Pan Trapping for Soybean Aphid (Homoptera: Aphididae) in Minnesota Soybean Fields[1]

E. W. Hodgson[2], R. L. Koch and D. W. Ragsdale

Department of Entomology, 219 Hodson Hall, University of Minnesota, St. Paul, MN 55108 USA

J. Entomol. Sci. 40(4): 409-419 (October 2005)

Abstract Soybean aphid, *Aphis glycines* Matsumura, can be an economically important pest in soybean, *Glycine max* (L.) Merrill. In 2002 and 2003, we evaluated the use of nonattractive pan traps to estimate soybean aphid densities in commercial soybean fields. A regression analysis indicated a strong relationship between log-transformed pan trap counts and whole-plant counts (r^2 = 0.70). To measure soybean aphid dispersion as characterized by each sampling method, Taylor's power law *a* and *b* values were calculated. The mean-to-variance ratios for pan trapping (*a* = 0.85, *b* = 1.63, r^2 = 0.96) were comparable to whole-plant counts (*a* = 1.67, *b* = 1.99, r^2 = 0.93). The precision and cost (i.e., time) of each sampling method was evaluated using relative net precision. Both sampling methods were generally precise throughout the season (<0.25). However, the relative net precision of whole-plant counts (4.21) was greater than for pan traps (0.67), and therefore whole-plant counts are a more cost effective sampling method. We also evaluated trap placement within fields during the initial colonization period. Trap catches did not differ among directions within the field or at the edges of fields versus the interior of fields. This lack of a preference for alates to land at field edges may preclude the use of border sprays, which have proven effective in other systems.

Key Words *Aphis glycines*, green tile pan trapping, relative net precision, site-specific management

Since the initial detection in 2000, the soybean aphid, *Aphis glycines* Matsumura, has spread rapidly in soybean, *Glycine max* (L.) Merrill, throughout the United States and Canada. Every soybean-growing county in Minnesota was infested with soybean aphid by August 2001 (Venette and Ragsdale 2004). There are over 2.9 million ha of soybean grown in Minnesota every year; only corn precedes soybean as the top field crop in the state (NASS 2004). High densities of soybean aphid can severely reduce yield up to 45% (Ostlie 2001) and photosynthetic rates by 50% (Macedo et al. 2003). Soybean is an economically important crop and the invasion by soybean aphid necessitates development of an integrated pest management (IPM) program.

In southern Minnesota, temperatures are favorable for successful overwintering of the soybean aphid (McCornack et al. 2005). The overwintering host (*Rhamnus* spp.) is readily available (Ragsdale et al. 2004), and spring migrants can colonize early vegetative soybean (Hodgson 2005). These data suggest that soybean aphids may

[1]Received 4 January 2005; accepted for publication 20 June 2005.

[2]Address inquiries (email: hodgs005@umn.edu).

overwinter in southern Minnesota and subsequently migrate to more northern fields each summer.

Soybean aphids are migratory and continuously produce alatoid nymphs during soybean reproductive stages (Hodgson 2005). Favret and Voegtlin (2001) describe different types of aphid flight behavior, including migratory (i.e., long distance) and trivial (i.e., short distance) flight. Although the large-scale migratory dynamics of soybean aphid have been explored (Hodgson 2005), the within-field movement and trivial landing behavior is not fully understood. Specifically, sampling soybean aphids during spring colonization and describing the landing preference in soybean must be examined.

Sampling is a fundamental activity necessary for decision making in an IPM program (Pedigo 1994). To compliment an overall IPM strategy, sampling should be efficient and dependent upon the overall objectives of the decision maker (Hutchins 1994). In general, whole-plant counts are used to estimate soybean aphid densities (Hodgson et al. 2004, Hodgson 2005). Perhaps one of the most effective methods for sampling alate aphids is using nonattractive pan traps (Irwin 1980). Boiteau (1990) and Hanafi et al. (1995) used pan traps to monitor aphid colonization in potato, *Solanum tuberosum* L., but the effectiveness of pan trapping for soybean aphid has not be documented.

