Assessing the Invasion by Soybean Aphid (Homoptera: Aphididae): Where Will It End?

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ABSTRACT The invasion of soybean aphid, *Aphis glycines* Matsumura, into soybean (*Glycine max* L.) production areas of the northcentral United States has generated substantial concern over the ultimate impact of this pest on domestic agriculture. To evaluate the potential extent and severity of its invasion in the United States, we examined possible pathways for the arrival of the insect, considered the likelihood for establishment in different regions of the United States, and described patterns of spread. Historical records of aphid interceptions by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service suggest that populations of soybean aphid most likely arrived in the United States from Japan or China, either carried by an international airline passenger or associated with horticultural cargo. Two methods of climate comparison suggest that the aphid may ultimately be present in all soybean producing areas of the United States. However, the severity of infestations within these areas is likely to vary considerably in space and time.

KEY WORDS risk assessment, geographic information system, exotic species, climate matching

THE ARRIVAL OF SOYBEAN APHID, *Aphis glycines* Matsumura, was announced to much of the United States in the *Wall Street Journal* in mid-August of 2000 (Kilman 2000). At the time, concerns were expressed about the origin of the pest, the aphid's rate of spread, the ultimate extent of the invasion, and the possible degree of damage. Predicting the range and impact of exotic species in a new habitat has long been a goal of invasion biologists (e.g., Elton 1958), but practical tools to help generate these forecasts have been slow to evolve (Mack 1996). Invasion biologists conceptually divide the process of invasion into a series of nondiscrete phases, typically arrival, establishment, and spread (e.g., Brown 1993, Williamson 1996, Venette and Carey 1998, Mack et al. 2002). Recently, the National Research Council (NRC) developed a series of questions (partially listed in Table 1) about each of these phases to help structure a research agenda and guide future pest risk assessments (Mack et al. 2002). In pest risk assessments, the goal is to characterize the likelihood and impact of invasion by an exotic species in a new geographic region. Herein, we consider some of the questions raised by the NRC as they pertain to soybean aphid.

Arrival. Questions about the arrival of soybean aphid may seem trivial initially. Obviously, soybean aphid has successfully arrived in the United States. However, attempting to answer these questions forces a more careful consideration of the potential source of the current aphid infestation.

Frequent Interceptions, Wide Geographic Range? The U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Plant Protection and Quarantine (USDA, APHIS, PPQ) maintains a database of plant pests intercepted at U.S. ports of entry. The database, the Port Information Network (PIN), stores records of exotic pests intercepted by PPQ officers during inspections of such pathways as international airline passengers (or more specifically, their baggage), cargo, mail, and cruise ships. The oldest interception records in PIN date to 1984. In addition to pest identity, the database includes 38 other information categories. The NRC recognizes PIN as one of the most useful sources of information to examine patterns in the arrival of exotic pests into the United States (Mack et al. 2002). The PIN database was accessed to investigate potential routes for the introduction of soybean aphid.

Six aphids in the genus *Aphis* are considered reportable by PPQ: *A. affinis* del Guercio, *A. callunae* Theobald, *A. euphorbiae tirucallis* Hille Ris Lambers, *A. grossulariae* Kaltenbach, *A. intybi* Koch, and "*Aphis* sp." Reportable species are generally not found in the United States or are of limited distribution and have the capacity to cause economic or environmental harm. Species that occur within a broad geographic area within the United States are considered nonreportable, and PPQ has designated 19 *Aphis* spp. as such. PIN only retains records for reportable taxa. *A.*

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Table 1. Selected questions identified by the National Research Council to evaluate the potential arrival, establishment, and spread of exotic arthropods

Arrival
Has the arthropod been frequently and recently intercepted or detected in North America?
Does the arthropod have a wide geographic range (proportional to likelihood of transport)?
Does the arthropod, at some times, have high population densities in its native range?
Establishment
Is there a history of establishment in a similar environment elsewhere outside its native range?
Is climate similar between the current geographic range and potential destinations?
Are potential hosts spatially and temporally available?
Is there uniparental reproduction?
Does the arthropod have a high growth rate?
Spread
Are potential hosts contiguously distributed?
Does the arthropod have an effective means of dispersal (natural or human-assisted)?

