

# Probing Behavior of *Diuraphis noxia* and *Rhopalosiphum maidis* (Homoptera: Aphididae) Affected by Barley Resistance to *D. noxia* and Plant Water Stress

MICHAEL J. BREWER<sup>1</sup> AND JAMES A. WEBSTER<sup>2</sup>

Environ. Entomol. 30(6): 1041–1046 (2001)

**ABSTRACT** Probing behavior of *Diuraphis noxia* (Mordvilko), Russian wheat aphid, and *Rhopalosiphum maidis* (Fitch), corn leaf aphid, was measured on barley lines resistant and susceptible to *D. noxia* grown under low and high soil moisture. *R. maidis* reproduces similarly on both barley lines. Probing behavior was interpreted from waveforms of an alternating current electrical penetration graph (AC EPG) system of the Oklahoma design during 6-h monitoring periods. Significant effects were observed, particularly the aphid species by barley line interaction. Averaging across moisture levels, *D. noxia* took longer to first enter sieve element phase when probing *D. noxia*-resistant 'STARS-9301B' ( $306 \pm 19.9$  min [mean  $\pm$  SEM]) than when probing susceptible 'Morex' ( $180 \pm 21.6$  min). In contrast, *R. maidis* relatively quickly entered sieve element phase on the two barley lines (average of  $132 \pm 13.7$  min), with no detectable difference between lines. When measuring the total duration of sieve element phases, the stylets of *D. noxia* were in contact with phloem sieve elements of STARS-9301B for a shorter period ( $27 \pm 10$  min) than with sieve elements of Morex ( $111 \pm 21$  min). In contrast, stylets of *R. maidis* were in contact with sieve elements of the two barley lines for similar time periods (average of  $176 \pm 15.8$  min). Any mediating effect of soil moisture was slight, if at all measurable, using the AC EPG system, making any interpretation of probing behavior relative to previous observations of aphid population growth affected by plant water stress untenable. In contrast, monitoring probing behavior was beneficial in assessing how plant resistance may affect aphid species differently. The differences in probing behaviors between the two aphids fed barley resistant and susceptible to *D. noxia* corresponded well with previous observations that *D. noxia* population growth was lower on *D. noxia*-resistant barley than on susceptible barley, while *R. maidis* population growth was similar on the two barley lines.

**KEY WORDS** Russian wheat aphid, corn leaf aphid, alternating current electrical penetration graph system, probing behavior, plant resistance, plant water stress

FEEDING BY *Diuraphis noxia* (Mordvilko), Russian wheat aphid, adversely affects plant health of commercial cultivars of barley, *Hordeum vulgare* L., as expressed by chlorosis, rolled leaves, and reduced growth rates (Webster et al. 1991; Brewer et al. 1998). Barley germplasm resistant to *D. noxia* has been identified and characterized as partially antibiotic and tolerant (Webster et al. 1991). In further assessment of aphid response to plant resistance, Webster et al. (1993) found differences in the probing behavior of *D. noxia* between *D. noxia*-resistant and -susceptible barley using an alternating current electrical penetration graph (AC EPG) system, and these differences corresponded with reduced population growth on resistant barley (Oswald and Brewer 1997) and other characterizations of resistance (Webster et al. 1991).

Another aphid, *Rhopalosiphum maidis* (Fitch), corn leaf aphid, is less damaging to barley than *D. noxia* (Kieckhefer and Kantack 1986) and reproduces similarly on *D. noxia*-resistant and -susceptible barley (Oswald and Brewer 1997).

Plant water stress may affect population growth of insects (Jones and Coleman 1991; Waring and Cobb 1992), including *D. noxia*. Oswald and Brewer (1997) reported that plant water stress increased *D. noxia* population growth on barley, and this enhancement was greater on susceptible barley. Comparatively, *R. maidis* population growth on barley was less affected by plant water stress regardless of resistance status to *D. noxia*.

