

Genetic inheritance analysis of melon aphid (*Aphis gossypii* Glover) resistance in cucumber (*Cucumis sativus* L.)

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Abstract The melon aphid *Aphis gossypii* Glover is one of the most serious pests in cucumber production, often causing severe damage in commercial fields. Identifying and deploying resistant germplasm and understanding the inheritance of melon aphid resistance are required for cucumber geneticists to develop an effective breeding strategy. In this study, resistance of 30 cucumber selections to melon aphid was evaluated at the seedling stage. Six generations, P₁, P₂, F₁, BC₁, BC₂ and F₂ derived from the cross of JY30 (susceptible) × EP6392 (resistant), were used as genetic populations to study the inheritance of melon aphid resistance in cucumber with the mixed major gene plus polygene inheritance model with the joint analysis method of multiple generations. Eight of the 30 tested selections displayed resistance to the melon aphid. The resistance of cucumber to melon aphids was controlled by one additive and dominant major gene plus additive and dominant polygenes, and was affected by environment as well. The additive effect and the dominant effect of the major gene were greater than the additive effect and the dominant effect of the polygenes. The heritabilities of the major gene in BC₁, BC₂ and F₂ were 63.62 %, 0 % and 70.39 %,

respectively. The polygenic heritabilities were 22.62 %, 37.0 % and 9.32 %, and the ratios of the environmental variance to phenotype variance were 58.54 %, 63.16 % and 30.77 %. We conclude that selections of cucumber with high resistance to melon aphid could be screened in advanced generations.

Keywords Aphid resistance · Cucumber · Joint segregation analysis · Mixed inheritance model

Introduction

Cucumber (*Cucumis sativus* L.) belongs to the family *Cucurbitaceae* (Jeffrey 1980; Mliki et al. 2003) and is one of the most important vegetable crops in many countries of the world. The melon aphid (*Aphis gossypii* Glover) has occurred in most areas of China. It often causes severe damage and is one of the most serious pests in cucumber production. Identifying and deploying resistant germplasm and understanding the inheritance of melon aphid resistance in cucumbers is crucial for breeding aphid-resistant cucumbers with high quality.

Proper assessment of plant resistance is necessary for successful research on plant aphid resistance. It was reported that the aphid damage exponent could be used as the basis for identifying aphid resistance in cotton (Zhang and Yuan 1978) and alfalfa (Wu et al. 2007). The average number of aphids per plant was used as a basis for identifying aphid resistance in bean (Han et al.

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1991). There is evidence for genetic control of aphid resistance in many crops, including tomato (*Solanum lycopersicum*) (Rossi et al. 1998), wheat (*Triticum aestivum*) (Liu et al. 2005), barley (*Hordeum vulgare*) (Mittal et al. 2008), melon (*C. melo*) (Sarria et al. 2008; Brotman et al. 2002), barrel clover (*Medicago truncatula*) (Klingler et al. 2005), maize (*Zea mays*) (So et al. 2010) and soybean (*Glycine max*) (Kim et al. 2010a, b; Ohnishi et al. 2012). However, little is known about the inheritance of aphid resistance in cucumber.

It is assumed that in addition to the major gene, a polygenic component is included in the inheritance system for quantitative traits. Such a mixed major gene plus polygene inheritance model is derived from the mixed one major gene plus polygene inheritance theory according to Elston (1984). This theory accounts for some inheritance of quantitative traits that could not be explained by classical Mendelian genetics. The mixed major gene plus polygene genetic model has been widely used in genetic analysis of multiple traits in rice (Gai and Wang 1998), wheat (Zhang et al. 2007a), soybean (Wang and Gai 2001; Li et al. 2008) and rape (Zhang et al. 2006). This model is also applied to the genetic analysis of multiple traits of cucumber, including downy mildew resistance (Zhang et al. 2007b) and fruit stalk length (Ma et al. 2010). However, this model has not been used in the study of the inheritance of cucumber aphid resistance.