From Mack et al. (2002).

glycines does not yet appear on either list. Historically, if/when *A. glycines* had been intercepted, it would have been reported as "*Aphis* sp." or "Aphididae" and would have triggered an appropriate regulatory response.

PIN was queried for all interceptions of "*Aphis* sp." or "Aphididae." For each interception record, host plant, country of origin, port of entry, and pathway of introduction were requested. Because of differences in inspection techniques from port to port, analysis using traditional parametric statistics is not appropriate (Mack et al. 2002). As a result, simple summaries of the data are provided.

From 1985 to September 2002, PPQ officers reported 11,654 interceptions of *Aphis* sp. or Aphididae. The majority of interceptions were from pathways originating in Europe (25%) and South America (25%). The remainders were from Central America (14%), Asia (12%), North America (7%), Caribbean (7%), Pacific Islands (3%), Africa (2%), or unknown locations (2%). "*Aphis* sp." or Aphididae were intercepted on 802 plant taxa. Interceptions occurred most frequently from permit cargo (43%) and baggage (36%), which suggests that these pathways are the most likely means of aphid entry into the United States. However, *Aphis* sp. or Aphididae were also associated with ship stores (10% of all interceptions), general cargo (6%), ship quarters (3%), mail (1%), and ship holds and miscellaneous pathways (<1%). It is extremely unlikely that most or even many of these interceptions were of *A. glycines.* Taxonomists recognize 4,702 species of Aphididae (Remaudière and Remaudière 1997) and >400 species of *Aphis* (Blackman and Eastop 2000). Our knowledge of the geographic distribution and host range of *A. glycines* can help us select records that may be more indicative of pathways for the arrival of this particular aphid.

Soybean aphid occurs throughout much of eastern Asia (Fig. 1). The species has been reported from China, Japan, Malaysia, Philippines, Taiwan, Thailand (Raychaudhuri 1980, Blackman and Eastop 2000), India (West Bengal) (Raychaudhuri 1980), Korea (Paik 1966), Indonesia (van den Berg et al. 1997), Vietnam, and eastern portions of the former Soviet Union (CAB 2000). The aphid may also be present in Kenya (Singh and van Emden 1979), but the occurrence of the species in Africa is not generally recognized. In 2000, soybean aphid was reported as a newly introduced species in Australia. Aphids that spawned the U.S. infestation could have originated from any of these countries.

The host range for *A. glycines* is moderately restricted. The primary (i.e., overwintering) host was originally reported as *Ramnus davurica* Pallas but now includes many *Rhamnus* spp. (Zhang and Zhong 1982, Takahashi et al. 1993, Blackman and Eastop 2000, Voegtlin et al. 2004). Secondary (i.e., summer) hosts are restricted to members of Fabaceae. Preferred hosts include *Glycine max* L. Merr. (Zhang and Zhong 1982), *G. soja* Sieb. and Zucc. (Patch 1939), *Pueraria phaseoloides* (Roxb.) Benth., *Pueraria phaseoloides* variety *javanica* (Benth.) Baker, and *Desmodium intortum* (P. Mill.) Urban (Blackman and Eastop 2000). Soybean aphid also feeds and reproduces well on *Trifolium pratense* L., *T. alexandrinum* L., *T. incarnatum* L., and *T. ambiguum* M. Bieb. (Alleman et al. 2002). The aphid feeds but reproduces poorly on other clovers (*T. repens* L., *Melilotus alba* Medikus, and *M. officinalis* L. Lam.), snap beans (*Phaseouls vulgaris* L.), and alfalfa (*Medicago sativa* L.); aphid nymphs are unable to develop into adults on certain varieties of these species (Alleman et al. 2002). Soybean aphid may also probe, but not reproduce, on Solanaceae, such as tobacco (*Nicotiana tabacum* L., Fang et al. 1985) and potato (*Solanum tuberosum* L., Ragsdale and McCornack 2002) and is capable of transmitting several plant viruses (Hill et al. 2001, Clark and Perry 2002, Davis et al. 2003).

