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Resistance to Lettuce Aphid (*Nasonovia ribisnigri*) Biotype 0 in Wild Lettuce Accessions PI 491093 and PI 274378

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***Abstract*. The lettuce aphid, *Nasonovia ribisnigri* Mosley (Hemiptera: Aphididae), is a major insect pest of lettuce, *Lactuca sativa* L, in many commercial lettuce production areas around the world. Resistance to lettuce aphid biotype 0 (Nr:0) was first reported in *Lactuca virosa* L. accession IVT 280 and characterized as complete, i.e., virtually no aphids survived, and genetically dominant to partial resistance in *L. virosa* accession IVT 273. Complete and partial resistances to Nr:0 were conditioned by two alleles, *Nr* (complete resistance) and *nr* (partial resistance), but the genetic relationship to susceptibility was not reported. We previously reported two new potential sources of unique genes for resistance to Nr:0 in *Lactuca serriola* L. accession PI 491093 and *L. virosa* PI 274378. We report on the genetic and phenotypic nature of resistance to Nr:0 in these two wild lettuce accessions. Resistance to Nr:0 in PI 274378 is complete and allelic to complete resistance in IVT 280. Resistance to Nr:0 in PI 491093 was partial, recessive to complete resistance in 'Barcelona' that was derived from IVT 280, but dominant to susceptibility in 'Salinas'. We propose the revised gene symbols for resistance to Nr:0: $Nr{:}0^C$ for complete resistance and $Nr{:}0^P$ for partial resistance, which was originally designated as *nr* but may now be regarded as the symbol for susceptibility to all strains of lettuce aphid. The dominance relationships among these three alleles are $Nr{:}0^C$ (in IVT 280, 'Barcelona') > $Nr{:}0^P$ (in PI 491093) > *nr* (in susceptible genotypes). Expression of partial resistance in PI 491093 was variable in controlled infestation tests, but in a naturally infested field test provided a potentially useful level of resistance to Nr:0. Partial resistance, where complete resistance has not been widely deployed, may either alone or as a component of integrated pest management delay or prevent emergence of genotypes that overcome complete resistance controlled by $Nr{:}0^C$.**

Lettuce (*Lactuca sativa* L.) is a major leafy vegetable that is grown and harvested year-round in the United States (Davis et al., 1997). California and Arizona produce 68% and 22%, respectively, of the lettuce grown in the United States (Mou, 2009) with the balance produced in 17+ other states (USDA, 2011a). Head and leaf lettuce crops were harvested from 56,660 ha in Monterey County, CA, and valued at $1.24 billion in 2010 (Lauritzen, 2011). Fresh lettuce leaves are commonly consumed in salads or sandwiches in the United States, Europe, and Australia, but in some countries, elongated stems are eaten; raw in Egypt; and cooked in China (Ryder, 2002).

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Lettuce aphid, *Nasonovia ribisnigri* Mosley (Hemiptera: Aphididae), is an economically important pest of lettuce in Europe (Arend et al., 1999), Canada (Forbes and MacKenzie, 1982), the United States (Chaney, 1999; Palumbo, 2000), New Zealand (Stufkens and Teulon, 2003), Tasmania (Stufkens et al., 2002, 2004), and Australia (Anonymous, 2004). Lettuce aphid may colonize lettuce at any time from the seedling stage of growth onward. High densities of lettuce aphid can deform lettuce heads and change leaf color. Lettuce aphid is also listed as a vector of *Cucumber mosaic virus* and *Lettuce mosaic virus* (Blua, 1997), although no incidents of virus transmission have been reported from any lettuce production areas. Lettuce aphid not only reduces marketability of infested lettuce in domestic markets but poses as a phytosanitary barrier for lettuce exports to some overseas markets such as Japan and Taiwan where lettuce aphid is quarantined.

Lettuce aphid is difficult to manage. Its propensity for colonizing the young (core) leaves makes it virtually impossible to control with contact insecticides during head maturation (Liu, 2004). In addition, it can develop resistance to insecticides (Barber et al., 1999; Stufkens and Wallace, 2004). Postharvest control of lettuce aphid on exported lettuce is also challenging. Methyl bromide fumigation causes injuries to lettuce and there are no safe alternative fumigants. Although ultralow oxygen treatment was reported to be safe and effective to control lettuce aphid on harvested head lettuce, the treatment was not effective against leafminer, *Liriomyza langei* Frick, which is also quarantined in Japan and often intercepted on exported lettuce (Liu, 2005). Genetically based host plant resistance is an economical and environmentally desirable means to control lettuce aphid infestation of lettuce (Painter, 1980).

