

Evaluating the cost and gain from genetic resistance to Hessian fly (*Mayetiola destructor* (say)) in durum wheat in Morocco using recombinant inbred lines

Evaluation du coût et du gain liés à la résistance génétique à la cécidomyie (*Mayetiola destructor* (Say)) chez une collection de lignées recombinantes de blé dur

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ABSTRACT

Durum wheat (*Triticum turgidum* L. var. *durum*) is an important food crop in the Mediterranean region. Hessian fly is the most important insect pest of wheat in the dry land areas in Morocco. Breeding wheat for genetic resistance to pests is the most sustainable control strategy because genetic resistance brings yield advantage under pest attack. However, there are fears that this resistance could have its price in terms of yield potential under pest free situation. The objective of this study was to quantify the yield gains in the presence of H. fly and verify the assumption of resistance cost in the absence of the pest. One hundred and eighty recombinant inbred lines of durum wheat (RILs) derived from the crosses (CI115 / Bzaiz-AHF/CM829/Cando -H25) segregated for Hessian fly resistance and adapted to dry areas were planted in two experimental domains of INRA, differing in Hessian fly infestation levels (Sidi El Aidi and Jemaa-Shaim) in the 2012-2013 season. Plants were evaluated for agronomic and phenological traits as well as for yield components. The data indicated that under severe H. fly attacks, the yield losses avoided by resistant lines may reach 100% and that under pest free situation, the mean values of each parameter measured are similar between resistant and susceptible groups of lines. These results indicated that resistance had no negative effect on genetic potential of studied characters in this case study. In addition, the phenotypic correlations between different traits are similar between groups under differing situations and this confirms the above results. The conclusion is that incorporating genetic resistance to Hessian fly has a positive effect on phenological and agro-morphologic traits, as well as on yield and yield components under H. fly attack, and has no negative effect on these parameters in a fly free situation.

Keywords: Hessian fly, costs of resistance, durum wheat, agronomic traits, yield.

RESUME

Le blé dur (*Triticum turgidum* L. var. *durum*) est l'une des principales cultures vivrières dans la région méditerranéenne. La cécidomyie est l'un des principaux ravageurs du blé. L'amélioration du blé pour la résistance génétique aux ravageurs est la stratégie de lutte la plus durable. En effet, la résistance génétique apporte une amélioration de rendement en cas d'infestation par ce ravageur. Cependant, il a été suggéré que la résistance génétique pourrait avoir un coût en termes de potentiel de rendement en cas d'absence d'infestation. L'objectif de cette étude était de quantifier les gains en rendement et de vérifier l'hypothèse du coût de la résistance génétique. Cent quatre-vingt lignées recombinantes de blé dur (RILs) issues de croisements entre des lignées de blé dur résistantes à la cécidomyie et des lignées sensibles et adaptées aux conditions pédoclimatiques des zones arides et semi-arides (CI115 / Bzaiz-AHF / CM829 / Cando -H25). Ces lignées ont été plantées dans deux domaines expérimentaux de l'INRA: Sidi El Aidi et Jemaa Shaim durant la campagne 2012-13. Les plantes ont été évaluées pour des caractères agro-phénologiques ainsi que pour les composantes de rendement. Les données indiquent qu'en cas de forte infestation, les pertes de rendement évitées par les lignées résistantes peuvent atteindre 100% et qu'en absence d'infestation, les valeurs moyennes de chaque paramètre mesuré sont similaires entre les groupes de lignées résistantes et sensibles. Ces résultats indiquent que la résistance n'a aucun effet négatif sur le potentiel génétique des caractères étudiés. En outre, les corrélations observées entre les différents paramètres sont similaires entre les groupes de lignées sous des situations différentes et cela confirme les résultats ci-dessus. La conclusion tirée de ce travail est que l'incorporation de la résistance génétique à la cécidomyie dans le blé dur a un effet positif sur les caractères agro-phénologiques, le rendement, et les composantes de rendement sous une forte attaque par la cécidomyie, mais n'a aucun effet négatif sur les mêmes caractéristiques en cas d'absence du ravageur.

Mots clés: Cécidomyie, coût de la résistance, blé dur, caractères agronomiques, rendement.