Table 2 lists interceptions of *Aphis* sp. or Aphididae from countries known or believed to have soybean aphid. Reported interceptions from Japan are ≥1.8 times greater than from any other nation or province. Interceptions from Japan, China, Korea, Australia, and the Philippines are of the same order of magnitude. Not all of these records list a potential host for soybean aphid. Interceptions of aphids not clearly associated with any host material (i.e., "at large") or on unspecified plants are greater from China, Japan, and Korea than any other nation. No intercepted aphids have been reported from *Rhamnus* sp. Interceptions of *Aphis* sp. or Aphididae on Fabaceae have the greatest likelihood of being soybean aphid and are greater from Japan and the Philippines than from any other country. Relative to the total 11,654 interceptions of *Aphis* sp. or Aphididae, interceptions of soybean aphid have probably been infrequent historically.

High Densities in Native Range? Soybean aphid can reach high densities in eastern Asia. In the Philippines, Quimio and Calilung (1993) noted a high density of 236 individuals per leaf on V8-R1 staged soybeans. In China, Wang et al. (1996) observed a density of 856 aphids per plant at the early flower stage of soybean

Fig. 1. Distribution of soybean aphid outside the new world. Soybean aphid has been present historically in areas shaded in gray and was detected in 1999–2000 in Western Australia.

in Jilin Province, and Xincai (1997) reported 188 aphids per plant at a late vegetative stage in Hubei Province. In Korea, Chung et al. (1980) reported 50 aphids per leaf; van den Berg et al. (1997) noted ≈60 aphids per plant under high aphid pressure in Indonesia. Because the soybean aphid can achieve such high densities, it is considered an important pest of soybeans in China, Japan, Korea, Indonesia (van den Berg et al. 1997), and the Philippines (Quimio and Calilung 1993). In contrast, Hill (1983) lists soybean aphid as a pest of minor economic importance in southeast Asia. In Thailand, soybean aphid is only a seasonal pest, despite the fact that host plants are available year-round (Talekar and Chen 1983).

Table 2. Interceptions of "*Aphis* sp." or "Aphididae" by USDA, APHIS, PPQ from multiple pathways originating in a country or municipality with soybean aphid

Country of origin	Interceptions		
	Total[a]	At large or on unspecified plant	On Fabaceae
Australia	102	10	0
Cambodia	11	0	0
China	168	23	0
Hong Kong	35	3	0
India	49	10	0
Indonesia	7	0	0
Japan	299	22	4
Kenya	24	4	0
Korea	150	21	1
Laos	11	1	0
Malaysia	14	2	0
Philippines	108	12	5
Russian Federation	37	2	0
Singapore	35	3	1
Thailand	69	10	1

[a] Irrespective of associated host and including aphids at large, on an unspecified plant, or on Fabaceae.

Establishment. Soybean aphid survives winters in North America and maintains populations through local reproduction (Ragsdale et al. 2004). However, the invasion of all soybean producing regions within the United States is not yet complete and may not be possible. Addressing the following series of questions on establishment allows us to consider the potential future extent of the invasion.

