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Research Article

GENE ACTION IN ORIENTAL TOBACCO GENOTYPES UNDER *OROBANCHE AEGYPTIANA* PERS. INFESTATION

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ABSTRACT
This work was conducted at Urmia Tobacco Research Centre, Iran, in 2012 to study the genetic system and types of gene effects controlling resistance of tobacco (*Nicotiana tabacum* L.) against Egyptian broomrape (EBR) (*Orobanche aegyptiaca* Pers.) an obligate holoparasitic weed. Six Oriental tobacco varieties and their fifteen diallel hybrids from Fl generation were planted in a randomized complete block design with three replications to study the genotype components for inheritance of seven investigated traits: fresh weight of leaf (FWL), dry weight of leaf (DWL), number of leaves (NL), length of leaf (LL), width of leaf (WL), length of stem (LS), and diameter of stem (DS) under EBR stress. Analysis of variance showed significant for all traits except dry weight of leaf. Diallel analysis using Griffing's method 2, Model 1 showed significant mean squares of general combining ability (GCA) for NL and LS, of specific combining ability (SCA) for LL, WL, and DS and of both GCA and SCA for FWL. Based on significance of GCA and SCA, three kind of gene actions (additive, non-additive and both additive and non-additive) were concluded. For each investigated trait after assessment of genetic parameters, parents and hybrids were investigated for their general and specific combining ability respectively. Good and poor general combiners were determined among parents for each investigated traits and finally a set of hybrids appeared to be significant SCA which could be used in Oriental tobacco improvement against EBR.

***Keywords**: Diallel, Gene Effects, GCA, SCA, Oriental Tobacco, Broomrape*

INTRODUCTION
Nicotiana tabacum L. is the prevailingly cultivated species of the genus *Nicotiana* (Wersnman and Matzinger, 1980) and is the most industrially important non- food crop in the world's agriculture, planted on approximately 4.2 million hectares of crop land (Katarina *et al*., 2010). Oriental tobacco also called Turkish tobacco is one of the main types of *N. tabacum* which mainly grown in Iran, Turkey, Greece, Bulgaria, Lebanon and the Republic of Macedonia. It is of economic importance due to its place in worldwide crop production (8% of the tobacco world production) (Davis and Nielsen, 1999) and as a highly aromatic tobacco type used in blended cigarettes (Darvishzadeh and Hatami Maleki, 2011; and Hatami Maleki *et al*., 2013). Egyptian broomrape (EBR) (*Orobanche aegyptiaca* Pers.) as one of the 150 species of the genus *Orobanche* (Abbes *et al*., 2011) is an important holoparasitic flowering weed in the Middle East and Asia (Parker and Riches, 1993) and is one of the most important parasitic weeds in Iran (Hasannejad *et al*., 2006; Rumsey and Jury, 1991) particularly Northwestern Iran, one of the most favorable regions for Oriental tobacco cultivation (Darvishzadeh *et al*., 2010). This parasitic weed has a much broader spectrum of hosts and in addition to tobacco, parasitizing many other crops such as potato (*Solanum toberosum* L.), tomato (*Licopersicon esculentum* Mill.), faba bean (*Vicia faba* L.), grasspea (*Lathyrus sativus* L.), chickpea (*Cicer arietinum* L.), lentil (*Lens culinaris* Medic.), common vetch (*Vicia sativa* L.), cabbage (*Brassica oleracea* L.), oilseed rape (*Brassica napus* L.), carrot (*Daucus carota* L.), peanut (*Arachis hypogaea* L.) and several other crops (Parker and Riches, 1993; Press and Graves, 1995; Perezde-Luque *et al*., 2008). Eradication of this dangerous weed was and still is a worldwide aim. In Iran it is the most serious holoparasite on tobacco, with losses both in yield and quality with the former up to 100% (Ashrafi *et al*., 2008) thus, its control is of the utmost importance. Numerous non-genetically strategies (NGS) mechanical, cultural, nitrogen metabolism, biological, chemical, or a combination of

these (Ditomaso *et al*., 2006; Lym, 2005) have been tested over the years with limited effectiveness for various reasons such as: the high amount of parasite seed production, viability of seeds in the soil over several years, lack of seed germination in the absence of a chemical trigger from a suitable host, vigorous growth habit after emergence, and close association with the host crop (Buschmann *et al*., 2005; Ghannam *et al*., 2012).

