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Temporary Crowding as an Extrinsic Factor Affecting the Performance and Morph Determination in the Corn Leaf Aphid *Rhopalosiphum maidis* (Fitch)

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Abstract: The effects of crowding (intra-specific) as an extrinsic factor were studied on the corn-leaf aphid *Rhopalosiphum maidis* (Fitch). Larval (postnatal) and maternal (prenatal) artificial temporary crowding were carried out at different holding hours: 1(once), 3 (once), 3 (twice) and 24 (once). After postnatal crowding for less than a day during third larval instar: 3 h. (twice) crowding was the prime extrinsic stimulus affecting the larval survival. Crowding for 3 h (once) or twice) inhibited the adult emergence to 73.33%vs. 86.67% at 1 h (once)-crowding. Decreasing total longevity by increasing holding period was observed. Similar effect was also observed for the parturition period while the prenatal period reversely correlated to this sequence of crowding regimes. Natality/0 deceased by increasing holding periods. Some deaths were observed during the first three larval instars of the progeny by increasing crowding periods. More or less, various data were determined after the crowding of fourth (last instar larvae and teneral apterous mothers. Crowding for 1 h alatae among the first offspring while for 3 h (once) induced 12.22% alatae and for 3 h (twice) induced 15.88% alatae. Also, various responses of parental generation and its progeny were determined by crowding at different population density under short and long photo phases.

Key words: Corn-leaf aphid *Rhopalosiphum maidis*, crowding, population densities

INTRODUCTION

There is no doubt that the densities of population of an aphid species directly control wing dimorphism; that is, more alatae are produced by crowded aphid than by these in isolation condition. Bonnemaison (1951) and Haymaizu (1984), *Myzus persicae* and *Brevicoryne brassicae*; Lees (1961), *Megoura viciae*; Johnson, (1965), *M. viciae* and *Aphis craccivora;* Toba *et al.* (1967), *Therioaphis maculata*; Sutherland (1969) and El-Hawary (1980), *A. craccivora*; Watt and Dixon (1981), Ankersmit and Dijkman (1983), *Sitobion avenae;* Dixon and Glen (1971) and Rautapaa (1976), *Rhopalosiphum padi*; Kidd and Tozer (1984), *Cinara pinaa;* Lamb and Mackay (1987), *Acyrthosiphon pisum* and *A. kondoi*). The crowding response is mediated by tactile stimuli which are exchanged between aphids, two individuals will (Johnson (1965); the effect can also be initiated by allowing aphids to be jostled by other species of insects (Lees, 1961) or even by inducing them to walk through fibers of a coarse muslin surface (Surtherland, 1969). Crowding stimulus operates postnatal in some species while it operates parentally in other ones (Lees, 1961; Johnson and Birks, 1960; Toba *et al.,* 1967; White, 1968; Mittler and Kunkel, 1971; Tsitsipis and Mittler, 1976). The Corn Leaf aphid *rhopahum maidis* (Fitch) has widely spread and sometimes its infestations caused severe damage to corn crops in Egypt (Hassan, 1957; Habib and El-Kady, 1961; Hafez *et al.*, 1971; El-Ibrashy *et al.,* 1972; Tawfik *et al.*, 1974; Megahed *et al.,* 1983; Darwish, 1989; Yousef, 1990; Ghoneim, 1995a, b) in addition to its occurrence all over the world especially whose the middle east climate (ICARDA, 1987; Apablaza and Robinson, 1967; Lazzari and Foerster, 1983; Bhatia Singh, 1977; Sakuratani, 1977). The present paper describes various biological, morphogenic and reproductive responses of the aphid *R. maidis* (Fitch) to the prenatal and postnatal crowding under laboratory controlled conditions.

