup>	51.7 $\pm$ 0.1 <sup>c</sup>	31.0 $\pm$ 31.3 <sup>bc</sup>
	B2(50)	36.4 $\pm$ 11.4 <sup>d</sup>	19.4 $\pm$ 11.2 <sup>cd</sup>	27.8 $\pm$ 1.1 <sup>d</sup>	11.8 $\pm$ 9.1 <sup>de</sup>
	Pr(20)	20.3 $\pm$ 12.3 <sup>c</sup>	7.8 $\pm$ 9.8 <sup>d</sup>	4.0 $\pm$ 0.3 <sup>e</sup>	3.8 $\pm$ 6.7 <sup>e</sup>

\* = number of plants evaluated in each generation. Means followed by different letters within each column for each population and site were significantly different ( $p < 0.05$ , Duncan's test).

x Chili. The additive effect was more important than dominance effect and highly significant in all cases (Table 2). For the 6-7 leaf stage, an additive-dominance model did not adequately explain variation in the generation means for the two crosses and all combinations (cross - site - year) (Table 3). Instead, a digenic epistatic model was found to

be appropriate for the majority of cases. In two cases, both the additive-dominance and digenic epistatic models failed to explain the variation in generation means (Table 3).

Table 4 summarizes the estimates of different variance components and  $h^2_n$ . For the two growth stages, the variance components were estimated and used to calculate

**Table 2** - Estimates of additive and dominance effects (and their standard errors) for resistance to SNB at the 2-3 leaf stage in two crosses (Karim 80 x Chili and Razzak x Swabaa Eljia) at two sites (El Kef and Tunis) during two growing seasons (2008-2009 and 2009-2010).

Cross	Model	El Kef (2008-2009)	Tunis (2008-2009)	El Kef (2009-2010)	Tunis (2009-2010)
Razzak x Swabaa Eljia	m	46.1 ± 1.6**	51.7 ± 1.8**	48.4 ± 1.7**	54.9 ± 1.8**
	a	-36.4 ± 1.5**	-36.2 ± 1.6**	-36.2 ± 1.5**	-35.4 ± 1.6**
	d	-0.6 ± 2.9	-0.4 ± 3.3	-0.5 ± 3.1	-0.39 ± 3.2
	p	0.93	0.73	0.38	0.87
Karim 80 x Chili	m	47.2 ± 0.9**	49.3 ± 0.8**	40.8 ± 1.7**	50.8 ± 0.9**
	a	-44.5 ± 0.8**	-46.0 ± 0.7**	-36.8 ± 1.2**	-46.3 ± 0.8**
	d	0.3 ± 1.4	0.1 ± 1.4	0.3 ± 2.4	-0.1 ± 1.5
	p	0.93	0.98	0.99	0.97

m, a, d = mean, additive and dominance genetic effects, respectively. p = probability of adequateness of the model. \*\*p < 0.01 compared to zero.

**Table 3** - Estimates of additive, dominance and epistatic effects (and the standard errors) for resistance to SNB at the 6-7 leaf stage in two crosses (Karim 80 x Chili and Razzak x Swabaa Eljia) at two sites (El Kef and Tunis) during two growing seasons (2008-2009 and 2009-2010).