In the present study, identification of the differences among 30 cucumber selections to melon aphid resistance was carried out based on the numbers of aphids per seedling. JY30 and EP6392 were chosen as susceptible and resistant aphid parents to produce F₁, F₂, BC₁ and BC₂ generations for genetic analysis following a mixed inheritance model with the objective of elucidating the inheritance of aphid resistance in cucumber.

Materials and methods

Plant materials and aphid infection

The aphid resistance level of 30 cucumber selections, including ZaoerN, NingYang7, CaiLv2, A'Xin, JY30, RiJieCheng, PingWang cucumber, BaiGuiFei, BiYu, EP6392, WanLv, JIN5-508, XUE1, D8, JinPeng-BaiYu, GY14A, ZaoKang, Katya, DDX, EP326, RiYin2, ZhongNong115, EP6411, YuNv, JinZhou cucumber, MaPiHuang, Burpee, GY2, CiXi cucumber

and XiaoYe, was evaluated by counting the number of aphids per cucumber seedling. Seeds of each selection were sown in trays filled with potting substrate (nutrient available: 40–60 g/kg total NPK nutrients, ≥ 350 g/kg total humus content, 6.5–7.5 pH) in three environmental growth chambers maintained at 25 °C (18 h)/18 °C (6 h) day/night, light intensity of 12,000 lux (18 h)/0 lux (6 h), and relative humidity ranged from 50 to 60 % on 2 December 2012. Seven days after the germination, five apterous adult melon aphids were transferred to the back of the first true leaf per seedling. Ten plants of each selection were infested with aphids, and three replications were conducted.

JY30 (P₁, susceptible female parent), and EP6392 (P₂, resistant male parent) were used to produce F₁ progeny based on the number of aphids per plant and plant reaction trait during March and June 2011. Selfing F₁ plants produced an F₂ population, and F₁ was crossed with P₁ to produce BC₁ and F₁ was crossed with P₂ to produce BC₂ during March and June 2013. Experiments were performed at the Yangzhou University Department of Horticulture research farm. Seeds of P₁, P₂, F₁, F₂, BC₁ and BC₂ generations were sown in trays filled with potting substrate (nutrient available: 40–60 g/kg total NPK nutrients, ≥ 350 g/kg total humus content, 6.5–7.5 pH) in four environmental growth chambers maintained at 25 °C (18 h)/18 °C (6 h) day/night, light intensity of 12,000 lux (18 h)/0 lux (6 h), and relative humidity ranged from 50 to 60 % on 6 July 2013. The number of sown seeds of P₁, P₂, F₁, F₂, BC₁ and BC₂ were 60, 60, 60, 440, 100 and 100, respectively. Seven days after the germination, five apterous adult melon aphids were transferred to the back of the first true leaf per seedling.

Determination of aphid resistance

The numbers of aphids on individual plants were counted at 8 days after aphid infestation by assigning aphid scores ranging from 1 to 5, where 1 \leq 100 aphids per plant, 2 = 101–200 aphids per plant, 3 = 201–300 aphids per plant, 4 = 301–400 aphids per plant and 5 \geq 401 aphids per plant, modified from Jun et al. (2012).

Data analysis

Data from six generations were used for inheritance analysis by the joint segregation analysis (JSA)

method (Gai and Wang 1998). The principle of JSA is as follows: first, we assumed that the segregating population was composed of component distributions controlled by a major gene and was modified by both polygenes and the environment. A total of five groups and 24 types of genetic models were established, including a “one major gene inheritance” model (A), a “two major genes inheritance” model (B), a “polygenic inheritance” model (C), a “mixed one major gene and one polygene inheritance” model (D) and a “mixed two major genes and a polygene inheritance” model (E). Subsequently, a joint maximum-likelihood function was derived using data from six generations to estimate the parameters of component distributions through the iterated expectation and conditional maximization (IECM) algorithm. Additionally, the Akaike’s information criterion (AIC), likelihood-ratio test (LRT), and a set of goodness-of-fit tests were used for model selection and testing. The model with the least AIC value and best fitness was considered as the best-fitting model. Related genetic parameters, including gene effects and genetic variances of major genes and polygenes were obtained from estimates of component distributions. Finally, individuals from segregating populations were classified into major-gene genotypes according to their posterior probabilities (Gai and Wang 1998; Zhang et al. 2000; Gai et al. 2003; Yao et al. 2013). The AIC value and related genetic parameters were calculated using the Segreg Anal Soft Program (<http://jpkc.njau.edu.cn/swtj/show.asp?classid=35&articleid=44&classtype=26>) and Statistical Analysis System (SAS, Cary, NC, USA).

