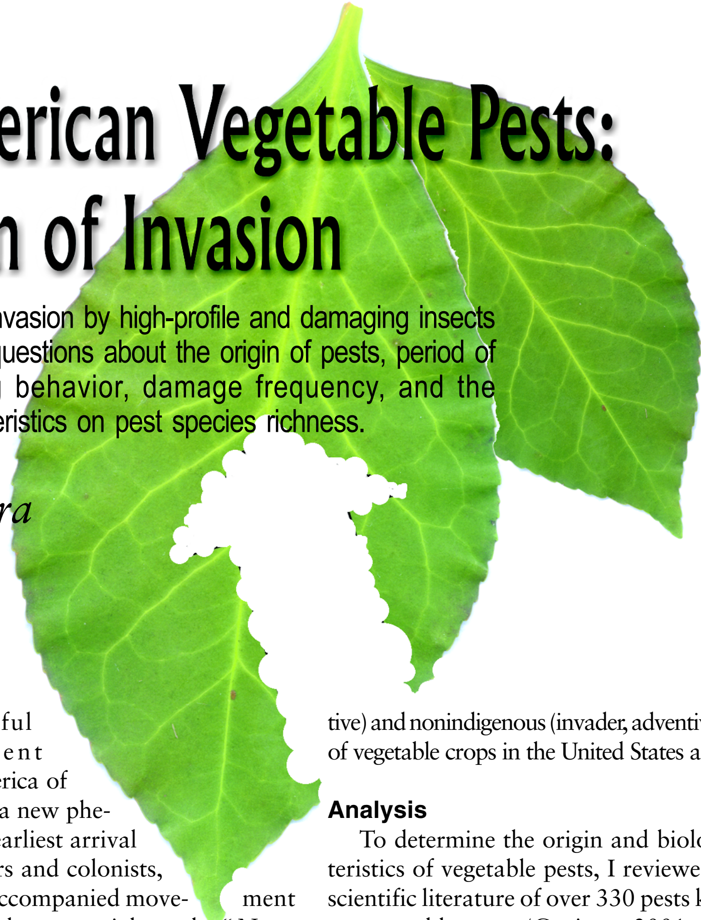
North American Vegetable Pests: The Pattern of Invasion



Increased concern over invasion by high-profile and damaging insects requires the answers to questions about the origin of pests, period of invasion, taxa, feeding behavior, damage frequency, and the influence of crop characteristics on pest species richness.

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The successful establishment in North America of invading pests is not a new phenomenon. Since the earliest arrival of European explorers and colonists, pests of plants have accompanied movement of people, food, and plant materials to the "New World." The long sea voyage during the initial stages of colonization likely inhibited extensive transport of many short-lived pests. Up until 1800, only about 36 species of insects invaded the United States (Simberloff 1986). However, by the late 1800s not only was the speed of transport greatly increased, but transport of living plant material (and associated pests) was commonplace.

Sailer (1978, 1983) analyzed the invasion of the United States by arthropods. He reported that initially the invaders (immigrants) consisted mostly of Coleoptera, which arrived principally in ship ballast. The dominance by beetles decreased as more Lepidoptera and then Homoptera invaded, often in association with living plant material. The rate of invasion increased greatly after the 1860s as international commerce expanded. Sailer also noted that there was a slight reduction in the rate of invasion commencing in the 1920s as the Plant Quarantine Act of 1912 was implemented.

Invasion by high-profile and damaging species in recent years has increased the awareness and concern by the scientific community, government, and the general public over invading species (U.S. Congress 1993, Simberloff et al. 1997, Sakai et al. 2001). The pattern of invasion is poorly documented, despite heightened concern, and many questions remain. Has the increase in international commerce and tourism in recent years resulted in higher rates of invasion and establishment of pests? Are we at greater risk from certain types of pests, or from certain sources? Are certain taxa of pests more likely to invade and establish successfully, and are all crops equally at risk? Here I address these questions and present a comparative analysis of indigenous (native) and nonindigenous (invader, adventive, exotic) pests of vegetable crops in the United States and Canada.

Analysis

To determine the origin and biological characteristics of vegetable pests, I reviewed the original scientific literature of over 330 pests known to feed on vegetable crops (Capinera 2001 and references therein), and compiled data on pest origin, period of introduction, host range, portion of plant damaged, and damage frequency. In most cases the literature contains reference to the likely source of these pests (126 of 135 invaders). However, for some cosmopolitan pests or poorly studied organisms the source is unknown or uncertain. Similarly, the period of detection in the United States and Canada varies from precise to unknown, with knowledge of the period of establishment (detection) limited to 87 of the 135 invading pests. Lack of data stems mostly from the early period of settlement, but invasions since 1900 are fairly well documented.

The host range of the vegetable pests is quite well documented in the literature, although there is a tendency for species that are better studied to have longer lists of hosts. Also, during periods of great abundance (outbreak), pests often use hosts that they will not normally accept. Thus, outbreak species probably have inflated host ranges. For the purposes of this analysis, I have defined a *narrow* host range to consist of consumption of vegetable plants from a single botanical family. A *moderate* host range consists of consumption of vegetable plants from two to five families, and a *wide* host range is defined as consumption of greater than five families of vegetable crops.

Damage frequency is based on the literature for each pest, as described elsewhere (Capinera 2001), and considers damage to both home gardens and commercial vegetable production. Damage frequency is designated as *rare* when there are few reports of serious injury in the literature. Damage frequency is considered *periodic* when there is general recognition that the organism is capable of causing crop injury, but the pest does not cause loss annually, and vegetable growers do not normally take preventative measures to guard against injury. Pest damage is considered *frequent* when the potential to cause injury exists annually in either home gardens or on farms, and characterizes pests for which vegetable producers annually plan for suppressive or preventive actions. Pests are designated as capable of periodic or frequent damage if this pattern is exhibited even in a limited geographic area, because most pests have limited geographic distribution.

Designation of the site of damage is based on the scientific literature, and consists of blossom (flower); fruit (seed-containing structure); foliage; stem or vine; tuber (below-ground storage organ); and root, bulb, or germinating seed (below-ground root-related structures).

The 332 pests considered in this analysis are, in nearly all cases, individual species. However, the economic literature tends to group some pests into complexes either because they are poorly known or difficult to differentiate. Therefore, a few pests (e.g., false wireworms, Coleoptera: Elateridae; white grubs, Coleoptera: Scarabaeidae) are treated as individual pests although more than one species is involved. Also, some literature is confusing because pests originally thought to be a single species have since been differentiated into species complexes (e.g., spinach and beet leafminers, *Pegomya* spp., Diptera: Anthomyiidae; dingy cutworms, *Feltia* spp., Lepidoptera: Noctuidae). These issues are minor, however, and likely have little effect on the analysis.