INTRODUCTION

Durum wheat is an important crop in the Mediterranean basin (Pedro & al., 2011) and is planted in 8 to 10% of the wheat cultivated area of the world (Mohammadi & al., 2011). It is an economically important crop because of its unique features related to grain end use products (Autran & al., 1986; Nachit & al., 1993). However, this crop is constantly exposed to a wide array of environmental stresses that cause major losses in productivity. Resistance and susceptibility to these biotic and abiotic stresses are complex phenomena, in part because stress may occur at multiple stages of plant development and often more than one stress simultaneously affects the plant (Subramanyam & al.,

2006). Hessian fly, *Mayetiola destructor* (Say) is a major source of stress that wheat plants endure during development. This pest has worldwide importance. In the United States, H. fly can be found in most wheat-growing regions (Ratcliffe & al., 2000; Shukle & al., 2010). In Morocco, Hessian fly is an important insect pest of wheat; it causes 32, and 36% average yield losses for durum and bread wheat, respectively (Lhaloui & al., 1992). The most effective means of control of this pest is the genetic resistance in the host plant (El Bouhssini & al., 2001). To date, 34 Hessian fly resistance genes have been identified (Li & al., 2013). This resistance is expressed as larval antibiosis and is controlled mostly by single genes that are partially or completely dominant (Buntin, 1999).

However, it is suspected that induced defense mechanisms can be costly to the plant, diverting resources that would otherwise be utilized toward yield (Karban & Baldwin, 1997; Baldwin & Preston, 1999). Thus, it is important to stress that curiosity over why resistance persist in plant populations has been the primary motivation for much of the research on the costs and benefits of resistance (Stahl & *al.*, 1999). The objective of this research was to evaluate the gains from resistance to H. fly and to verify the assumption of costs of resistance in a durum wheat recombinant inbred lines population.

MATERIALS AND METHODS

Genetic materials and experimental design

A durum wheat recombinant inbred lines population (RILs) of 180 entries (84 resistant and 95 susceptible) was developed from crosses between durum wheat lines with resistance to Hessian fly and adapted to dry land areas (CI115/Cando-H25) and (CM829/ BZAIZ-AHF). These lines were planted in two locations (Sidi El Aidi (SEA), low pest infestation and Jemaa Shaim (JS) heavy pest infestation) during the 2012/2013 growing season. The lines were sown early November in moist conditions, in two rows, 1m long plots, with 0.3m spacing. Sowing was carried out by hand, at a depth of approximately 3 to 5cm. Evaluation of this collection was based partly on the observations that have been made throughout the vegetative cycle on phenological and agro-morphological traits. Determination of grain yield and its components took place after harvest. This experiment was laid out as an augmented randomized complete block design of six blocks. Controlled testing for Hessian fly resistance was conducted in a parallel

experiment in the greenhouse using reared fly population.

Parameters recorded

Resistance to Hessian fly was confirmed by the presence of dead larvae in the greenhouse experiment. In the field experiment, traits including number of days to heading, plant height, total plant's weight, thousand kernels weight, number of days to maturity, grain weight per line, grain weight per spike, number of grain per spike and number of spikes per line, were measured in both the H. fly resistant and susceptible lines.

Statistical analysis

Analysis of variance according to the RCBD design was performed on all traits measured. Frequency distributions were computed and normality was tested. Comparing means results of both susceptible and resistant lines was made. The analysis of relationship between different measured traits by correlation was also conducted.

RESULTS

There were different levels of Hessian fly infestation in the two sites. JemaaShaim was subject to a heavy infestation and only the resistant entries continued their growth and development until harvest. The susceptible entries started to be destroyed from the jointing stage to the heading stage. At Sidi El Aidi, there has been little to no attack and plants from all entries continued their growth and development normally. For all remaining materials and trials, the evaluation of the phenological and Agro-morphologic traits was made in good conditions.

The analysis of variance indicated that differences due to genotypes were highly (0.01 level) significant in both sites.

When the lines were subdivided into resistant and susceptible groups, the differences among lines within groups remained highly significant. The analysis of variation within and between resistant and susceptible groups was continued within sites (Jemaa Shaim and Sidi El Aidi). Furthermore, the distribution of all traits was normal within and between groups of lines (tables 1 to 3).

The results of the descriptive analysis of all characters evaluated at Sidi El Aidi indicated that while the differences in measured traits within groups were significant, the means values for groups were not significantly different. The student test for mean comparison between resistant and susceptible groups' means indicated levels of significance less than 0.05 for all traits group's means.

