

Influence of Barley Yellow Dwarf Virus-Infected Oats and Barley on Morphology of Aphid Vectors

F. E. Gildow

Assistant professor, Department of Plant Pathology, University of California, Berkeley 94720.
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ABSTRACT

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Maturation of aphids as winged forms (alatae) was favored when cereal grain aphids, *Sitobion avenae* and *Rhopalosiphum padi*, were reared from birth on barley yellow dwarf virus (BYDV)-infected oats or barley. In six experiments involving approximately 300 *S. avenae* per treatment, 85% matured as alates when reared on BYDV-infected oats, but only 31% matured as alates on healthy oats. Aphid clones from California and New York produced more alates on BYDV-infected hosts. Similar results were obtained with *R. padi* reared on healthy or BYDV-infected oats and barley. When first and second instar nymphs of *R. padi* were collected from barley

in the field and were reared to maturity, the percentage of *R. padi* developing as alates from healthy or BYDV-infected barley was 24 and 87%, respectively. Brome mosaic virus-infected barley and insecticide-treated oats also induced increased alate production by *R. padi*. Differences in the ratio of winged to nonwinged aphid progeny may reflect changes in host plant physiology that affect aphid nutrition and development. Cereal grain aphids developing on infected plants are more likely to mature as alates, which would favor aphid dispersal and secondary spread of BYDV.

Additional key words: epidemiology, luteovirus.

Cereal grain aphids are of interest to plant pathologists not only for the damage they cause as insect pests, but also for their key role as vectors of barley yellow dwarf virus (BYDV) (19). During the spring and summer growing season, populations of cereal grain aphids consist of parthenogenetic viviparous females. Nymphs produced at this time may mature as either winged (alate) or nonwinged (apterous) adults, depending upon several environmental factors that influence the induction or inhibition of wing development (15). Effects of population density on aphid morphology are well known (23). Generally, aphid crowding stimulates maturation of nymphs as alatae. In a similar manner, aphid nutrition also influences wing development (20). Laboratory rearing of aphids on artificial diets (17) or selected plant tissues (12,21) indicates that nutritionally deficient diets inhibit wing

development of some species. In this regard, nutritional quality of the host plant is of practical importance to cereal aphid population dynamics. Increased alatae production by cereal aphids occurs in response to nutritional changes associated with cereal grain maturation in the field (2,7,25).

While rearing aphids for electron microscope studies of BYDV transmission, I noted more alatae consistently produced on BYDV-infected oats than on healthy oats. This observation was verified in a study utilizing genetically stable clones of *Sitobion avenae* (F.) and *Rhopalosiphum padi* (L.) maintained for 20 yr under controlled conditions (9). If cereal aphids born on BYDV-infected grains are more likely to mature as winged alatae, they could also have an increased probability of contributing to secondary spread of the virus, profoundly influencing BYDV epidemiology. Insecticide treatments of oat plants also influenced wing development. In early experiments at Berkeley, oats to be used for rearing experiments were inoculated with BYDV by aphids, which were then removed by spraying the plant with nicotine sulfate and acephate. The plants were then used for rearing aphids 4 wk after

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spraying. On sprayed plants, winged aphids predominated when reared on either BYDV-infected or uninoculated oats.

The purpose of this study was to determine whether other populations of aphids responded similarly to virus-infected host plants and whether this phenomenon occurs with aphids produced under field conditions. The influence of insecticide treatment of host plants on aphid morphology was also examined.