Two biotypes of lettuce aphid have been known in Europe since 2007 and were designated by The Netherlands Inspection Service for Horticulture (Naktuinbow) as Nr:0 and Nr:1 (Thabuis et al., 2011). Biotype Nr:0 is known worldwide, and biotype Nr:1 is, thus far, known only in Europe. Complete and partial types of resistance to Nr:0 were described in *Lactuca virosa* L., a wild, distant relative of cultivated lettuce (Eenink and Dieleman, 1983). Complete resistance to Nr:0 was the result of a single gene (*Nr*) that was partially dominant in segregating (F_2) families from resistant *L. virosa* × susceptible *L. virosa* crosses but completely dominant after introgression to cultivated lettuce, *L. sativa* (Eenink and Dieleman, 1983; Eenink et al., 1982b). Partial resistance to Nr:0 in *L. virosa* was the result of a recessive allele, *nr*, at the same locus (Eenink and Dieleman, 1983). Complete resistance to Nr:0 in *L. virosa* accession IVT 280 was transferred to cultivated lettuce (Arend et al., 1999) and is highly effective against California strains of Nr:0 (Liu and McCreight, 2006).

Sixty-four *L. serriola* and *L. virosa* accessions in the Center for Genetic Resources, The Netherlands (CGN) collection were reported resistant to Nr:1 (Anonymous, 2008). Dominant resistance to Nr:0 and Nr:1 was claimed in *L. serriola* accession 10G.913571 (Thabuis et al., 2011).

The potential for the breakdown or failure of resistance conferred by the *Nr* gene was recognized shortly after release of Nr:0-resistant cultivars (Arend, 2003) and subsequently realized in Europe where the *Nr* gene was widely deployed (Thabuis et al., 2011). Although the gene has not been widely deployed in the United States as a result of different market requirements and numerous production niches (Davis et al., 1997), alternative sources of resistance to Nr:0 conditioned by other genes or mechanisms are desirable to prolong the effective life of Nr:0-resistant lettuce cultivars. Two potentially unique sources of resistance to Nr:0 were found in a survey of ≈1200 cultivated and wild lettuce accessions (McCreight, 2008). Our objectives were to characterize and determine the inheritance of resistance to Nr:0 in *Lactuca serriola* accession PI 491093 and *L. virosa* accession PI 274378.

Materials and Methods

This work was done using controlled infestations in greenhouses (13 experiments) and field cages (one experiment) and natural infestations in open fields (two experiments) in Salinas, CA. Eight of the experiments determined inheritance of resistance in PI 491093 (three) and PI 274378 (five); eight experiments evaluated the resistance phenotype of PI 491093.

Plant materials. The nine lettuce aphid-susceptible, resistant, or partially resistant accessions and cultivars used in these experiments were from various sources (Table 1). The seeds used in this research were produced in insect-free greenhouses at Salinas, CA. 'Salinas' served as the susceptible control (Ryder, 1979a). IVT 280 (Eenink and Dieleman, 1983), and 'Barcelona', which carries the *Nr* gene from IVT 280, served as resistant controls. Lettuce aphid-resistant 'Dynamite' (Arend et al., 1999) was included in one test for comparison with 'Barcelona'.

Crosses for genetic studies were made in a greenhouse using standard procedures for hand pollination of lettuce (Ryder, 1979b). PI 491093 was crossed with *L. sativa* cultivars Barcelona and Salinas. PI 274378 was crossed with four *L. virosa* accessions: completely resistant IVT 280, partially resistant CGN05332 (McCreight, unpublished data), susceptible PI 273597 (McCreight, unpublished data), and partially resistant PI 274375 (McCreight, unpublished data).

Lettuce aphid strain. Lettuce aphids were collected from a lettuce field at the USDA-ARS research station, Salinas, CA, in 2001 and reared on lettuce plants, usually 'Parris Island' and 'Salinas', in large, insect-proof, screened cages in a greenhouse. The colony was periodically supplemented with field-collected lettuce aphids through the duration of the testing to ensure representation of populations in commercial fields and on one occasion was completely re-established when infested by parasitoids. Resistance in IVT 280 and 'Barcelona' was always expressed against the lettuce aphids used in these studies; they may thus be regarded as Nr:0 (Thabuis et al., 2011).

Greenhouse tests. Seeds of each entry were sown in coarse, washed sand in 10 cm × 10 cm × 10-cm plastic pots and covered with Tencate Mirafi® geosynthetic fabric (<http://www.tencate.com/>) through germination in a greenhouse. Seedlings were transplanted at the one to two true leaf stage into 7.6 cm × 7.6 cm × 7.6-cm plastic pots filled with a 1 potting mix:1 sand mixture (by volume). Plants were watered daily, fertilized weekly with 119 15N–2.2P–12.5K–5Ca–2Mg (Peters Excel Cal-Mag; Scotts-Sierra Horticultural Products, Marysville, OH) at a rate of 3.6 $g\cdot L^{-1}$ to deliver 540 $mg\cdot L^{-1}$ N, and grown under the natural photoperiod at 4 to 20 °C (winter) and 10 to 40 °C (summer).

Plants were infested with 24 h or less or 24- to 48-h-old nymphs of lettuce aphid (five or 10 nymphs per plant). Infested plants were placed in insect-proof cages (≈63 cm × 63 cm × 63 cm) with one entry per cage. Total numbers of aphids (nymphs + alates) were counted periodically from as early as 2 d through 111 d post-infestation (dpi).