Host Plant Resistance is one of the key strategies in the fight against this parasite (Perez-Luque *et al*., 2009) since resistant cultivars can grow satisfactorily and yield well in infested fields thus alleviating the hazards of *Orobanche* attacks. Thus, resistance breeding combined with an appropriate NGS (integrated management methods) seems to be capable of crop production its yield is not adversely affected by broomrape.

However, absence of mono- or oligogenic donors that are resistant to the tobacco–parasitizing EBR and polygenic nature of broomrape resistance (Cubero and Moreno 1999) cause selection the resistant genotypes become the main problem in tobacco resistance breeding. Marker assisted breeding (MAB) based on selection assisted via molecular marker (MAS) as a promising method to streamline resistance breading due to its high selection efficiency seems to be the most suitable method to solve this problem. Using this approach needs breeder-friendly markers tightly linked to the quantitative trait loci (QTLs) for resistance against EBR.

This in turn needs high costs and high equipment demands which are not practical in every plant breeding agencies. Diallel analysis (one of the several biometrical techniques of conventional plant breeding which has the potentiality of determining information used in cultivar development), on the other hand, seems still have prestige in resistance breeding against biotic and abiotic stresses. Information about genetic parameters (such as gene action, heritability, combining ability, heterosis) which are required in selection of desirable parents to develop resistant cultivars, could be determined by diallel analysis. Principles of diallel were proposed by Jinks and Hayman, (1953); Jinks, (1954); Hayman, (1954a); Hayman, (1954b); Griffing, (1956a); and Griffing (1956b). Diallel has been utilized in investigation of gene action effects and type of inheritance in tobacco (Pandeya and Zilkey, 1981; Ogilvie and Kozumplik, 1983; Pandeya *et al*., 1985; Rao, 1989; Legg and Collins, 1991; Chen, 1992; Honarnejad and Shoai, 1996; Kurobin and Matterskim, 2002; Xiaobing *et al*., 2005; Newaz and Uddin, 1992; Shoaei and Honarnejad, 1996; Butorac *et al*., 2004). Little is known associated with gene action in tobacco under broomrape stress. The aims of the present study were: 1) to estimate gene action and define the type of inheritance patterns of investigated traits under broomrape stress; and 2) to select the superior F1 diallel crosses via identification of valuable sources of resistance in Oriental tobacco germplasm.

MATERIALS AND METHODS

This study was performed at Urmia Tobacco Research Centre (UTRC), with cooperation of Department of Plant Breeding and Biotechnology, University of Urmia, during 2012.

Parents and their Hybrids

The parents used for the present study, comprised of six Oriental tobacco genotypes, G.D.165, Kromovgraid, Xanthi, SPT410, SPT406, Basmaseres31. The seeds of fifteen intercrossed combinations (G.D.165 × Kromograid, G.D.165 × Xanthi, G.D.165 × SPT410, G.D.165 × SPT406, G.D.165 × B.S.31, Kromovgraid × Xanthi, Kromovgraid × SPT410, Kromovgraid × SPT406, Kromovgraid × B.S.31, Xanthi × SPT410, Xanthi × SPT406, Xanthi × B.S.31, SPT410 × SPT406, SPT410 × B.S.31, and SPT406 × B.S.31) of six parents which prepared based on a half-diallel design at UTRC, were used along with their parents in this study.