To compare sampling methods of soybean aphid, we examined the precision and cost (i.e., time) of pan trapping and whole-plant counts. Pan trapping is a passive sampling method for collecting alate aphids and is generally effective for most aphid species (Irwin 1980). Pan traps can also be monitored on a weekly basis, minimizing the frequency of trips to the field and eliminating time of day trapping conflicts. However, pan trapping requires supplies, some of which may be relatively expensive (e.g., propylene glycol, green tiles, and a microscope). Pan trapping can only account for alate forms, and therefore it does not estimate apterous adults and immatures in the population. To sort through insects and other aphid species caught in pan traps takes training that goes beyond counting on plants. Identifying aphids to species is tedious, but bias is virtually eliminated once that skill is learned because generally one person is sorting and counting weekly samples.

Nondestructive, whole-plant counts may be preferable because populations can be estimated in "real-time", generally require few supplies, are convenient for most exposed insects, and can target specific parts of the plant (Musser et al. 2004). Few insect pests resemble soybean aphid in soybean, so a relatively inexperienced sampler can learn to estimate densities with little training. Disadvantages of whole-plant counts include a prominent sampling bias among observers, especially for estimating high populations (Powell et al. 1996). Also, costs may be incurred walking through fields (Stephens and Losey 2004), and the time at which samples are taken may affect overall counts (Musser et al. 2004). Despite these limitations, enumerative and binomial sequential sampling plans were developed for soybean aphid in soybean (Hodgson et al. 2004).

The intent of this paper was to evaluate pan trapping as a sampling method for soybean aphid in commercial soybean. Objectives were to describe the seasonal dynamics of the soybean aphid using pan trap counts and whole-plant counts and to compare these two different sampling methods. Also, we wanted to estimate the precision throughout the growing season and calculate the relative net precision of each sampling method. Finally, we evaluate trap placement by testing for soybean aphid landing preference within fields during spring colonization.

Materials and Methods

In 2002, fields 1 and 2 (4 and 20 ha, respectively) were located at the University of Minnesota Outreach, Research and Extension Park, Rosemount, MN. Also, in 2002, fields 3 and 4 (4 ha and 20 ha, respectively) were located 2 km west of Owatonna, MN, and 1 km north of Potsdam, MN, respectively. The pan trapping layout was similar in all fields, with eight traps arranged into four pairs. For each pair, one trap was placed directly on the field edge; the other trap was 25 m into the field for fields 1 and 3 and 75 m into the field for fields 2 and 4 (Fig. 1A, 1B). In 2003, fields 5 and 6 (4 ha each) were located at the University of Minnesota Outreach, Research and Extension Park, Rosemount, MN. Pan traps were organized in four north-south transects. Each transect consisted of two pairs of pan traps: one trap was placed along the northern field edge and the complimentary trap was 45.7m from the border trap, and the second trap was placed along the southern field edge with the complimentary trap placed 45.7 m from the border trap (Fig. 1C).

Each pan trap consisted of a 10.8-cm^2 green tile (D-22 green Dal-Tile Corp., Dallas, TX) placed into a 1.32-L plastic round container and filled with 750 ml of propylene glycol. Each container was held in a metal tomato cage, and the container was adjusted weekly to align with canopy height. Pan traps operated for 8 wk from June until mid-September in both years. Once per week, all aphids were removed from the samples and permanently stored in 1.5-mL vials with 70% ethanol, and containers were refilled with fresh propylene glycol. For the purpose of this study, alate aphids were classified as “soybean aphids” or “other”. The total number of soybean aphids in each trap for each sampling week was determined for 2002 and 2003.

For comparison of pan trapping counts to plant counts, the same six soybean fields were systematically sampled, ensuring all areas of the field were covered for all stages and morphs of soybean aphid. Whole-plant counts were nondestructive, and fields were sampled once per week from early vegetative stages to pod set. Each field had different sample sizes, ranging from 120-1500 plants per field depending on field size, plant stage and soybean aphid density.

