

Multiple Pest Interactions in Soybean: Effects on *Heterodera glycines* Egg Populations and Crop Yield¹

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Abstract: Population changes of *Heterodera glycines* eggs on soybean in small field plots were influenced by the lepidopterous insect pest, *Helicoverpa zea*; however, few effects on eggs due to the presence of annual weeds were detected. Soybeans defoliated 15–35% by *H. zea* during August remained green and continued to produce new flowers and pods later into the season than soybeans without *H. zea*, resulting in higher numbers of *H. glycines* eggs at harvest on insect-defoliated soybeans. Final *H. glycines* populations also were influenced by soil population density (Pi) of the nematode at planting. Fecundity of *H. glycines* was generally greater at the undetected and low Pi than at high Pi levels. Soybean yields were suppressed 12, 22, and 30% by low, moderate, and high *H. glycines* Pi, respectively. When weed competition and *H. zea* feeding damage effects were added, yields were suppressed 34, 40, and 57% by the three respective nematode Pi levels. Effects among the three pests on soybean yield were primarily additive.

Key words: Annual weed, *Glycine max*, *Helicoverpa zea*, *Heterodera glycines*, nematode, pest complex, population dynamics, soybean, weed, yield.

The soybean cyst nematode (*Heterodera glycines* Ichinohe), the corn earworm (*Helicoverpa zea* (Boddie)), and annual weed species compose a common and economically important pest complex on soybean (*Glycine max* (L.) Merr.) in eastern North Carolina. Although substantial yield loss has been attributed to each pest individually (7,10,18,19), it is necessary to quantify the simultaneous effects of these multiple-stress factors on soybean and on each other. Such information is crucial to the development of integrated pest management strategies for soybean.

Soybean growth and seed yield are inversely related to the initial soil population density (Pi) of *H. glycines* (4,24). The negative impact of the nematode on soybean canopy size and development results in better *H. zea* larval establishment and survival and more late-season weed biomass (1–3).

Infestations of plant-parasitic nematodes may be related to direct and indirect effects of other biotic stress agents (20,22, 26). Weed-induced stresses in sugarcane reduce accumulations of free amino acids in plants and consequently suppress late-season population development of plant-parasitic nematodes (26). *Heterodera glycines* population development is enhanced on insect-damaged soybeans with lower levels of photosynthate (22).

Soybean has a tremendous ability to compensate for insect feeding damage on leaves, flowers, and seeds (9,13,16,28). New foliage and flowers can develop during pre- to midbloom growth stages of soybean following *H. zea* feeding damage (16,17). The altered and extended plant growth may affect late-season *H. glycines* population dynamics (12).

The objectives of this study were to determine the effects of *H. zea* and annual weeds on *H. glycines* population changes and the interactive effects of the three pests on soybean yield.

MATERIALS AND METHODS

Field experiments were conducted from 1985 to 1987 in eastern North Carolina. Study sites were located near Elizabeth City, Pasquotank County, and Tarboro, Edgecombe County, in 1985 and 1986; Como, Hertford County, in 1986 and

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1987; and Edenton, Chowan County, in 1987. Soil texture was sandy loam (62–69% sand, 24–32% silt, and 3–7% clay) at Elizabeth City, Como, and Edenton, and loamy sand (77% sand, 18% silt, and 5% clay) at Tarboro.

Soil samples were collected from 400 plots (4 rows [0.75–1.03 m row-spacing] × 4.6 m long) at each location to determine initial *H. glycines* egg population densities (Pi) in soil before planting. The soil samples consisting of 10–12 cores 2.5 cm d and 15–20 cm deep were collected from the two center rows of plots and mixed, and a 500-cm³ aliquant of soil was then processed by a combination of elutriation (8) and centrifugation (14). *Heterodera glycines* cysts were crushed with a glass tissue grinder to free eggs for counting (4). The *H. glycines* populations at Elizabeth City and Tarboro were race 5, and those at Como and Edenton were race 2.