History of Establishment in Climatically Similar Regions? During the 1999–2000 growing season, soybean aphid was reported for the first time from Australia (Fletcher and Desborough 2000). Populations were noted in Queensland and New South Wales (Fletcher and Desborough 2000). The lowest annual temperature for these two Australian states on average is between −10 and 5°C, which roughly corresponds to USDA plant hardiness zones 8–10 (Dawson 1991), which are present in the far southeastern portion of the U.S. soybean production region. Thus, the invaded area in Australia shows some degree of climatic sim-

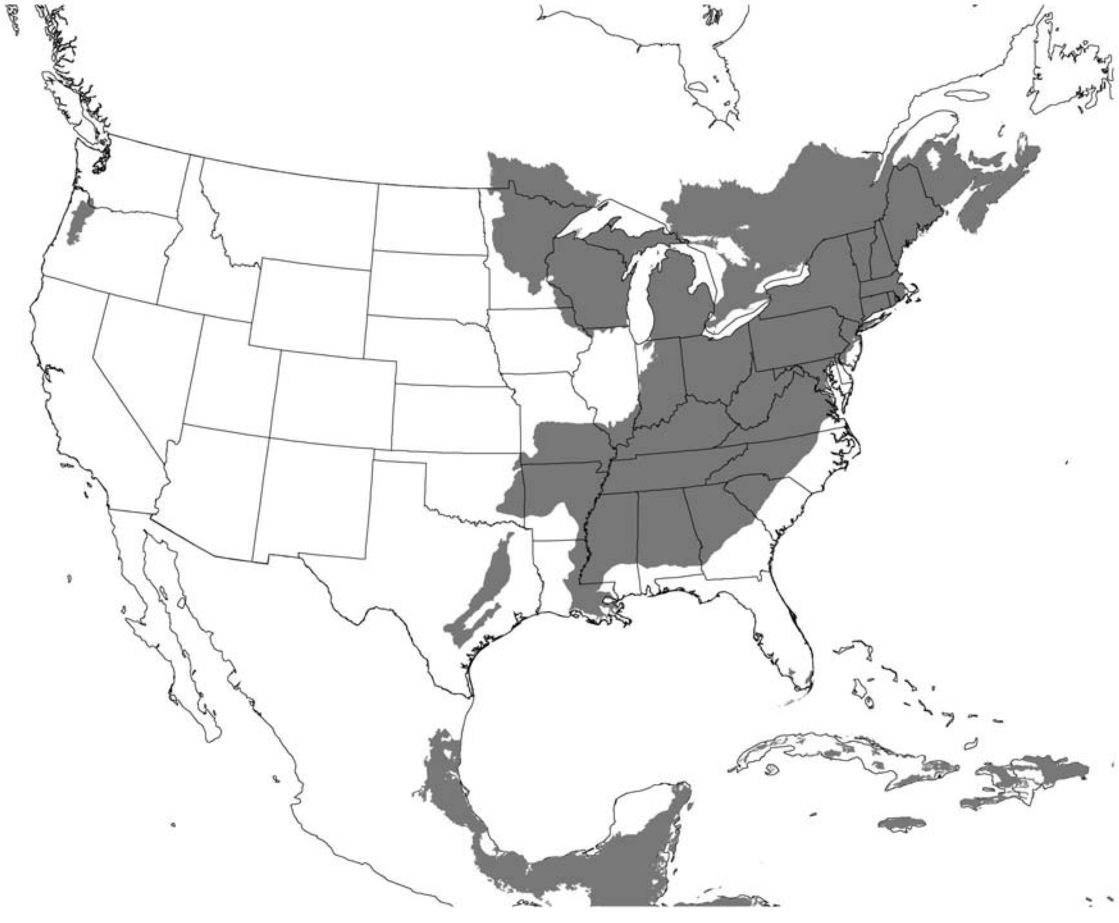

Fig. 2. Predicted regions within North America (shaded gray) likely to provide a suitable climate for soybean aphid as estimated by the similarity of biomes in Asia and North America.

ilarity to the United States, and the invasion of Australia by soybean aphid should have been cause for concern in the United States. We note, however, that until recently, soybean aphid had not been reported from zones 8–10 in the United States.

Climatic Similarity? Climatic comparisons have long been used to evaluate where introduced species might become established within a new geographic region (Mack et al. 2002). Such predictions are useful for establishing the maximum area that might support populations of a species, although additional biotic and abiotic constraints may further limit the distribution of a species. Nevertheless, we present two methods of climate matching to describe the potential distribution of soybean aphid in the United States.