MATERIALS AND METHODS

Aphid clones of the English grain aphid, *S. avenae*, and the oat bird-cherry aphid, *R. padi*, were developed from single apterous parthenogenetic virginoparae collected at Berkeley and Davis, CA, respectively. Virus-free stock colonies of aphids were reared on caged barley, *Hordeum vulgare* (L.) 'Briggs,' plants at 15 C with a 24-hr photoperiod in a growth chamber. Chamber light intensity, measured with a quantum sensor (Li-Cor, Inc., Lincoln, NE 68504) within a wavelength range of 400–700 nm was approximately $80 \mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$. A clone of green peach aphid, *Myzus persicae* (Sulzer) from Salinas, CA, was maintained on radish (*Raphanus sativus* L.) as described above. Two BYDV isolates collected at Davis, CA, were used: CA-RPV, which is transmitted specifically by *R. padi*, and CA-PAV, which is transmitted by *R. padi* and *S. avenae*. Plants used in rearing experiments were grown in U.C. soil mix (4) in 10-cm-diameter clay pots and watered with tap water. Seven-day-old seedlings of oats or barley were inoculated by aphids previously fed on BYDV-infected oats (*Avena sativum* L. 'California Red'). Viruliferous second and third instar nymphs were allowed a 48-hr inoculation access feeding on the seedlings and then were removed manually. The plants were allowed to develop symptoms over a 3-wk period before use. Healthy plants used as controls were infested with nonviruliferous aphids and treated similarly. Brome mosaic virus (BMV) was mechanically inoculated to 7-day-old seedlings of cultivar Prato barley, which were used for rearing experiments 3 wk after inoculation.

Controlled rearing experiments were done in growth chambers at 15 C with a 24-hr photoperiod and a light intensity of $80 \mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$. Leaves that developed yellowing symptoms typical of luteovirus infection or senescence were removed. Aphids fed only on the younger leaves that showed no visible symptoms. To begin an experiment, 10 or 20 nonviruliferous alate adults were placed on each test plant, and allowed to feed and produce nymphs for 24 hr. The adults were removed, and the nymphs were allowed to mature on the plant for 12 days. Alate and apterous forms on each plant were then counted.

Small colonies of first and second instar nymphs, closely associated with a single adult, were collected from barley plants in fields at Davis, CA. Sections of leaves bearing the colonies were carefully removed from the plant and transported to the laboratory in dishes with tight-fitting lids. The nymphs were transferred to healthy oats and reared to maturity in the growth chamber, as previously described. Leaf tissue from each field plant was bioassayed for BYDV infection by aphid transmission tests utilizing *R. padi*, *S. avenae*, *Metopolophium dirhodum* (Walk.), and *R. maidis* (Fitch), and oats used for rearing were observed for symptom development for 4 wk.

To test the effect of insecticides on aphid development, populations of *R. padi* were reared on uninoculated healthy California Red oats that were sprayed 3 wk prior to use with either nicotine sulfate (Black Leaf Products Co., Elgin, IL 60120) or acephate (*O*, *S*-dimethylacetylphosphoamidothiolate; Chevron Chemical Co., San Francisco, CA 94104). Aphids reared on healthy unsprayed oats were used as controls.

To determine whether other luteoviruses increased alatae production in other aphid species, green peach aphids (*M. persicae*) were reared 2 wk on several species of healthy plants, or on plants previously inoculated with beet western yellows virus or potato leafroll virus.

RESULTS

Results of controlled rearing experiments indicated that the California and New York clones of *S. avenae* developed more

alatae on BYDV-infected oats than on healthy oats (Table 1). These results verified those of a preliminary study (9) of *S. avenae* in New York, and suggested that other populations of the same species responded similarly to BYDV-infected oats. Increased alatae production was also observed in populations of *R. padi* reared on several cultivars of oats or barley (Table 2). A greater percentage of winged *R. padi* matured on BYDV-infected California Red oats and Briggs barley, which develop severe symptoms, as well as on Kanota oats and Prato barley, which are more tolerant to BYDV and produce few symptoms.

The experiments described above were conducted with aphid clones maintained for several generations under controlled conditions. To determine the potential significance of this phenomenon relative to aphid population dynamics in the field, early instar aphid nymphs were collected from healthy or BYDV-infected barley and reared to maturity on healthy oats. The results of previous work (9) show that wing development is determined within 24 hr of birth and thereafter the condition of the host plant has no effect on morphology. Results (Table 3) of three field collections made in April of 1980 and 1981 at Davis showed that 87% of 907 nymphs of *R. padi* born on BYDV-infected barley matured as alatae, while only 25% of 400 nymphs born on uninoculated barley developed wings. Smaller collections of *M. dirhodum* and *S. avenae* reacted similarly.