The aforementioned data on pest characteristics were analyzed by 2 × 2 contingency table analysis using Fisher's exact test (Zar 1984). In the case of feeding behavior, I compared the number of species with wide host range to the number of species with narrow host range for both indigenous and nonindigenous species. For the noctuid and pyralid analysis, I also analyzed the number of species with narrow and wide host ranges for each family. For damage frequency, I compared the number of species causing damage rarely or frequently for both indigenous and nonindigenous species.

Regression analyses were conducted on area planted to major commercial vegetable crops, total crop value, and unit value in relation to the total number of pest species or number of major pest species per crop. Major pest species were those capable of "frequent" and "periodic" damage, as described previously. Correlation analyses were performed on crop acreage and crop value data, and on crop acreage and crop unit value data. All data were log-transformed prior to linear regression or correlation (Graphpad Software 1993). Such transformation linearizes curvilinear relationships, and normalizes residuals and makes them homocedastic. Although not always improving the fit of the model (Conner and McCoy 1979), this is a common practice in analysis of species-area relationships. The crops analyzed in this manner were artichoke, asparagus, bean, broccoli, cabbage, cauliflower, carrot, celery, cucumber, lettuce, melons (primarily cantaloupe and honeydew), onion, pea, pepper, potato, spinach, sweet corn, sweet potato, tomato, and watermelon. Data on crop acreage and value are from Capinera (2001), and consist of summed American and Canadian values.

Origins of Vegetable Pests

Of the 332 vegetable pests considered in this analysis, 99% were successfully classified as either indigenous (native) or nonindigenous (invaders), and 59% appeared to be indigenous to the United States or Canada (*Appendix 1*). Similarly, Pimentel (1993) estimated that 63% of major American vegetable pests are indigenous, though this figure is based on a subset of vegetable crops. It is evident that our native fauna displays considerable plasticity in acquiring new hosts. This trend has been noted previously, and we can expect the number of pests to increase with time, and especially with the area planted to each particular crop (Strong 1974, Strong et al. 1977, McCoy and Rey 1983, Capinera et al. 1984a), as indigenous species adapt to imported host plants, or crops are exposed to additional potential pests in new geographic areas. However, species accrual on introduced crops occurs most rapidly soon after plant introduction, and species richness on crops does not increase indefinitely, leveling off after fewer than 300 years if there is not an increase in crop acreage (Strong 1974). Also, it is important to note that though indigenous pests form a large assemblage, they do not necessarily cause damage frequently (see discussion of pest damage below).

Europe is the principal origin of the nonindigenous vegetable pests found in North America. About 54% are thought to have originated there, or to have arrived in North America via that region (Fig. 1). This is not surprising because the United States and Canada were colonized principally by Europeans, who introduced European crops, and possibly allowed European pest "hitchhikers" to arrive. The introduction of crops, the repeated waves of European immigration, the extensive trade between Europe and North America, and the introduction of European ornamental plants to North America all contributed to the pre-

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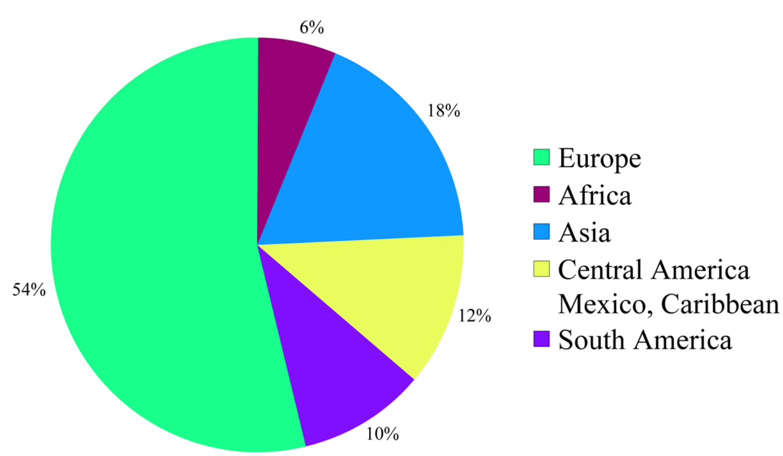

Fig. 1. Origins of vegetable pests (*n* = 126) that successfully invaded the United States and Canada, expressed in percentage.

The invasion of large numbers of European pests is not limited to North America, as it also has occurred in Australia, New Zealand, and South Africa

ponderance of European pests. Sailer (1978) also reported that non-indigenous species came predominantly from the European region (western Palearctic), although beneficial insects introduced for biological suppression of pests also were included in his calculations. Pimentel (1993) estimated that 37% of major American pests originated in Europe, although this estimate is based on a large number of crops, not just vegetables. Lindroth (1957) provided a long list of fauna common to Europe and North America. The invasion of large numbers of European pests is not limited to North America, as it also has occurred in Australia, New Zealand, and South Africa (Simmonds and Greathead 1977). Interestingly, North America has contributed relatively few insects to Europe's pest fauna. Lindroth (1957) suggested that North America contributed few species to Europe because shipments to Europe contained heavy, raw materials that did not necessitate ballast, whereas many sailing ships traveling to North America required ballast because they carried only small cargoes of refined goods.

Less well represented are pests from South America (10%), and Central America, Mexico, and the Caribbean region (12%). We might expect that with the proximity of these regions, and the Neotropical origins of many important crops cultivated in the United States and Canada (e.g., corn, beans, squash, potato), we might have a larger contingent of pests from Latin America. However, the aforementioned values are larger estimates than were developed by Sailer (1978) for immigrant (invaders plus deliberate introductions) fauna from these regions (6% for South America, and 7% for Mexico, Central America, and the Caribbean region). Sailer suggested that environmental resistance may account for the relatively small number of Neotropical pests in North America; invaders from the Southern Hemisphere are most likely to gain access to commercial transport during the southern summer months but may arrive in the Northern Hemisphere during the inhospitable northern winter months. Evidence for this is perhaps found in the very high pest invasion rates of Hawaii, Florida, and California (Sailer 1978, Dowell and Gill 1989, Frank and McCoy 1992), where environmental resistance is less of an issue for invaders (Sailer 1978).

Asia is well represented as a source of vegetable pests (18%), although Africa is poorly represented (6%), and Australia apparently contributed no pests to North America's vegetable pest fauna. The paucity of crops grown in North America that originate in Africa and Australia, as well as the relatively low level of commerce between North America and these continents, may account for these low figures.