First, we used a geographic information system (ArcView 3.2; ESRI, Redlands, CA) to determine which terrestrial biomes, as defined by Olson et al. (2001), may support populations of soybean aphid within its native range. In this simple analysis, we presume those biomes would provide climatically suitable habitat for soybean aphid if they occur in the United States. The known geographic distribution of soybean aphid (Fig. 1) was overlaid on a map of the worldwide distribution of biomes. A list was prepared of the biomes that occurred within each respective country or municipality where soybean aphid had been reported.

Because soybean aphid may not be distributed throughout a country, using all biomes from all countries reporting soybean aphid as a basis of prediction is likely to overestimate the potential distribution of the species. As a result, an analysis of parsimony was conducted to identify the minimum number of biomes that could account for the worldwide distribution of soybean aphid. If only one biome was reported for a location where soybean aphid occurs, this biome must be suitable for the species. A short list was prepared of the biomes that occurred in states or countries with just one biome. This list was compared with the biomes reported for other countries or states. If a country or state had a biome that already appeared on the short list, we assumed this area was accounted for. For locations with biomes that did not appear on the short list, those biomes that occurred in the greatest number of countries or states were added to the short list. The process of adding additional biomes to the short list continued until at least one biome was noted from each location with soybean aphid. Biomes on the short list were evaluated for their presence in the United States.

In a second analysis, we matched the climates of five Asian cities to the climate of North America. Asian cities were Harbin (China), Seoul (South Korea), Sapporo (Japan), Osaka (Japan), and Echague (Philippines). Soybean aphid has been reported as problematic in or near these locations. Because soybean aphid is not generally considered problematic in mainland Southeast Asia, no cities were selected from this region. Climate comparisons were performed in Climex (Sutherst et al. 1999) based on 30-yr average minimum temperature, maximum temperature, precipitation (annual total), and precipitation pattern. Similarity based on each climatic parameter is expressed as an index from 0 to 100. The four indices are combined into a single measure of overall climatic similarity (Sutherst et al. 1999).

Three biomes account for the reported distribution of soybean aphid in Africa and eastern Asia. The biomes are temperate broadleaf and mixed forests; tropical and subtropical dry broadleaf forests; and tropical and subtropical moist broadleaf forest. Tropical and subtropical dry broadleaf forests do not occur in the United States. Temperate broadleaf and mixed forests account for 27.9% of the area of the conterminous United States, whereas tropical and subtropical moist broadleaf forests represent <0.1%. Figure 2 illustrates the distribution of habitat types predicted to be suitable for soybean aphid in North America. This admittedly crude prediction suggests that the mid-Atlantic states, the Great Lakes states, the northeastern United States, and much of the Southeast should provide a suitable habitat for soybean aphid.

The climate in areas of Asia where soybean aphid has been reported as a pest is similar to much of the United States. In general the degree of climatic similarity is greater in the eastern United States than in the West. Figure 3 illustrates that the pattern and degree of climatic similarity changes considerably depending on which Asian city is examined. The climate of Harbin is most similar to that of central North America (Fig. 3A). Seoul is only moderately similar (50–70%) to any location in North America (Fig. 3B). The climate of Sapporo is most similar to that of the Great Lakes states, the mid-Atlantic region, and New England (Fig. 3C). The climate of Osaka is most similar to much of the southeastern United States (Fig. 3D). Echague is only moderately similar to the southern portions of the Gulf Coast states (Fig. 3E). Presumably, as the degree of climatic similarity increases between a North American location and an Asian city reporting soybean aphid as a pest, the likelihood that soybean aphid would act as a pest in North America also increases. However, the relationship between climatic similarity and pest status may be nonlinear (Venette and Hutchison 1999), complicating the interpretation of the match indices. The environmental conditions that are likely to support outbreaks of soybean aphid have yet to be determined. Both the comparison of biomes and the climate matching analysis indicate that much of the eastern United States is