Monitoring probing behavior by use of an electronic monitoring system can aid in discerning mechanisms of plant resistance to aphids (Reese et al. 1994). However, little is apparently known of the effect of plant water stress on insect probing behavior monitored by these systems (e.g., no citations of this type in review publications: Ellsbury et al. [1994]; Tjallingii [1998]; and Walker and Backus [2000]); even though the phenomenon of plant water stress affecting insect population dynamics is well documented, including

This article reports the results of research only. Mention of a proprietary product does not constitute an endorsement or a recommendation by USDA for its use.

<sup>1</sup> Department of Renewable Resources, Entomology, P.O. Box 3354, University of Wyoming, Laramie, WY 82071 (e-mail: elmich@uwyo.edu).

<sup>2</sup> USDA-ARS Plant Science and Water Conservation Research Laboratory, 1301 N. Western, Stillwater, OK 74075.

the population dynamics of sucking insects (Waring and Cobb 1992). Are the differences in *D. noxia* and *R. maidis* population growth as mediated by barley resistance and plant water stress explained, at least in part, by differences in probing behavior? To address this question, an AC EPG system was used to evaluate the probing behavior of *D. noxia* and *R. maidis* on barley resistant and susceptible to *D. noxia*, grown under high and low soil moisture conditions. The same test conditions were previously used to observe population growth of these aphids (Oswald and Brewer 1997).

### Materials and Methods

**Aphid and Plant Cultures.** *D. noxia* and *R. maidis* were obtained from laboratory cultures established from aphids intermittently collected in southeastern Wyoming and placed in mixed-clonal cultures from 1992 to 1997. The aphids were reared on the aphid-susceptible spring barley cultivar 'Klages' in a growth chamber maintained at  $20 \pm 1^\circ\text{C}$ ,  $\approx 80\%$  RH, and a photoperiod of 14:10 (L:D) h. To promote aphid population growth, plants of the *R. maidis* colony had water continuously available while plants of the *D. noxia* colony were watered only when the soil surface appeared dry (Oswald and Brewer 1997).

For experimentation, pretillering plants with three expanded leaves were used. Barley plants resistant and susceptible to *D. noxia* were maintained individually in pots (14 cm diameter) with drainage holes. The soil was a sandy-loam texture of  $\approx 85\%$  sand and 15% silt/clay. Plants were kept in the greenhouse at  $29 \pm 5^\circ\text{C}$  with a photoperiod of 16:8 (L:D) h. To prevent unintended aphid infestation, plants were covered with ventilated clear plastic tubes ( $\approx 24$  cm high and 14 cm diameter). As done by Oswald and Brewer (1997), plants grown in low soil moisture were sparingly watered and were used when the top 0.5 cm of soil was dry to touch. Plants grown in high soil moisture were kept in pots placed in water-filled plastic trays, four to six per tray, and used as needed. Soil samples ( $\approx 2.5$  cm diameter by 10 cm depth using a soil probe) were removed from each pot before experimental use. To calculate gravimetric water content ( $100 \times [M_w - M_d/m_d]$ ), wet weight ( $M_w$ ) of each sample was taken, and the sample was then oven-dried for 48 h at  $50^\circ\text{C}$  before measuring dry weight ( $M_d$ ).

**Monitoring Probing Behaviors.** Waveforms of six AC EPG monitors of the Oklahoma design operating at 20 Hz (Backus et al. 2000) were displayed on computer monitor with a six-channel custom data acquisition software program (G. E. Young, Oklahoma State University, Stillwater, OK). Data were saved to an electronic file at 1-s intervals. Although the level of waveform detail is less than other systems operating higher frequency (Backus et al. 2000, Reese et al. 2000), waveforms detected with AC EPG monitors of the Oklahoma design have been successfully used to investigate aphid probing behavior (Webster et al. 1993, Hays et al. 1999, Reese et al. 2000).