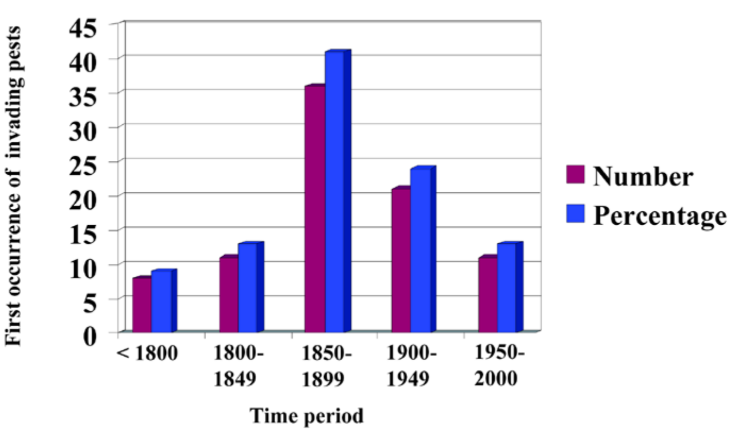

Fig. 2. Temporal pattern of invasion of United States and Canada by vegetable pests (n = 87), expressed as number and percentage in each time period.

Period of Invasion

Establishment of invading vegetable pests appears to have reached a maximum in the period of 1850-1899 (Fig. 2). This corresponds to a period of more rapid transport and increased commerce between North America and the rest of the world. However, the date of invasion of a considerable number of vegetable pests (36%) is uncertain. It is likely that many pests with unknown dates of invasion were established before 1800 or early in the 1800s, so the apparent increase in rate of invasion shown in Fig. 2 may be exaggerated. However, the establishment rate data since 1900 are quite reliable, reflecting advances in both the science of entomology and government support for regulatory activities. Thus, there is good evidence that the rate of invasion of vegetable pests has declined markedly during the 20th century. There remain in Europe many important vegetable pests that have not invaded North America, so I do not think that the "species pool" of good invaders has been depleted. In Asia and South America there are even larger numbers of prospective pests, and the level of commerce and speed of transport would suggest that more pests might be introduced successfully. Thus, the quarantine procedures and eradication efforts implemented by state and federal governments are producing benefits for the United States and Canada, at least with respect to vegetable pests.

The decreasing rate of establishment of invading pests reported herein should not be entirely surprising. Long-term analyses of arthropod introduction rates into California (Dowell and Gill 1989) and Florida (Frank and McCoy 1992, Florida Department of Agriculture unpublished data) demonstrate no increase in establishment rate, despite massive increases in tourism and commerce between the United States and elsewhere. Those data and the data reported herein on decreased vegetable pest invasion rates are hopeful signs, but hardly signal an end to problems with invading pests. Not only are invasions continuing, but we must bear the economic burden of the cumulative effects of a 300-year period of pest invasion. In an annoying number of cases, pests that were serious threats to vegetable production 100 years ago remain as significant pests. Thus, the economic burden (costs associated with old and new pests) tends to increase as new pests establish successfully, even if the rate of introduction is diminishing and suppressive technology is improving.

Taxa of Invading Pests

The number of vegetable-feeding pests in each taxon might be expected to reflect the number of plant-feeding species in that taxon. Indeed, some of the largest groups of vegetable-feeding species are in the large plant-feeding orders Coleoptera, Lepidoptera, Heteroptera, and Homoptera. Also, the species richness of taxa containing vegetable pests largely parallels that of pests in general as documented by the Commonwealth Institute of Entomology's world-wide perspective (Simmonds and Greathead 1977). Specifically, taxa such as the order Heteroptera, family Aphididae (order Homoptera), families Pyralidae and Noctuidae (order Lepidoptera), and families Curculionidae and Scarabaeidae (order Coleoptera), which contain many pests, also are especially well represented in the North American vegetable pest compilation. There are some exceptions, however, and taxa such as the families Chrysomelidae and Elateridae (order Coleoptera), families Agromyzidae and Anthomyiidae (order Diptera), family Miridae (order Heteroptera), and family Acrididae (order Orthoptera) tend to be slightly over-represented because North American vegetable pests as compared with pests in general as compiled by the Commonwealth Institute of Entomology.

There are some marked differences in taxonomic association of vegetable pests when the abundance of invading organisms is compared with the abundance of indigenous organisms (Fig. 3). The proportion of invading Coleoptera, Lepidoptera, Heteroptera, and Orthoptera is about one-half the level observed among indigenous species, whereas Homoptera, Diptera, and Gastropoda are several-fold more abundant among invaders. The greater abundance of invading Diptera and Gastropoda is likely due to the dumping of soil ballast containing these pests in American ports during the early period of colonization when ballast was needed by sailing ships, because these organisms are commonly associated with soil. In contrast, Homoptera are excellent "hitch-hikers" on plant material, and many undoubtedly were introduced accidentally with ornamental plants (Sailer 1978). Some examples of successful invaders are shown in Fig. 4.

Association of pests into large taxa (i.e., orders or classes) is convenient, but masks some important trends. Family-level analysis suggests some important differences in biological characteristics of insects that may account for pest status. The vegetable-feeding ground beetles (Carabidae), tortoise beetles (Chrysomelidae, subfamily Cassidae), blister beetles (Meloidae), sap beetles (Nitidulidae), seed bugs (Lygaeidae), woollybears (Arctiidae), hornworms (Sphingidae), grasshoppers (Acrididae), and field crickets (Gryllidae) are exclusively indigenous species. The flea beetles (Chrysomelidae, subfamily Alticinae), wireworms (Elateridae), cutworms (Noctuidae), and plant bugs (Miridae) are predominantly indigenous. Possibly these species are not good "stow-aways," although there are other explanations. The European fauna and the North American fauna are not completely equivalent, with groups such as grasshoppers (Acrididae) and wireworms (Elateridae) not particularly numerous or damaging in Europe, so there is little likelihood that they would be transported. Similarly, ground beetles (Carabidae) have been frequently transported to North America, where they successfully established (Lindroth 1957), but few species are considered to be pests. In contrast, the seed beetles (Bruchidae), mole crickets (Gryllotalpidae), and nearly all snail and slug (Gastropoda) pests are not indigenous. Invasion by seed beetles was likely unavoidable due to the dependency of early colonists on legume seeds which stored well for long periods of time. Mole crickets and slugs undoubtedly were accidentally introduced with soil ballast (Sailer 1978), though most snails were deliberately introduced as a source of food (Mead 1971). Other important taxa containing numerous invaders include the weevils (Curculionidae), white grubs (Scarabaeidae), root maggots and leaf miners (Anthomyiidae), and aphids (Aphididae). The curculionids, scarabaeids, and anthomyiids have soil-borne or cryptic stages, and aphids are difficult to detect, especially in the egg stage, so transport of these groups is understandable. Some of the more numerous plant-feeding taxa, including leaf beetles (Chrysomelidae), leaf miners (Agromyzidae), stalk borers (Pyralidae),