Eighty plots were selected from the 400, and 20 plots each were categorized into four groups (undetected, low, moderate, and high) based on *H. glycines* Pi at each location (Table 1). Because of the aggregated spatial pattern of *H. glycines* in soybean (4), plots with the various Pi levels were scattered throughout each field and selected at random for inclusion in the study. The low, moderate, and high Pi levels were assigned based on relative nematode abundance at each site and expected plant damage (e.g., slight, moderate, and severe soybean plant stunting). No nematocides were used.

Experiments were set up in completely randomized 4 × 2 × 2 factorial designs

with five replications. Factors were *H. glycines* Pi (undetected, low, moderate, or high); weed densities (natural infestation or elimination with acifluorfen [0.28–0.56 kg a.i./ha], bentazon [0.56–1.11 kg a.i./ha] [BASF Corp., Parsippany, NJ], and imazaquin [0.07–0.14 kg a.i./ha] [American Cyanamid Co., Wayne, NJ] depending on the weed species present); and *H. zea* densities (natural infestation or elimination with thiocarb [0.14 kg a.i./ha] [Rhone Poulenc Chemical Co., Research Triangle Park, NC]). The herbicides and insecticides were applied at 414 KPa with a CO₂ backpack sprayer. The herbicides were applied postemergence at monthly intervals, and the insecticide was applied 5–8 August each year, prior to *H. zea* egg hatch.

Seeds were planted 3–9 June 1985 and 1986, and 26–27 May 1987. Soybean 'Coker 156', susceptible to all races of *H. glycines*, was planted at all locations. Soybeans at the Edenton site were damaged by deer feeding. Two rows per bed (alternate 0.3 m and 0.8 m row-spacing) were replanted 22 June 1987.

Numbers of *H. glycines* eggs were determined at three sampling dates during the growing season. Soil samples were collected from plots at planting (or at replant at Edenton, 1987), 30–36 days after planting (28 June–15 July), and at harvest (30 October–23 November).

The major annual weed species present in the fields included large crabgrass (*Digitaria sanguinalis* (L.) Scop.), broadleaf signalgrass (*Brachiaria platyphylla* (Griseb.) Nash), fall panicum (*Panicum dichotomiflorum* Michx.), common lambsquarters (*Che-*

TABLE 1. Initial population density (Pi) ranges of *Heterodera glycines* represented as number of eggs per 500 cm³ soil for 1985–87 field sites.

| Year | Location | Undetected | Low | Moderate | High |
|------|----------------|------------|---------|-------------|---------------|
| 1985 | Elizabeth City | 0 | 300–400 | 1,200–2,000 | 8,000–17,900 |
| | Tarboro | 0 | 100–200 | 900–2,000 | 4,800–15,800 |
| 1986 | Elizabeth City | 0 | 300–600 | 3,000–4,000 | 8,800–14,400 |
| | Tarboro | 0 | 100–200 | 800–1,700 | 4,900–8,800 |
| 1987 | Como | 0 | 400–600 | 2,800–4,000 | 9,500–21,500 |
| | Como | 0 | 600–900 | 6,000–8,000 | 15,000–20,000 |
| | Edenton | 0 | 200–400 | 700–1,000 | 1,300–4,300 |

nopodium album L.), redroot pigweed (*Amaranthus retroflexus* L.), common ragweed (*Ambrosia artemisiifolia* L.), and morning-glory (*Ipomoea* spp.). The major ground cover plant species at Elizabeth City in 1985 was volunteer wheat (*Triticum aestivum* L.). Fresh weed weights were determined in a randomly selected square-meter area in plots during mid-September to mid-October.

To elucidate the interactive effects of the three pest groups on soybean yield, seeds were harvested mechanically at maturity from the center two rows of plots and expressed in kg/ha at a standard moisture content of 13%.

Factorial analyses of the General Linear Models Procedure (23) were used to test the main effects of *H. glycines* Pi, weed and *H. zea* population densities, and all two- and three-way interactions. Main effects and the interactions were partitioned into orthogonal polynomial contrasts for comparisons. Data values for *H. glycines* egg densities and soybean yields were averaged across levels of weed and insect treatments based on no significance of interaction terms. The change in *H. glycines* egg population densities from planting to harvest was determined by dividing the final (at harvest) egg densities (Pf) by $P_i + 1$ for each plot and then averaged across values in a given Pi class.