Caged field test. Seedlings from seeds sown in the greenhouse as described previously were transplanted to standard lettuce beds in a field and included 'Salinas', 'Barcelona', PI 491093, and IVT 280. Plants were spaced 30 cm apart along the center of the bed and drip-irrigated as needed. Tests were arranged in randomized complete blocks with five replications. Plants were individually enclosed in aphid-proof cages (≈46 cm × 46 cm × 46 cm) at the time of transplanting. One plant of each entry in each replication was infested with five aphids at the time of transplanting and at 2 and 4 weeks post-transplanting. Numbers of aphids were counted at 7-d intervals through 28 dpi. Other aphid species present were also counted.

Open-field tests. There were two naturally infested, open-field tests. The first test was started from seed, and entries were planted on standard lettuce beds, two entries per bed (one per seed line) and thinned to one plant per 30-cm; each experimental unit was 3.0 m long. The test included 'Salinas', 'Barcelona', PI 491093, IVT 280, seven families of F_2 Salinas × PI 491093, and one family of F_2 Barcelona × PI 491093. The entries were arranged in a randomized complete block design with four replications. Natural infestation of the control cultivar Salinas by lettuce aphid was monitored weekly in both tests. When lettuce aphids were numerous on 'Salinas', three plants were randomly selected from each plot and taken to the laboratory where only lettuce aphids were counted.

The second open-field test was transplanted as described previously for the caged field test; included 'Salinas', 'Barcelona', PI 491093, and IVT 280; and was located in a commercial lettuce production area, 8.9 km away from the caged field test. The entries were arranged in a randomized complete block design with three replications. Each replication included three plants of IVT 280 and five plants each of the other three entries. Natural infestation of the control cultivar Salinas by lettuce aphid was monitored weekly, and when aphids were numerous on 'Salinas' (40 dpi), the plants were taken to the laboratory where all aphids were counted. Lettuce aphid counts were totaled separately from other aphid species.

Data analysis. Statistical analyses and means comparisons were done using JMP 8.0.1 (SAS Institute, Cary, NC). Greenhouse data were analyzed as complete random designs. Caged and open-field data were analyzed as randomized complete block designs.

Results and Discussion

Inheritance of partial resistance in PI 491093. Mean numbers of lettuce aphids on 'Salinas' at 14 and 40 dpi were significantly ($P = 0.05$) higher than on PI 491093 and six F_1 progenies from crosses of PI 491093 with 'Salinas' and 'Barcelona' (Table 2). Numbers of lettuce aphid on the three F_1 Salinas × PI 491093 progenies were not significantly higher than the numbers on three F_1 Barcelona × PI 491093 progenies (Table 2). These data suggest that resistance to lettuce aphid in PI 491093 is dominant to susceptibility. Although the F_1 data suggest that resistance in PI 491093 is comparable to that in IVT 280, F_2 data reveal the difference in their gene expression. In the greenhouse experiment on the F_2 Salinas × PI 491093, mean numbers of lettuce aphids on 'Salinas' were many fold and significantly ($P = 0.05$) higher than on PI 491093 and their F_2 at 15 and 36 dpi (Table 2). There was a considerable overlap in aphid distributions on the parents and their F_2 at 15 dpi (Fig. 1A), but by 36 dpi, lettuce aphids on the susceptible 'Salinas' increased significantly and resulted in higher densities per plant than on PI 491093 and their F_2 (Fig. 1B). The wide range in number of lettuce aphids per plant of PI 491093 indicates that the resistance is partial in contrast to the complete resistance in IVT 280 (Eenink and Dieleman, 1983). The F_2 segregated 87 partially resistant:33 susceptible at 36 dpi when the break point for partial resistant vs. susceptible was set at 73 (= mean + SE of the F_2; Table 2) lettuce aphids per plant, an acceptable fit to the expected 3:1 ratio for a single dominant gene ($\chi^2 = 0.40$, $P = 0.54$).

In the naturally infested field test of the F_2 Salinas × 491093 and the F_2 Barcelona × 491093, 'Salinas' had significantly ($P = 0.05$) higher aphid density than PI 491093, 'Barcelona', and IVT 280 on 8 July and 20 July (Table 2). 'Salinas' differed significantly from three of the seven F_2 Salinas × PI 491093 progenies and the F_2 Barcelona × PI 491093 (Table 2) on 8 July. Mean numbers of lettuce aphids increased on all entries except IVT 280 by 20 July, and 'Salinas' had significantly higher aphid density than all seven of the F_2 Salinas × PI 491093 progenies. Mean number of aphids on F_2 Barcelona × PI 491093 was

Table 1. Plant materials used in experiments to determine the inheritance of lettuce aphid resistance in PI 491093 and PI 274378.