Each adult apterous aphid was attached, with colloidal silver as adhesive (Ted Pella, Redding, CA), on its dorsal side to a 8-cm length of 10- $\mu\text{m}$ -diameter gold wire (Johnson Matthey, Ward Hill, MA) that served as the input wire to the AC EPG system. The tethered aphid was placed in the center of the adaxial surface of the third expanded leaf. Current was conducted to the soil by a 6 cm long copper rod (AWG12) inserted near the root base and attached to the output wire of the monitor. If an aphid fell off the leaf, became detached from the insect electrode, died during a trial, or never penetrated the plant surface, the test was reinitiated with a new aphid. A 6-h monitoring period was selected because it was previously found to be sufficient to detect differences in *D. noxia* probing behaviors among resistant and susceptible barley (Webster et al. 1993).

To begin a trial, *D. noxia* and *R. maidis* were taken directly from the stock cultures, tethered onto gold wire, and placed separately on resistant and susceptible barley grown in low and high soil moisture conditions. Treatments were randomly assigned to the six available AC EPG monitors. Remaining treatments representing a full replication were assigned to a supplemental trail, conducted within 1 d of the initial trial. The trials were done in a laboratory maintained at  $\approx 25^\circ\text{C}$ , RH of 30–40%, and fluorescent lighting measured at  $8.8 \mu\text{mole/m}^2\text{-s}$  (Webster et al. 1993). There were 13 replications of eight treatments, consisting of all possible combinations of the two aphid species and two soil moisture conditions as described above, and two barley lines that were resistant ('STARS-9301B' [= PI 366450]) and susceptible ('Morex') to *D. noxia* (Webster et al. 1991). Different aphids and plants were used for each replicate.

**Waveform Interpretation and Analysis.** Reese et al. (1994) reviewed previous probing behavior studies using aphids and concluded that waveforms were similar among 11 species. They found that characteristic waveforms corresponded well with the sequence of probing behaviors from stylet penetration of the plant to stylet insertion into a phloem sieve element, based on histological work. Girma et al. (1992) specifically confirmed this correspondence with *D. noxia*. Therefore, the waveforms generated in this study were directly interpreted (Reese et al. 1994, 2000) into the following probing behaviors: (1) plant contact with no probing, (2) stylet penetration phase (stylet contact with plant tissue), and (3) sieve element phase (sieve element puncture with extended contact with a sieve element).

Reese et al. (1994) reported antibiotic plant resistance was closely associated with two probing behavior measures linked to the above waveform interpretations: a relatively long time to enter the aphid's first sieve element phase (time from initiation of the experiment to the first X-I sequence [Reese et al. 2000]) and a relatively short duration of the total duration of all sieve element phases recorded. Effects of plant water stress have not been previously reported in probing behavior tests (Ellsbury et al. 1994, Tjallingii 1998, Walker and Backus 2000); therefore preliminary

experiments were conducted (Oswald 1995). The time required to the first sieve element phase and the total duration of sieve element phases were less variable than other measurements (Oswald 1995). Based on this result and the plant resistance data summarized in Reese et al. (1994), analyses reported here were centered on these two measurements.

Data adjustment was required when an aphid's stylets penetrated the plant surface but did not enter sieve element phase in the 6-h monitoring period (18 of these cases occurred). In these cases, some waveforms associated with probing behaviors of interest were recorded and some were not. These data were prepared for analysis in two ways: without data adjustment, allowing unobserved probing behaviors to be treated as missing; and with data adjustment, inserting 360 min (6-h) for the time to first enter sieve element phase and 0 min for duration of sieve element phase. Analyses with and without the data adjustments were compared to determine if a consistent interpretation of the results could be derived.

The experiment was analyzed as a two (barley line: STARS-9301B and Morex) by two (aphid species: *D. noxia* and *R. maidis*) by two (moisture level: high and low soil moisture) factorial with replication as a blocking factor. We selected the barley lines and moisture levels with emphasis on extreme conditions to optimize detection of differences in probing behaviors among treatments. Therefore, the three factors were considered fixed effects for analysis, using the residual term of the analysis of variance (ANOVA) as error for all significance tests (Snedecor and Cochran 1980).