Cross	Model parameter	El Kef (2008-2009)	Tunis (2008-2009)	El Kef (2009-2010)	Tunis (2009-2010)
Three parameter model					
Razzak x Swabaa Eljia	m	31.5 ± 1.6**	39.8 ± 1.6**	33.0 ± 1.6**	40.7 ± 1.9**
	a	-27.0 ± 1.5**	-33.5 ± 1.4**	-28.7 ± 1.5**	-31.2 ± 1.8**
	d	-6.4 ± 2.7**	-13.2 ± 3.0	-0.5 ± 2.7	-13.4 ± 3.8**
	p	< 0.001	< 0.001	< 0.001	< 0.001
Karim 80 x Chili	m	40.3 ± 1.4**	39.7 ± 1.4**	38.7 ± 1.5**	41.1 ± 1.5**
	a	-35.9 ± 1.3**	-36.2 ± 1.4**	-34.7 ± 1.4**	-37.1 ± 1.5**
	d	-15.8 ± 2.4	-18.0 ± 2.3	-20.0 ± 2.9**	-22.1 ± 2.4
	p	< 0.001	< 0.001	< 0.001	< 0.001
Best-fit model					
Razzak x Swabaa Eljia	m	41.8 ± 5.8**	60.0 ± 13.1**	52.5 ± 12.6**	1365.1 ± 15.3**
	a	-28.0 ± 1.8**	-32.7 ± 1.4**	-28.7 ± 1.5**	-33.6 ± 2.1**
	d	-22.3 ± 8.2**	-33.8 ± 28*	-51.8 ± 27.3**	-129.2 ± 35.7**
	aa	-9.9 ± 6.3*	-22.7 ± 13.1**	-18.1 ± 12.6*	-48.5 ± 15.2**
	dd	ns	-12.3 ± 16.4*	14.5 ± 10.5**	24.3 ± 14.6**
	ad	8.6 ± 5.8	ns	ns	28.0 ± 8.7**
	p	0.36	0.77	0.25	
Karim 80 x Chili	m	59.3 ± 5.4*	1792.8 ± 15.3**	1382.1 ± 13.0**	634.4 ± 14.0**
	a	-36.0 ± 1.6**	-40.3 ± 1.6**	-37.1 ± 1.7**	-39.4 ± 1.7**
	d	-41.1 ± 7.0**	-101.3 ± 33.2**	-123.0 ± 29.1**	-75.2 ± 31.3**
	aa	-20.3 ± 5.9**	-33.8 ± 15.2**	-36.3 ± 13.0**	-16.6 ± 13.9*
	dd	ns	21.5 ± 10.7**	21.9 ± 8.3**	12.5 ± 6.0**
	ad	4.8 ± 5.5	ns	ns	11.6 ± 5.9**
	p	0.69	0.50	0.58	

m, a, d, aa, dd, ad = mean, additive, dominance, additive x additive, dominance x dominance and additive x dominance genetic effects, respectively. p = probability of adequateness of the model. ns = not significant. \*p < 0.05 and \*\*p < 0.01 compared to zero.

**Table 4** - Estimates of variance components and narrow-sense heritability ( $h^2_n$ ) at the 2-3 and 6-7 leaf stages for two crosses (Karim 80 x Chili and Razzak x Swabaa Eljia) at two sites (El Kef and Tunis) during two growing seasons (2008-2009 and 2009-2010).

Variance components	VE	VA	VD	$\chi^2$ (df)	$h^2_n$
2-3 leaves					
Razzak x Swabaa Eljia					
Site (year)					
El Kef (2008-2009)	69.8 ± 12.7*	2268 ± 349*	1108 ± 177*	ns (3)	0.65
Tunis (2008-2009)	149.8 ± 27.3*	2228 ± 359*	1118 ± 185*	ns (3)	0.63
El Kef (2009-2010)	113.7 ± 22.1*	1622 ± 262*	817 ± 136*	ns (3)	0.63
Tunis (2009-2010)	148.9 ± 27.2*	2052 ± 333*	1034 ± 172*	ns (3)	0.63
Karim 80 x Chili					
El Kef (2008-2009)	23.0 ± 4.2*	3311 ± 474*	1658 ± 237*	ns (3)	0.66
Tunis (2008-2009)	27.3 ± 5.0*	3483 ± 499*	1745 ± 250*	ns (3)	0.66
El Kef (2009-2010)	57.1 ± 10.4*	2300 ± 343*	1144 ± 173*	ns (3)	0.65
Tunis (2009-2010)	25.0 ± 4.6*	3652 ± 521*	1834 ± 261*	ns (3)	0.66
6-7 leaves					
Razzak x Swabaa Eljia					
El Kef (2008-2009)	30.4 ± 5.6*	1408 ± 214*	681 ± 108*	ns (3)	0.66
Tunis (2008-2009)	47.8 ± 10.7*	1783 ± 618*	854 ± 309*	ns (3)	0.66
El Kef (2009-2010)	62.7 ± 14.0*	1494 ± 541*	701 ± 272*	ns (3)	0.66
Tunis (2009-2010)	112.7 ± 25.2*	1795 ± 671*	848 ± 338*	ns (3)	0.65
Karim 80 x Chili					
El Kef (2008-2009)	25.83 ± 5.8*	2165 ± 734*	1031 ± 367*	ns (3)	0.67
Tunis (2008-2009)	19.05 ± 4.3*	2364 ± 791*	1132 ± 396*	ns (3)	0.67
El Kef (2009-2010)	49.6 ± 11.1*	1598 ± 541*	792 ± 271*	ns (3)	0.65
Tunis (2009-2010)	50.6 ± 11.3*	1739 ± 620*	810 ± 311*	ns (3)	0.66

VE, VA, VD = environmental, additive and dominance variance components, respectively. df = degrees of freedom, calculated as the number of generations minus the number of estimated variance parameters. ns = non-significant. \* $p < 0.05$  compared to zero.

