

December 1999

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Recommended Citation

Giebink, Bruce L.; Scriber, J. Mark; and Wedberg, John 1999. "Survival and Growth of Two *Hydraecia* Species (Noctuidae: Lepidoptera) on Eight Midwest Grass Species," *The Great Lakes Entomologist*, vol 32 (3)

Available at: <https://scholar.valpo.edu/tgle/vol32/iss3/3>

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SURVIVAL AND GROWTH OF TWO *HYDRAECIA* SPECIES
(NOCTUIDAE: LEPIDOPTERA) ON EIGHT MIDWEST GRASS SPECIESBruce L. Giebink^{1,2}, J. Mark Scriber¹ and John Wedberg³

ABSTRACT

Grasses play a critical role in the life cycles of both the hop vine borer (*Hydraecia immanis*) and potato stem borer (*H. micacea*), two potentially serious agriculture pests. Neonate larvae of both species (Noctuidae: Lepidoptera) were reared on eight selected grasses and corn for 14–18 days under greenhouse conditions to determine their survival and growth. These were quackgrass (*Agropyron repens*), smooth brome grass (*Bromus inermis*), orchardgrass (*Dactylis glomerata*), large crabgrass (*Digitaria sanguinalis*), barnyardgrass (*Echinochloa crusgalli*), giant foxtail (*Seteria faberii*), wild proso millet (*Panicum millaceum*), Johnsongrass (*Sorghum halepense*), and corn (*Zea mays*). In a separate, concurrent experiment, *H. immanis* and *H. micacea* larvae were reared on quackgrass, smooth brome grass and orchardgrass (narrow-stemmed grasses) and sampled after 7, 10 and 14 days. *H. immanis* larvae generally grew more slowly and dispersed less quickly than *H. micacea* larvae.

The fewest *H. immanis* and *H. micacea* larvae were recovered from giant foxtail. *H. immanis* larvae reared on quackgrass, smooth brome grass and orchardgrass (thin-stemmed grasses) “outgrew” their hosts by the third instar and rapidly dispersed, particularly from quackgrass. Due to the unique internal stem-feeding behavior of these larvae the stem thickness becomes a constraining factor regarding duration of suitability to serve as a larval host. Grass feeding has tremendous significance regarding the geographic spread, local population densities, phenological damage periods, and cultural control methods such as crop rotation for these two noctuid species.

Populations of two related, but rare, stem boring noctuid caterpillars, *Hydraecia immanis* Guenée (hop vine borer) and *H. micacea* [Esper] (potato stem borer), suddenly increased to damaging levels in cornfields of the midwestern United States and Canada after 1976 (Muka 1976, Scriber 1980, Giebink et al. 1984). Larvae of both species initially feed within the stems of various grasses and then switch to other host plants including corn (*Zea mays* L.) and hops (*Humulus lupulus* L.) (Hawley 1918, Giebink et al. 1984). This early association with grasses is critically important and is demonstrated by the pattern of damage in cornfields which tends to be the most in-

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tense in the rows adjacent to weedy vegetation (Deedat et al. 1983, Giebink et al. 1984).

Late in the summer, the females of both species oviposit within the leaf sheaths of grasses. The eggs overwinter and hatch the following spring (Deedat et al. 1983, Giebink et al. 1984). Initially larvae feed within stems of the new growth and we believed that they eventually outgrow their hosts (especially thin-stemmed species) and are therefore forced to disperse to plants which have thicker stems. This study was designed to evaluate the stem-size hypothesis.

Weeds in and around corn fields, particularly perennial grasses, often serve as pest reservoirs by providing oviposition sites for the females and food for emerging larvae. Although a number of hosts have been reported for *H. immanis* (Tietz 1972, Hawley 1918) and *H. micacea* larvae (Deedat 1980, Brittain 1918, Guenée 1852, Nordstrom et al. 1941, 1974, Seppanen 1970, West 1984, Zwolfer 1962), relatively little is known about their feeding behavior and performance across a range of potential weed hosts commonly found in plant communities in and around midwestern corn fields (Scriber 1999). We conducted experiments to assess larval survival and growth on selected grasses that differ in phenology, stem thickness, growth form, and root system. Such information is fundamental to determining the limits to geographic spread and locations of potentially high population densities of these two noctuids across the Midwest.