RESULTS

The increase in *H. glycines* egg population densities by the end of the season was influenced by nematode Pi at all test locations, except Tarboro, in all years (Table 2). In general, fecundity of *H. glycines* was greatest at undetected or low nematode Pi and decreased with increasing Pi. The reproductive rate of *H. glycines* within a Pi level was less at Tarboro in 1985 and 1986 than that at all other sites. *Heterodera glycines* egg densities were different ($P = 0.01$) among nematode Pi levels preplant, at planting (Table 2), and 30–36 days after planting (data not presented) at all locations. Numbers of nematode eggs at har-

vest were similar in all plots at Elizabeth City 1985 and 1986 and Edenton 1987 because of the differential reproductive rate at the various Pi levels. Plots with no detectable *H. glycines* eggs at planting contained 215–15,070 eggs/500 cm³ soil at harvest.

Fresh weed weights in weedy plots ranged from 95 to 613 g/m² for 1985 and 1987 field studies (data not presented). Establishment of weeds in 1986 studies was poor. In general, weed biomass was greater in the moderate and high *H. glycines* Pi plots with more open soybean canopies (1). The presence of weeds in plots generally did not influence numbers of *H. glycines* eggs in the soil (Fig. 1). However, at Elizabeth City in 1985, numbers of eggs at harvest were higher ($P = 0.05$) in weed-free than in weedy soybean plots (Fig. 1A).

Soybeans fed on by *H. zea* during August had higher *H. glycines* egg population densities at harvest than soybeans without *H. zea* damage at Elizabeth City ($P = 0.02$) and Como ($P = 0.04$) in 1986 (Fig. 2). Natural *H. zea* infestation levels were very low in 1985, but sufficient in 1986 and 1987 to cause 15–35% defoliation of soybeans. Soybeans damaged by *H. zea* matured later than those treated with insecticide. Numbers of *H. glycines* eggs at harvest were also greater on soybeans with *H. zea* in 1987 studies than those without *H. zea* damage, although differences were not significant ($P = 0.33$ – 0.07) (Fig. 2D,E).

Seed yields were less ($P = 0.05$ – 0.01) at high than undetected and low *H. glycines* Pi at Tarboro 1985, and undetected, low, and moderate nematode Pi at Como 1986 and 1987 (Table 3). Yields at Elizabeth City were highest overall and followed similar trends, but were not different ($P = 0.29$ and 0.12) (Table 3). Seeds were not harvested at Tarboro 1986 or Edenton 1987 due to equipment and weather related difficulties.

Yield suppression for an individual pest, averaged across levels of the other pests, was greatest due to weed competition at Tarboro in 1985 ($P = 0.02$) and *H. zea* feeding damage at all locations in 1986 (P

TABLE 2. Influence of preplant *Heterodera glycines* Pi levels on mean number of eggs per 500 cm³ soil at planting and harvest, and on egg fecundity (Pf/(Pi + 1)).