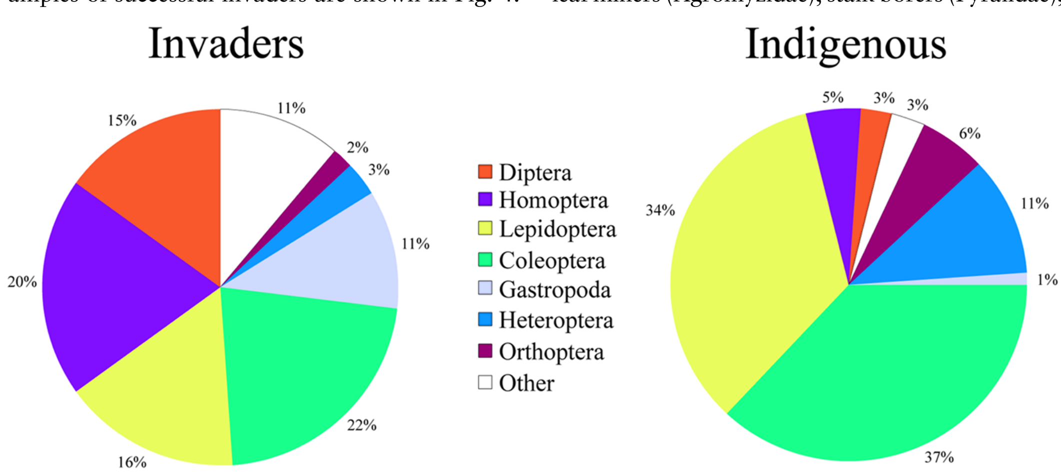

Fig. 3. Taxonomic distribution of invaders (*n* = 135) and indigenous vegetable pests (*n* = 197) expressed as percentage.

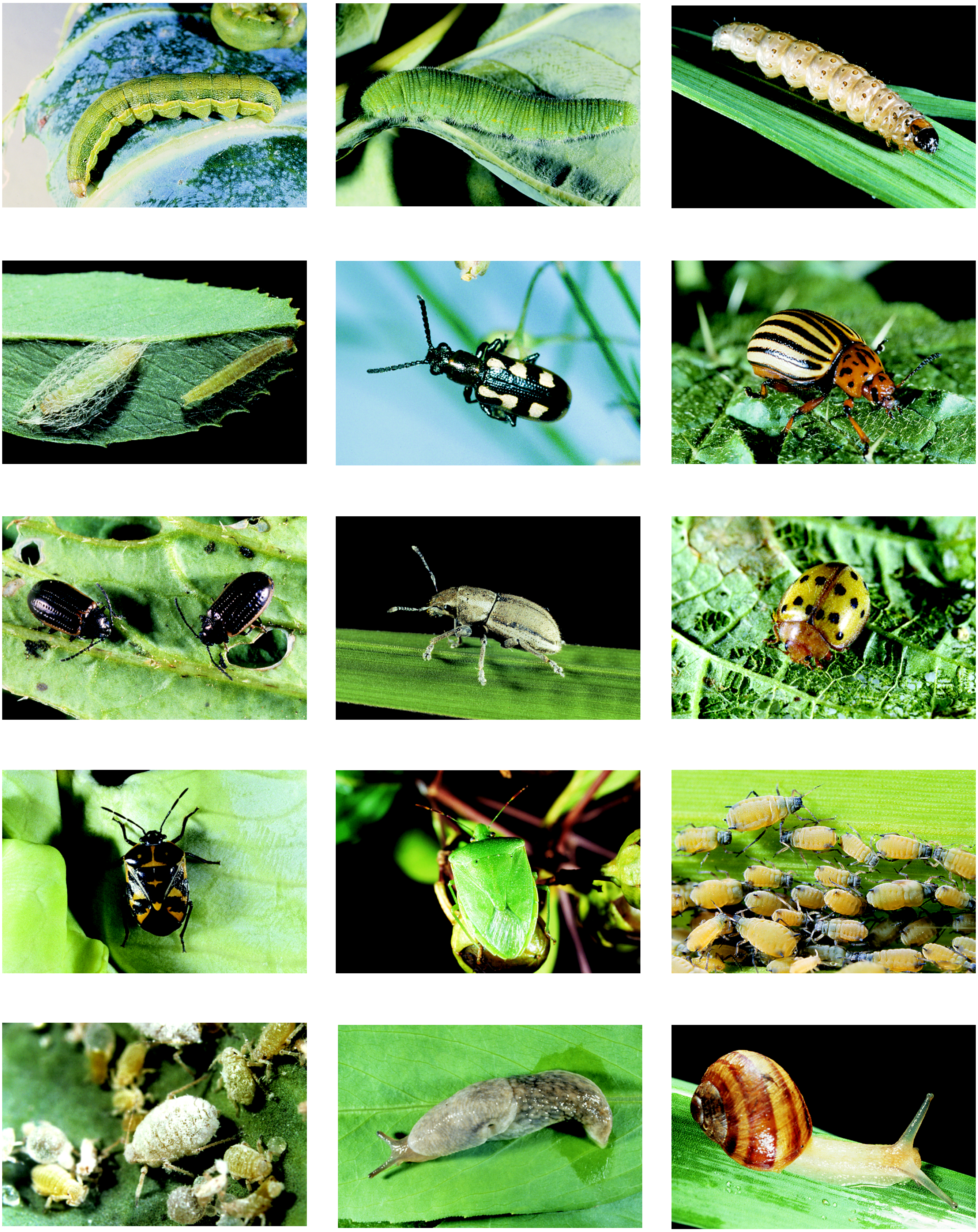

Fig. 4. A rogue's gallery of representative non-indigenous pests affecting North American vegetable crops. Top row (left to right): beet armyworm, imported cabbageworm, European corn borer. Second row: diamondback moth pupa and larva, asparagus beetle, Colorado potato beetle. Third row: yellowmargined leaf beetle, whitefringed beetle, Mexican bean beetle. Fourth row: harlequin bug, southern green stink bug, corn leaf aphids. Bottom row: cabbage aphids, gray garden slug, brown garden snail.

thrips (Thysanoptera), and mites (Acari) consist of both indigenous and nonindigenous species. Again, these groups have below-ground or cryptic stages.