Table 1: Mean performance values for phenologic traits of resistant and susceptible lines in pest free condition

Group	Resistant lines			Susceptible lines		
Traits	PH (cm)	MD	HD	PH (cm)	MD	HD
Mean	70.36	168.84	130.13	71.98	170.17	130.13
Median	70.00	172.00	130.00	70.50	172.00	130.00
S. E.	11.34	6.80	2.052	11.567	5.602	2.050
Minimum	40.50	154.00	127.00	50.00	154.00	128.00
Maximum	100.50	185.00	135.00	100.00	183.00	136.00
C. V.	16.117	4.027	1.577	16.069	3.2920	1.575

PH: plant height, **MD:** number of days to maturity; **HD:** number of days to heading; **S. E.:** standard error, **C.V:** Coefficient of variation.

Table 2: Mean performance values of yield components of resistant and susceptible lines in pest free condition

Group	Resistant lines			Susceptible lines		
Traits	NSL	TKW (g)	GWS (g)	NSL	TKW (g)	GWS(g)
Mean	212.48	30.23	0.533	203.06	30.89	0.499
Median	207.00	30.00	0.520	207.00	31.10	0.504
S. E.	54.261	4.180	0.181	46.22	3.343	0.156
Minimum	86.00	19.40	0.17	109.00	24.00	0.16
Maximum	352.00	40.10	1.03	330.00	41.80	0.99
C. V.	25.536	13.827	33.958	22.761	10.822	31.262

NSL: number of spikes per line; **TKW:** thousand kernels weight; **GWS:** grain weight per spike; **S. E.:** standard Error; **C.V.:** Coefficient of variation.

Table 3: Mean performance values for yield of resistant and susceptible lines in pest free condition

Group	Resistant lines			Susceptible lines		
Traits	PW (g)	GWL (g)	NGS	PW (g)	GWL (g)	NGS
Mean	663.21	114.41	17.64	623.78	103.59	16.12
Median	630.20	108.20	17.37	584.20	97.20	16.75
S. E.	217.37	48.66	5.522	207.26	45.29	4.562
Minimum	271.70	19.40	6.10	261.50	26.50	5.58
Maximum	1130.20	250.00	32.95	1200.00	231.20	28.76
C. V.	32.775	42.531	31.303	33.226	43.720	28.300

PW: total plants weight; **GWL:** grain weight per line; **NGS:** number of grain per spike; **S. E.:** standard Error. **C.V.:** Coefficient of variation.

The trial at Jemaa Shaim showed a maximum level of attack due to late planting. The analysis of variance indicated that differences among genotypes were highly significant. Further, the distribution of lines' means was normal. In accordance, the results shown in tables 4 and 5 indicate that there is a wide variation between lines of the resistant group in yield and yield components. The lines belonging to the susceptible group all died and therefore are not accounted for.

Comparison between the susceptible and resistant group's means under heavy infestation is a comparison between a nil

value for the susceptible group and any value found for the resistant group.

Comparison between group's means between heavy infestation and no or low infestation using Students test for mean comparison indicated that the values are not significantly different.

These results indicate that incorporating genetic resistance to Hessian fly in durum wheat has positive effect under H. fly attack and has no negative effect on phenological and agro-morphologic traits, and yield component in an attack free situation (figures 1 and 2).

Table 4: Mean performance values of yield components of resistant and susceptible lines under heavy H. fly infestation

Group	Resistant lines			Susceptible lines
traits	TKW (g)	NSL	GWS (g)	All traits
Mean	27.259	179.51	0.5681	Nil
Median	28.068	169.00	0.5451	Nil
S. E.	4.995	94.688	0.17384	Nil
Minimum	8.37	14.00	0.24	Nil
Maximum	37.90	399.00	1.04	Nil
C. V.	18.324	52.748	30.600	Nil

NSL: number of spikes per line. **TKW:** thousand kernels weight; **GWS:** grain weight per spike, **S. E.:** standard Error. **C.V.:** Coefficient of variation.

Table 5: Mean performance values for yield of resistant and susceptible lines under heavy H. fly infestation (Jemaa Shaim site)

Group	Resistant lines			Susceptible lines
traits	PW (g)	GWL (g)	NGS	All traits
Mean	546.35	103.03	21.09	Nil
Median	528.00	84.30	20.47	Nil
S. E.	211.55	68.605	6.519	Nil
Minimum	114.80	8.80	8.77	Nil
Maximum	1213.40	319.50	40.82	Nil
C. V.	38.720	66.587	30.910	Nil

PW: plants weight. GWL: grain weight per line. NGS: number of grains per spike; S. E.: standard Error; C.V.: Coefficient of variation.