MATERIALS AND METHODS

We measured larval survival and growth of hop vine borer and potato stem borer on eight grass species and corn with each treatment replicated five times per borer species. The study, completely randomized and conducted under controlled-environment greenhouse conditions with Metalarc® full spectrum illumination and temperature regulation was also repeated three times with *H. immanis* (spring, summer, fall) and twice with *H. micacea* (spring, fall) larvae.

Grass species tested were quackgrass (*Agropyron repens* (L.) Beauv), smooth bromegrass (*Bromus inermis* Leyss), orchardgrass (*Dactylis glomerata* (L.)), large crabgrass (*Digitaria sanguinalis* (L.) Scop.), barnyardgrass (*Echinochloa crusgalli* (L.) (Beauv)), giant foxtail (*Setaria faberii* Hermm.), wild proso millet (*Panicum milliaceum* (L.)), Johnsongrass (*Sorghum halepense* (L.) Beauv), and corn (*Zea mays*). Plants were all 51–55 days old when larvae were placed on them. The first two grasses are generally rather narrow-stemmed (1–2 mm) compared to the orchardgrass and foxtail and also usually less than 3 mm diameter.

Grass seed was obtained from either wild plants or F & J Seed Service, P.O. Box 82, Woodstock, IL 60098. Seeds were planted directly into plastic pots (21 cm diam. × 20 cm ht.) filled with autoclaved soil (equal parts compost, field soil, and sand), grown under Metalarc® high-intensity lamps (15L:9D photoperiod), watered as necessary and fertilized every two weeks. Two weeks prior to introducing the larvae, the plants were thinned to ca. 30 plants per pot. Temperatures ranged from 14°C (evening) to 30°C (day).

Larvae were obtained from eggs deposited on grasses in greenhouse cages during late June through July the previous season. After remaining in the greenhouse for 3–4 weeks, these eggs were then removed from the plants, chilled (5.6°C) for eight or more weeks, and then incubated at 21°C for one-to-two weeks prior to starting the experiment.

To prevent larval escape, a combination of screen cylinders and Teflon®

coatings were used on each pot. The Teflon® coating (Phillips and Burkholder 1976), applied in a 3 cm band to the inside of the pot rim with a cotton-tipped applicator prevented any larvae from crawling out of the pot. The screen cylinders (81 cm diam. × 50 or 80 cm high) kept all foliage directly above the pots, thereby preventing escapes via overhanging foliage. Nonetheless, some larvae disappeared.

At first hatch, Parafilm® packages of 20 eggs each (all viable and ready to hatch) were pinned to the base of a centrally located stem in each pot/replication (i.e., 100 neonate larvae per grass species). This was done at dusk to maximize larval establishment. After 14–18 day larval feeding periods, all plants were gently uprooted, placed in labeled plastic bags, refrigerated, and later examined for damage and dissected for larvae. Surviving larvae were characterized for instar and weight.

Using temperatures recorded by hygrothermographs placed at opposite ends of the study bench, degree-day accumulations were calculated as in Giebink et al. (1985) with the sine-wave method and developmental thresholds of 4.9°C (*H. immanis*) and 6.8°C (*H. micacea*). Centigrade Degree Days (CDD) accumulated during these feeding periods ranged from 230–324 for *H. immanis* and 203–300 for *H. micacea*. This averaged 12.7–21.4 CDDs per day. Data from the replicate study dates were pooled because the controlled greenhouse conditions were variable enough to simulate the likely variance that would be encountered from field to field or among sites in a single field.

In a separate experiment, involving only *H. immanis* larvae and three thin-stemmed grasses (quackgrass, smooth bromegrass and orchardgrass) three pots (replications) of each treatment were sampled after 7, 10 and 14 days to observe changes in larval survival and growth over time. Corresponding thermal unit accumulations for these sample dates were 108, 158, and 230 CDD, respectively (Giebink et al. 1985). Again, a completely randomized design was used. In addition to measuring larval survival, instar, and weight, the numbers of damaged plants and stem diameters were also measured.

Statistical analyses of larval survival differences (Scheffe, $p < 0.05$) were made after arcsine square root (%/100) transformations and analysis of variance using SAS GLM procedures (SAS, 1988). We chose Scheffe's test because it is extremely conservative. The differences indicated are sure to be real. A less conservative test would doubtless indicate more significant differences between the means. For *H. immanis* the averages of 15 replications of 20 larvae per grass species were used (except giant foxtail, which had only 10 replications). *H. micacea* values (Table 1) are expressed as averages of 10 replications of 20 larvae each (except foxtail, smooth bromegrass, quackgrass and orchardgrass that had five replications).