MATERIALS AND METHODS

Culturing of the experimental aphid: A culture of the corn leaf aphid *Rhopalosiphum maidis* (Fitch) for this study was maintained in laboratory of Entomology, Faculty of Science Al-Azhar University, Cairo in December, 2002. The culture was originally established by an initial sample of this species collected from leaves of maize plant (*Zea mais*) cultivated at Ashmon district, Al-Minofiya Governorate. Aphids were reared for a number of successive generation before the experimental work

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under the laboratory conditions: 25±3°C. long photophase (17 h per diem) 60-80% R.H. as described by Ghoneim (1994). The culture was maintained in transparent glass cages (60×40×15 cm) tightly covered with muslin cloth sheets and placed inside black painted cabinets which were fitted with automatic light and temperature regulators and provided with front black cloth flap to facilitate the daily routine work and at the same time to prevent spread of room light into the cabinets. Fresh and clean (free from any infestation and dust) maize leaves of mature plants (35-45 days of age) were offered to aphids as a green food every two days. Examination and daily routine work with aphids were carried out on black coated table using an illuminated round lens (10×25 cm diameter) with a jointed stand. A moistened fine-tipped camel hair brush is an indispensable tool of the aphidologist to remove, transfer and manipulate the aphids.

Crowding: Different holding periods [1 h (once), 3 h (twice) and 24 h (once) were passed for 15 individuals without feeding except the last category which was allowed to feed on fresh corn leaves. Thereafter, aphids were transferred separately into small pieces of fresh corn leaves and confined inside small glass Petri dishes (6 cm diameter) provided with moistened cotton-wools to maintain a high relative humidity. All experimental aphids were kept under constant conditions: 25±0.17:7 LD photoperiodic regime and renewed corn leave every day. All Petri dishes were daily checked to record the possible observations. Another set of experiments was carried out under tow levels of population density (low: 15 and high: 40 individuals) and tow photoperiodic regimes, favorable (17:7 LD) and unfavorable (7:17 LD). For conducting the crowding regime of 3 h (twice), the apterous aphids were temporarily crowded to 3 h a day then separated and provided with food. The same aphids were re-crowded other 3 h at the next day and separated again to live individually under the controlled laboratory conditions.

RESULTS AND DISCUSSION

There is no doubt that the density of aphid population directly control wing dimorphism; that is, crowded aphids than produce more alatae by uncrowded ones. The crowding and not the nutritional stimulus were firstly demonstrated by Bonnemaison (1951), Lees (1961), Johnson (1965) and Toba *et al.* (1967). On the contrary, Wiktelius (1992), found that both plant growth stage and crowding play an important role in alate formation but plant growth stage has the most prominent effect, especially after beginning of ear emergence of corn plant when a major proportion of the fourth instar larvae become alatae, irrespective of aphid density. This control mechanism may operate either prenatal, postnatal, or both, depending on the species. Also, the proportion of alatae in the progeny of crowded aphids depends upon both the duration of the treatment and the density of the aphid population when crowded (Sutherland, 1969).

In the present study, *Rhopalosiphum. maidis* was undergone to crowding prenatal and postnatal, at different holding periods and different levels of the population density. On the other hand, the food source was available as fresh corn leaves (of 35-45 days in age). The crowding space was constant for all crowded categories (transparent glass Petri dish of 6 cm diameter and 1 cm height). Crowding of the third instar larvae of parental generation for 1 h (once), 3 h (once) and 3 h (twice) (under long photophase, 17 h light per diem and at a level of population density of 15 individuals) enhanced various populations of alatae among the progeny which

Table 1: Effects of temporal crowding[(a)] of (apterous) third instar larvae (without food) on progeny performance of Corn Leaf aphid *Rhopalsiphum maidis*[(b)]

	Natality (Progeny production)			Progeny fitness	
Holding Period	Av. No. of larvae/+O±SD	Av. No. of larvae/+O/day±SD	% change of progeny	% survival	% alate/apteroues
1 h (once) (c)	14.38±3.58	1.31±0.84	------	80.43	2.50
3 h (once)	7.45±1.30***	0.83±0.62Ns	- 48.19	74.54	4.50
3 h (Twice)	5.64±1.23***	0.63±0.532*	- 41.06	74.07	4.90

[(a)]: Crowding was held on a period less than day, without food. [(b)]: The whole generation and produced offspring were raised at 25±0.1 °C and 17:7 LD, at one level only of density: 15 aphids. [(C)]: Data in this row were used as a statistical basis. NS: Not significant (p>0.05), *: significant (p<0.05), **: highly significant (p>0.01). ***: very highly significant (p<0.001)