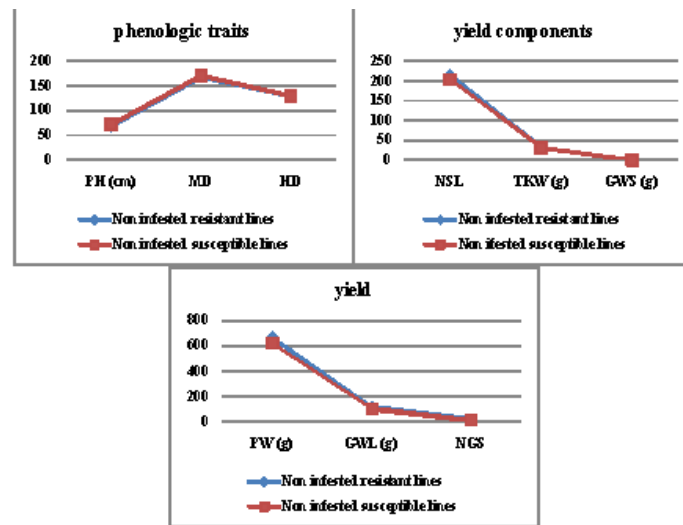


Figure 1: Mean values for phenologic traits, yield and yield components of resistant and susceptible lines under pest free condition (PH: plant height, MD: number of days to maturity, HD: number of days to heading; NSL: number of spikes per Line, TKW: thousand kernels weight, GWS: grain weight per spike; PW: plants weight, GWL: grain weight per line, NGS: number of grains per spike).

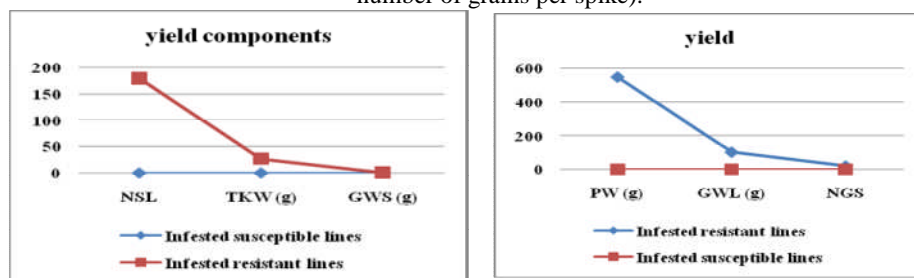


Figure 2: Mean values for yield and yield components of infested resistant and susceptible lines (NSL: number of spikes per Line, TKW: thousand kernels weight, GWS: grain weight per spike; PW: plants weight, GWL: grain weight per line, NGS: number of grains per spike).

Phenotypic and agro-morphologic correlation among traits

The phenotypic and agro-morphologic correlation coefficients of each character evaluated are presented in tables 6 to 8.

The correlations between traits in the pest free situation in the resistant group (table 6) showed that the number of spikes per line is correlated with the total plant weight and grain weight per line. Total plant weight showed positive correlations with grain weight per line, grain weight per spike, number of grains per spike, plant height and number of days to maturity. Furthermore, the grain weight per line was correlated with the grain weight per spike, number of grains per spike, total plant weight and thousand kernels weight. The latter was also correlated with grain weight per

spike. This result is similar with the grain weight per spike which has a correlation with the number of grains per spike and plant height. The number of grains per spike was positively correlated with plant height. The number of days to maturity was correlated with the number of days to heading. These associations show that many of the individual characters are positively correlated to the same effect. On the other hand, the number of days to heading had a strong negative correlation with the number of spikes per line, grain weight per line, number of grains per spike and plant height. These associations are generally seen in all similar studies and their cause may be genetically and/or environmentally controlled.