Cultural Practices

Seeds of six parents and their F1 progenies were sown at a rate of approximately 5 g/m^2 followed by spreading a fine layer of sieved well fermented sheep manure on beds. Seedlings on 12 cm in height stage were transplanted to ceramic pots (one healthy and strong seedling in each pot) containing 5 kg of sterilized soil prepared from alfalfa fields as a representative of soils in which Oriental tobacco type is usually planted mixed with 0.06 g Egyptian broomrape seeds. Harvests were done at technical maturity and leaves were sun-cured. The plants were not topped as is common with most other tobacco types such as Virginia and burley (Bayat *et al*., 2014).

Experiment

Parents and their hybrids were conducted in an experiment which was arranged in randomized complete block design (RCBD) with three replications. Each replication consisted of one pot with one plant.

Traits Measured

The data on seven agronomic and morphological traits namely fresh weight of leaf (FWL), dry weight of leaf (DWL), number of leaves (NL), length of leaf (LL), width of leaf (WL), length of stem (LS), and diameter of stem (DS) were measured and recorded after flowering stage for each plant per pot in each replication.

Variance and Diallel Analysis

The general linear model (GLM) procedure in the SAS version 9.1 software (SAS Institute Inc, NC, USA) was used for analysis of variance. Diallel analysis were conducted according to Griffing's method 2 and model 1 (Griffing, 1956b) using the SAS program for Griffing's diallel analysis (Zhang *et al.*, 2005). Baker ratio was used for approximate estimations of gene effects (Baker, 1978).

RESULTS AND DISCUSSION

Variance analysis of experiment showed significant differences among genotypes for investigated traits except dry weight of leaf (Table 1). This indicated presence of adequate genetic variability among Oriental tobaccos, could be exploited in different crossing programs. Obtaining significant differences among genotypes allowed total variation to be partitioned into variation due to general and specific combining abilities.

The mean squares (MS) of GCA of the six parental genotypes and SCA of the F1 diallel crosses for the investigated traits are summarized in the Table 1. Based on significant mean squares for GCA and SCA, three kind of gene actions (additive for NL and LS, non-additive for LL, WL and DS and both additive and non-additive genes for FWL) were concluded. For each investigated trait after assessment of genetic parameters, parents and hybrids were investigated for their general and specific combining ability respectively.

Table 1: Variance Analysis for Studied Traits, GCA and SCA under EBR Infestation

Source of Variation	df	MS						
		FWL	**DWL**	**NL**	**LL**	**WL**	**LS**	**DS**
Genotype	20	49.93*	0.64	21.46**	19.57**	8.14**	352.67*	5.52**
GCA	5	44.51*	0.94	21.69*	14.31	4.69	450.72*	20.64
SCA	15	54.26*	0.65	17.36	22.58*	10.22*	320.14	6.86*
2GCA/2GCA+SCA		0.621	0.74	0.714	0.55	0.47	0.73	0.725

*: *Significant at 5% probability level*, **: *Significant at 1% probability level*

Fresh Weight of Leaf

Significant mean squares for GCA and SCA and Baker ratio of 0.621 showed contributions of both additive and non-additive gene effects with more positive actions for additive effects on controlling trait (Table 1).

Chen *et al*., (1992) reported both additive and non-additive effects of genes under stress free condition. SPT 410 with maximum positive GCA effects (1.92) (Table 2) and with mean weight of 7.19 gram/plant (Table 4) was the best general combiner, while G.D.165 with highest negative GCA effects (-1.92) (Table 2) and with mean weight of 4.07 gram/plant (Table 4) showed the poor one. The best specific combination with highest (9.25) positive SCA effects was Kromovgraid × SPT410 followed by Xanthi × B.S.31 (7.95) (Table 3). The highest (-4.61) negative SCA effects was recorded in the cross Kromovgraid × Xanthi (Table 3).