Table 2: Effects of temporal crowding[(a)] of (apterous) fourth (last) instar larvae (without food) on progeny performance of Corn Leaf aphid *Rhopalsiphum maidis*[(b)]

	Natality (Progeny production)			Progeny fitness	
Holding Period	Av. No. of larvae/+O±SD	Av. No. of larvae/+O/day±SD	% change of progeny	% survival	% alate/apteroues
1 h (once) (c)	15.27±2.26	1.52±1.07	------	84.0	0.00
3 h (once)	8.14±1.80***	0.68±0.62NS	- 46.69	75.86	12.22
3 h (twice)	7.08±1.93***	0.77±0.69*	- 53.63	73.91	15.88

[(a)], [(b)], [(c)], NS, *, **, ***: See footnote of Table (1)

Table 3: Effects of temporal crowding[(a)], at various photoperiods, of apterous third instar larvae on progeny performance of Corn Leaf aphid *Rhopalsiphum maidis*[(b)]

Photoperiod (hours)		Natality (Progeny production)				Progeny fitness	
L	D	Pop. density	Av. No. of larvae /±O±SD	Av. No. of larvae/±O/day±SD	% change of progeny	% survival	% alate/apteroues
7	17(c)	15	16.60±1.99	1.48±0.89	----	83.00	12.4
17	7	15	19.67±0.94**	1.51±0.87NS	+18.49	88.78	0.0
7	17	40	15.93±1.57Ns	1.34±0.75NS	- 4.04	82.65	15.6
17	7	40	19.40±1.20***	1.50±0.83NS	+16.87	87.63	3.5

[(a)], [(b)], [(c)], NS, *, **, ***: See footnote of Table (1). Pop. density: Population density

Table 4: Effects of temporal crowding[(a)], at various photoperiods, of apterous fourth (last) instar larvae on progeny performance of Corn Leaf aphid *Rhopalsiphum maidis*[(b)]

Photoperiod (hours)		Natality (Progeny production)				Progeny fitness	
L	D	Pop density	Av. No. of larvae /±O±SD	Av. No. of larvae/±O/day±SD	% change of progeny	% survival	% alate/apteroues
7	17(c)	15	14.87±1.93	1.23±0.86	----	80.80	10.2
17	7	15	18.33±2.24**	1.53±0.83NS	+23.27	85.00	0.0
7	17	40	14.13±1.57NS	1.36±0.77NS	- 4.98	80.39	12.2
17	7	40	20.13±1.99***	1.68±0.81NS	+35.37	84.16	1.2

[(a)], [(b)], [(c)], NS, ***: see footnote of Table (1). Pop. density: see footnote of Table (3)

Table 5: Effects of temporal crowding[(a)], of (apterous) third instar larvae on survival, development and adults, of Corn Leaf aphid *Rhopalsiphum maidis*[(b)]

		Larval instars					Adult stage				
								Mean longevity (days±SD)			
		% Survival		Mean duration							
Holding Period	No larvae	3rd inst.	4th inst.	3r dinstar	4th instar	% Emerg.	% Survival	Prenatal period	Parturition period	Postnatal period	Total
1 h (once)[(c)]	1	93.3	92.90	1.71±0.45	1.62±0.62	86.67	100.0	1.07±0.47	6.85±1.74	1.30±0.46	9.23±1.42
3 h (once)	15	93.3	78.57	1.71±0.45NS	1.90±1.08NS	73.33	100.0	1.09±0.51NS	5.27±1.21*	1.55±0.78NS	7.91±1.16*
3 h (twice)	15	73.3	77.25	1.27±0.45*	1.00±0.00*	73.33	100.0	1.18±0.39NS	4.73±1.21**	1.45±0.50NS	7.36±1.49**

(a), (b), (c), NS, *, **, ***: See footnote of Table (1)

Table 6: Effects of temporal crowding[(a)], of (apterous) fourth instar larvae on survival, development, adult performance and progeny of Corn Leaf aphid *Rhopalsiphum maidis*[(b)]