Table 6: Coefficients of correlation between phenological traits and yield components of resistant lines in pest free conditions

	NSL	PW	GWL	TKW	GWS	NGS	PH	MD
PW	0.735**							
GWL	0.694**	0.688**						
TKW			0.302**					
GWS		0.400**	0.813**	0.341**				
NGS		0.389**	0.730**		0.907**			
PH		0.266*	0.295**		0.359**	0.393**		
MD		0.307**						
HD	-0.246*		-0.411**		-0.378**	-0.415**	-0.313**	0.323**

PW: plants weight, **GWL:** grain weight per line, **NGS:** number of grains per spike. **NSL:** number of spikes per Line, **PH:** plant height, **TKW:** thousand kernels weight, **GWS:** grain weight per spike. **MD:** number of days to maturity, **HD:** number of days to heading.

The correlations between traits observed in the susceptible group under no infestation are shown in table 7. The data revealed that the number of spikes per line presented strong and positive correlations with total plant weight, grain weight per line, number of grains per spike and number of days to maturity. Total plant weight showed positive

correlations with grain weight per line, thousand kernels weight, and grain weight per spike, number of grains per spike, plant height, and number of days to maturity and to heading. These results are similar for grain weight per line which had a positive correlation with thousand kernels weight, grain weight per spike, number of grains per spike,

plant height and number of days to maturity. In addition, thousand kernels weight was also correlated with grain weight per spike and plant height. The grain weight per spike had a positive and significant correlation with plant height

and the number of grains per spike. The latter was also correlated with plant height and number of days to heading. Finally, the number of days to maturity and number of days to heading were positively correlated.

Table 7: Coefficients of significant correlations between phenological traits and yield components of susceptible lines in pest free conditions

	NSL	GWL	TKW	GWS	NGS	PH	MD
GWL	0.707**						
TKW		0.334**					
GWS		0.808**	0.453**				
NGS	0.204*	0.774**		0.933**			
PH		0.288**	0.215*	0.319**	0.267**		
MD	0.322**	0.222*					
HD					-0.203*		0.211*
PW	0.756**	0.681**	0.243*	0.336**	0.289**	0.280**	0.501**

PW: plants weight, **GWL:** grain weight per line, **NGS:** number of grains per spike, **NSL:** number of spikes per line, **PH:** plant height, **TKW:** Thousand kernels weight, **GWS:** grain weight per spike, **MD:** number of days to maturity, **HD:** number of days to heading.

The correlations between traits under high level of infestation are shown in table 8. The data revealed that total plant weight is significantly and positively correlated with grain weight per line, thousand kernels weight and grain weight per spike. Grain weight per line presented correlations with thousand kernels weight, number of spikes per line

and grain weight per spike. In addition, thousand kernels weight was correlated with number of spikes per line, grain weight per spike and number of grain per spike. The number of spikes per line was correlated with number of grains per spike. Also, grain weight per spike was positively correlated with number of grains per spike.

Table 8: Coefficients of correlation between grain yield and yield components under heavy H. fly infestation

	PW	GWL	TKW	NSL	GWS
GWL	0.797**				
TKW	0.411**	0.581**			
NSL	0.755**	0.884**	0.556**		
GWS	0.320**	0.468**	0.310**		
NGS			-0.373**	-0.316**	0.733**

PW: plants weight, **GWL:** grain weight per line, **NGS:** number of grains per spike, **NSL:** number of spikes per Line, **TKW:** thousand kernel weight, **GWS:** grain weight per spike.

Grouping traits according to similarities

To better describe the correlations observed previously, grouping of traits according to their similarities was performed within both resistant and susceptible groups of lines in pest free condition and under heavy H. fly infestation (Figure 3, 4 and 5).

Under pest free situation, the dendrogram of progressive similarity of traits within the resistant group showed three groups of characters: in the first cluster we found the number of grains per spike, the grain weight per spike, and the grain weight per line. This first cluster is then tied to the number of spikes per line and the total plant's weight. The last group to join the cluster is made of the number of days to heading and the number of days to maturity (figure 3). In the same sense, cluster analysis showed that all traits for susceptible group were grouped into two clusters (Figure 4). The first cluster constituted by the number of grains per spike, the grain weight per spike, and the grain weight per line followed by the second cluster which included the number of spikes per line and the plants

weight. These traits were located in the same groups that were already classified in the clustering of resistant group, indicating that groupings of these traits are similar for both susceptible and resistant group under pest free situation.

Under heavy H. fly infestation, the clustering of traits within the resistant group can be subdivided into two groups and one character; thousand kernels weight. The first cluster included the plants weight, the number of spikes per line and the grain weight per line. The last cluster was constituted by the number of grains per spike and the grain weight per spike (figure 5).