In addition to BYDV infection, other factors affecting host plant physiology also influenced aphid wing development. In two experiments, *R. padi* were reared on healthy barley or barley infected with brome mosaic virus (BMV), which *R. padi* does not transmit. Of approximately 200 aphids in each treatment, the percentage of aphids maturing as alatae when reared on healthy or

TABLE 1. Development of winged adults by California and New York clones of *Sitobion avenae* reared 10 days on either healthy cultivar California Red oats or on oats infected with the PAV isolate of barley yellow dwarf virus (BYDV)

Aphid clone ^a	Winged in each treatment (%) ^b	
	Healthy	BYDV-infected
<i>Sitobion avenae</i> -CA	12	90
	36	84
	22	67
<i>S. avenae</i> -NY	36	95
	40	75
	42	99
Mean	31	85

^a *S. avenae*-NY were obtained from Ithaca, NY, and *S. avenae*-CA were collected from Berkeley, CA.

^b Number of aphids per treatment was 50 ± 15 (S.E.). Mean values between treatments are significantly different ($P = 0.01$) by *t*-test.

TABLE 2. Development of winged adults by *Rhopalosiphum padi* reared 10 days on either healthy plants or on plants infected with the RPV isolate of barley yellow dwarf virus (BYDV)^a

Plant host	Winged adults in each treatment (%) ^b	
	Healthy	BYDV-infected
Oats		
California Red	49	95
Kanota	49	77
Barley		
Prato	40	74
Briggs	40	64

Seven-day-old seedlings of each variety were inoculated with BYDV 4 wk prior to use. Healthy control plants were grown in parallel.

Results are combined data from three replicates per treatment. Number of aphids per treatment was 120 ± 10 (S.E.). Chi-square analysis indicated significant differences ($P = 0.01$) in paired comparisons between healthy and BYDV-infected treatments for each cultivar.

BMV-infected barley was 42 and 77% respectively. Values between treatments were significantly different ($P = 0.01$).

In my experiments on the effects of nicotine sulfate and acephate on the development of alatae, the percentage of aphids maturing as alates when reared on unsprayed oats or on oats sprayed with nicotine sulfate or acephate was 44% (of 353), 77% (of 265), and 76% (of 337), respectively. Insecticide treatments were significantly different from unsprayed controls at $P = 0.01$. Apparently, the insecticide treatments induced wing development in aphids reared on both BYDV-infected and healthy oats. For all subsequent studies, only early instar nymphs were used to inoculate test plants, and these were removed individually without fumigation or spraying.

Luteovirus inoculated plants failed to induce a significant increase in alate aphid production by *M. persicae* (Table 4). Although luteovirus infection of these plant species did not influence wing development under the conditions tested, there was an obvious differential response by the aphids to the species of host plant. The majority of *M. persicae* reared on *Chenopodium quinoa* L., *Physalis floridana* Rydb., and *Raphanus sativus* L. matured as nonwinged apterae. On *Capsella bursa-pastoris* (L.) Medic., however, most aphids matured as winged alatae.

DISCUSSION

Differences in the ratio of winged to nonwinged progeny were observed among cereal aphids reared on healthy or BYDV-infected oats or barley. Maturation of winged aphids was favored on virus-infected plants. Results suggest these differences reflect changes in host-plant physiology influencing aphid nutrition. It is assumed that other factors, such as crowding, photoperiod, temperature, and mother-aphid morphology, also influenced wing production. These factors, however, contributed equally to all treatments, and the only known experimental variable was the condition of the host plant. Alate aphids selected as mothers were exposed equally to a crowding stimulus under colony conditions, and similar numbers

of nymphs were produced and reared on test plants. All aphids fed only on green, symptomless leaf tissue; therefore, yellowing and senescing leaves were not a factor influencing aphid development. Ability of the aphids to transmit virus was not a factor, since barley infected with the aphid-nontransmissible BMV also favored alate production. Increased alate maturation following insecticide treatment of host plants may have resulted from induced changes in plant components, or from the effects of sublethal doses of insecticide directly on aphid physiology. Similar results under field conditions could favor alate development of aphid vectors of plant viruses.