RESULTS

The mean larval survival of both noctuid species after 14–18 days was consistently highest on corn and barnyardgrass, the grasses with the thickest stems (Table 1). Giant foxtail was the poorest of all plants tested for both *H. immanis* and *H. micacea*. Generally larval survival and growth of *H. micacea* is greater than the survival and growth of *H. immanis* on these grasses. This was reflected in the overall larval growth during each of the studies (all treatments combined), where significantly higher weights were observed for *H. micacea* than *H. immanis* larvae (on thin-stemmed grasses *H. micacea* was 9.4 ± 2.1 compared to 3.6 ± 0.2 for *H. immanis*; and on other

Table 1. Host suitability criteria for two *Hydraecia* spp. larvae reared on grasses in the greenhouse. Feeding periods ranged from 14–18 days.

Grass species ^a	% Larval survival Mean ± SE	Developmental index ^b Mean ± SE	Larval weigh (mg) Mean ± SE	Total no. surviving larvae	No. plants damaged ^c Mean ± SE	Plant stem diam. (mm) ^d Mean ± SE
Hop Vine Borer						
Barnyardgrass	38.2 ± 4.4 a	3.7 ± 1.1 a	11.6 ± 1.1 a	115	13.5 ± 1.4 a	5.8 ± 0.2
Corn	28.3 ± 5.2 ab	3.8 ± 0.2 a	18.0 ± 4.7 a	85	8.5 ± 2.0 ab	3.9 ± 0.2
Wild proso millet	17.9 ± 4.5 abc	3.4 ± 1.4 a	5.1 ± 0.7 a	54	11.9 ± 1.5 ab	3.0 ± 0.1
Large crabgrass	17.3 ± 3.5 abc	3.2 ± 0.2 a	6.4 ± 2.8 a	52	7.3 ± 1.4 ab	3.7 ± 0.3
Orchardgrass	16.7 ± 4.0 abc	3.1 ± 0.2 a	3.2 ± 0.5 a	50	9.2 ± 1.8 ab	2.6 ± 0.2
Smooth bromegrass	15.5 ± 4.5 abc	3.0 ± 0.3 a	2.8 ± 0.7 a	47	13.4 ± 1.5 a	1.5 ± 0.1
Johnsongrass	12.8 ± 3.6 bc	3.6 ± 0.2 a	7.6 ± 2.2 a	38	7.3 ± 2.2 ab	3.8 ± 0.4
Quackgrass	6.1 ± 2.4 bc	3.3 ± 0.2 a	4.0 ± 1.4 a	18	8.6 ± 1.3 ab	1.4 ± 0.2
Giant foxtail	3.0 ± 0.0 c	3.5 ± 1.2 a	3.5 ± 1.2 a	6	3.8 ± 0.9 b	2.6 ± 0.3
Potato Stem Borer						
Corn	45.0 ± 10.7 a	4.2 ± 0.1 a	27.6 ± 4.8 a	90	12.1 ± 1.1 a	4.3 ± 0.1
Barnyardgrass	23.8 ± 5.6 ab	3.9 ± 0.3 a	7.3 ± 0.5 a	48	18.4 ± 2.4 a	4.7 ± 0.2
Smooth bromegrass	22.0 ± 8.0 ab	3.7 ± 0.2 a	5.9 ± 0.7 a	22	15.0 ± 1.0 a	2.0 ± 0.0
Large crabgrass	18.6 ± 6.3 ab	4.1 ± 0.2 a	13.7 ± 3.2 a	37	6.9 ± 0.8 a	3.2 ± 0.3
Quackgrass	10.0 ± 5.5 ab	4.0 ± 0.0 a	15.8 ± 2.6 a	10	11.2 ± 3.1 a	1.9 ± 0.1
Johnsongrass	7.1 ± 3.6 ab	4.0 ± 0.4 a	18.4 ± 3.1 a	14	6.4 ± 1.8 a	4.6 ± 0.3
Orchardgrass	6.0 ± 6.0 ab	4.0 ± 0.0 a	4.3 ± 0.0 a	6	17.0 ± 3.6 a	3.3 ± 0.6
Wild proso millet	5.0 ± 3.3 ab	3.1 ± 0.1 a	7.3 ± 0.2 a	13	8.3 ± 2.3 a	2.7 ± 0.1
Giant foxtail	0 b			0	6.2 ± 2.3 a	2.8 ± 0.7

Means within each column followed by the same letter did not differ according to the Scheffe test ($P < 0.05$).