Accession or cultivar	*Lactuca* sp.	Lettuce aphid resistance	Sources	Reference
Barcelona	*sativa*	Resistant	Rijk Zwaan	
CGN05332	*virosa*	Partially resistant	Italy	(CGN, 2011)
Dynamite	*sativa*	Resistant	Rijk Zwaan	(Arend et al., 1999)
IVT 280	*virosa*	Resistant	Rijk Zwaan	(Eenink and Dieleman, 1983)
PI 273597	*virosa*	Partially resistant	Germany	(USDA, 2011b)
PI 274378	*virosa*	Resistant	France	(McCreight, 2008; USDA, 2011c)
PI 274375	*virosa*	Susceptible	Poland	(USDA, 2011d)
PI 491093	*serriola*	Partially resistant	Turkey	(McCreight, 2008; USDA, 2011e)
Salinas	*sativa*	Susceptible	USDA	(Ryder, 1979a)

Table 2. Mean ± SE numbers of lettuce aphids per plant of ‘Salinas’, ‘Barcelona’, PI 491093, IVT 280, and their F_1 and F_2 offspring in two greenhouse tests at different days post-infestation and on two dates in a naturally infested, open field test, Salinas, CA.

	F_1			F_2 Greenhouse			F_2 Field		
Entry or cross	No.	14 dpi[z]	40 dpi	No.	15 dpi	36 dpi	No.	8 July[z]	20 July[z]
Salinas	15	16.7 ± 2.3 a	69.1 ± 13.5 a	25	162.1 ± 14.0 a	378.9 ± 13.5 a	27	16.1 ± 5.3 a	54.0 ± 7.8 a
Barcelona							21	0.0 cd	0.3 ± 0.1 d
PI 491093	11	1.3 ± 0.6 b	0.2 ± 0.2 b	23	70.9 ± 88.9 b	85.2 ± 20.7 b	25	4.1 ± 1.6 bcd	3.9 ± 1.0 cd
IVT 280							27	0.0 cd	0.0 d
Salinas × PI 491093	10	0.5 ± 0.3 b	0.9 ± 0.3 b	120	84.1 ± 5.2 b	66.3 ± 6.5 b	30	10.9 ± 2.5 ab	23.7 ± 4.7 b
	10	1.9 ± 1.0 b	3.5 ± 0.6 b				25	7.4 ± 1.8 bc	16.7 ± 3.7 b
	9	2.0 ± 0.8 b	1.3 ± 0.3 b				15	11.9 ± 3.8 ab	21.8 ± 6.0 b
							25	6.9 ± 3.2 bcd	20.3 ± 4.8 b
							23	11.9 ± 3.1 ab	17.0 ± 3.9 b
							22	11.8 ± 3.3 ab	23.1 ± 5.0 b
							24	8.2 ± 3.9 bc	14.8 ± 5.0 bc
Barcelona × PI 491093	4	1.0 ± 0.6 b	0.0 ± 0.0 b				23	0.3 ± 0.2 cd	1.0 ± 0.4 d
	10	0.0 ± 0.0 b	1.4 ± 0.3 b						
	7	0.4 ± 0.3 b	0.7 ± 0.4 b						

[z]Means within columns followed by different letters are significantly different ($P = 0.05$).
dpi = days post-infestation.