Table 2: GCA Values of Studied Traits under EBR Infestation for the Six Parents

Genotypes	FWL	DWL	NL	LL	WL	LS	DS
G.D.165	-1.92*	-0.04	-1.44	-0.72	-0.61	-8.11*	-1.02*
Kromovgraid	0.44	-0.19	1.34	-0.54	0.25	1.67	0.41
Xanthi	0.06	-0.26	-0.26	0.11	-0.15	2.28	-0.08
SPT410	1.92*	0.28	-0.32	1.11	0.71*	-1.02	0.05
SPT406	-1.41	0/06	-0.26	-0.76	-0.32	-0.37	0.001
B.S.31	0.89	0.15	0.95	0.821	0.11	5.35*	0.62*

*: *Significant at 5% probability level*

Table 3: SCA Values of Studied Traits under EBR Infestation for the Fifteen F1 Hybrids

Genotypes	FWL	DWL	NL	LL	WL	LS	DS
G.D.165 × Kromovgraid	1.44	-0.04	0.82	1.85	0.77	4.87	0.71
G.D.165 × Xanthi	-1.71	-0.26	-1.56	-1.47	-0.54	-8.92	-1.53*
G.D.165 × SPT410	-0.05	0.09	0.82	1.64	1.49	4.24	0.59
G.D.165 × SPT406	0.15	-0.33	0.11	-0.95	-1.07	-2.06	-0.15
G.D.165 × B.S.31	-1.19	-0.09	-3.38	-0.24	-2.09	-12.11	-1.81
Kromovgraid × Xanthi	-4.61*	-0.27	-3.0*	-2.52	-1.28	-2.37	-0.32
Kromovgraid × SPT410	9.25*	0.79*	2.37	4.51*	2.34*	12.46	1.77**
Kromovgraid × SPT406	-0.38	0.03	-0.34	-0.88	1.59	-4.84	-0.91
Kromovgraid × B.S.31	-3.73	-0.58	-6.61**	-0.88	0.52	-14.33	-0.74
Xanthi × SPT410	-1.54	0.09	1.65	1.51	0.19	8.15	0.23
Xanthi × SPT406	-1.32	0.01	-1.06	-0.49	-1.15	-7.64	-0.21
Xanthi × B.S.31	7.95*	0.31	3.44	2.79	1.66	28.47**	2.36*
SPT410 × SPT406	2.52	0.22	0.32	1.64	1.03	2.85	1.08
SPT410 × B.S.31	2.98	0.81	2.05	6.53*	4.69*	9.31	3.06**
SPT406 × B.S.31	0.49	1.14	-1.55	0.85	1.29	6.61	0.32

*: *Significant at 5% probability level*, **: *Significant at 1% probability level*

Table 4: Mean Values of Studied Traits under EBR Infestation for the Six Parents

Genotypes	FWL g/plant	DWL g/plant	NL n/plant	LL cm	WL cm	LS cm	DS mm
G.D.165	4.07	2.33	9.33	12.48	7.5	15.67	5.9
Kromovgraid	7.19	1.81	11.33	15.28	8.4	23.33	6.93
Xanthi	3.67	1.53	7.33	12.61	6.7	10.33	4.2
SPT410	7.19	2.43	9.66	16.71	9.58	20.0	6.46
SPT406	4.05	1.78	9.0	12.26	6.0	14.33	5.66
B.S.31	5.71	2.44	8.33	14.15	6.13	17.0	5.75

Number of Leaves

Significant mean squares for GCA showed the positive actions for additive effects on controlling number of leaves (Table 1). Also, Baker ratio equal to 0.714 showed more positive actions for additive effects on controlling this trait (Table 1).

Additive gene action due to significant mean squares for GCA were reported by Gopinath *et al*., (1996) and Shoaei and Honarnejad, 1996, under normal condition, while for the same condition, Korubin and Matterskin (2002); Sadeghi *et al*., (2009) and Sadeghi *et al*., (2011), reported additive and non-additive gene effects.

For the number of leaves there was no significance for GCA values of parents. The worst specific combination with highest (-6.61) negative SCA effects was Kromovgraid × B.S.31 with mean number of

15 leaves/plant followed by G.D.165 × B.S.31 which showed the maximum negative (-3.38) SCA effects with mean number of 9.66 leaves/plant (Tables 3 and 5).