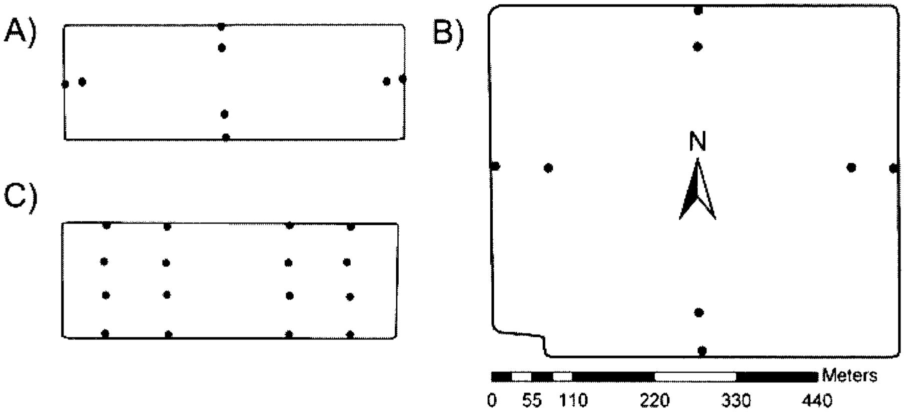

Fig. 1. Field layout for pan traps. A) Fields 1 and 3 in 2002 (4 ha each), B) fields 2 and 4 in 2002 (20 ha each), and C) fields 5 and 6 in 2003 (4 ha each).

A regression analysis was performed to better understand the relationship between whole-plant counts and pan trapping counts throughout the season using the six fields described above. The mean number of soybean aphids trapped per week from all traps for a given field was compared with the mean number of soybean aphids sampled in whole-plant counts per week from all sampled plants for that field. A linear regression of the log(x + 1) transformed mean number of soybean aphids per plant per week versus the log(x + 1) transformed mean number of soybean aphids per trap per week across both years was performed (PROC REG; SAS Institute 2001).

To understand the mean-to-variance relationship and dispersion pattern resulting from each sampling method, we calculated Taylor's power law ($s^2 = a\bar{x}^b$) *a* and *b* values (Taylor 1961) for soybean aphids sampled in 2002 and 2003.

Although data for two sampling methods may be closely related over a wide range of densities, one method may be consistently more precise and hence preferred. Precision is defined by the following equation:

$$D = (\mathrm{SE}/\bar{x}) * 100,$$

where *D* is precision, SE is the standard error, and $\bar{x}$ is the mean. Greater precision (i.e., a low value) is preferred to minimize sampling error. Southwood (1978) recommends precision to be at most 25% for pest management purposes. The precision of pan trapping and whole-plant counts throughout the sampling period was examined so they could be directly evaluated. A strong relationship between sampling methods could potentially indicate a consistent bias and a reliable estimate with either sampling method (Musser et al. 2004).

Comparing the precision of sampling methods can be useful; however, evaluating relative net precision could ultimately aid in deciding which method is most practical (e.g., Pedigo et al. 1972). Relative net precision includes the precision and cost (i.e., time) of a sampling method so that sampling plans can be directly compared and is calculated by the following equation:

$$\text{relative net precision} = [1/(D * c)] * 100,$$

where *D* is precision [$(\mathrm{SE}/\bar{x}) * 100$] set at 25% (Southwood 1978), and *c* is the total cost related to collecting the desired number of sample units. A higher relative net precision value indicates a more efficient sampling plan. The minimum number of soybean aphid pan traps needed to attain 25% precision is unknown, but was set at eight traps because of the design of this study. The weekly cost of sampling eight pan traps for soybean aphids over a range of densities was 6 person-hours, and includes preparing fresh traps, changing and sorting traps and identifying soybean aphids among other species. Hodgson et al. (2004) determined the minimum number of field count samples needed to attain 25% precision is 38 plants. The estimated weekly cost of sampling 38 plants over a range of densities was 0.95 person-hours, and includes 1 min to sample each plant and 0.5 min walk time between plants.

To determine if trap catches may be affected by trap placement within a field, we compared trap catches among location within a field in 2002 and 2003. Here, we define spring colonization as the period of time when alates are moving from primary overwintering hosts to secondary summer hosts in addition to the absence of alatoid nymph production in soybean (Hodgson 2005). Field counts showed an absence of alatoid nymphs on plants until the second sampling week in 2002 and 2003, indicating alatae collected in traps during this period were immigrants. The origin of alates found in pan traps for the remainder of the sampling season is unknown but likely represents a mixture of alates arising from within the field and immigrants from outside the field. Consequently, spring colonization (i.e., movement from overwintering hosts to soybean fields) is perhaps the most accurate time to describe landing preferences of alate aphids (Hodgson 2005).