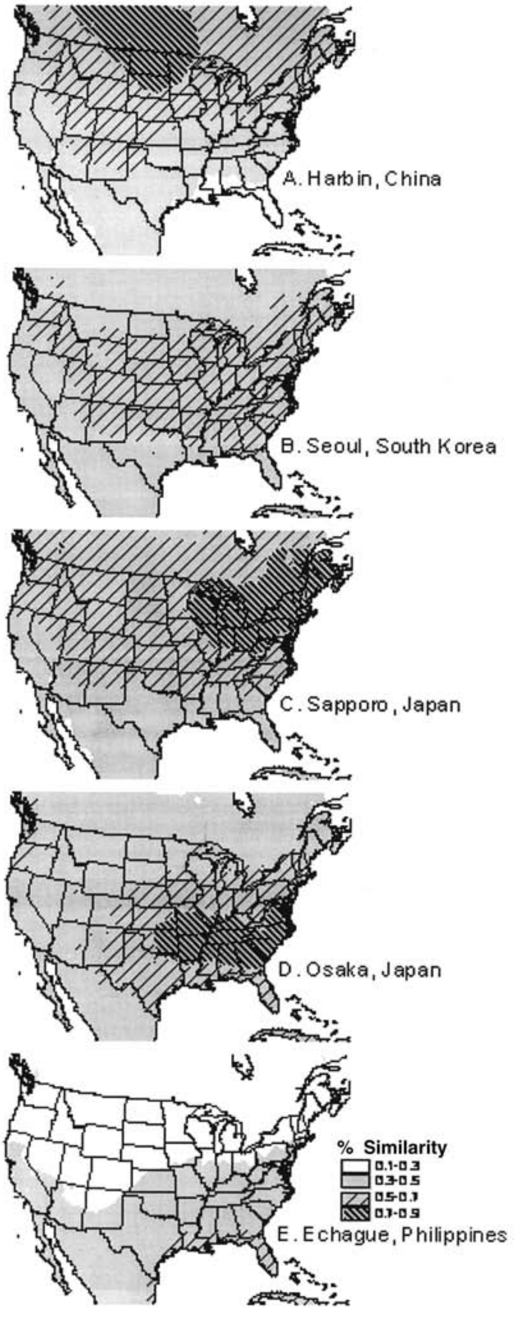

Fig. 3. Similarity of the climate in North America to five Asian cities in or near regions reporting soybean aphid as a pest.