### Results and Discussion

Soil moisture content was  $3.7 \pm 0.21\%$  (mean  $\pm$  SEM,  $n = 52$ ) in the low moisture condition and  $9.7 \pm 0.37\%$  ( $n = 52$ ) in the high moisture condition. The probing behavior measurements were in the ranges as found by others working with *D. noxia* (e.g., Girma et al. 1992, Kindler et al. 1992, Webster et al. 1993). Despite fairly high variability of the data (SEMs measured as percent of the mean as high as 85%) which is common to EPG recordings (van Helden and Tjallingii 2000), significant differences in the time to first sieve element phase and the total duration of sieve element phases were detected ( $P < 0.05$ ) for the barley line and aphid species main effects, but the moisture level main effect was not significant ( $P > 0.20$ ). Some two-way interactions among these factors were detected at  $\alpha = 0.05$ , and marginally significant patterns were also seen at  $\alpha = 0.10$ . The three-way interaction was not significant for these two probing behavior measurements ( $P > 0.10$ ). Because of the previously observed joint effect of these factors when measuring population growth of these two species in similar test conditions (Oswald and Brewer 1997), we focused attention on the significant two-way interactions, and these are discussed below.

**Time to First Sieve Element Phase.** Setting the time to first sieve element phase at 360 min when sieve element phase waveforms were not observed, there

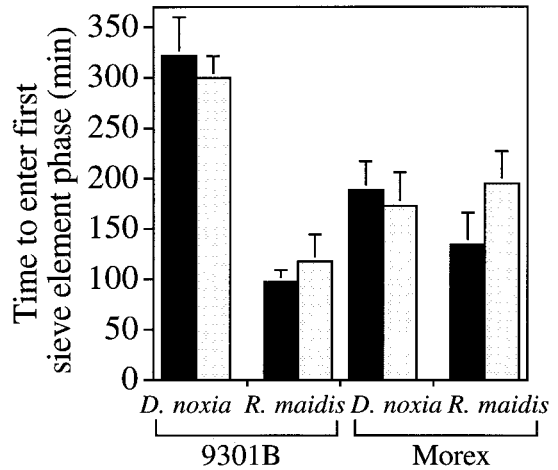


Fig. 1. Mean time for *Diuraphis noxia* and *Rhopalosiphum maidis* to first enter sieve element phase during a 6-h monitoring period. Aphids were placed on a *D. noxia*-resistant (9301B [= STARS-9301B]) and -susceptible (Morex) barley, grown under low (dark bars) and high (light bars) soil moisture conditions. Means reflect the data adjustment of 360 min for aphids penetrating the plant but not entering sieve element phase within the 6-h test. Vertical lines are SEMs.

was a significant interaction between aphid species and barley lines ( $P < 0.05$ ). Averaging across moisture levels, *D. noxia* took longer to enter first sieve element phase when probing resistant STARS-9301B ( $306 \pm 19.9$  min [mean  $\pm$  SEM]) than when probing the susceptible Morex ( $180 \pm 21.6$  min). In contrast, *R. maidis* relatively quickly entered sieve element phase on both barley lines (average of  $132 \pm 13.7$  min) (barley line by aphid species interaction:  $F = 26.5$ ;  $df = 1, 63$ ;  $P < 0.0001$ ) (Fig. 1). The results were similar when not using the data adjustment ( $F = 5.36$ ;  $df = 1, 45$ ;  $P < 0.025$ ). Assuming a longer time period to first sieve element phase is an indication of feeding difficulties (Reese et al. 1994) and can lead to reduced population growth, this measure corresponded well with the previous observation that *D. noxia* population growth was lower on STARS-9301B than on Morex, while *R. maidis* population growth was similar on the two barley lines (Oswald and Brewer 1997).