Results

Evaluation of cucumber aphid resistance

Screening germplasm for aphid resistance led to the discovery of aphid-resistant selections within the 30 tested cucumber selections (Table 1). We identified eight aphid-resistant cucumber selections, including Katya, EP326, JIN5-508, Burpee, ZaoKang, EP6392, EP6411 and GY14A, as well as two highly susceptible selections, JY30 and BaiGuiFei.

The leaves of aphid-resistant cucumber selections were curled slightly upwards, whereas those of aphid-susceptible selections were more obviously curled upwards. Plants with aphid resistance performed

normally in growth and development, but plants with aphid susceptibility were severely stunted at 8 day after aphid infestation.

Variation of aphid resistance among the six generations

‘EP6392’ showed significant resistance to aphid infestation, whereas ‘JY30’ was susceptible (Table 2). The F_1 population had a tendency toward the resistant parent; BC_1 and BC_2 showed a single mode in the susceptible direction and resistant direction, respectively; and the F_2 population showed two modes in both the susceptible and resistant directions (Table 2).

Inheritance analysis

To estimate the number of genes and heritability parameters, the aphid scores of individual plants of six generations were analyzed using the Segreg Anal Soft Program. The maximum log likelihood value (MLV), AIC value and the maximum-likelihood estimates in each genetic model were calculated. The model D-4 had the smallest AIC value of 1508.00, followed by E-1 (1536.07) (Table 3). Therefore, D-4 and E-1 were chosen as candidates for a best-fitting model to explain the inheritance of aphid resistance in ‘JY30’ × ‘EP6392’ progenies according to Akaike’s hypothesis on maximizing expected entropy (Akaike 1977).

The tests for goodness-of-fit between the expected values from the selected model and the observed values were conducted to determine whether the selected model sufficiently explained the data. LRT and test of goodness-of-fit for the models D-4 and E-1 indicated that model D-4 was the best-fitting genetic model to explain the inheritance of aphid resistance in the cross (Table 4). This means that aphid resistance in the cross of ‘JY30 × EP6392’ was controlled by one additive and dominant major gene plus additive and dominant polygenes.

The results of genetic components of each segregated generation showed that the additive effect and the dominant effect of the major gene were greater than the additive effect of the polygenes (Table 5). The dominant degrees of the major gene and polygenes were about -1.00 and -0.8 . The heritability of the major gene in BC_1 , BC_2 and F_2 was 63.62 %, 0.00 % and 70.39 %, respectively. The polygenic heritability was 22.62 %, 37.00 % and 9.32 %, respectively, and

Table 1 The results of the evaluation of cucumber aphid resistance

Cultivars	Mean	Aphid scores	Resistance level	Cultivars	Mean	Aphid scores	Resistance level
JY30	508.60	5	HS	WanLv	245.40	3	MR
BaiGuiFei	449.40	5	HS	NingYang7	240.60	3	MR
AXin	379.40	4	S	D8	235.00	3	MR
XiaoYe	369.20	4	S	JinZhou cucumber	227.40	3	MR
ZaoerN	345.80	4	S	DDX	226.20	3	MR
CaiLv2	334.00	4	S	YuNv	220.00	3	MR
RiJieCheng	314.20	4	S	CiXi cucumber	213.60	3	MR
BiYu	314.20	4	S	Katya	198.00	2	R
GY2	313.20	4	S	EP326	192.20	2	R
PingWang cucumber	310.00	4	S	JIN5-508	189.20	2	R
RiYing2	300.00	3	MR	Burpee	176.60	2	R
XUE1	295.80	3	MR	ZaoKang	173.80	2	R
JinPengBaiYu	286.80	3	MR	EP6392	159.40	2	R
ZhongNong115	257.60	3	MR	EP6411	158.80	2	R
MaPiHuang	249.40	3	MR	GY14A	123.60	2	R