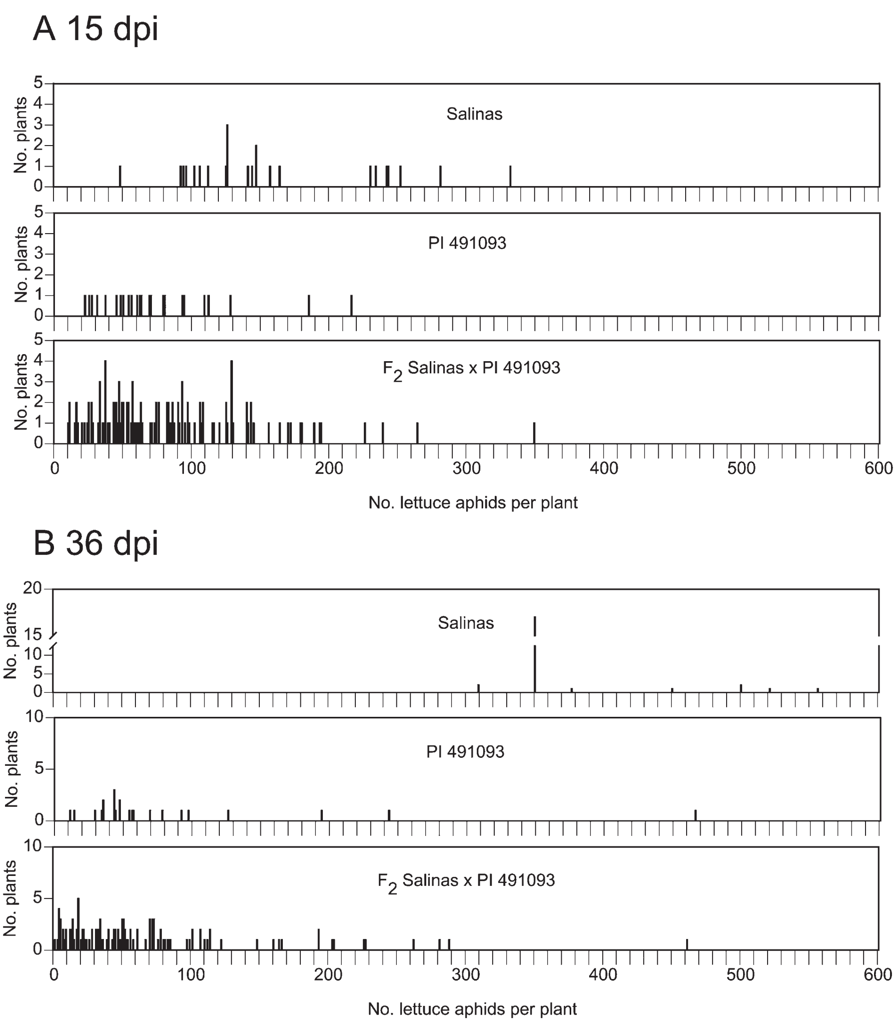

Fig. 1. Frequency distributions of numbers of lettuce aphids per plant of susceptible ‘Salinas’, partially resistant PI 491093 and F_2 Salinas × PI 491093 at 15 dpi (**A**) and 36 dpi (**B**); infested with five 24- to 48-h-old nymphs per plant in the greenhouse. dpi = days post-infestation.

1.0; this was significantly lower than on the F_2 Salinas × PI 491093 progenies, which ranged from 14.8 to 23.7.

Frequency distributions of lettuce aphid from the F_2 field tests further revealed the difference in dominance and, possibly, the number of resistant alleles between the *L. virosa*-derived (IVT 280) resistance conditioned by the single dominant gene, *Nr*, and the resistance in PI 491093 (Fig. 2). Numbers of lettuce aphids on susceptible ‘Salinas’ ranged from zero (one plant) to 100 (Fig. 2). Distributions of IVT 280 (all zero lettuce aphids per plant) and ‘Barcelona’ (zero to two lettuce aphids per plant) were similar to each other. Numbers of lettuce aphids per plant of PI 491093 ranged from zero (16 plants) to 17 (one plant). The small sample of the F_2 Barcelona × PI 491093 segregated 20 completely resistant:three partially resistant where, based on the range of ‘Barcelona’, completely resistant ranged from zero to two lettuce aphids per plant and partially resistant had three or more lettuce aphids per plant, an acceptable fit to the expected 3:1 ratio for a single dominant gene ($\chi^2 = 1.17$, $P = 0.28$) with Yates correction (Yates, 1931). Mean number of lettuce aphids per plant for the seven F_2 Salinas × PI 491093 progenies was 19.7 ± 1.8; the combined data ranged from zero (36 plants) to 106 (one plant) lettuce aphids per plant (Fig. 2). The combined F_2 families in this naturally infested field test segregated 120 partially resistant:54 susceptible when the break point for partial resistant vs. susceptible was set at 22 (= mean + SE of the combined F_2) lettuce aphids per plant, an acceptable fit to a three partially resistant:one susceptible ($\chi^2 = 3.38$, $P = 0.07$).

These results suggest that resistance to lettuce aphid strain Nr:0 is likely conferred by multiple alleles. IVT 280 is the source of *Nr*, which confers complete resistance and is dominant to partial resistance in other *L. virosa* accessions as previously reported (Eenink and Dieleman, 1983). The F_2 Barcelona × PI 491093 segregation had no susceptible segregants, which indicates that complete resistance in ‘Barcelona’ is allelic to partial resistance in PI 491093. Partial resistance in PI 491093 was dominant to susceptibility in ‘Salinas’. We propose the revised gene symbols for resistance to lettuce aphid strain Nr:0: $Nr{:}0^C$ for complete resistance and $Nr{:}0^P$ for partial resistance, which was originally designated as *nr* (Eenink and Dieleman, 1983) but may now be regarded as the symbol for susceptibility to all strains of lettuce aphid. The dominance relationships among these three alleles are $Nr{:}0^C$ (in IVT 280, ‘Barcelona’) > $Nr{:}0^P$ (in PI 491093) > *nr* (in susceptible genotypes).

Inheritance of resistance in PI 274378. Mean numbers of lettuce aphids on susceptible 'Salinas' and PI 273597 were significantly higher in three tests done in different seasons of the year than on resistant 'Barcelona', PI 2742378, IVT 280, and reciprocal F_1 progenies from crosses of PI 273597 and PI 274378 with IVT 280 and F_1 PI 274378 × CGN05332 (Table 3). There were no significant differences in number of lettuce aphids per plant between 'Salinas' and PI 273597 (*L. virosa*). Resistance to lettuce aphid in PI 274378 was dominant in the F_1 PI 274378 × CGN05332 (Spring test) and was comparable to IVT 280 and 'Barcelona'.

CGN05332 exhibited partial resistance in a separate greenhouse test with 'Salinas'; their respective mean number of lettuce aphids per plant 28 dpi were 6.8 ± 1.6 and 40.3 ± 10.0. The F_2 PI 274378 × CGN05332 did not segregate; mean numbers of aphids per plant 14 and 21 dpi were less than 1.0 (Table 3); at 28 dpi, no aphids were on 114 plants, one plant had a single aphid, and one plant had seven aphids. These data are comparable with the F_2 Barcelona × PI 491093 data. Likewise, the F_2 IVT 280 x PI 274378 did not segregate and mean numbers of aphids per plant 14 and 21 dpi were also less than 1.0 (Table 3). These data demonstrate that complete resistance to lettuce aphid in PI 274378 is not the result of a unique new gene, but is allelic with the *Nr:0*^{C} gene in IVT 280.