The number of soybean aphids trapped during spring colonization was defined as the mean number of aphids per trap for the first 2 wk. An analysis of variance was used to test for differences in trap catches among field sizes (4 versus 20 ha), directions (cardinal directions) and locations (edge versus interior) in 2002, and directions and locations in 2003 (PROC GLM; SAS Institute 2001). In addition to these main effects, the model included all interactions of the main effects. Prior to analysis, trap catches were $\log(x + 1)$ transformed to stabilize variances. Because 2- and 3-way interactions were not significant ($P > 0.05$) they were omitted from the models.

Results and Discussion

For our study, pan traps operated for 8 wk (2002: 9 July-2 September; 2003: 2 July-26 August). The mean number of soybean aphids at both trapping locations (i.e., field edge and field interior) was calculated for each sampling week at each field. In general, trap catches at the field edge and interior were similar in all fields (Fig. 2). The peak number of trapped aphids occurred during 6-12 August in 2002 and 30 July-5 August in 2003 (Fig. 2). During the peak trapping week, soybeans were at the pod set stage in both years. Similarly, Hodgson (2005) showed peak alate migration at pod set stage in Minnesota.

Soybean aphid counts for each sampling method were greater in 2003 compared with 2002 (Fig. 3). During the initial spring colonization period, soybean plants were in the vegetative stages, and the number of soybean aphids for each sampling method was relatively low. This suggests that only a few alates provide the foundation of apterous colonies within fields, and the subsequent increasing production of alates colonize within a field or between fields during soybean reproductive stages. For both years, the peak number of soybean aphids in pan traps was preceded by a midseason peak in aphid numbers on plants (Fig. 3). The peak number of soybean aphids in pan traps was delayed and could potentially be a result of alatoid production from crowded plant conditions during the previous sample week.

The regression analysis demonstrated a positive relationship between $\log(x+1)$ transformed pan traps and whole-plant counts ($n = 48$; $y = [0.758 \pm 0.09\ (\pm SE)]\ x - [0.782 \pm 0.08]$; $r^2 = 0.63$) (PROC REG; SAS Institute 2001) (Fig. 4). Although pan traps only collect alates, this equation could be useful for estimating soybean aphid densities on plants. Knowing that pan trapping provides a relative measure of soybean aphids on plants could be implemented in future studies regarding seasonal aphid movement. Elberson and Johnson (1995) found a relationship between suction trap counts and field counts for *Diuraphis noxia* (Kurdjumov), and suggest suction traps can be an effective sampling method for predicting immigrating populations.

Taylor's power law *a* and *b* dispersion values for pan trapping ($a = 0.85$, $b = 1.63$, $r^2 = 0.96$) were comparable to field counts ($a = 1.67$, $b = 1.99$, $r^2 = 0.93$). The *b*-value was significantly greater than 1 for pan trap counts ($t = 14.82$; $df = 64$; $P < 0.0001$) and whole-plant counts ($t = 14.01$; $df = 64$; $P < 0.0001$). A *b*-value significantly greater than 1 indicates an aggregated dispersion pattern. In China, the soybean aphid also has