Feeding Behavior and Damage Frequency

Feeding behavior varies considerably among both invading and indigenous species. Some species attack only a single vegetable crop (e.g., asparagus aphid and asparagus, artichoke plume moth and artichoke, sweetpotato leaf beetle and sweet potato), others consume 20 or more crops (e.g., green peach aphid, onion thrips, twostriped grasshopper), and of course many species are intermediate in host acceptance between these extremes. Of the 332 pests evaluated, 38% were determined to have a narrow host range (a single plant family), 16% have a moderate host range (two to five plant families), and 45% have a wide host range (more than five plant families). Interestingly, the breadth of host feeding behavior is not equally distributed among the indigenous and nonindigenous species. The nonindigenous species display a greater proportion of species with a narrow host range (45%) and a lesser proportion of species with a wide host range (38%) as compared to indigenous species (34 and 50%, respectively) (significant by Fisher's exact test: $P = 0.027$). This trend is even more marked if only the arthropods are included (the gastropods are excluded); in the absence of gastropods the invaders' host range is 50% narrow and 31% wide, and the indigenous species' host range is 34% narrow and 50% wide (Fishers exact test: $P < 0.001$). From an evolutionary perspective, it makes sense that the indigenous species having a wide host range would be the ones associated with introduced crops, whereas the invading species that are most intimately associated with introduced crops (i.e., those with a narrow host range) would most likely accompany the introduced crops. This is perhaps best seen in the families Noctuidae and Pyralidae (both order Lepidoptera). Noctuid pests of vegetables are overwhelmingly indigenous, and only 5% are classified as possessing a narrow host range, whereas 70% are classified as having a wide host range. The vegetable pests of the family Pyralidae, however, are mixed in origin, and 71% are classified as possessing a narrow host range, whereas 21% have a wide host range. Thus, the noctuid vegetable pests, which are overwhelmingly indigenous, have a broad host range, and the pyralid vegetable pests, which include a great number of nonindigenous species, are predominantly narrow in host range (significantly different by Fisher's exact test: $P < 0.001$). A study of adoption of conifer hosts by British moths (Fraser and Lawton 1994) showed a similar trend: species adopting new hosts had wider host ranges. North America possesses close relatives to nearly all the introduced crops among its indigenous flora, so it might seem equally likely that specialist herbivores associated with the native plants would adapt to the introduced crops. Indeed, we see the results of specialists expanding their host range to include introduced host plants, but even more important is the invasion by specialist herbivores which are co-evolved and are preadapted to accept the foreign crops.

Damage frequency varies significantly among indigenous and nonindigenous species, with invaders considered to be damaging far more frequently (significantly different by Fisher's exact test: $P < 0.001$). Among nonindigenous species, 50% were classified as causing damage rarely and 22% were classified as causing damage frequently. In contrast, among indigenous species, 65% were classified as causing damage rarely and only 9% as causing damage frequently. Thus, the specialist herbivores that typify invasive pests are well adapted for their host plants, and more damaging than the generalist indigenous species that have expanded their host range to include the introduced vegetable crops. There seems to be no relationship between the site of attack, or the number of sites attacked on a plant, and the origin of pests or their frequency of damage (*Appendix 1*).

Invading organisms are often thought to be particularly damaging because they lack the normal complement of natural enemies found in their native land. This is largely true, and substantiated by the decreased abundance and economic impact of some invaders following introduction of predators and parasitoids (Sailer 1978). However, the differing feeding behavior/host range of invaders relative to indigenous species is perhaps a significant element accounting for frequent and damaging outbreaks of nonindigenous species in North America. Pre-adapted specialist species, with relatively narrow host ranges, are especially well equipped to exploit crop resources when they are inadvertently introduced. More than 99% of the cultivated acreage in North America is planted to introduced crops, and seems to be unusually vulnerable to invading species (Kim 1993).

The importance of herbivore pre-adaptation to the host, or selective feeding behavior, is not generally recognized as an important element leading to frequent damage by invading species, though intuitively most economic entomologists would acknowledge its importance. For example, in a review of the ecological basis for pest problems, Pimentel (1977) listed numerous factors that account for pest status, including introduction into new areas without their natural enemies, change in climatic regions, monoculture, plant spacing, continuous culture, plant nutrition, timing of planting, and pesticide-induced changes in plant physiology. Though these all are valid elements contributing to the suitability of host plants to pests, these characteristics are all extrinsic to the pest, representing climatic and host-plant attributes only. However, in Pimentel's discussion of genetic diversity, where the notion of co-evolution is presented, one begins to appreciate the significance of plant-insect relationships, including elements intrinsic to the insects, such as selective feeding behavior. In a later treatment (Pimentel 1993), food is suggested as the number one factor in determining success of

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invading insects, but again pre-adaptation or feeding specialization is not explicitly stated as a major factor determining success of, or frequency of damage by, invaders. Similarly, Sakai et al. (2001) reviewed the life history characteristics of invasive species, and although they noted the significance of pre-adaptation to climatic conditions, they failed to note the importance of diet specialization. The lack of data on pest origins, severity, and other factors perhaps accounts for the under-appreciation of pre-adaptation or selective feeding behavior as a key element in determining damage by introduced pests. However, in the biological control community the importance of selectivity, or narrow host range due to pre-adaptation, is widely recognized as an important element in determining the potential effectiveness (i.e., host location and exploitation) of introduced biological control agents (Huffaker et al. 1971, Zwolfer et al. 1976). There is no reason to expect that the pattern of host-parasite relationships would be any different in crop plant-crop pest relationships than it would be in weed-biological control agent relationships or insect-parasitoid relationships. The ecological community also has a good appreciation of pre-adaptation, identifying host plant taxonomic affinity as an element in host adoption by insect herbivores, and hence in species richness (Connor et al. 1980, Neuvonen and Niemela 1983, Capinera et al. 1984b).

Influence of Crop Characteristics on Pest Species Richness

North American vegetable crops differ greatly in the extent of commercial acreage, crop value, and the number of pests associated with each crop (Capinera 2001). Mean area (±SD) planted to vegetable crops averaged 108,000 ha (±150,720 ha) per crop, ranging from artichoke at only 3,683 ha, to potato at 662,020 ha. The mean value (±SD) of vegetable crops was about $617 million (±769 million) or $7,986/ha (±5,785). Correspondingly, the least valuable crop was artichoke, valued at $67.6 million, whereas the most valuable was potato, valued at $3,121 million. However, examination of crop unit value provided a different picture of vegetable crop worth, with pea the least valuable crop at $1,162/ha, and celery the most valuable at $24,340/ha. Vegetable crops averaged (±SD) 110 known pests/crop (±36), with a mean of 39 major pests (±19) per crop. Although the value and area planted to crops can vary considerably from year to year, the pest fauna should display relatively little short-term change.