Nature of resistance in PI 491093. Partial resistance permits lettuce aphids to reproduce; the numbers of aphids per plant ranges over a wide range as these and previous (Eenink and Dieleman, 1983) data show. Numbers of live lettuce aphids were counted at different intervals starting 2 dpi for periods ranging up to 40 dpi in tests in which plants of PI 491093, 'Barcelona', 'Dynamite', IVT 280, and 'Salinas' were infested with 10 24-h-old nymphs (Fig. 3A–C). Numbers of live aphids declined on susceptible, partially resistant, and completely resistant genotypes by 2 dpi in the three tests (Fig. 3A–C). The reduction was minimal or approximately one-third on susceptible and partially resistant genotypes; reduction was more severe on resistant genotypes, from approximately half to 100%. After a short lag time, numbers of aphids on susceptible and partially resistant genotypes increased with a much greater increase on susceptible 'Salinas'. In one test, the numbers of aphids per plant on PI 491093 were virtually indistinguishable from completely resistant genotypes from 14

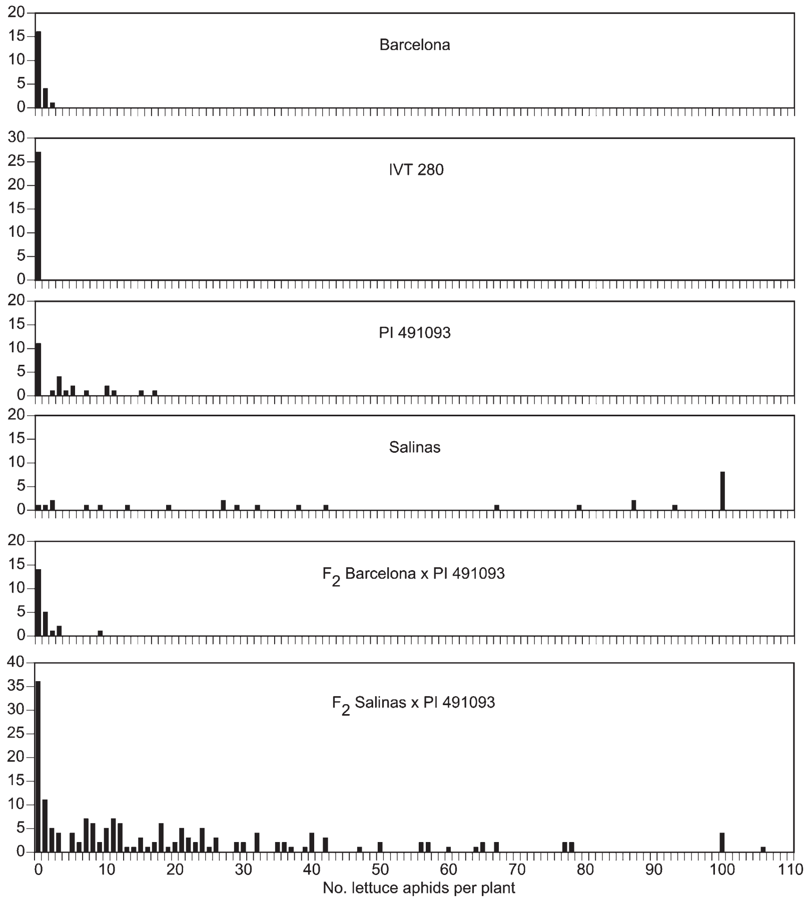

Fig. 2. Frequency distributions of numbers of lettuce aphids per plant in a naturally infested, open field; completely resistant 'Barcelona' and IVT 280, susceptible 'Salinas', partially resistant PI 491093, F_2 Barcelona × PI 491093, and F_2 Salinas × PI 491093 (composite of seven families).

Table 3. Mean numbers ± SE of lettuce aphids per plant at various days post-infestation in three greenhouse tests that included 'Salinas', 'Barcelona', PI 273597, PI 2742378 and IVT 280, and PI 274375, and F_1 and F_2 progenies from crosses among the *L. virosa* accessions; each plant infested with five 24- to 48-h-old nymphs; greenhouse; Salinas, CA.