| Year | Location | Preplant | | At planting | At harvest | Pf/(Pi + 1)‡ |
|------|----------------|---------------------|----------|-------------|------------|--------------|
| | | <i>H. glycines</i> | Pi level | | | |
| 1985 | Elizabeth City | Undetected | 0 | 0 | 8,105 | 8,105.0 |
| | | Low | 316 | 360 | 7,925 | 22.0 |
| | | Moderate | 1,585 | 1,575 | 10,835 | 6.9 |
| | | High | 12,589 | 12,520 | 9,325 | 0.7 |
| | | <i>P</i> > <i>F</i> | 0.01 | 0.01 | 0.51 | 0.01 |
| | Tarboro | Undetected | 0 | 130 | 1,565 | 11.9 |
| | | Low | 158 | 308 | 925 | 3.0 |
| | | Moderate | 1,585 | 1,050 | 5,250 | 5.0 |
| | | High | 10,000 | 9,899 | 10,090 | 1.0 |
| | | <i>P</i> > <i>F</i> | 0.01 | 0.01 | 0.01 | 0.26 |
| 1986 | Elizabeth City | Undetected | 0 | 160 | 15,070 | 93.6 |
| | | Low | 398 | 540 | 14,019 | 25.9 |
| | | Moderate | 3,162 | 2,940 | 17,320 | 5.9 |
| | | High | 12,400 | 7,055 | 18,815 | 2.7 |
| | | <i>P</i> > <i>F</i> | 0.01 | 0.01 | 0.20 | 0.01 |
| | Tarboro | Undetected | 0 | 95 | 230 | 2.4 |
| | | Low | 121 | 275 | 863 | 3.1 |
| | | Moderate | 950 | 720 | 1,733 | 2.4 |
| | | High | 5,486 | 4,795 | 12,467 | 2.6 |
| | | <i>P</i> > <i>F</i> | 0.01 | 0.01 | 0.01 | 0.72 |
| | Como | Undetected | 0 | 153 | 215 | 1.4 |
| | | Low | 452 | 978 | 29,725 | 30.4 |
| | | Moderate | 3,822 | 2,710 | 35,535 | 13.1 |
| | | High | 15,850 | 10,058 | 32,778 | 3.3 |
| | | <i>P</i> > <i>F</i> | 0.01 | 0.01 | 0.01 | 0.01 |
| 1987 | Como | Undetected | 0 | 388 | 7,925 | 20.4 |
| | | Low | 631 | 3,456 | 4,495 | 1.3 |
| | | Moderate | 6,584 | 7,270 | 5,040 | 0.7 |
| | | High | 17,191 | 18,230 | 10,310 | 0.6 |
| | | <i>P</i> > <i>F</i> | 0.01 | 0.01 | 0.03 | 0.01 |
| | Edenton | Undetected | 0 | 60 | 4,289 | 70.3 |
| | | Low | 320 | 200 | 6,401 | 31.8 |
| | | Moderate | 914 | 833 | 9,906 | 11.8 |
| | | High | 3,532 | 3,610 | 10,830 | 3.0 |
| | | <i>P</i> > <i>F</i> | 0.01 | 0.01 | 0.10 | 0.01 |

† For *H. glycines* Pi effects *df* = 3; error *df* = 64.

‡ Final (at harvest) mean egg population density/initial (at plant) egg population density + 1; at plant samples collected 26 May to 9 June, and 22 June at Edenton; at harvest samples collected 30 October to 23 November.

= 0.07–0.01) and 1987 (*P* = 0.01) (Table 3). Very low *H. zea* infestation levels in 1985 experiments and poor establishment of weeds in 1986 studies negated the impact of these pests on yield loss in these years. In all experiments, the greatest yield losses were attributed to the occurrence of *H. zea* and weeds together across all *H. glycines* Pi levels (18–57%) (Table 4). When considered alone, the high *H. glycines* Pi suppressed soybean seed yields by an average of 30% compared to the undetected Pi for all locations and years (Table 4), and

the individual effects of weeds and *H. zea* suppressed yields by 6–32% and 9–35%, respectively. There were no significant (*P* = 0.05) two-way or three-way interactive effects among pests on soybean yields. Therefore, effects among the three pests on yield were primarily additive (Table 4).

DISCUSSION

Population fluctuations of *H. glycines* are influenced by Pi, soybean root growth pattern, and edaphic and environmental con-