Pest species richness was positively related to area planted to vegetable crops. The number of indigenous pests, nonindigenous pests, as well as indigenous plus nonindigenous pests, were significantly related to crop area. This was true for both major pests and all pests (Table 1). Richness of indigenous species was more directly related to crop area than was richness of nonindigenous species.

The positive species-area relationship is a fundamental expression of community biogeography (Strong 1979), and is well documented for insects feeding on trees (Cornell and Washburn 1979; Claridge and Wilson 1982; MacGarvin 1982; Stevens 1986; Leather 1985, 1990) and crop plants (McCoy and Rey 1983; Capinera et al. 1984a, 1984b). However, there is continuing debate concerning the basis for the greater herbivore species richness associated with more extensive host area or range. Three general explanations have been proposed: area per se, habitat heterogeneity, and passive sampling (Connor and McCoy 1979).

The area per se explanation considers that crop area is the favorable or preferred habitat for crop pests, and that when the pests disperse into other (noncrop) areas their survival is diminished. With larger crop "islands," or more extensive plantings, dispersing insects are more likely to be retained within the crop habitat, resulting in enhanced survival and species richness. A dynamic balance is postulated between immigration and emigration/extinction, with a higher equilibrium level established on larger crop islands or on crops grown more extensively.

Habitat heterogeneity is greater when crops are planted over a more extensive area, providing for differing topological, climatological, or microhabitat differences that may favor accrual of more species of herbivores inhabiting the same crop. Similarly, crops planted more extensively cross the range limits of more insect species. In an area as extensive as North America, it is easy to find many examples of pests that are limited by climatological factors to a portion of the range inhabited by a crop. Thus, diversity of physical or biological environment rather than equilibrium biogeography is emphasized in this explanation of the species-area relationship.

The passive sampling explanation is perceived as more of a statistical artifact than a biological explanation. In this scenario, larger crop areas are thought to accumulate larger numbers of herbivores through random dispersal, leading to increased species richness. Alternatively, crops grown more extensively may be sampled more frequently or extensively, leading to greater discovery and the perception of enhanced species richness. Another aspect of the sampling explanation is that host species lists may not be accurate, reflecting collector bias.

Examination of species richness in North American vegetable crops is revealing because it allows us to dispose of some of the sampling issues effectively. The pest fauna of vegetable crops is well studied, with extent of research effort and taxonomic bias not likely to be significant impediments to determination of true host ranges. Also, if there is an entomologist-based bias, it should be reflected in relation to crop value. With an entomologist-based bias we might expect to find vegetable crops of greater value to be studied more carefully, and to have longer host lists.

Pest species richness had relatively little relationship to crop value (Table 1). The relationships between major pest species richness and total crop value were marginally significant, although when all pests were considered the relationships were not

Table 1. Regression equations describing the relationship (log/log) of species richness (number of pests per crop) to crop area (ha), crop value ($), and unit value ($/ha)

X	*Y*	Equation	Residual mean square	*F*	r²	*P*
Area	Major pests, indigenous	*Y* = (0.38)*X* - 0.54	0.071	10.18	0.361	0.005**
	Major pests, invaders	*Y* = (0.19)*X* + 0.22	0.035	5.32	0.228	0.033*
	Major pests, total	*Y* = (0.31)*X* + 0.07	0.039	11.83	0.396	0.003**
	All pests, indigenous	*Y* = (0.22)*X* + 0.78	0.025	9.63	0.348	0.006**
	All pests, invaders	*Y* = (0.22)*X* + 0.50	0.032	7.58	0.296	0.013*
	All pests, total	*Y* = (0.22)*X* + 0.95	0.027	9.18	0.337	0.007**
Crop value	Major pests, indigenous	*Y* = (0.29)*X* + 0.53	0.094	3.45	0.161	0.079
	Major pests, invaders	*Y* = (0.18)*X* + 0.67	0.039	3.09	0.147	0.094
	Major pests, total	*Y* = (0.25)*X* + 0.90	0.054	4039	0.196	0.050*
	All pests, indigenous	*Y* = (0.08)*X* + 1.60	0.038	0.63	0.034	0.438
	All pests, invaders	*Y* = (0.19)*X* + 1.15	0.040	2.07	0.116	0.141
	All pests, total	*Y* = (0.31)*X* + 1.62	0.036	2.39	0.117	0.139
Unit value	Major pests, indigenous	*Y* = (-0.33)*X* + 2.54	0.978	2.56	0.124	0.127
	Major pests, invaders	*Y* = (-0.19)*X* + 1.85	0.041	1.91	0.096	0.184
	Major pests, total	*Y* = (-0.27)*X* + 2.55	0.056	2.87	0.137	0.107
	All pests, indigenous	*Y* = (-0.23)*X* + 2.70	0.031	3.92	0.176	0.063
	All pests, invaders	*Y* = (-0.21)*X* + 2.36	0.041	2.48	0.121	0.132
	All pests, total	*Y* = (-0.23)*X* + 2.88	0.034	3.48	0.162	0.078

*, significant; **, highly significant

significant. The relationships of pest species richness and crop value were positive. The marginal positive relationships are likely due to the fact that, not surprisingly, crop area and value are correlated ($r = 0.758$; $P < 0.001$; $n = 20$). Thus, pest species richness and value are auto-correlated but there is no causative basis. Conversely, when crop unit values were analyzed, there were no significant relationships between crop values and the richness of major pests, and only near significance for crop values and richness of all pests. These latter relationships were consistently negative. Crops grown extensively are less valuable, and there is a significant negative correlation ($r = -0.506$; $P = 0.023$; $n = 20$) between crop area and unit area values. Again, autocorrelation accounts for the marginal trends observed with respect to crop unit values and species richness. In a previous study of crop pests in Colorado, I similarly found no evidence that species richness was positively correlated with crop value, and in the case of vegetable crops I found a significant negative relationship (Capinera et al. 1984a). Thus, there seems to be little evidence for entomologist-bias, allowing us to largely exclude sampling-based explanations for the species-area relationships

It is difficult to determine the relative contribution of the two remaining explanations, area per se and habitat heterogeneity, to species richness. As pointed out by Strong (1979), heterogeneity is often correlated with area. However, heterogeneity seems the most logical basis for the species-area relationship. Many crop pests, particularly specialists, are adept at locating small patches of plants, even including individual plants. Also, the vegetable crops in North America have had 200 years or more to be "located" by indigenous insect herbivores, so relationships should be fairly well defined. Lastly, because of the extensive observations of vegetable crops made in North America during the last 150 years, there are few undiscovered relationships/host associations. There seems to be little evidence, therefore, to justify area per se as the basis for species richness unless higher extinction rates in smaller "patches" leads to failure of entomologists to detect colonizing species. On the other hand, habitat heterogeneity is a significant element affecting species distribution. Northern and southern latitudes differ markedly with respect to vegetable fauna, and a moisture-based longitudinal gradient also affects host associations significantly in North America. Plant species grown more extensively will undoubtedly accrue longer host lists on a continent as climatologically diverse as North America.