Table 5: Mean Values of Studied Traits under EBR Infestation for the Fifteen F1 Hybrids

Genotypes	FWL g/plant	DWL g/plant	NL n/plant	LL cm	WL cm	LS cm	DS mm
G.D.165 × Kromovgraid	7.13	1.74	16.66	12.45	6.53	30.33	7.41
G.D.165 × Xanthi	3.13	1.36	8.66	11.75	6.81	26.66	6.84
G.D.165 × SPT410	18.83	2.97	14.0	19.76	11.3	38.0	9.04
G.D.165 × SPT406	5.89	1.99	11.33	12.52	9.51	21.33	6.33
G.D.165 × B.S.31	3.86	1.51	9.66	13.18	6.91	19.67	6.86
Kromovgraid × Xanthi	7.97	1.62	10.33	15	8.25	21	6.41
Kromovgraid × SPT410	7.68	2.21	11.66	17.42	8.75	34.5	7.03
Kromovgraid × SPT406	4.58	1.92	9.0	13.55	6.38	19.33	6.53
Kromovgraid × B.S.31	16.74	2.35	15.0	18.5	10.16	52.33	9.46
Xanthi × SPT410	4.48	1.65	6.33	9.0	4.56	4.33	3.56
Xanthi × SPT406	10.25	2.66	10.33	16/67	9.42	26.33	796
Xanthi × B.S.31	6.44	2.33	9.66	15.25	8.65	20.0	7.21
SPT410 × SPT406	3.71	1.67	11.33	13.07	6.5	26.66	6.76
SPT410 × B.S.31	6.49	2.91	11.0	15.52	8.24	39.0	7.71
SPT406 × B.S.31	9.49	1.97	15.66	16.55	8.56	33.33	7.73

Length of Leaf

Significant mean squares for SCA and Baker ratio of 0.55 showed the positive actions for non-additive effects on controlling of leaf length (Table 1). Shamsuddin *et al*., (1980) and Pandeya *et al*., (1985) observed non-additive gene action for this trait under stress free condition while for the same condition, Gopinath *et al*., (1996); Shoaei and Honarnejad (1996); Sadeghi *et al*., (2011) reported additive and non-additive gene action with more importance for non-additive one.

Width of Leaf

Significant mean squares for SCA and Baker ratio of 0.47 showed the positive actions for non-additive effects on controlling of trait (Table 1). Additive gene action was reported by Pandeya *et al*., (1985); Rao (1989); Ogilvie and Kozumplik (1983); Shoaei and Honarnejad (1996) under stress free condition. Sadeghi *et al*., (2011) reported additive gene action and dominance with more important for the former case under normal condition. SPT 410 with maximum positive GCA effects (0.71) (Table 2) and with mean leaf width of 9.58 cm (Table 4) was the best general combiner, while Xanthi showed the lowest combiner with maximum negative GCA effects (-0.61) (Table 2) and mean leaf width of 7.5 cm (Table 4). The best specific combination with the highest (4.69) positive SCA effects was SPT410 × B.S.31 with mean leaf width of 8.24 cm followed by Kromovgraid × SPT410 which showed the positive (2.34) SCA effects (Tables 3 and 5). The highest (-2.09) negative SCA effects were recorded in the cross GD165 × B.S.31.

Length of Stem

Significant mean squares for GCA and Baker ratio of 0.73 showed the positive actions for additive effects on controlling of Length of stem (Table 1). Chen (1992) reported that length of stem is controlled by additive gene action under stress free condition, while Gupoyl *et al.*, (1987); Shoaei and Honarnejad (1996) and Chang and Shyu (1991) emphasized to non-additive gene effects under normal condition. B.S.31 with maximum positive GCA effects (5.35) (Table 2) and with mean stem length of 17 cm (Table 4) was the best general combiner, while G.D.165 with highest negative GCA effects (-8.11) (Table 2) and with mean stem length of 15.67 cm (Table 4) showed the lowest one. The best specific combination with highest (28.47) positive SCA effects with mean stem length of 20 cm was Xanthi × B.S.31 (Tables 3 and 5).