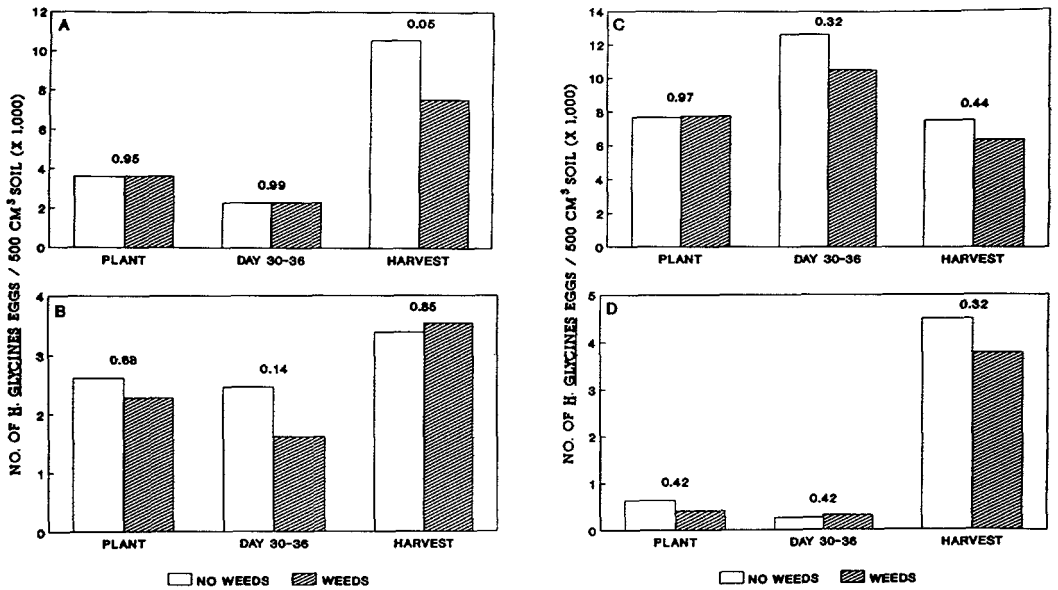


FIG. 1. Mean number of *Heterodera glycines* eggs per 500 cm³ soil during the season as influenced by weed infestation level in soybean. A) Elizabeth City 1985, B) Tarboro 1985, C) Como 1987, and D) Edenton 1987. Numbers above bars indicate level of significance between treatments.

ditions (4,6,25). Initial nematode population density is important because it can be related to the amount of damage to annual crops (5). Reproductive potential of *H. glycines* is also negatively related to Pi, and the carrying capacity of a field is usually reached by the end of the season, regardless of Pi (4,6). In these studies, fecundity of *H. glycines* was greatest at the undetected and low nematode Pi levels, except for Tarboro, where there were no differences among Pi. Soil at the Tarboro site had the highest percentage sand content (77% compared to 62–69% at the other sites) and the lowest soybean seed yields. Soybean plants at Tarboro appeared stressed due to lack of moisture and generally poor growing conditions in both years, which may explain the low reproductive rate of *H. glycines* across all Pi levels at this site.

High *H. glycines* Pi can cause so much damage to soybean roots that late season populations are limited by the shortage of food (6). This differential reproductive rate of *H. glycines* at the various Pi levels was especially evident at Elizabeth City 1985 and 1986 and Edenton 1987, where fecundity was substantially higher at lower

nematode Pi, resulting in similar egg densities at harvest in all Pi levels. Therefore, although *H. glycines* Pi may be low at planting, substantial populations can develop by harvest.

Weeds present in these experiments are not known to be hosts for *H. glycines* (15,27). Weed-stressed soybeans harbored fewer *H. glycines* than weed-free plants in some fields. The ability of *H. glycines* to reproduce on weed-stressed soybeans may be reduced through weed competition for nutrients and moisture and indirect effects of the weeds on the physiological mechanisms of the plant.

Soybeans may produce new foliage and flowers following insect defoliation during pre- to midbloom stages (18,28), which delays plant maturation and senescence (16,17). This additional period of plant growth may allow *H. glycines* to continue egg production longer, which would explain the higher end-of-season numbers on insect-damaged plants. Increases in numbers on *H. glycines* eggs in late season soybeans are associated with diapause induction in eggs (4,12) and with increased nematode reproduction on reproductive