Crop area is not the only plant characteristic to affect species richness. The architecture or complexity of plants (Lawton 1983), taxonomic relatedness (Connor et al. 1980, Niemela and Neuvonen 1983, Kennedy and Southwood 1984), and degree of polyphagy and habitat generalism (Quinn et al. 1997) have been implicated, though these factors are usually less important than is area. In a previous analysis of crop plants grown in Colorado, I found that the plant architecture and taxonomic relatedness factors affected species richness on crop plants, but not in a consistent manner (Capinera et al. 1984a).

Characterization of North American Vegetable Pests

Of the 332 pests considered to be damaging to vegetable crops in the United States and Canada, 59% apparently are indigenous. The invaders come principally from Europe, the source of many of our vegetable and ornamental crops, the major source of human immigrants that populated North America, and a continuing source of tourists and trade. Latin America and Asia are secondarily important as sources of vegetable pests, though they remain significant potential sources of invaders. The rate of invasion by vegetable pests has decreased in the 20th century, though pests continue to enter North America. The regulatory processes developed to curtail the influx of exotic pests seem to have had considerable benefit.

The major plant-feeding insect orders are well represented among North American vegetable pests, principally the orders Coleoptera, Lepidoptera, Heteroptera and Homoptera. Invaders are more likely to be the orders Homoptera and Diptera, and the class Gastropoda, whereas indigenous pests are more likely to be the orders Coleoptera, Lepidoptera, Heteroptera, and Orthoptera. Among the groups that are particularly good invaders are the insect families Bruchidae, Curculionidae, and Scarabaeidae (all order Coleoptera), family Pyralidae (order Lepidoptera), family Anthomyiidae (order Diptera), family Aphididae (order Homoptera), family Gryllotalpidae (order Orthoptera), and the class Gastropoda. We seem to be at greatest risk from pests that have soil-dwelling or cryptic stages, as these pests gain entry frequently. North American vegetable crops have numerous pests, averaging 110 per crop, and with a mean of 39 major pests per crop.

Invading vegetable pests are more likely to have a narrow host range (a single vegetable plant family) whereas indigenous pests are more likely to have a wide host range (more than five plant families). Nonindigenous pests are more likely to be classified as serious pests than are indigenous pests. Thus, preadaptation to feed on imported vegetable crops is identified as a major factor in attainment of pest status. Species richness of both indigenous and nonindigenous vegetable crop pests is positively related to the extent of commercial crop production in North America, so the crops most at risk of acquiring new pests are those grown most extensively. Although economics usually determines whether or not an insect is considered to be serious pest, crop values do not affect our perception of pest species richness.

Acknowledgments

This research was supported by the Florida Agricultural Experiment Station, and approved for publication as Journal Series No. R-08132. J. H. Frank, R. McSorley, and J. R. Rey kindly provided useful reviews of the manuscript.

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Appendix 1. Insects and other invertebrate pests affecting vegetable crops in the United States and Canada

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
Order Coleoptera - beetles, weevils, white grubs, and wireworms						
Family Bruchidae - seed beetles and weevils						
Acanthoscelides obtectus (Say), bean weevil	Invader	Central America, Mexico, Caribbean	Narrow	1800-1850	Rare	Fruit
Bruchus pisorum (L.), pea weevil	Invader	Africa	Narrow	Before 1800	Rare	Fruit
Bruchus rufimanus Boheman, broadbean weevil	Invader	Asia	Narrow	1850-1900	Rare	Fruit
Callosobruchus chinensis (L.), southern cowpea weevil	Invader	Africa	Narrow	?	Rare	Fruit
Callosobruchus maculatus (F.), cowpea weevil	Invader	Africa	Narrow	1800-1850	Rare	Fruit
Family Carabidae—ground beetles						
Clivina impressifrons LeConte, slender seedcorn beetle	Native		Narrow		Rare	Root/ seed/bulb
Stenolophus comma (F.), seedcorn beetle	Native		Narrow		Periodic	Root/ seed/bulb
Stenolophus lecontei (Chaudoir), seedcorn beetle	Native		Narrow		Rare	Root/ seed/bulb
Family Chrysomelidae, subfamily Alticinae - flea beetles						
Chaetocnema confinis Crotch, sweetpotato flea beetle	Native		Moderate		Rare	Foliage, root/ seed/bulb

Appendix continued on next page

Appendix 1. (continued)