HS high susceptible, S susceptible, MR middle resistant, R resistant

Table 2 The frequency distribution of aphid numbers on individual seedling in six generations

Generation	Numbers	The aphid scores				
		1	2	3	4	5
P ₁	50	–	–	–	18	32
P ₂	57	30	27	–	–	–
F ₁	57	22	35	–	–	–
BC ₁	94	–	–	8	42	44
BC ₂	94	41	46	7	–	–
F ₂	432	80	226	86	34	6

the ratios of the environmental variance to phenotype variance was 58.54 %, 63.16 % and 30.77 %, respectively. These results indicated that the environmental effect was also important in cucumber resistance to melon aphids.

Discussion

The melon aphid is one of the major pests in cucumber production. It feeds specifically from the sieve element and causes damage by removing plant nutrients and carbohydrates. Severe aphid infestation may cause many visible symptoms, including curling, wilting, yellowing and plant stunting. Use of aphid-resistant

Table 3 The maximum log likelihood values (MLV) and AIC values under various genetic models estimated through the iterated ECM (IECM) algorithm

Model	MLV	AIC	Model	MLV	AIC
A-1	–877.73	1763.46	D	–835.13	1694.25
A-2	–1022.99	2051.99	D-1	–836.60	1691.20
A-3	–1227.76	2461.52	D-2	–836.61	1689.21
A-4	–885.54	1777.09	D-3	–769.89	1555.79
B-1	–825.89	1671.79	D-4	–746.00	1508.00
B-2	–803.88	1619.76	E	–830.84	1697.68
B-3	–1084.71	2177.42	E-1	–753.03	1536.07
B-4	–999.44	2004.88	E-2	–841.29	1704.59
B-5	–1205.31	2418.62	E-3	–837.79	1693.58
B-6	–1205.31	2416.62	E-4	–922.54	1861.08
C	–853.34	1726.69	E-5	–932.52	1883.03
C-1	–932.55	1879.10	–	–	–

selections increases yields and improves cucumber quality, and also protects the environment by allowing reduced insecticide application. Identification of germplasm with aphid resistance is an effective way to explore the crop’s genetic resources; however, proper assessment is necessary. The ratio of aphid number was used as the basis for identifying aphid resistance in chrysanthemum (He et al. 2010). Aphid

Table 4 Test for goodness-of-fit of genetic models of aphid resistance

Model	Generation	Maximum likelihood estimates of component distribution parameters				
		U_1^2	U_2^2	U_3^2	nW^2	D_n
D-4	P ₁	0.11 (0.5689)	1.24 (0.2912)	16.50 (0.0439)*	2.737 (>0.05)	0.405 (>0.05)
	P ₂	0.06 (0.6181)	1.73 (0.2515)	49.73 (0.0079)*	3.331 (>0.05)	0.395 (>0.05)
	F ₁	0.00 (0.8759)	0.35 (0.4423)	183.06 (0.0002)*	2.982 (>0.05)	0.360 (>0.05)
	BC ₁	11.46 (0.0658)	12.24 (0.0614)	0.02 (0.7218)	0.194 (>0.05)	0.609 (<0.05)*
	BC ₂	0.00 (0.8067)	0.00 (0.8869)	5.29 (0.1294)	3.385 (>0.05)	0.286 (>0.05)
	F ₂	0.20 (0.5043)	2.41 (0.2128)	33.04 (0.0165)*	34.053 (>0.05)	0.263 (>0.05)
E-1	P ₁	0.20 (0.5055)	30.87 (0.0184)*	2200.64 (0.0000)*	6.254 (>0.05)	0.462 (>0.05)
	P ₂	0.00 (0.8667)	19.19 (0.0363)*	3556.33 (0.0000)*	7.630 (>0.05)	0.437 (>0.05)
	F ₁	0.29 (0.4649)	56.42 (0.0061)*	36196.20 (0.0000)*	15.614 (>0.05)	0.498 (>0.05)
	BC ₁	2501.50 (0.0000)*	2191.83 (0.0000)*	0.00 (0.9831)	43.097 (>0.05)	0.541 (>0.05)
	BC ₂	77.39 (0.0030)*	99.14 (0.0016)*	1.66 (0.2566)	6.334 (>0.05)	0.381 (>0.05)
	F ₂	189.56 (0.0002)*	390.02 (0.0000)*	134.44 (0.0007)*	47.803 (>0.05)	0.322 (>0.05)