^aPlant ages ranged from 51–55 days old.

^bFor calculations of the developmental index, a numerical assignment was made for each stage (e.g., 1–6 = larval instars and 7 = pupa, with molting larvae assigned the mean value of the two instars). Replications with no survivors were excluded from the calculations.

^cAny degree of larval feeding was regarded as damage.

^dValues are averages of 15 and 10 replications of ca. 30 stems each for *H. immanis* and *H. micacea*, respectively.

species of grasses *H. micacea* was 18.4 ± 3.7 compared to 10.8 ± 0.0 for *H. immanis*; $p = 0.05$, Scheffe's test).

In the concurrent study, *H. immanis* larvae were reared on orchardgrass, smooth brome grass and quackgrass and sampled after 7, 10 and 14 days (108, 158, 230 CDD). Larval survival rapidly diminished as the larvae matured and "outgrew" their hosts. This was most pronounced on quackgrass, on which *H. immanis* survival decreased from 42% to 7% within a week. Survival on other hosts was still 28% to 32% at 14 days when the experiment was terminated. This dramatic decrease was undoubtedly due to dispersal (or perhaps starvation in the soil without a larger host to switch to) since larvae feeding on quackgrass tended to grow faster than larvae feeding on orchardgrass or smooth brome grass and "outgrew" their hosts more quickly. In fact, after 230 CDD, the surviving *H. immanis* larvae, on average, reared on quackgrass weighed at least twice as much (10.6 mg) as the larvae on other hosts (3.6 to 3.8 mg). Bigger larvae may have escaped despite containment attempts and would explain the drop in survival from 10 days to 14 days on quackgrass.

DISCUSSION

All the grasses used in these studies support the survival and growth of *Hydraecia* sp. larvae for varying periods of time. Larval developmental rates and survival to later instars depend on the host's stem thickness. *H. micacea* larvae developed faster than *H. immanis* larvae on all the grasses tested except barnyardgrass. Of the thin-stemmed grasses, larval developmental rates were fastest on quackgrass (mean weights were 2-3 times those of larvae reared on other grasses). In a mixed grass community, it is quite probable that larvae feed within quackgrass stems for the first few instars, then disperse to smooth brome grass or orchardgrass before moving on to available grasses with even thicker stems such as corn, barnyardgrass, or Johnsongrass, much as was observed with common stalkborer, *Papaipema nebris* (Alvarado 1985).

The higher mean instar and weight values of *H. immanis* and *H. micacea* larvae recovered from barnyardgrass, Johnsongrass and corn suggests better capability to support larger larvae. For instance, these grasses, plus large crabgrass, were the only hosts that sustained larvae much past the third instar.

Phenology is a critical determinant as to whether or not a particular plant species can serve as a host for *Hydraecia* spp. larvae. When *H. immanis* and *H. micacea* larvae begin feeding in early spring the number of plant species *Hydraecia* spp. can utilize as primary hosts is limited; relatively little "green" plant material is available. Typically, perennial grasses, such as quackgrass or smooth brome grass are among the primary host species. The unique stem-boring feeding behavior of the *Hydraecia* spp. larvae may restrict feeding durations on a particular plant on the basis of stem thickness alone. Of course different phytochemical and nutritional qualities will vary among plant species and within plants (i.e. geographically, Johnson and Scriber 1994). For example, Johnsongrass has thick stems, but is of low suitability for both *H. immanis* and *H. micacea*.

With *Hydraecia* spp., an important change in the feeding behavior occurs by the fourth instar. Initially, the larvae feed above ground within grass stems (until they outgrow them). But, by the fourth instar, the majority feed either within or beside stems/roots below the soil surface. This contrasts with most other stalk borers, which feed exclusively with the host above the soil

surface. For example, *P. nebris* feeds in the above ground portion of the stem and may even pupate within it (Alvarado 1985, Decker 1931).

We have shown that many grasses lack sufficient stem or root mass to support *Hydraecia* larvae throughout their development (Table 1). However, in wetter or marsh-type areas, a number of perennials have thick, fleshy culms, rhizomes, or underground roots capable of sustaining larvae until they complete their development. These primarily include the sedges, reeds and several aquatic grasses. The polyphagous *H. micacea* has been reported feeding on a wide variety of these wild plants from swampy or marsh-edge habitats in Europe (Seppanen 1970, Zwolfer 1962) and Canada (Jobin 1963, French et al. 1973). Since its recent discovery in Wisconsin and Michigan, *H. micacea* has, thus far, only been reported on quackgrass, reed canary grass, and corn—usually adjacent to marshy, low-lying habitats. However, because over 200 sedge species inhabit these states (Fassett 1976) and *H. micacea* populations generally occur near marshy habitats, it is possible that endemic *H. micacea* populations are already well-established inside these uncultivated areas.