	F_1 generation						F_2 generation			
	Winter[z]		Spring[y]		Fall[x]		Test 1[w]		Test 2[v]	
Entry	No.	27 dpi	No.	21 dpi	No.	28 dpi	No.	21 dpi	No.	28 dpi
Salinas (S)	10	119.1 ± 9.9 a	15	186.4 ± 21.2 a	15	53.7 ± 9.0 a	20	237.8 ± 24.0 a	20	344.0 ± 39.8 a
Barcelona (CR)			15	0.3 ± 0.1 b	15	0.1 ± 0.1 b				
PI 273597 (S)	10	104.7 ± 16.0 a								
PI 2742378 (CR)			14	0.0 b						
IVT 280 (CR)	15	6.5 ± 1.5 b	23	0.0 b	24	0.0 b			20	0.0 b
PI 274375 (PR)	9	16.6 ± 3.1 b								
PI 274378 (CR)	6	7.7 ± 1.4 b			15	0.0 b	20	0.0 c		
F_1 PI 274375 × IVT 280	17	8.6 ± 1.4 b	2	0.0 b						
F_1 PI 274378 × IVT 280	8	3.6 ± 1.0 b			5	0.0 b				
F_1 IVT 280 × PI 274378			3	0.0 b	12	0.0 b				
F_1 PI 274378 × CGN05332			4	0.0 b						
F_2 PI 274378 × CGN05332							77	0.1 ± 0.1 c		
F_2 IVT 280 × PI 274378									122	0.1 ± 0.1 b

[z]Planted 2 Feb. 2009, infested 4 Mar. 2009.
[y]Planted 4 Apr. 2006, infested 10 May 2006.
[x]Planted 20 Oct. 2006, infested 17 Nov. 2006.
[w]Planted 26 June 2009; infested 10 July 2009.
[v]Planted 24 July 2009; infested 6 Aug. 2009.
dpi = days post-infestation.

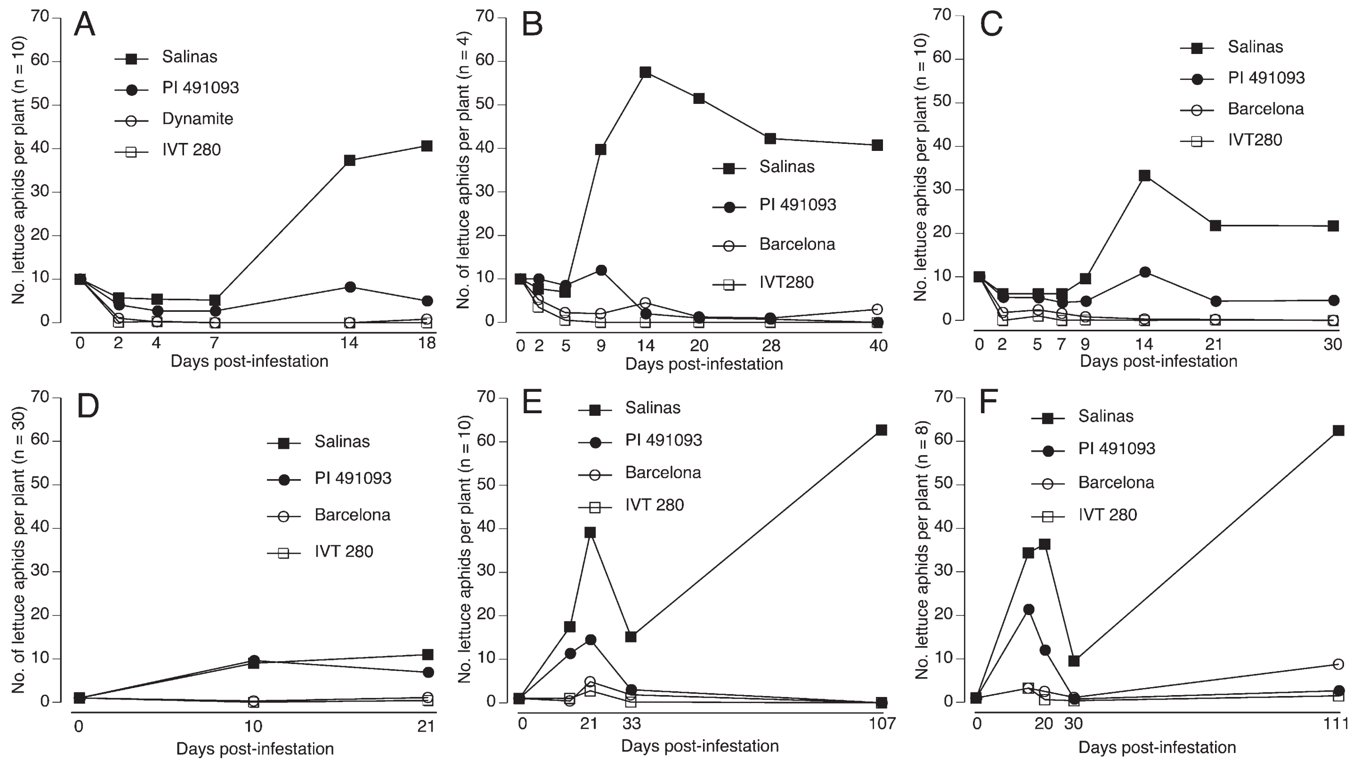

Fig. 3. Mean numbers of lettuce aphids per plant on resistant and susceptible lettuce at various days post-infestation. Plants infested with 10 24-h-old nymphs per plant (**A–C**) or a single 24-h-old nymph per plant (**D–F**) in the greenhouse.