U_1^2, U_2^2, U_3^2 uniformity test, nW^2 Smirnov test, D_n Kolmogorov test

* Means significance at 0.05

Table 5 Estimates of genetic parameters for resistance in the ‘JY30’ × ‘EP6392’ cross

1st parameter	Estimate	2nd parameter	BC ₁	BC ₂	F ₂
m	3.03	σ_p^2	0.41	0.38	0.78
d	1.05	σ_{mg}^2	1.11	0.00	0.83
h	−1.05	σ_{pg}^2	0.39	0.14	0.11
[d]	0.53	σ_e^2	0.24	0.24	0.24
[h]	−0.42	h_{mg}^2 (%)	63.62	0.00	70.39
h/d	−1.00	h_{pg}^2 (%)	22.62	37.00	9.32
[h]/[d]	−0.80	h_{mg+pg}^2 (%)	86.24	37.00	79.71
		$1 - h_{mg+pg}^2$ (%)	13.76	63.00	20.29

d additive effects of the major genes, h dominant effects of the major genes, [d] additive effects of the polygenes, [h] dominant effects of the polygenes, h/d dominance degree of the major gene, [h]/[d] dominance degree of the polygenes, σ_p^2 phenotypic variance, σ_{mg}^2 variance of major gene, σ_{pg}^2 variance of polygenes, σ_e^2 environmental variance, h_{mg}^2 inheritability of major gene, h_{pg}^2 inheritability of polygenes

damage index was used as a basis for identifying aphid resistance in soybean (Meng et al. 2010), cotton (Zhang and Yuan 1978) and alfalfa (Wu et al. 2007). In this study, an assessment of cucumber aphid resistance was conducted by assigning aphid scores according to the number of aphids per seedling in chambers. The results showed that eight of the 30 tested selections were resistant to the melon aphid. Our results may provide aphid-resistant materials for the study of genetic mechanisms of aphid resistance in cucumber and for breeding work.

Previous studies have shown that inheritance of aphid resistance may be monogenic or polygenic. For example, inheritance of greenbug resistance is controlled by a single dominant resistance gene (*Gb3*) in wheat (Weng and Lazar 2002; Weng et al. 2005; Azhaguvel et al. 2012). *Mi* was also found to confer resistance to the potato aphid (*Macrosiphum euphorbiae*) and whitefly (*Bemisia tabaci*) and the *Mi-1* gene was cloned (Milligan et al. 1998; Rossi et al. 1998; Vos et al. 1998). A dominant gene (*Dp-1*) provides resistance to the pear aphid (*Dysaphis pyri*) (Evans

et al. 2008). Three dominant genes, *Rag1*, *Rag2* and *Rag3*, for resistance to the soybean aphid (*A. glycines*) were mapped to independent soybean linkage groups (Hill et al. 2009; Zhang et al. 2010). Four quantitative trait loci (QTLs) and two pairs of epistatic QTLs for resistance to melon-cotton aphid were mapped, and the major gene *vat* gene was cloned (Boissot et al. 2010; Pauquet et al. 2004). Different species might have different inheritance models for aphid resistance. The present results showed that genetic model D-4 was the best fitting genetic model for melon aphid resistance in cucumber. It indicated that melon aphid resistance in cucumber was controlled by one additive and dominant major gene plus additive and dominant polygenes. The heritability of the major gene and polygenes in F_2 was about 70.39 and 9.32 %. This result showed that cucumber selections with aphid resistance could be screened in advanced generations. The environmental and other variances in F_2 were approximately 20.29 %. This indicated that aphid resistance in cucumber could be enhanced by improving cultivation conditions and optimizing cultivation techniques.

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Conflict of interest The authors declare that they have no competing interests.

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