The natural host preferences of *H. immanis*, however, are quite different from those of *H. micacea*. *H. immanis* is a stenophagous feeder that does exceptionally well on hops (Giebink et al. 1992), but it is not known to complete its life cycle on any grass other than corn. To date, the only grasses naturally hosting *H. immanis* are quackgrass, smooth brome grass, and wirestem muhly, *Muhlenbergia frondosa* (Poir.) (Giebink et al. 1984, Fritz Breitenback, pers. commun.), which are all small perennials. In Canada, several researchers (Jobin 1963, Deedat et al. 1983) reported *H. micacea* feeding on several annual grass species: orchardgrass, *Dactylis glomerata* L., green foxtail, *Setaria viridis* (L.) Beauv, and barnyardgrass, *Echinochloa crusgalli* L. (which is a thick-stemmed grass) and sustained larval growth much better than any of the other annuals). Moreover, *E. crusgalli*, (barnyardgrass or watergrass) also grows best in moist, low-lying areas.

In addition to thick-stemmed perennials already mentioned (e.g., reed canary grass, sedges, and reeds) we have shown that Johnsongrass could potentially serve as an alternate larval host. Both its perennial phenology and growth form make it a good candidate as a new larval host for these *Hydraecia* spp. It is an early spring perennial and its primary and secondary rootstocks and thick (up to 12 mm) fleshy culms could provide the larvae with suitable feeding sites both above and below the soil surface, a characteristic necessary for supporting all the stages of larval development. It could serve as an alternate host for both species in the southern portions of their range. This may result in additional *Hydraecia* spp. problems in the Corn Belt if the weed continues to spread across the southern portions of the Midwest.

The composition of the plant community has important implications with regard to cultural controls such as crop rotation (Southwood 1977). Based on our results, crop rotation should be able to locally eliminate *H. immanis* populations if wild hops, curly dock, or any thick-stemmed grass such as Johnsongrass or barnyardgrass do not exist in the local plant community. However, the wide host range of *H. micacea* may overcome such constraints by using reed, canary grass, curly dock, or other broad-leaved plants (Giebink et al. 1992).

Historical spread of *Hydraecia* spp. into the USA. *H. immanis* is very similar in many respects to the morphology and ecology of *H. micacea* (Smith 1899, Forbes 1954, Godfrey 1981, Giebink et al. 1984). Diagnostic electrophoretic allozymes have been determined for distinguishing *H. micacea* and *H. immanis* in the USA and Canada (Scriber et al. 1992). Morphological differences are described by Godfrey (1981). *Hydraecia immanis*

pupae are slightly larger (heavier) than *H. micacea* (Giebink et al. 1985). The life history of this North American native has been described in Giebink et al. 1984, Scriber and Hainze 1988, CABI 2000).

The potato stem borer, *Hydraecia micacea*, is a European noctuid moth that is currently univoltine (as is *H. immanis*), having a single generation annually. It lays eggs in masses of 80–300 along the sides of grass stems with loose leaf sheaths, and the eggs are the overwintering stage, which is 7–9 months long. The species was introduced into North America around the turn of the century (Gibson 1908), and has slowly spread from initial establishment in Eastern Canada across the Great Lakes region of North America in Canada (Deedat et al. 1983) and the USA (Muka 1976, Scriber 1980, Giebink et al. 1984).