These results indicate that grouping characters according to their similarities differs only by a few characters in resistant group under heavy H. fly infestation but in general most of these associations were substantially similar in both situations for each group of lines. The clusters or the single traits that were linked the least to the others are the ones that are subject to change from one group to the other.

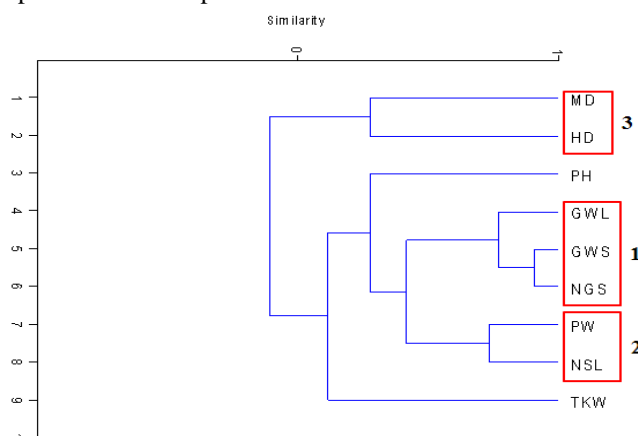


Figure 3: Dendrogram representing the clustering of the measured characters of resistant group under pest free condition according to their successive similarities (PW: plants weight; GWL: grain weight per line; NGS: number of grains per spike, NSL: number of

spikes per Line; **PH**: plant height; **TKW**: thousand kernels weight; **GWS**: grain weight per spike, **MD**: number of days to maturity; **HD**: number of days to heading).

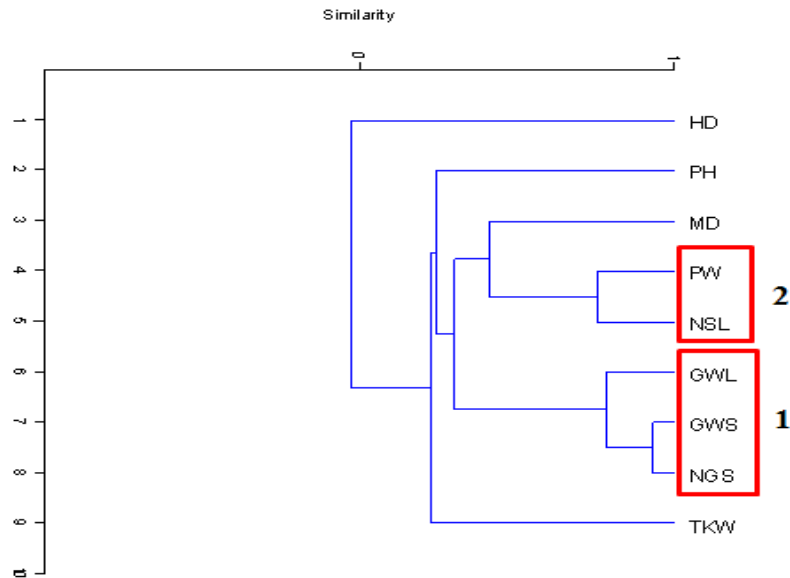


Figure 4: Dendrogram representing the clustering of the measured characters of susceptible group in pest free condition according to their successive similarities (**PW**: plants weight; **GWL**: grain weight per line; **NGS**: number of grains per spike, **NSL**: number of spikes per Line; **PH**: plant height; **TKW**: thousand kernels weight; **GWS**: grain weight per spike, **MD**: number of days to maturity; **HD**: number of days to heading).