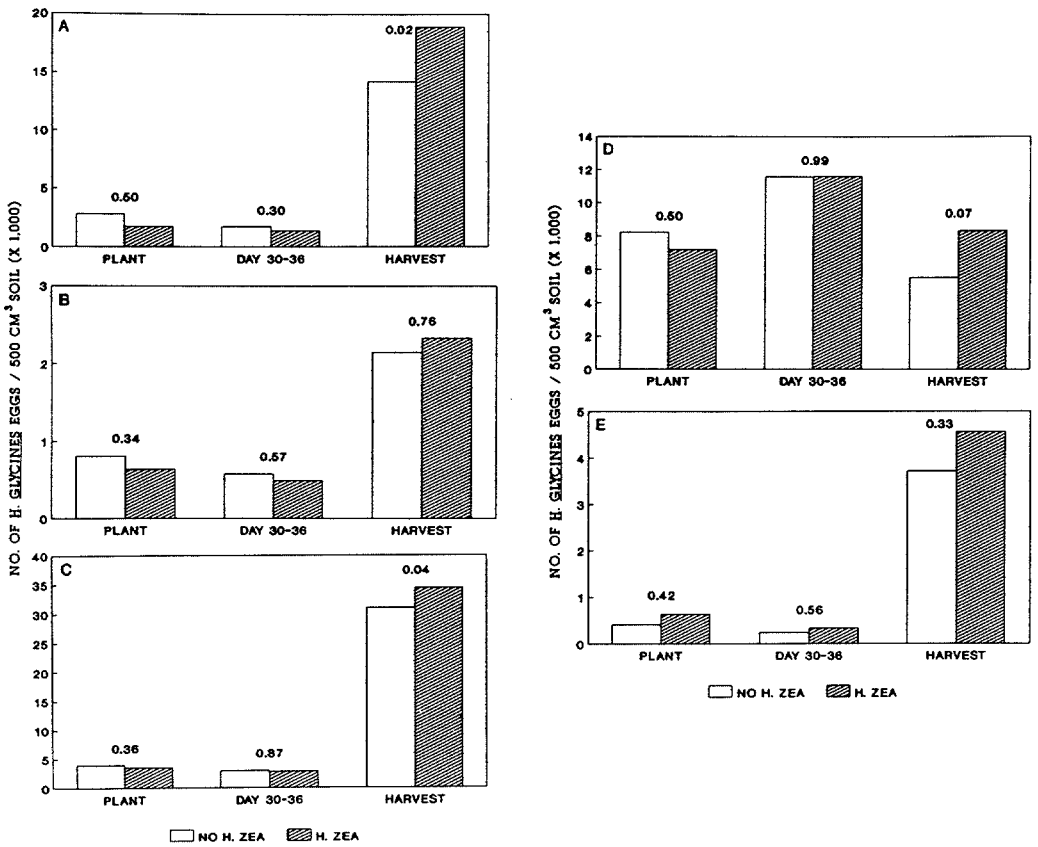


FIG. 2. Mean number of *Heterodera glycines* eggs per 500 cm³ soil during the season as influenced by *Helicoverpa zea* infestation level in soybean. A) Elizabeth City 1986, B) Tarboro 1986, C) Como 1986, D) Como 1987, and E) Edenton 1987. Numbers above bars indicate level of significance between treatments.

soybeans and delayed maturing cultivars (12). An early diapause in 1987, possibly related to cool fall temperatures, may have prevented *H. glycines* populations from de-

veloping as they did in 1986, when diapause appeared to occur later. An enhanced reproductive rate for *H. glycines* was also documented in greenhouse stud-

TABLE 3. Effects of *Heterodera glycines*, weed, and *Helicoverpa zea* population densities on soybean yield (kg/ha) ± S.E.