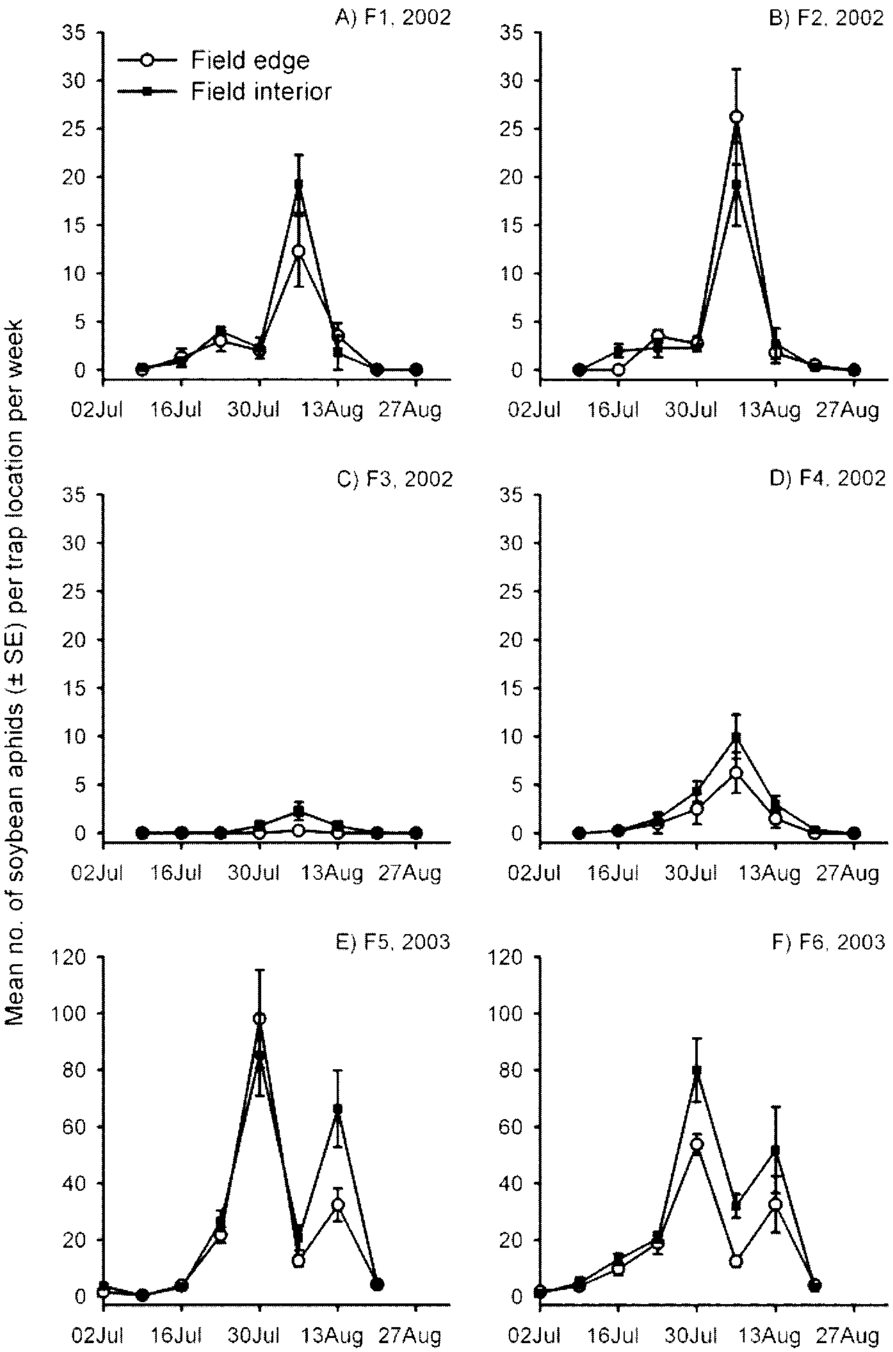

Fig. 2. Comparison of soybean aphids trapped at the field edge versus field interior in 2002 and 2003.

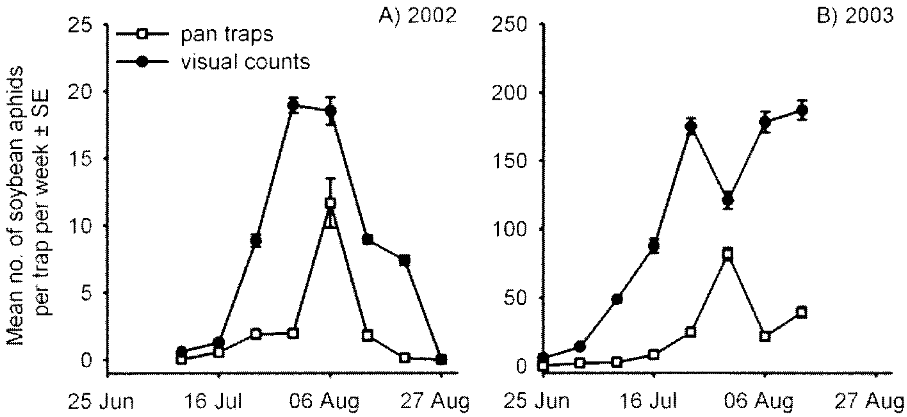

Fig. 3. Phenology of soybean aphids (averaged across fields) from pan trapping counts and whole-plant counts in 2002 and 2003.