Diameter of Stem

Significant mean squares for SCA and Baker ratio of 0.725 showed contributions of both additive and non-additive gene effects with more positive actions for non-additive effects on controlling trait (Table 1). Two genotypes displayed maximum and minimum GCA effects were B.S.31 (0.62) with mean stem diameter of 5.75 mm and G.D.165 (-1.02) with mean stem diameter of 5.9 mm respectively (Tables 2 and 4). Best cross combination showing high positive SCA effects was SPT 410 × B.S.31 (3.06) with mean stem diameter of 7.71 mm (Tables 3 and 5). The hybrid G.D.165 × Xanthi showed the maximum negative (-1.53) SCA effects with mean stem diameter of 6.84 mm (Tables 3 and 5).

Conclusions

Partitioning of total mean squares of genotypes to general and specific combining abilities showed additive and non-additive gene effects for fresh weight of leaf, non-additive gene effects for length of leaf, width of leaf and diameter of stem, and additive gene effects for number of leaves and length of stem. In traits controlled by additive gene effect (number of leaves and length of stem) or in two modes via-controlled traits with more importance of additive inheritance such as fresh weight of leaf, it is supposed that relevant hybrids may produce transgressive segregants in the early generations which is more appropriate for pedigree selection could be employed to achieve genetic progress. In non-additively controlled traits such as width of leaf in this study single plant selections in later generation could be more effective.

Based on investigated traits, parents were considered as the good or poor general combiners. For the former case, these were SPT410 for fresh weight of leaf (1.92), and width of leaf (0.71), and B.S.31 for length of stem (5.35), and diameter of stem (0.62) (Table 6). While for the latter case, G.D.165 for the three traits including fresh weight of leaf (-1.92), length of stem (-8.11) and diameter of stem (-1.02), was the poor general combiner (Table 6). Four out of fifteen hybrids appeared to be positive and significant SCA which based on breeding aims could be exploited in Oriental tobacco improvement. These were Kromovgraid × SPT 410 for fresh weight of leaf (9.25) and width of leaf (2.34), Kromovgraid × B.S. 31 for number of leaves (6.61), xanthi × B.S. 31 for length of stem (28.47) and SPT 410 × B.S. 31 for diameter of stem (3.06) (Table 7). Hybrids with negative SCA in this research were Kromovgraid × xanthi for fresh weight of leaf (-4.61) and number of leaves (-3.0) and G.D.165 × xanthi for diameter of stem (-1.53) (Table 7).

Table 6: Significant GCAs of Studied Traits under EBR Infestation for the Six Parents

		FWL	DWL	NL	LL	WL	LS	DS
Positive	A	4	ns	ns	ns	4	6	6
	B	1.92*				0.71*	5.35*	0.62
Negative	A	1	ns	ns	ns	-	1	1
	B	-1.92*					-8.11*	-1.02*

**: Significant at 5% probability level, ns: Non-significant, A: Parent, 1: G.D.165, 2: Kromovgraid, 3: Xanthi, 4: SPT 410, 5: SPT 406, 6: B.S.31, B: Significant GCA*

Table 7: Significant SCAs of Studied Traits under EBR Infestation for the Fifteen F1 Hybrids

		FWL	DWL	NL	LL	WL	LS	DS
Positive	A	2×4	ns	2×6	ns	2×4	3×6	4×6
	B	9.25*		6.61*		2.34*	28.47*	3.06
	C	0.44×1.92*		1.34×0.95		-0.25×0.71*	2.28×5.35*	0.05×0.62*
Negative	A	2×3	ns	2×3	ns	-	-	1×3
	B	-4.61		-3.0*				-1.53*
	C	0.44×0.06		1.34×-0.26				-1.02*×-0.08

**: Significant at 5% probability level, ns: Non-significant, A: Hybrid, 1: G.D.165, 2: Kromovgraid, 3: Xanthi, 4: SPT 410, 5: SPT 406, 6: B.S.31, B: Significant SCA, C: GCAs of respective parents*

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