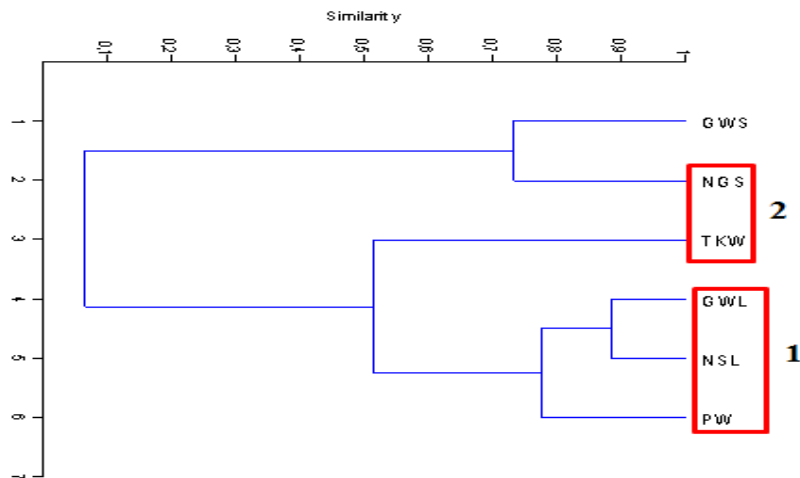


Figure 5: Dendrogram representing the clustering of the measured characters of resistant group under heavy H. fly infestation according to their successive similarities. (**PW**: plants weight; **GWL**: grain weight per line; **NGS**: number of grains per spike, **NSL**: number of spikes per Line; **TKW**: thousand kernels weight; **GWS**: grain weight per spike).

DISCUSSION

Under the pest free situation, the mean values of measured parameters are similar between resistant and susceptible lines. Analysis of variance for all characters indicates that there is no statistically significant difference between groups in plant phenology and yield components in the no infested trial. Theoretically, when several generations of breeding result in a reduction or elimination of costs, the most likely explanation is that the loss of linked alleles, rather than the often-invoked phenomenon of compensatory mutations, new mutations, that somehow decrease the fitness cost of the resistant phenotype (Purrlington, 2000). In this study, and under drought and heavy Hessian fly infestation, the susceptible lines gave no yield. This result is confirming those of Lidell & Schuster (1990) who found that Hessian fly reduces grain production of wheat by killing plants, stunting and killing vegetative tillers, preventing spike development, reducing grain filling, and by harvest losses through stem breakage. They are also corroborated by Buntin (1999) who revealed that the Hessian fly injury during grain filling significantly reduced all yield components including grain weight per spike and number of grains per spike. The resistant lines had a regular number of grains per spike and spikes per line.

This study is showing that there is no cost to resistance under no infestation situation and that there is a high benefit from resistance when plants are grown under high levels of infestation. These results corroborate those of Anderson and Harris (2006). The theory of "cost of resistance" indicates that the frequency of a resistance polymorphism in a plant species is very closely related to the level

of virulence of the plants primary pest, and when resistant genotypes have relatively low fitness (poor seed production) in the absence of pests, it is often assumed that their poor performance must be explained by the energetic drain involved in making and maintaining a chemical or structural defense, even if such a character has not been identified (Berenbaum & Zangerl, 1998; Ardesai & *al.*, 2005). This theory was not confirmed in this study.

Concerning the correlation analysis, significant correlations were observed between total plant weight, grain weight per line, weight and number of grains per spike for both resistant and susceptible lines. Total plant weight is of major interest in selection as well as the performance since it is positively related to yield (Mekhlouf & Bouzerzour, 2000). Grain weight per line is also correlated with grain weight per spike, number of grains per spike, thousand kernels weight and plant height, and showed also that the number of grains per line and thousand kernels weight are the main components of yield. They are influenced by the varietal characteristics (Baldwin & Preston, 1999). Similarly, Simane & *al.*, (1993) & Radhouane (2004) noted that the number of grains per spike contributes directly to increase the grain yield in durum wheat. The susceptible lines revealed that number of days to heading is significantly and negatively correlated with grain weight per spike and number of grains per spike. These correlations are also in agreement with Mekhlouf & Bouzerzour (2000), who confirmed the relationship between plants life-cycle development and yield. In general, the relationships between phenotypic traits, yield and yield components advantage are similar for both Hessian fly resistant and susceptible

lines. These results indicate that incorporating genetic resistance to Hessian fly has no negative effect on the studied characters.

CONCLUSION

This work showed that no significant difference existed between studied traits of Hessian fly resistant and susceptible lines, under pest free conditions. However, in the infested trial, all traits revealed that there is a highly significant difference between the two groups since all plant parts were affected to the maximum in the heavily infested site.

Analysis of correlation coefficients indicated that there is a similarity in the patterns of correlations between traits within the resistant and susceptible lines, under both the no infested and the heavily infested situation.

The conclusion drawn from this work is that incorporating genetic resistance to Hessian fly in durum wheat has positive effect on yield related performances under heavy fly attack, and has no negative effect on neither performance nor agro-morphological and phenological traits, and yield components in a fly free situation.

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