		4th instar		Adult Stage				
					Mean longevity (days±SD)			
Crowding (h)	No. of larvae used	% Survival	Mean duration	%	Prenatal period	Parturition period	Postnatal period	Total
1 h (Once)[(c)]	15	100.00	1.20±0.40	100.00	1.07±0.25	6.27±1.29	1.20±0.40	8.53±1.31
3 h (Once)	15	93.33NS	1.20±0.41	93.33	1.14±0.35NS	5.71±2.19NS	1.79±0.67**	8.64±2.55NS
3 h (Twice)	15	80.00NS	1.50±0.50	80.00	1.58±0.64**	4.50±1.12***	1.25±0.92NS	7.33±1.55*

[(a)], [(b)], [(c)], NS, *, **, ***: See footnote of Table (1)

generally increased by the increasing holding hours (Table 1). Crowding of last (4th) instar larvae for 1 h did not cause alate production, for 3 h (once) led to 12.22% and for 3 h (twice) led to 15.88% alatae (Table 2). When the holding period was extended to a whole day crowding of third instar larvae under long day condition did not cause alata production, irrespective of the population density level (Table 3). After crowding of last instar larvae, only few (1.2%) alatae were produced under long photophase (17 h light per diem) with high level (40 individuals), they increased (10.2%) under short photophase (7 h light per diem) with low level (15 individuals) of population density. More alatae (12.2%) were engendered under short photophase with high level of population density (Table 4). Prenatal crowding at all levels of population density under all photo phases failed to induce wing development in mothers and all progeny appeared as apterous aphids.

Thus, it is obvious that not the parental (mother crowding) but the postnatal crowding (larval crowding of parental generation) enhanced the wing development in *R. maidis*. These findings agreed with those of Scheefers and Judge (1971) on *Chaetosiphum fragaefolii*; Dixon and Glen (1971) on *R. padi*; while disagreed with Johnson (1965) on *Aphis craccivora;* Mittler and Kunkel (1971) who recorded an enhancement in alata production as a response to interaction between adults of *Myzus perssicae*; Lees (1961) on *Megoura vicae* who found that a relatively brief contact between wingless adults caused them to produce winged offspring even after the parents

Table 7: Effects of temporal crowding[a], of (apterous) third instar larvae on survival, development and adults, of Corn Leaf aphid *Rhopalsiphum maidis*[b]

Photoperiod (hours) L	D	No. of larvae	Larval instars: % Survival 3rd inst.	4th inst.	Mean duration 3r dinstar	4th instar	% Emerg.	% Survival	Adult stage: Mean longevity (days±SD) Prenatal period	Parturition period	Postnatal period	Total
7	17(c)	15	100.0	100.0	1033±0.47	1.40±0.49	100.0	100.0	1.73±0.44	8.00±0.97	1.06±0.23	10.80±0.90
17	7	15	100.0	100.0	1.40±0.49NS	1.40±0.61NS	100.0	100.0	1.06±0.25***	9.53±1.20***	1.20±0.54NS	11.80±1.28*
7	17	15	100.0	100.0	1.00±0.44*	1.26±0.44NS	100.0	100.0	1.33±0.47*	7.73±0.68NS	1.33±0.47NS	10.40±0.71NS
17	7	15	100.0	100.0	1026±0.44NS	1.26±0.44NS	100.0	100.0	1.33±0.47*	9.27±1.24**	0.93±0.44NS	11.67±1.40*

[a]: Crowding was held on a whole day. [b]: The whole generation and produced offspring were raised under controlled conditions: 25±0.1°C and at two levels of population density: 15 and 40 aphids provided the food. [c] Data in this row were used as a statistical basis. not-significant (p>0.05), *: significant (p<0.05), **: highly significant (p>0.01), ***: very highly significant

Table 8: Effects of temporal crowding[a], at various photoperiods, of (apterous) fourth (last) instar larvae on survival, development and adults of Corn Leaf aphid *Rhopalsiphum maidis*[b]