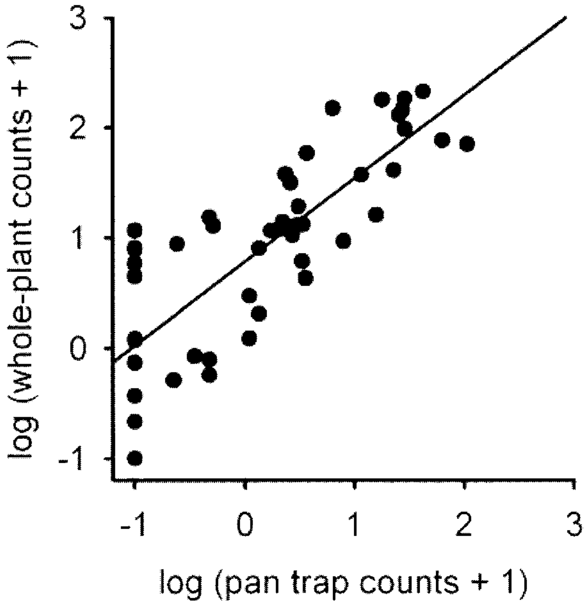

Fig. 4. Relationship of whole-plant counts to pan trap counts ($n = 48$; $y = [0.758 \pm 0.09$ (±SE)] $x - [0.782 \pm 0.08]$; $r^2 = 0.63$).

been reported as an aggregated species in soybean (Liu 1986, Su et al. 1996, Huang et al. 1992).

The precision for whole-plant counts was always greater than recommended for pest management purposes (i.e., 25%; Southwood 1978); however, precision for pan trapping was less than 25% when alate counts were low in 2002 (Fig. 5). Overall, whole-plant counts were more precise than pan trapping throughout the entire growing season for both years (Fig. 5). The relative net precision for pan trapping (0.67) was less than whole-plant counts (4.21) and indicates pan trapping requires considerably more effort; therefore, pan trapping is not likely to be a practical option for crop professionals. However, future research possibilities could include the use of pan trapping to study the landing preference on different varieties, various growth stages, or in the presence of some crop protection chemicals with a repellent effect.

During spring colonization (2002: 9-22 July; 2003: 2-15 July) there were no significant differences in trap catch among field sizes, directions within fields or locations within fields (Table 1). In addition, all interactions were also not significant ($P > 0.05$). The lack of a significant difference in trap catches among directions and locations in a field indicates that such traps can be placed anywhere in the field without introducing bias during spring colonization.

Site-specific management (i.e., targeted insecticide applications) is appropriate for insects that are aggregated during initial colonization; targeted applications can direct control, improve cropping economics, reduce exposure to animals and the environment, and provide refuge to natural enemies (Weisz et al. 1995, 1996). Site-specific management is currently recommended for green peach aphid, *Myzus persicae* (Sulzer), on potato, *Solanum tuberosum* L., field edges (Suranyi et al. 1999, Carroll 2005). Our results contrast with the field edge colonizing behavior of grain aphid, *Sitobion avenae* F. (Winder et al. 1999) and green peach aphid (Carroll 2005). However, Nault et al. (2004) suggest soybean aphid, pea aphid (*Acyrthosiphon pisum* (Harris)), corn leaf aphid (*Rhopalosiphum maidis* (Fitch)), and yellow clover aphid (*Therioaphis trifolii* (Monell)) all disperse randomly in snap bean, *Phaseolus vulgaris* L. Differences in alate spring colonization may be due to the overwintering potential of the aphid species and proximity to secondary hosts in the spring. Landing behavior appears to vary among aphid species and cropping systems; therefore, one management tactic is not appropriate for all aphids. Because soybean aphid does not preferentially land

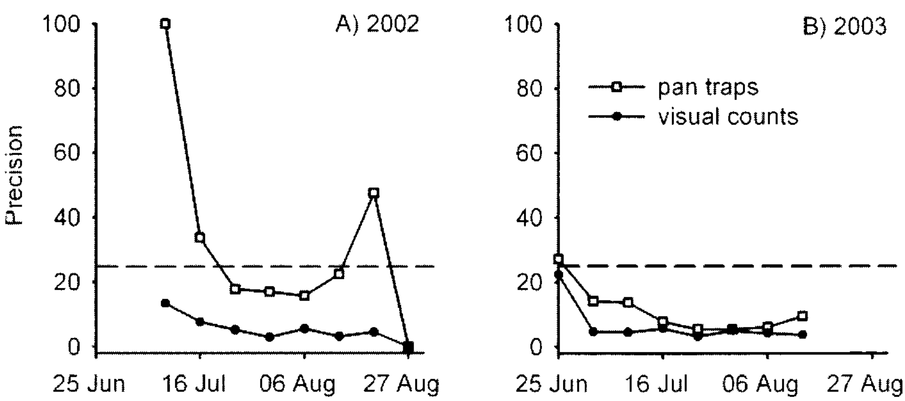

Fig. 5. Precision [$D = (SE/\bar{x}) * 100$] of pan trapping counts and whole-plant counts for soybean aphid throughout the growing seasons of 2002 and 2003; dashed line indicates acceptable precision for pest management purposes ($D < 0.25$).