$h^2_n$  for both crosses at the two sites and for the two replications. In all cases, the additive variance was highly significant and of greater magnitude than the environmental and dominance variance. The range of  $h^2_n$  was 0.63-0.67 in the two crosses and for all combinations.

## Discussion

In this study, we examined the role of growth stage in the mechanism of resistance to SNB. There was considerable variation in susceptibility among the varieties, with reactions ranging from moderately resistant to highly susceptible at both development stages. Karim 80 and Razzek, the most cultivated and productive cultivars in Tunisia, were very susceptible where Swabaa Eljia and Chili were the most resistant of all the varieties evaluated. For all varieties, the incidence of SNB was greater at the 2-3 leaf stage than at the 6-7 leaf stage at the two sites during the two seasons. The decrease in severity seen at the 6-7 leaf stage may reflect the ability of the plant to exploit a variety of genetic interactions. In contrast, at the 2-3 leaf stage, the necessary defense mechanisms may not yet have been established so that only additive and dominance effects were implicated in

resistance to SNB. The difference in resistance between the two leaf stages was particularly pronounced for the varieties Om Rabiaa, Chili and Inrat 69. There was also a significant difference in resistance between the two stages for the variety Swabaa Eljia, and any breeding program based on this resistant variety would more efficient than using Chili.

In all cases, there were significant differences among the generation means for resistance to SNB for the two developmental stages and the two crosses, indicating genetic diversity for this attribute. For the 2-3 leaf stage, the variation among the generation means was best fitted by a model that included only additive and dominance effects for the two crosses and all combinations. For the 6-7 leaf stage, the significant digenic terms indicated that epistasis was responsible for departure from the additive-dominance model. In two cases, both the additive-dominance and digenic epistatic models failed to explain the variation among generation means, indicating that other mechanisms of genetic control such as higher order interactions or linkage effects were important. Further analyses of additional generations are needed to determine whether the cause of the model failure was the presence of higher order interactions or linkage effects.

Significant estimates of additive gene effects (a and aa) and dominance effects (d) were usually negative, indicating that these effects contributed more to resistance than to susceptibility (Mather and Jinks, 1982). There is no consensus in the literature on the type of inheritance involved in resistance to SNB. Some reports have concluded that additive and dominance effects are very important for SNB resistance (Wilkinson *et al.*, 1990; Bostwick *et al.*, 1993; Wicki *et al.*, 1999; Kim *et al.*, 2004). In contrast, others have indicated that epistasis has a significant role in the expression of SNB, *e.g.*, Bruno and Nelson (1990) and Friesen *et al.* (2007) who reported that epistatic effects contributed to the resistance to SNB in winter wheat. Our results indicated that genetic interactions were expressed only when the plant was vigorous. At the 2-3 leaf stage the genetic mechanism of resistance is not well developed and the plant is unable to establish genetic interactions. In maize, resistance to the European corn borer was found to increase from the 3-leaf through to the 10-leaf stage (Bergvinson D, 1993, PhD thesis, University of Ottawa, Ottawa, Canada). Shaik *et al.* (1989) reported an effect of leaf stage on the variability of the reactions of *Phaseolus vulgaris* to *Uromyces appendiculatus*. Broers (1989) observed a large growth stage effect on latency period, infection frequency and urediosorus size during resistance to leaf rust in wheat.

The estimated  $h^2_n$  was consistent between growth stages for the two crosses in all cases and ranged from 0.63 to 0.67. A greater range of narrow-sense heritability (48%-68%) was reported by Fried and Meister (1987). The stability of narrow-sense heritability between development stages indicated that resistance to SNB was not under separate genetic control. However, a genetic interaction was evident only when the plants were vigorous.

There was some discrimination among varieties at the more advanced vegetative stage, where the genetic mechanism of resistance was functional. Our results showed higher narrow-sense heritability values, suggesting that genetic effects had a major role in resistance to SNB and that selection for this trait should be highly efficient. The presence of non-additive effects (dominance and epistasis) seen here suggested that the expected progress from selection during early segregating generations would be limited.

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