A possible mediating effect of soil moisture was seen (detected at  $\alpha = 0.10$ ) when setting a 360 min data adjustment when sieve element phase waveforms were not observed (aphid species by moisture level interaction:  $F = 3.61$ ;  $df = 1, 63$ ;  $P = 0.061$ ). *D. noxia* tended to take longer to enter first sieve element phase when probing barley grown in low moisture conditions than when probing barley grown in high moisture conditions; whereas, *R. maidis* tended to take longer to enter first sieve element phase in high moisture conditions than in low moisture conditions (Fig. 1). This marginally significant pattern did not correspond to the previous observation that *D. noxia* population growth was higher when fed barley grown in low soil moisture conditions, and *R. maidis* population

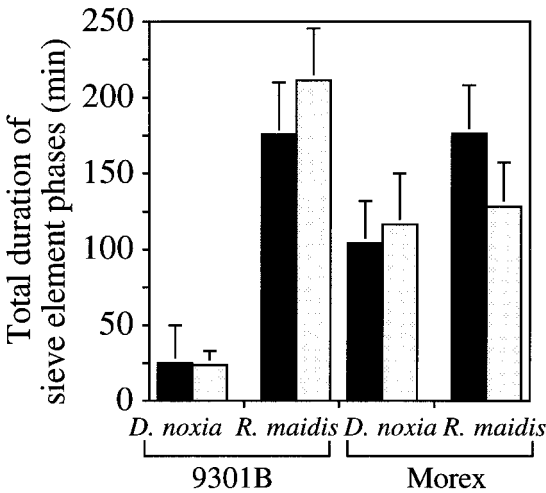


Fig. 2. Mean of the total duration of sieve element phases for *Diuraphis noxia* and *Rhopalosiphum maidis* during a 6-h monitoring period. Aphids were placed on a *D. noxia*-resistant (9301B [= STARS-9301B]) and -susceptible (Morex) barley, grown under low (dark bars) and high (light bars) soil moisture conditions. Means reflect the data adjustment of 0 min for aphids penetrating the plant but not entering sieve element phase within the 6-h test. Vertical lines are SEMs.

growth was higher when fed barley in high soil moisture conditions (Oswald and Brewer 1997).

**Duration of Sieve Element Phase.** Setting 0 min for the duration of sieve element phase when sieve element phase waveforms were not observed, the barley line by aphid species interaction was again highly significant ( $F = 12.9$ ;  $df = 1, 61$ ;  $P = 0.0007$ ). Averaging across moisture conditions, *D. noxia* spent less time in contact with a sieve element of STARS-9301B ( $27 \pm 10$  min) than with a sieve element of Morex ( $111 \pm 21$  min). In contrast, for *R. maidis* feeding on both barley lines, the sieve element phase was about the same (average of  $176 \pm 15.8$  min) (Fig. 2). As with the first measurement, the data interpretation was consistent with the aphid population growth data (Oswald and Brewer 1997), assuming a shorter duration of sieve element phase is an indication of feeding difficulties and can lead to reduced population growth. But unlike the time to enter sieve element phase, the barley line by aphid species interaction was not significant when not using the data adjustment and deleting observations when sieve element phase waveforms were not detected ( $F = 2.34$ ;  $df = 1, 45$ ;  $P = 0.13$ ).

There was no indication of soil moisture playing a mediating role in the duration of sieve element phase ( $P > 0.20$  for all interactions involving the moisture level factor for the two ways in which the data were analyzed). As noted above, the moisture level main effect was also not significant ( $P > 0.20$ ).

**Comparison with Past Studies.** Spiller et al. (1990) varied water stress conditions, but in their case worked with water-deprived aphids and healthy plants. Electronic monitoring studies specifically considering plant water stress were not found in the lit-

erature; therefore there was little basis to compare our lack of plant water stress effect with past work. To possibly increase sensitivity in detecting a plant water stress effect in our initial work on this subject, the data were decomposed into other measurements considered by Webster et al. (1993), and analyzed. No significant effects associated with the moisture level factor (the main effect and the moisture level interactions with the barley line and aphid species factors) were detected for any of the measurements, using the same ANOVA analysis described above ( $P > 0.05$  in analyses of five measurements, each of which produced an insignificant moisture main effect and interactions involving the moisture factor [20 total significance tests], and for only one of the 20 tests was marginal significance detected at  $\alpha = 0.10$ ). Reese et al. (2000) provided good argument in using more focused and behaviorally appropriate measurements (the two principal measurements described in the two previous sections) when using AC EPG monitors, and the other measurements appeared to be of no value in considering the effect of plant water stress.