Table 1. Analysis of variance for log(x + 1) transformed soybean aphid counts collected with pan traps in soybean fields in 2002 and 2003

Source	df	*F*	*P*
2002			
Field size*	1, 31	0.06	0.81
Direction**	3, 31	1.40	0.27
Location†	1, 31	1.43	0.24
2003			
Direction**	3, 31	0.74	0.54
Location†	1, 31	0.83	0.37

All two- and three-way interactions were not significant ($P > 0.05$) for each year.
* 4 vs. 20 ha.
** Four carcinal directions.
† Field edge versus field interior.

at field edges, we cannot recommend the use of border or perimeter treatments as a means of control.

Soybean aphid populations in pan traps tracked the population found using whole-plant counts except pan traps showed a slight lag. Both sampling methods had acceptable levels of precision ($D < 0.25$) for most of the season, and in general, pan traps seem to be a good tool for monitoring aphid populations. However, the additional cost and resulting lower relative net precision may preclude the use of pan trapping for some projects. Despite the additional costs, pan trapping holds value for monitoring aphid colonization and migration.

Acknowledgments

The authors thank A. Pereira and A. Jensen for helping sample fields and collect samples. We also thank W. D. Hutchison (Department of Entomology, University of Minnesota) and two anonymous reviewers for critical comments of this manuscript. This work was funded by the North Central Soybean Research Program, the Minnesota Soybean Research and Promotion Council, and the University of Minnesota College of Agriculture, Food and Environmental Sciences Rapid Agricultural Response Fund.

References Cited

Boiteau, G. 1990. Effect of trap color and size on relative efficiency of water-pan traps for sampling alate aphid (Homoptera: Aphididae) on potato. J. Econ. Entomol. 83: 937-942.

Carroll, M. W. 2005. Spatial distribution of the green peach aphid, *Myzus persicae* (Sulzer), and management applications in seed potato. Ph.D. Diss., Univ. Minnesota, St. Paul, MN.

Elberson, L. R. and J. B. Johnson. 1995. Population trends and comparison of sampling methods for *Diuraphis noxia* and other cereal aphids (Homoptera: Aphididae) in Northern Idaho. Environ. Entomol. 24: 538-549.

Favret, C. and D. J. Voegtlin. 2001. Migratory aphid (Hemiptera: Aphididae) habitat selections in agricultural and adjacent natural habitats. Environ. Entomol. 30: 371-379.

Hanafi, A., E. B. Radcliffe and D. W. Ragsdale. 1995. Spread and control of potato leafroll virus in the Souss Valley of Mororcco. Crop Prot. 14: 145-153.

Hodgson, E. W. 2005. Population dynamics and sampling for soybean aphid. Ph.D. Diss., Univ. Minnesota, St. Paul, MN. Pp.146.

Hodgson, E. W., E. C. Burkness, W. D. Hutchison and D. W. Ragsdale. 2004. Enumerative and binomial sequential sampling plans for soybean aphid (Homoptera: Aphididae) in soybean. J. Econ. Entomol. 97: 2127-2136.

Huang, F., X. Ding, X. Wang and Z. Huang. 1992. Studies on the spatial distribution pattern of soybean aphid and sampling techniques. J. Shenyang Agric. Univ. 23: 81-87.

Hutchins, S. H. 1994. Techniques for sampling arthropods in integrated pest management, Pp. 73-97. *In* L. P. Pedigo and G. D. Buntin (eds.), Handbook of sampling methods for arthropods in agriculture. CRC, Boca Raton, FL.

Irwin, M. E. 1980. Sampling aphids in soybean fields, Pp. 239-259. *In* M. Kogan and D. C. Herzog (eds.), Sampling methods in soybean entomology. Springer-Verlag, New York, NY.

Liu, Z. 1986. Spatial distribution pattern and sequential sampling of soybean aphid. Plant Prot. 12: 16-18.