Photoperiod (hours) L	D	4th instar: No. of larvae	% Survival	Mean duration (days±SD)	% Emerg.	% Survival	Adult stage: Mean longevity (days±SD) Prenatal period	Parturition period	Postnatal period	Total
7	17[b]	15	100.0	1.20±0.40	100.0	100.0	1.13±0.34	7.66±0.87	1.27±0.44	10.07±0.93
17	7	15	100.0	1.13±0.34NS	100.0	100.0	0.73±0.57*	9.73±0.85***	1.30±0.47NS	11.26±0.77
7	17	40	100.0	1.30±0.47NS	100.0	100.0	1.00±0.00NS	7.93±0.93NS	1.53±0.50NS	10.46±0.62NS
17	7	40	100.0	1.10±0.34NS	100.0	100.0	0.13±0.34***	9.80±1.22***	1.13±0.40NS	11.46±0.00***

[a], [b], [c], NS, *, **, ***: See footnote of Table (7)

have been re-isolated. The present findings, also, disagree with El-Hawary (1980) on *A. craccivora* who obtained alatae progeny by prenatal crowding; and with Watt and Dixon (1981) and Ankersmit and Dihkman (1983) on *Sitobion avenae* who found both prenatal and postnatal crowding induced alatae among progeny. However, crowding of aphids during the larval stage, of parental generation, has the prime factor in the factor in the alatae diversion which finding was recorded, also, by Sourial (1995) for the present aphid species *R. maidis* in addition to tow other species, *R. padi* and *Schizaphid graminum.* To interpret the physiological action of crowding as an extrinsic factor affecting the wing dimorphism in aphids, Lees (1961) has proposed that embryos of *Meguora viciae* are prenatally determined as presumptive alatae by a maternal factor, probably of a hormonal nature, originating in the head of the mother. Similar idea been suggested for the aphid *Brevicoryne brassicae* (White and Lamb, 1968). White (1968) clarified that suggestion which is acceptable until now as the isolation of *B. brassicae* enhances a hyperactivity of corpora alatae leading to an increase of juvenile hormone titer in the haemolymph which prohibits the development of wing tissues and consequently ensures the apterousness in aphids. Precisely, Sutherland (1969) suggested that the production and release of this hormone is initiated by an appropriate tactile stimulation and then vary with time. On the other hand, crowding stimulus-or tactile stimulation-suppresses the activity of corpora alata leading to gradual diminishing of juvenile hormone titer and this allows operating the wing formation. This may be substantiated by the apterizing effect of juvenile hormone analogues when applied to alatiform larvae of *B. brassicae* (White and lamb, 1968) of *M. viciae* (Lees, 1966) and of *R. maidis* (Ghoneim, 1994; Helwah, 1995).

In addition to the effect of crowding on the wing dimorphism that has intensively attracts the attention of many workers allover the world, the present study shows several other effects of crowding on aphid bio-potentials. As shown in Table 5 and 6, temporary crowding of third or fourth instar for 3 h (twice) has the supreme effect on the survival of larval which may be due to poor nutrition as mentioned by Dixon and Glen (1971), Watt and Dixon (1981) and Sourial (1995). Crowding of third instar larvae for 3 h (once or twice) inhibited the adult emergence to be only 73.33% vs. 86.67% at 1 h (once)-crowding (Table 5). As well as crowding of the fourth instar larvae for 3 h (twice) inhibited it to be 80.0% while 1 h (once)-crowding of these larvae had no effect (Table 6). Crowding of third or fourth instars larvae for a whole day led to longer longevity under long photophase and vice versa (Table 7-8). Crowding of fourth instar larvae at high level of population density prolonged the adult longevity, irrespective of the length of photophase. Moreover, at the same level of population density, all photo phases resulted in shortened prenatal period which was shortened also by all levels of population density under the long photophase. Crowding of mothers (prenatal crowding) for less than a day tremendously shortened the parturition period under long photophase (Table 9).