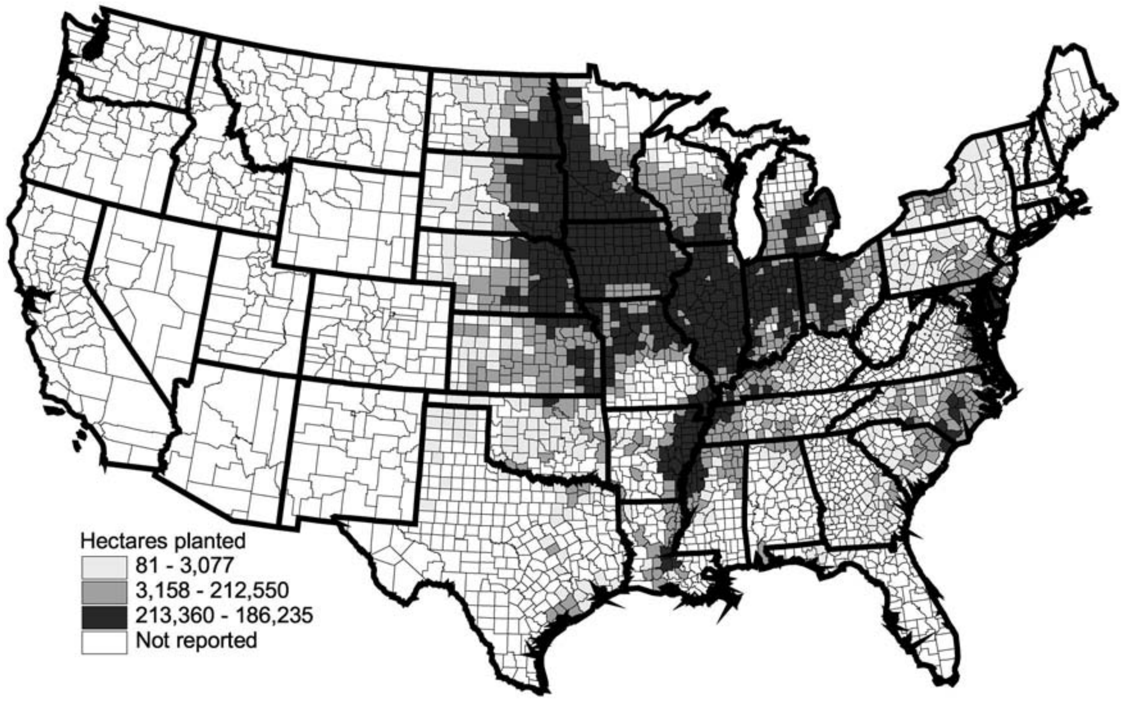

Fig. 4. County-level estimates of the area planted to soybeans (Data from U.S. Dep. Agric. 2001).

likely to provide a suitable climate for soybean aphid; climate matching adds most states in the Great Plains to the potentially suitable area.

Hosts Available? Within areas of high climatic similarity (>70%), both summer and winter hosts are readily available. *Rhamnus cathartica* L. and *Frangula alnus* P. Mill (Rhamnaceae) were both introduced to the United States and are present in the eastern and central United States and Canada (USDA 1999). Voegtlin et al. (2004) have shown that alderleaf buckthorn, *R. alnifolia* L'Hér, a native species distributed throughout much of the northern half of the continental United States (USDA 1999), also serves as a primary host. Soybeans are widely produced in these areas (Fig. 4). In 2001, the area planted to soybean (*G. max*) was greatest in Iowa (4.5 million ha), Illinois (4.3), Minnesota (3.0), Indiana (2.3), Missouri (2.0), and Nebraska (2.0) (USDA 2001). Collectively, these five states accounted for 60% of the area planted to soybean in the United States.

Uniparental Reproduction, High Growth Rate? Local reproduction is not likely to be constrained by the availability of mates. Soybean aphids reproduce parthenogenetically during the summer. If summer hosts were available and weather conditions were suitable, soybean aphids could presumably overwinter as apterae and avoid the sexual stage altogether. Because all individuals in a summer population are female, soybean aphid can have an exceptionally high population growth rate. Hirano et al. (1996) measured a maximum intrinsic rate of increase (r_m) at 27°C of $0.533\ d^{-1}$, which translates to a doubling time of 1.3 d.

Spread. In 2000, soybean aphid was first detected in Wisconsin (Alleman et al. 2002). Subsequent surveys detected the pest in Michigan, Indiana, Illinois, Missouri, Iowa, Ohio, West Virginia, Kentucky, and Minnesota (Fig. 5). In 2001, distribution of the aphid expanded to 15 states, with new finds in Virginia, Pennsylvania, New York, and North and South Dakota. In 2002, the range of the aphid in the United States continued to expand, with a total of 20 states reporting the presence of the aphid. Nebraska, Kansas, Delaware, Georgia, and Mississippi reported the aphid for the first time in 2002. Thus, soybean aphid could reasonably be expected to occur on nearly 80% of U.S. soybean production acreage.

The rapid spread of soybean aphid occurred despite the fact that aphids are generally considered weak flyers (e.g., Dixon and Howard 1986). However, it is well known that aphids are readily moved by wind, which has the potential to carry these insects long distances in a short period of time. Currently, no information suggests that commerce or other human activities commonly move soybean aphid.