The difficulty of *D. noxia* entering sieve element phase under some of the test conditions was likely responsible for the different results when measuring duration of sieve element phase. There was a significant barley line by aphid species interaction when using the data adjustment of 0 min when sieve element phase waveforms were not detected, and an insignificant barley line by aphid species interaction when not using the data adjustment and deleting observations when sieve element phase waveforms were not detected. Of the 18 cases in which an aphid's stylets penetrated the plant surface but did not enter sieve element phase in the 6 h monitoring period, 12 were of *D. noxia* placed on STARS-9301B. Webster et al. (1993) also reported that the vast majority of time was spent in probing behaviors other than sieve element contact when *D. noxia* was placed on STARS-9301B. Although Webster et al. (1991) found a 6 h monitoring period effective when measuring barley resistance to *D. noxia*, it would be valuable to use a longer trial period in future tests when studying a wide range of test species and conditions. It is possible that a longer monitoring period would result in more aphids, particularly *D. noxia*, successfully entering sieve element phase. Time periods of 24 h commonly have been used to monitor aphids in host plant resistance work (see citations in Reese et al. 1994).

The effect of barley resistance on these aphid species was clarified using the AC EPG system. Based on aphid population growth data of Oswald and Brewer (1997), we expected that the resistant barley STARS-9301B would affect *D. noxia* differently than *R. maidis*. *D. noxia* spent more time in sieve phase when probing Morex than when probing STARS-9301B. This result was consistent with *D. noxia* probing behaviors reported by Webster et al. (1993). The current study added the contrast of *R. maidis*, which performed similarly on STARS-9301B and Morex as measured by the two principal probing behaviors considered here (Figs. 1 and 2), and the species differences in these

probing behaviors corresponded well with differences in *D. noxia* and *R. maidis* population growth on these two barley lines (Oswald and Brewer 1997). Maxwell et al. (1972) also reported a dissimilarity of barley susceptibility between two aphid species. The barley cultivar 'Omugi' was resistant to *Schizaphis graminum* (Rondani) but susceptible to *R. maidis*. Auclair (1989) reviewed the literature on plant resistance to aphids and reported similar contrasts of plant susceptibility to different aphid species.

In contrast, the mediating effect of plant water stress on aphid population growth did not correspond well with measurements of probing behavior. Aphid species differences in response to plant water stress may lead to considerable variation in aphid population dynamics (Kennedy et al. 1958; Wearing 1972; Waring and Cobb 1992). Kennedy et al. (1958) observed aphid restlessness on water stressed plants, suggesting a plant water stress effect on feeding behavior generally. But a mediating effect of the moisture treatment on probing behavior measured by an AC EPG system was slight, if at all measurable (Figs. 1 and 2). Moisture stress may have been more critically measured and a gradient of soil moisture conditions used (e.g., Waring 1972; Holtzer 1988), but we note the use of extreme soil moisture levels to optimize detection of probing behavior differences among treatments in our initial study. We conclude that probing behaviors measured by an AC EPG system were not good detectors of the effect of plant water stress on *D. noxia* and *R. maidis* population growth. This conclusion does not preclude use of EPG systems with enhanced sensitivity that may detect finer differences in probing behaviors (Reese et al. 2000, Tjallingii 2000).