| Pest | Level | 1985 | | 1986 | | 1987 |
|--------------------|---------------------|----------------|----------|----------------|-------------|-------------|
| | | Elizabeth City | Tarboro | Elizabeth City | Como | Como |
| <i>H. glycines</i> | Undetected | 1,685 ± 162 | 451 ± 43 | 1,728 ± 107 | 1,189 ± 96 | 1,082 ± 78 |
| | Low | 1,620 ± 70 | 421 ± 30 | 1,686 ± 142 | 1,300 ± 69 | 1,021 ± 147 |
| | Moderate | 1,518 ± 59 | 390 ± 44 | 1,413 ± 95 | 1,231 ± 144 | 965 ± 82 |
| | High | 1,414 ± 99 | 304 ± 43 | 1,476 ± 86 | 920 ± 95 | 649 ± 64 |
| | <i>P</i> > <i>F</i> | 0.16 | 0.05 | 0.12 | 0.03 | 0.01 |
| Weeds | None | 1,634 ± 91 | 437 ± 30 | 1,615 ± 83 | 1,144 ± 81 | 971 ± 73 |
| | Present | 1,484 ± 52 | 346 ± 27 | 1,537 ± 75 | 1,175 ± 72 | 788 ± 73 |
| | <i>P</i> > <i>F</i> | 0.16 | 0.02 | 0.48 | 0.75 | 0.04 |
| <i>H. zea</i> | None | 1,563 ± 80 | 390 ± 29 | 1,675 ± 73 | 1,325 ± 77 | 1,066 ± 81 |
| | Present | 1,556 ± 70 | 393 ± 29 | 1,477 ± 82 | 994 ± 67 | 692 ± 52 |
| | <i>P</i> > <i>F</i> | 0.95 | 0.94 | 0.07 | 0.01 | 0.01 |

TABLE 4. Average percentage of soybean seed yield losses† attributed to *Heterodera glycines*, annual weeds, and *Helicoverpa zea* in 1985–87 studies.

| <i>H. glycines</i> Pi | Weeds | <i>H. zea</i> | |
|--------------------------|---------|---------------|---------|
| | | None | Present |
| Undetected | None | 0 | 9 |
| | Present | 6 | 18 |
| Low | None | 12 | 22 |
| | Present | 13 | 34 |
| Moderate | None | 22 | 27 |
| | Present | 24 | 40 |
| High | None | 30 | 35 |
| | Present | 32 | 57 |

† Average percentage of seed yield losses = 100%—([average yield of each treatment over all locations and years/average yield of no pest treatment over all locations and years] × 100).

ies on soybeans fed on by another defoliating insect, the soybean looper (*Pseudoplusia includens* (Walker)) (22). Simulated insect damage reduced the concentration of sugars in soybean stem sap as compared to undefoliated plants (9). Changes in translocation and concentration of photosynthates in soybean plant parts due to stresses imposed by insect feeding may affect *H. glycines* development and reproductive rates.

The three pests must be considered in the design of an integrated management system for soybean. For example, low population densities (100–200 eggs per 500 cm³ soil) of *H. glycines* in the absence of other pest species usually are not a significant factor for economic soybean production, but if *H. zea* and (or) weeds are also present, the additive potential for yield loss is great. An additive effect on soybean yield also occurred in a field study in Arkansas, among a pest complex composed of *H. glycines*, annual weeds, and a stem-girdling insect, the threecornered alfalfa hopper (*Spissistilus festinus* Say) (21). The combined yield loss for the three pests was 35–56% in the Arkansas study, compared to 34–57% in this study.

The three pests can affect photosynthate available to soybean nodules, thereby limiting fixation of nitrogen (11) and yield. Soybean seed growth rates may not be directly related to current photosynthate

production if storage carbohydrates are available to serve as a buffer source (9). However, a stable rate of seed growth requires either accumulation or mobilization of storage carbohydrates or changes in photosynthate production (9). Despite the tremendous compensatory nature of soybean (9,28), this pest complex severely suppressed seed production. Although defoliation by *H. zea* and weed biomass are disproportionately increased in soybeans with open canopies due to moderate to high *H. glycines* Pi levels (1,2), yield reduction effects of the three pests are only additive. It appears that *H. zea* is primarily a foliage feeding insect that does not consistently cause seed damage. Difficulties in obtaining coincident yield damaging levels of the three pests in field studies limited our abilities to detect interactive effects on yield loss.

The integration of host–pest and pest–pest interactions into integrated crop management systems is a great challenge that needs to be met by agricultural researchers and extension personnel. It is imperative that crop–pest management systems are developed that incorporate such information on biological interactions and yet will be accepted and implemented by the grower.

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