Table 9: Effects of temporal crowding[a], of apterous virginoparous teneral adults (without food) on longevity, natality and progeny of Corn Leaf aphid *Rhopalsiphum maidis*[b]

Holding Period	No. of larvae	Adult longevity: Mean duration (days±SD) Prenatal period	Parturition period	Postnatal period	Total	Natality: Av. No. of larvae/±O±SD	Av. No. of larvae/±O/day±SD	% progeny change	Progeny fitness: % Survival	% alatc/ aptcrous
1 h (once)	15	1.30±0.44	8.20±2.04	0.87±0.40	10.33±2.15	15.67±1.78	1.06±0.88	---	84.870.0	
3 h (once)	15	1.07±0.25NS	4.40±1.58***	1.20±1.22NS	8.67±2.27NS	7.47±1.59***	0.62±0.77NS	-52.23	97.55	0.0
3 h (twice)	15	1.03±0.59*	3.13±2.25***	1.20±0.75NS	5.67±2.36***	6.33±3.55***	0.76±0.80NS	-59.60	76.67	0.0

[a]: Crowding was held on a period less than day for one level only of population density (15 individuals) and kept under 17:7 LD. [b], [c], NS, *, ***: See footnote of Table (7)

Table 10: Effects of temporal crowding[a], at various photoperiods, of apterous teneral virginoparous adults on longevity, natality and progeny of Corn Leaf aphid *Rhopalsiphum maidis*[b]

Photoperiod (hours) L	D	No. of larvae	Adult longevity: Mean duration (days±SD) Prenatal period	Parturition period	Postnatal period	Total	Natality: Av. No. of larvae/±O±SD	Av. No. of larvae/±O/day±SD	% progeny change	Progeny fitness: % survival	% alatc/ aptcrous
7	17(c)	15	1.0±0.0	9.00±0.63	1.27±0.44	11.27±0.85	15.33±1.25	1.28±0.79	---	83.0	0.0
17	7	15	1.0±0.0NS	9.33±1.07NS	1.13±0.34NS	11.46±1.02NS	19.06±1.39***	1.58±0.81NS	+24.33	88.54	0.0
7	17	40	1.0±0.0NS	8.70±0.70NS	1.30±0.44NS	10.90±0.72NS	15.16±1.23NS	1.47±0.93	+4.76	79.21	0.0
17	7	40	1.0±0.0NS	9.00±1.37NS	1.40±0.71NS	11.30±1.44NS	19.40±2.12***	1.62±0.96NS	+26.55	90.09	0.0

[a]: Crowding was held on a whole day for two levels of population density (15 individuals) and kept under two different photoeriodic regimes (17:7 LD and 17:7 LD). [b], [c], NS, ***: See footnote of Table (7)

When the holding period was extended to a whole day, longer photophase led to longer adult longevity and parturition period while higher level of population density resulted in a shortage of these periods (Table 10).

Regarding the reproductive capacity as affected by crowding of the aphids, mother fecundity decreased by increasing holding period in the case of crowding of third instar larvae for less than a day (Table 1) and vice versa in the case of crowding the fourth instar larvae (Table 2). As distributed in Table 3 and 4, after crowding for a whole day, natality% increased under long photophase at low level of population density and decreased under short photophase at high level of population density, regardless of the instar under experimentation. Similar finding was recorded by Walters and Dixon (1982) where progeny production was inversely related to the degree of crowding. Also, the high population density of crowded *M. persicae* resulted in decreased fecundity (crowding along the whole larval stage) (Haymaizu, 1984). Chongrattanameteekul *et al.* (1991) observed lower fecundity of *R. padi* and *S. avenae* by higher population density of crowding. On the other hand, compact aggregation of *B. brassicae* led to increasing fecundity (Way and Cammell, 1970). By the crowding of mothers for less than day in the present study, longer holding period detrimentally suppressed the reproductive capacity but long photophase-at each population density-very highly enhanced the fecundity. These results go in accordance to those obtained by Sourial (1995) for the same aphid species *R. maidis*. The decreasing natality% of the crowded mothers may be contributed to starvation during this important duration of developing embryos.

Finally, although a big lot of literature focused on the major extrinsic factors of the environment as affecting and regulation the aphid performance and polymorphism (such as temperature, photoperiod, nutrition, crowding and ants), there are some other causative factors such as decapitation, removal of rostrum, amputation of leg extremities, carbon dioxide, ether anesthesia and nitrogen narcosis, which one or more operations or treatments of them regulate the alate diversion during the embryonic development in adults (Johnson and Birks, 1960 ; Bradley, 1962; Lees, 1967, 1977, 1984; Ghoneim, 1995a,b). Some of these operations and treatments will be investigated against the present aphid *R. maidis* in future.

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