In summary, the effect of soil moisture was slight, if at all measurable, using the AC EPG system (Oklahoma design), making any interpretation relative to previous observations of aphid population growth affected by plant water stress untenable. In contrast, monitoring probing behaviors was beneficial in assessing how plant resistance may affect aphid species differently. *R. maidis* probing behavior was very different than that of *D. noxia* when fed barley resistant to *D. noxia* (Webster et al. 1991, 1993). The risk in breeding plants resistant to selected insect species in isolation of others insects (Maramorosch 1980) is apparent by review of other work on plant susceptibility to different aphid species (e.g., Maxwell et al. 1972; Auclair 1989). We reported here measurements of aphid probing behavior by which such differences in aphid population growth may result.

#### Acknowledgments

We thank J. Donahue (currently USDA ARS, Newark, DE) and K. Mirkes (USDA ARS, Stillwater, OK) for assistance. The data acquisition program was provided by G. Young (Oklahoma State University). We also thank two anonymous reviewers, whose comments greatly improved the presentation of this work. This study was supported, in part, by a grant to M.J.B. from the USDA CSRS NRI Competitive Grants Program (#93-37311-9512).

#### References Cited

- Auclair, J. L. 1989. Host plant resistance, pp. 225–264. In A. K. Minks and P. Harrewijn (eds.), *Aphids, their biology, natural enemies and control*, vol. C. Elsevier, New York.
- Backus, E. A., M. J. Devaney, and W. H. Bennett. 2000. Comparison of signal processing circuits among seven AC electronic monitoring systems for their effects on the emf and R components of aphid (Homoptera: Aphididae) waveforms, pp. 102–143. In G. P. Walker and E. A. Backus (eds.), *Principles and applications of electronic monitoring and other techniques in the study of Homopteran feeding behavior*. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, MD.
- Brewer, M. J., D. W. Mornhinweg, J. M. Struttman, and C. J. Oswald II. 1998. Russian wheat aphid (Homoptera: Aphididae) and parasitoids (Hymenoptera: Braconidae and Aphelinidae) found on field-grown barley lines varying in susceptibility to Russian wheat aphid, pp. 258–269. In S. S. Quisenberry and F. B. Peairs (eds.), *Response model for an introduced pest—the Russian wheat aphid*. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, MD.
- Ellsbury, M. M., E. A. Backus, and D. L. Ullman. 1994. History, development, and application of AC electronic insect feeding monitors. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, MD.
- Girma, M., G. E. Wilde, and J. C. Reese. 1992. Russian wheat aphid (Homoptera: Aphididae) feeding behavior on host and nonhost plants. *J. Econ. Entomol.* 85: 395–401.
- Hays, D. B., D. R. Porter, J. A. Webster, and B. F. Carver. 1999. Feeding behavior of biotypes E and H greenbug (Homoptera: Aphididae) on previously infested near-isolines of barley. *J. Econ. Entomol.* 92: 1223–1229.
- Holtzer, T. O. 1988. Host plant suitability in relation to water stress, pp. 111–137. In E. A. Heinrichs (ed.), *Plant-stress-insect interactions*. Wiley, New York.
- Jones, C. G., and J. S. Coleman. 1991. Plant stress and insect herbivory: toward an integrated perspective, pp. 249–280. In H. A. Mooney, W. E. Winner, and E. J. Pell (eds.), *Response of plants to multiple stresses*. Academic Press, San Diego, CA.
- Kennedy, J. S., K. P. Lamb, and C. O. Booth. 1958. Responses of *Aphis fabae* Scop. to water shortage in host plants in pots. *Entomol. Exp. et Applicata* 1: 274–291.
- Kieckhefer, R. W., and B. H. Kantack. 1986. Yield losses in spring barley caused by cereal aphids (Homoptera: Aphididae) in South Dakota. *J. Econ. Entomol.* 79: 749–752.
- Kindler, S. D., L. G. Greer, and T. L. Springer. 1992. Feeding behavior of the Russian wheat aphid (Homoptera: Aphididae) on wheat and resistant and susceptible slender wheatgrass. *J. Econ. Entomol.* 85: 2012–2016.
- Maramorosch, K. 1980. Insects and plant pathogens, pp. 137–155. In F. B. Maxwell and P. R. Jennings (eds.), *Breeding plants resistant to insects*. Wiley, New York.
- Maxwell, F. G., J. N. Jenkins, and W. L. Parrott. 1972. Resistance of plants to insects. *Advan. Agron.* 24: 187–265.
- Oswald, C. J. II. 1995. Russian wheat aphid and corn leaf aphid (Homoptera: Aphididae) competition and plant response as mediated by plant water stress and aphid-resistant and -susceptible barley, M.S. thesis, University of Wyoming, Laramie.
- Oswald, C. J. II, and M. J. Brewer. 1997. Aphid-barley interactions mediated by water stress and barley resistance to Russian wheat aphid (Homoptera: Aphididae). *Environ. Entomol.* 26: 591–602.