Table 4. Mean numbers ± SE of lettuce aphid and other unidentified aphid spp. on lettuce aphid-susceptible 'Salinas', partially resistant PI 491093, and completely resistant 'Barcelona', and IVT 280 at 28 d post-infestation after three infestation dates of plants in field cages (No. = 5) and in a naturally infested open field; 2008.[z]

	Field cages						Open field		
	8 Aug.		15 Aug.		1 Sept.				
Entry	Lettuce aphid	Other aphid spp.	Lettuce aphid	Other aphid spp.	Lettuce aphid	Other aphid spp.	No.	Lettuce aphid	Other aphid spp.
Salinas	180.4 ± 187.8 a	85.6 ± 59.0	173.8 ± 232.7 a	119.2 ± 196.0	96.8 ± 120.1 a	80.2 ± 44.3	15	48.7 ± 5.9 a	0.0 ± 0.0
PI 491093	17.4 ± 17.3 b	84.2 ± 34.6	12.2 ± 11.9 b	180.0 ± 118.7	1.6 ± 0.9 b	80.8 ± 28.9	15	3.3 ± 1.4 b	2.3 ± 1.3
Barcelona	0.6 ± 0.9 b	70.8 ± 22.7	0.0 ± 0.0 b	152.4 ± 180.1	0.0 ± 0.0 b	100.0 ± 0.0	15	0.0 ± 0.0 b	0.0 ± 0.0
IVT 280	0.0 ± 0.0 b	61.4 ± 51.5	0.0 ± 0.0 b	48.8 ± 47.5	0.0 ± 0.0 b	72.8 ± 40.6	9	0.0 ± 0.0 b	0.3 ± 0.3

[z]Lettuce aphid means followed by different letters are significantly different, $P = 0.05$. Numbers of other aphid spp. did not differ significantly among the entries in any test.

through 40 dpi (Fig. 3B). In another test, mean numbers of aphids remained approximately five per plant except for a period ≈14 dpi (Fig. 3C).

In three similar tests, plants were infested with a single 24-h nymph. The initial count was made 10 to 20 dpi and the final count was made from 21 to 111 dpi (Fig. 3D–F). In one test (Fig. 3D) there was no significant difference between 'Salinas' and PI 491093 for number of aphids at 10 dpi, but by 21 dpi, PI 491093 had significantly fewer aphids than 'Salinas', although the mean number of aphids per plant on either was very low. Numbers of lettuce aphids on 'Salinas' and PI 491093 followed similar patterns through ≈30 dpi (Fig. 3E–F), although the numbers on PI 491093 were significantly lower than on 'Salinas' but not significantly greater than on IVT 280 or 'Barcelona' through the end of the tests.

Numbers of lettuce aphids per plant were significantly higher on 'Salinas' than 'Barcelona', IVT 280, and PI 491093 in a caged field test (Table 4). 'Barcelona' and IVT 280 were essentially aphid-free, whereas mean numbers of aphids on PI 491093 ranged from 17.4 when infested immediately after transplanting to 1.6 when infested 4 weeks post-transplanting. Partial resistance provided a marked and significant level of protection against lettuce aphid infestation in this test. The cages were not completely insect-proof as indicated by high numbers of other aphid species on the plants regardless of their aphid resistance genotype (Table 4). These data confirm the specificity resistance in lettuce aphid as previously reported (Reinink et al., 1995). Other crops have been noted as hosts of different aphid species, whereas their resistance to aphids is species- or biotypes-specific (Dogimont et al., 2010). A given lettuce genotype may possess resistance to more than one aphid (Reinink and Dieleman, 1989).

Partial resistance in PI 491093 provided protection against natural infestation by lettuce aphid in a replicated, naturally infested field test. 'Salinas' had significantly greater numbers of lettuce aphids than PI 491093, 'Barcelona', and IVT 280 (Table 4). Other aphid species were present at very low levels.

Partial resistance to lettuce aphid in *L. serriola* accession PI 491093 is dominant to susceptibility in *L. sativa* cultivars, e.g., 'Salinas'. Partial resistance is controlled by a single dominant gene that appears to be identical to the gene in *L. virosa* accession IVT 273 and allelic to the gene for complete resistance in *L. virosa* accession IVT 280, the source of resistance for all currently available lettuce aphid-resistant lettuce cultivars. Transfer of complete resistance from IVT 280 was a lengthy, complicated process that involved interspecific crosses to introgress a unique gene from a tertiary gene pool into cultivated lettuce (Arend et al., 1999; Eenink et al., 1982a; Lebeda et al., 2007).

Partial resistance to lettuce aphid provides a level of protection that is of potential value to lettuce production. Greenhouse data suggest increased expression or effectiveness of partial resistance with plant growth. Partial resistance may, either alone or as a component of integrated pest management, delay or prevent emergence of resistance-breaking strains where complete resistance has not been widely deployed. *Lactuca serriola* is in the primary gene pool for cultivated lettuce; transfer of partial resistance from PI 491093 is, therefore, expected to be easier than transfer from the tertiary gene pool.

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