In Europe, the potato stem borer is a major pest of hops (French et al. 1973). The hop vine borer is a native North American species (Guenée 1852) that was closely affiliated with hops as a severe pest in the 1840–1870s across the region from New York to Wisconsin (Dodge 1882, Comstock 1883, Fletcher 1893, Howard 1897, Hawley 1918). It then disappeared from view for approximately 100 years (1875–1975) as the hop industry moved completely out of the area to the West coast states (Washington, Oregon, northern California and Idaho, Scriber and Hainze 1988). Only in 1975 did this mysterious species resurface as a pest in continuous corn in a few central Wisconsin counties (Sauk, Dane, Livingston and Richland) where the old hop production was most intense during the 1850s and 1860s. While no significant production of hops occurred in Wisconsin since 1880 (except a brief attempt after prohibition in the 1930s, Scriber and Hainze 1988), there were escaped hop vines or wild hops that occurred in central Wisconsin and in 28 states from Maine to Washington. Apparently the insect had survived at very low densities basically unknown to 20th century entomologists (Godfrey 1981). After this 100 year period hop vine borer suddenly arose to prominence as a new corn pest, spreading (in noticeable damage) from this central Wisconsin location rapidly into the adjacent states of Minnesota, Iowa and Illinois (Scriber 1980, Giebink et al. 1984). Its presence in New York and Michigan was not associated with pest status on corn as it was on hops 100 years earlier (Comstock 1883, Hawley 1918).

The elimination of chlorinated hydrocarbon insecticides, combined with continuous corn production (which provided stable, dependable and excellent food and protection for the larger instars, as hop plants did earlier), and the increase in conservation tillage, grassy contour strips, and field-wide reduced tillage practices (with associated grassy weeds throughout the fields, rather than just at the fencelines) all contributed to the rapid spread and severe damage inflicted from grass feeding larvae moving out into the corn during the period from 1975–1985. While thousands of acres of corn were destroyed and required replanting during this decade, little serious damage has occurred subsequently, perhaps because of pest recognition and cultural controls for this localized and sporadic pest. As with the hop vine borer, so too the potato stem borer with nearly identical ecology (except for its wider diet range than the stenophagous hop vine borer) showed an increased rate of spread (or local outbreaks) during this decade across Canada (Deedat et al. 1983) and into Wisconsin (Scriber 1980, Giebink et al. 1984), Michigan (M. Nielsen and H. Russell, pers. comm.), New York (Muka 1976), and possibly Minnesota.

The possibility of these closely related species (*H. micacea* and *H. immanis*) hybridizing (Forbes 1954) may be a significant concern in the Great Lakes region where they are becoming sympatric. The increased hybrid vigor, expanded potential host plant range, and the faster larval development

(and lower developmental thresholds for temperature) of some hybrids might lead to a polyphagous and multivoltine genotype emerging much as has happened with the European corn borer in the same geographic area (Scriber and Hainze 1988). Largely free of natural enemies, both species and their hybrids would likely enjoy a tremendous potential for rapid and unchecked geographic spread, especially with two generations per season.

In Europe, parasites such as *Lydella stabulans* Fall (Diptera: Tachinidae) kill as many as 57% of the potato stem borer larvae, and another species, *Lydella radialis* (Townsend) may kill as many as 61% of the larvae in corn fields near Guleph, Canada (West et al. 1984). Skunks supposedly hear the chewing grubs and then dig up and eat larger larvae of *Hydraecia* in corn (Dodge 1882, Howard 1897), but few other natural enemies are known or reported (Hawley 1918).

Since 1985, the incidence of hop vine borer and potato stem borer damage in corn has been almost non-existent. We have not seen a continued geographic spread in damaging population levels in Michigan, Minnesota or Wisconsin, and only sporadic, isolated, non-economic observations have been made (M. Nielsen 1997, K. Ostlie and P. Pelliteri, pers. comm.). The long term ecological research (LTER) study of various farming systems at the Kellogg Biological Station in southwest Michigan has not observed the occurrence of either species in the past 13 years of intense biological monitoring.

What then has caused the disappearance of both species from the prominent status they were achieving in Midwest cornfields? We do not really know, although better weed control, rotation out of long term continuous corn cropping systems, and better scouting for early damage in local pockets could partially explain their scarcity during the past decade. Perhaps natural enemy pressure (parasites, predators, or pathogens) has increased somehow (Hunter et al. 1997). In any case, grassy areas provide early instar hosts, and we must continue to watch for local population build-ups of these two pest species, whether or not they hybridize.

ACKNOWLEDGMENTS

This research was supported by the College of Agriculture of the University of Wisconsin, Madison (Hatch Project 5134) and in part by the Michigan State University Agricultural Experiment Station (MAES Project #8051 and 1644) and Regional Research Projects NC-180 and NC-205. It was supported in part by N.S.F. (L.T.E.R. "Agroecology") Project BSR #8702332. We are grateful for assistance of Dr. Jeffrey Wyman, Jeffrey Beehler, Mo Nielsen, Ken Ostlie, and Phil Pellitteri.

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