- Reese, J. C., D. C. Margolies, E. A. Backus, S. Noyes, P. Bramel-Cox, and A.G.O. Dixon. 1994. Characterization of aphid host plant resistance and feeding behavior through use of a computerized insect feeding monitor, pp. 52–72. *In* M. M. Ellsbury, E. A. Backus, and D. L. Ullman (eds.), History, development, and application of AC electronic insect feeding monitors. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, MD.
- Reese, J. C., W. F. Tjallingii, M. van Helden, and E. Prado. 2000. Waveform comparisons among AC and DC electronic monitoring systems for aphid (Homoptera: Aphididae) feeding behavior, pp. 70–101. *In* G. P. Walker and E. A. Backus (eds.), Principles and applications of electronic monitoring and other techniques in the study of Homopteran feeding behavior. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, MD.
- Snedecor, G. W., and W. G. Cochran. 1980. Statistical methods, 7th ed. Iowa State University Press, Ames, Iowa.
- Spiller, N. J., L. Koenders, and W. F. Tjallingii. 1990. Xylem ingestion by aphids—a strategy for maintaining water balance. *Entomol. Exp. Appl.* 55: 101–104.
- Tjallingii, W. F. 1998. Electronic recording of stylet penetration activities, pp. 95–108. *In* A. K. Minks and P. Harrewijn (eds.), Aphids, their biology, natural enemies and control. vol. 2B. Elsevier, Amsterdam.
- Tjallingii, W. F. 2000. Comparison of AC and DC systems for electronic monitoring of stylet penetration activities by Homopterans, pp. 41–69. *In* G. P. Walker and E. A. Backus (eds.), Principles and applications of electronic monitoring and other techniques in the study of Homopteran feeding behavior. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, MD.
- van Helden, M., and W. F. Tjallingii. 2000. Experimental design and analysis in EPG experiments with emphasis on plant resistance research, pp. 144–171. *In* G. P. Walker and E. A. Backus (eds.), Principles and applications of electronic monitoring and other techniques in the study of Homopteran feeding behavior. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, MD.
- Walker, G. P., and E. A. Backus (eds.). 2000. Principles and applications of electronic monitoring and other techniques in the study of Homopteran feeding behavior. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, MD.
- Waring, G. L., and N. S. Cobb. 1992. The impact of plant stress on herbivore population dynamics, pp. 167–226. *In* E. Bernays (ed.), Insect-plant interactions, vol. 4. CRC, Boca Raton, FL.
- Wearing, C. H. 1972. Responses of *Myzus persicae* and *Brevicoryne brassicae* to leaf age and water stress in brussels sprouts grown in pots. *Entomol. Exp. Appl.* 15: 61–80.
- Webster, J. A., C. A. Baker, and D. R. Porter. 1991. Detection and mechanisms of Russian wheat aphid (Homoptera: Aphididae) resistance in barley. *J. Econ. Entomol.* 84: 669–673.
- Webster, J. A., D. R. Porter, C. A. Baker, and D. W. Mornhinweg. 1993. Resistance to Russian wheat aphid (Homoptera: Aphididae) in barley: effects on aphid feeding. *J. Econ. Entomol.* 86: 1603–1608.

Received for publication 7 August 2000; accepted 9 July 2001.