Results of this study cannot be extrapolated to other aphid species, as indicated by data obtained for *M. persicae*. The obvious effect of host plant species on *M. persicae* development, however, does support the idea that nutrition influences aphid morphology.

The role of host plant physiology in cereal aphid population dynamics, recently described (10,24,25), indicates that alate production and dispersal are favored by mature plants. Senescing tissues generally possess increased levels of soluble nitrogen components, compared to actively growing tissues (6,22), suggesting that increased availability of amino acids or other nitrogenous components favors wing development. Apterous forms have been reported to predominate early in the growing season (2,7,25), and cereal aphids reared uncrowded on wheat (8) or oat (3) seedlings produced few alates. Increased development of apterae has also been described for other aphid species reared on seedlings (12) or etiolated plants (1), or when aphids were temporarily prevented from feeding (20). Studies of aphids reared on artificial diets have demonstrated that poor nutrition inhibits wing development (17). Virus-infected plants also possess increased concentrations of amino acids and soluble nitrogen resulting from interference with normal host metabolism (16). Virus infection of host plants has been shown to influence fecundity of several aphid species (5,11,14). Kennedy (13) observed that virus-infected or senescing plant tissues tended to similarly influence aphid growth.

Increased amino acid content of BYDV-infected oats and increased alate development of cereal aphids have been discussed (9). The work reported here suggests that, since it occurred in populations of cereal aphids from California and New York, alate development in response to BYDV infection may be a general phenomenon. More importantly, increased alate production was shown to occur in field-collected aphids, indicating an influence of plant virus infection on vector population dynamics and, therefore, BYDV epidemiology. If aphid progeny developing on infected plants are more likely to mature as alates, then the infected condition of the host plant would favor aphid dispersal and, as a result, secondary spread of the virus. This fact could be especially significant early in the season when migrant viruliferous aphids first enter the crop. Field studies (18) indicate only a small percentage of early migrant grain aphids are viruliferous. Progeny maturing on a plant previously inoculated by a viruliferous mother aphid would be selectively favored for the alate condition. These aphids would themselves be viruliferous and tend to disperse early in the season when small grains are most vulnerable to barley yellow dwarf. The interaction among the virus, the vector, and their plant host influences BYDV epidemiology and warrants further study for better understanding this important disease complex.

TABLE 3. Number of *Rhopalosiphum padi* maturing as winged (W) or nonwinged (NW) adults when collected in the field as nymphs from healthy or barley yellow dwarf virus (BYDV)-infected barley^a

Experiment	Healthy		BYDV-infected ^b	
	W	NW	W	NW
1	11	47	64	23
2	28	105	124	30
3	59	150	605	61
Total	98	302	793	114
Percentage	25	75	87	13

^a First and second instar nymphs were reared to maturity on healthy oats in a growth chamber at 15 C with a 24-hr photoperiod.

^b Results are combined data from counts made of aphids collected from 10–22 plants for each experiment. Chi-square values of paired comparisons within each experiment indicated significant differences ($P = 0.01$) between healthy and BYDV-infected treatments.

TABLE 4. Number of *Myzus persicae* maturing as winged (W) or nonwinged (NW) adults when reared on healthy plants or plants infected with beet western yellows virus (BWYV) or potato leafroll virus (PLRV)^a

Plant species	Healthy		BWYV-infected		PLRV-infected	
	W	NW	W	NW	W	NW
<i>Chenopodium quinoa</i>	19	230	40	174	62	390
<i>Physalis floridana</i>	30	99	3	121	7	159
<i>Raphanus sativus</i>	2	380	28	542	34	520
<i>Capsella bursa-pastoris</i>	316	110	251	34	212	47

^a Data are the combined results of two experiments. Virus-infected plants were inoculated 3 wk prior to use and were subsequently tested to verify infection.

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