Macedo, T. B., C. S. Bastos, L. G. Higley, K. R. Ostlie and S. Madhavan. 2003. Photosynthetic response to soybean aphid (Homoptera: Aphididae) injury. J. Econ. Entomol. 96: 188-193.

McCornack, B. P., M. A. Carrillo, R. C. Venette and D. W. Ragsdale. 2005. Physiological constraints on the overwintering potential of the soybean aphid (Homoptera: Aphididae). Environ. Entomol. 34: 235-240.

Musser, F. R., J. P. Nyrop and A. M. Shelton. 2004. Survey of predators and sampling method comparison in sweet corn. J. Econ. Entomol. 97: 136-144.

Nault, B. A., D. A. Shah, H. R. Dillard and A. C. McFaul. 2004. Seasonal and spatial dynamics of alate aphid dispersal in snap bean fields in proximity to alfalfa and implications for virus management. Environ. Entomol. 33: 1593-1601.

National Agricultural Statistics Service. 2004. Statistics of oilseeds, fats, and oils, Pp. 13-20. *In* Agricultural Statistics 2004, http://www.usda.gov/nass/pubs/agr04/04_ch3.pdf (25 April 2005).

Ostlie, K. 2001. Soybean aphid reduces yields: harvest results from insecticide strip trials. University of Minnesota, St. Paul, MN. http://www.soybeans.umn.edu/crop/insects/ aphid/ studyresults/htm (27 January 2004).

Pedigo, L. P. 1994. Introduction to sampling arthropod populations, Pp. 1-11. *In* L. P. Pedigo and G. D. Buntin (eds.), Handbook of sampling methods for arthropods in agriculture. CRC, Boca Raton, FL.

Pedigo, L. P., G. L. Lentz, J. D. Stone and D. F. Cox. 1972. Green cloverworm populations in Iowa soybean with special reference to sampling procedure. J. Econ. Entomol. 65: 414-421.

Powell, W., M. P. Walton and M. A. Jervis. 1996. Populations and communities, Pp. 223-292. *In* M. Jervis and N. Kidd (eds.), Insect natural enemies: practical approaches to their study and evaluation. Chapman & Jall, London, England.

Ragsdale, D. W., D. J. Voegtlin and R. J. O'Neil. 2004. Soybean aphid biology in North America. Ann. Entomol. Soc. Am. 97: 204-208.

SAS Institute. 2001. PROC user's manual, 8.02. SAS Institute, Cary, NC.

Southwood, T. R. E. 1978. Ecological methods, with particular reference to the study of insect populations. Chapman and Hall, London.

Stephens, E. J. and J. E. Losey. 2004. Comparison of sticky cards, visual and sweep sampling of coccinellid populations in alfalfa. Environ. Entomol. 33: 535-539.

Su, J., K. Hai and X. Shi. 1996. Spatial distribution and sampling techniques of *Aphis glycines* Matsumara. J. Nanjing Agric. Univ. 19: 55-58.

Suranyi, R. A., E. B. Radcliffe, D. W. Ragsdale, I. V. MacRae and B. E. L. Lockhart. 1999. Aphid alert: A research/outreach initiative addressing potato virus problems in the northern

Midwest. *In* E. B. Radcliffe and W. D. Hutchison (eds.), Radcliffe's IPM World Textbook. http://ipmworld.umn.edu/ (11 Nov 2004).

Taylor, L. R. 1961. Aggregation, variance and the mean. Nature 189: 732-735.

Venette, R. C. and D. W. Ragsdale. 2004. Assessing the invasion by soybean aphid (Homoptera: Aphididae): where will it end? Ann. Entomol. Soc. Am. 97: 219-226.

Weisz, R., S. Fleischer and Z. Smilowitz. 1995. Map generation in high-value horticultural integrated pest management: appropriate methods for site-specific pest management of Colorado potato beetle (Coleoptera: Chrysomelidae). J. Econ. Entomol. 88: 1650-1657.

1996. Site-specific integrated pest management for high-value crops: impact on potato pest management. J. Econ. Entomol. 88: 501-509.

Winder, L., J. N. Perry and J. M. Holland. 1999. The spatial and temporal distribution of the grain aphid *Sitobion avenae* in winter wheat. Entomol. Exp. Appl. 93: 277-290.