Summary Assessment. Soybean aphid poses significant risks to U.S. agriculture. This threat was recognized by the Entomological Society of America as they prepared their list of "least wanted" insects that had not (yet) occurred in the United States (S. Halbert, personal communication). The origins of the U.S. infestation are not precisely known, but circumstantial evidence suggests that Japan could have been the source. A significant number of aphids have been intercepted from Japan, and the extent of the current

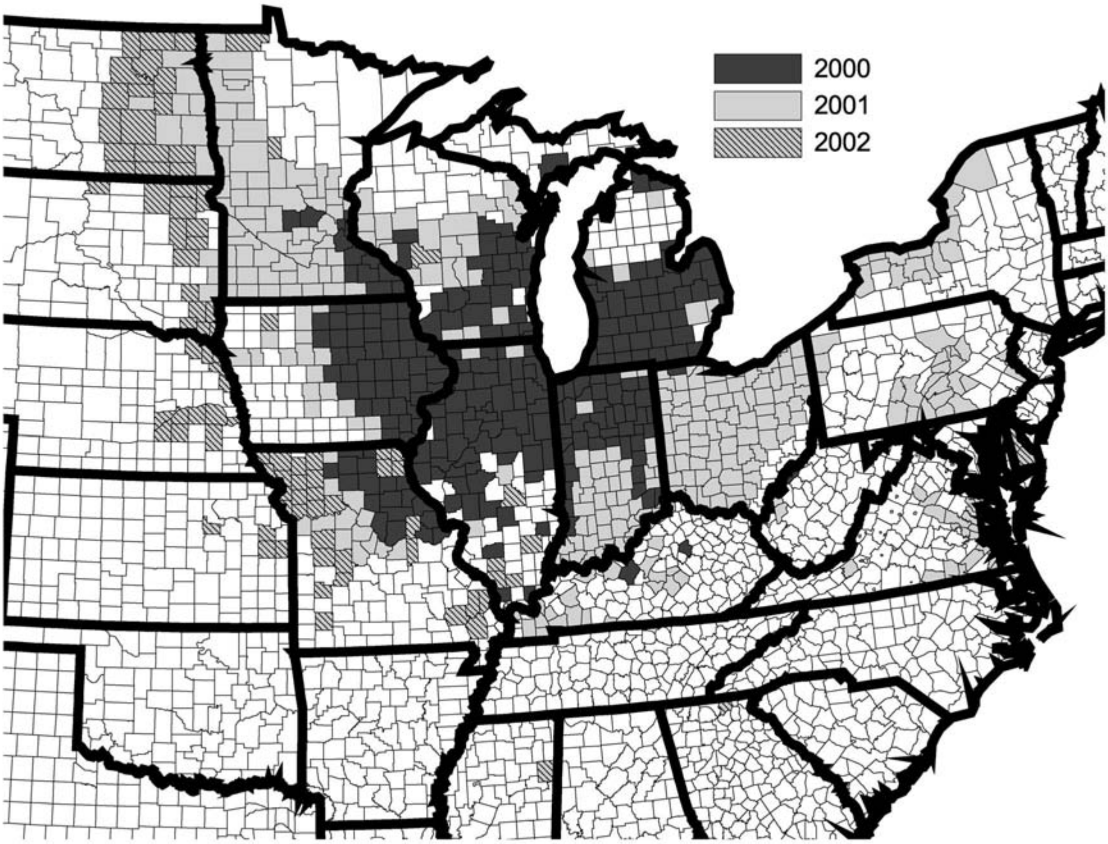

Fig. 5. Year in which soybean aphid was first detected in U.S. counties.

infestation seems consistent with patterns suggested by climate matching to Sapporo, Japan. The occurrence of soybean aphid in parts of the southeastern United States, as suggested by biome comparison, has only recently been observed (Fig. 5). Ultimately, soybean aphid is likely to spread into most, if not all, soybean producing areas of the United States. However, the arrival and establishment of soybean aphid in a particular production area does not automatically translate into lost production or income. The circumstances required for populations to outbreak and cause adverse economic impacts are the focus of future research.

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