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
Order Coleoptera - beetles, weevils, white grubs, and wireworms (continued)						
Chaetocnema denticulata (Illiger), toothed flea beetle	Native		Narrow		Rare	Foliage
Chaetocnema ectypa Horn, desert corn flea beetle	Native		Moderate		Rare	Foliage, root/ seed/bulb
Chaetocnema pulicaria Melsheimer, corn flea beetle	Native		Narrow		Periodic	Foliage
Disonycha mellicollis Say, yellownecked flea beetle	Native		Narrow		Rare	Foliage
Disonycha triangularis (Say), threespotted flea beetle	Native		Narrow		Rare	Foliage
Disonycha xanthomelas (Dalman), spinach flea beetle	Native		Narrow		Rare	Foliage
Epitrix cucumeris (Harris), potato flea beetle	Native		Wide		Rare	Foliage, tuber, root/ seed/bulb
Epitrix fasciata Blatchley, southern tobacco flea beetle	Invader	Central America, Mexico, Caribbean	Moderate	?	Rare	Foliage, root/ seed/bulb
Epitrix fuscula Crotch, eggplant flea beetle	Native		Narrow		Periodic	Foliage, tuber, root/seed/bulb
Epitrix hirtipennis (Melsheimer), tobacco flea beetle	Native		Moderate		Periodic	Foliage, root/ seed/bulb
Epitrix subcrinata LeConte, western potato flea beetle	Native		Wide		Rare	Foliage, tuber, root/seed/bulb
Epitrix tuberis Gentner, tuber flea beetle	Native		Wide		Periodic	Foliage, tuber, root/seed/bulb
Phyllotreta albionica LeConte, cabbage flea beetle	Native		Narrow		Rare	Foliage, root/ seed/bulb
Phyllotreta armoraciae (Koch), horseradish flea beetle	Invader	Europe	Narrow	1850-1900	Rare	Foliage, root/ seed/bulb
Phyllotreta cruciferae (Goeze), crucifer flea beetle	Invader	Europe	Moderate	1900-1950	Frequent	Foliage, root/ seed/bulb
Phyllotreta pusilla Horn, western black flea beetle	Native		Wide		Rare	Foliage, root/ seed/bulb
Phyllotreta ramosa (Crotch), western striped flea beetle	Native		Narrow		Rare	Foliage, root/ seed/bulb
Phyllotreta striolata (F.), striped flea beetle	Invader	Europe	Narrow	Before 1800	Periodic	Foliage, root/ seed/bulb
Phyllotreta zimmermanni (Crotch), Zimmermann's flea beetle	Invader		Moderate	?	Rare	Foliage
Psylliodes punctulata Melsheimer, hop flea beetle	Native		Wide		Rare	Foliage
Systena blanda Melsheimer, palestriped flea beetle	Native		Wide		Periodic	Foliage, root/ seed/bulb
Systena elongata (F.), elongate flea beetle	Native		Wide		Rare	Foliage, root/ seed/bulb
Systena frontalis (F.), redheaded flea beetle	Native		Wide		Rare	Foliage, root/ seed/bulb
Systena hudsonias (Förster), smartweed flea beetle	Native		Wide		Rare	Foliage, root/ seed/bulb
Family Chrysomelidae, subfamily Cassidinae - tortoise beetles						
Agroiconota bivittata (Say), striped tortoise beetle	Native		Narrow		Rare	Foliage
Charidotella bicolor (F.), golden tortoise beetle	Native		Narrow		Rare	Foliage
Chelymorpha cassidea (L.), argus tortoise beetle	Native		Narrow		Rare	Foliage, root/ seed/bulb
Deloyala guttata (Olivier), mottled tortoise beetle	Native		Narrow		Rare	Foliage
Gratiana pallidula (Boheman), eggplant tortoise beetle	Native		Narrow		Rare	Foliage
Jonthonota nigripes (Olivier), blacklegged tortoise beetle	Native		Narrow		Rare	Foliage
Family Chrysomelidae, several subfamilies - leaf beetles						
Acalymma trivittatum (Mannerheim), western striped cucumber beetle	Native		Wide		Periodic	Blossom, fruit, foliage, root/seed/bulb
Acalymma vittatus (F.), striped cucumber beetle	Native		Wide		Frequent	Blossom, fruit, foliage, root/seed/bulb
Cerotoma trifurcata (Förster), bean leaf beetle	Native		Narrow		Rare	Foliage, root/ seed/bulb
Colaspis brunnea (F.), grape colaspis	Native		Wide		Rare	Foliage, root/ seed/bulb
Crioceris asparagi (L.), asparagus beetle	Invader	Europe	Narrow	1850-1900	Periodic	stem/vine, foliage

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
Crioceris duodecimpunctata (L.), spotted asparagus beetle	Invader	Europe	Narrow	1850-1900	Periodic	Fruit, foliage
Diabrotica balteata LeConte, banded cucumber beetle	Native		Wide		Periodic	Blossom, fruit, foliage, tuber, root/seed/bulb
Diabrotica barberi Smith & Lawrence, northern corn rootworm	Native		Moderate		Rare	Root/ seed/bulb
Diabrotica undecimpunctata Mannerheim, spotted cucumber beetle	Native		Wide		Frequent	Blossom, fruit, foliage, root/seed/ bulb
Diabrotica virgifera LeConte, western corn rootworm	Native		Moderate		Frequent	Blossom, fruit, foliage, root/seed/ bulb
Entomoscelis americana Brown, red turnip beetle	Native		Narrow		Rare	Stem/vine, foliage
Leptinotarsa decemlineata (Say), Colorado potato beetle	Invader	Central America, Mexico, Caribbean	Narrow	1800-1850	Frequent	Foliage
Microtheca ochroloma Stål, yellowmargined leaf beetle	Invader	South America	Wide	1900-1950	Periodic	Foliage
Typophorus nigritus (Crotch), sweetpotato leaf beetle	Native		Narrow		Rare	Stem/vine, foliage, tuber, root/ seed/bulb
Family Curculionidae - billbugs, curculios, and weevils						
Anthonomus eugenii Cano, pepper weevil	Invader	Central America, Mexico, Caribbean		1900-1950	Frequent	Blossom, fruit
Ceutorhynchus assimilis (Paykull), cabbage seedpod weevil	Invader	Europe		1900-1950	Rare	Fruit
Ceutorhynchus rapae Gyllenhal, cabbage curculio	Invader	Europe		1800-1850	Rare	Stem/vine, foliage
Chalcodermus aeneus Boheman, cowpea curculio	Native				Periodic	Blossom
Cylas formicarius (Summers), sweetpotato weevil	Invader	Africa		1850-1900	Frequent	Foliage, tuber
Diaprepes abbreviatus (L.), West Indian sugarcane rootstalk borer weevil	Invader	Central America, Mexico, Caribbean		1950-present	Rare	tuber
Listroderes difficilis Germar, vegetable weevil	Invader	South America		1900-1950	Periodic	Foliage, root/seed/ bulb
Listronotus oregonensis (LeConte), carrot weevil	Native				Frequent	Stem/vine, root/seed/ bulb
Listronotus texanus (Stockton), Texas carrot weevil	Native				Periodic	Stem/vine, root/seed/ bulb
Lixus concavus Say, rhubarb cuculio	Native				Rare	Stem/vine, foliage
Naupactus spp., whitefringed beetle	Invader	South America		1900-1950	Periodic	Foliage, tuber, root/ seed/bulb
Sitona lineatus (L.), pea leaf weevil	Invader	Europe		1900-1950	Periodic	Foliage, root/seed/ bulb
Sphenophorus callosus (Oliver), southern corn billbug	Native				Rare	Stem/vine, root/seed/ bulb
Sphenophorus maidis Chittenden, maize billbug	Native				Rare	Stem/vine, root/seed/ bulb
Trichobaris trinotata (Say), potato stalk borer	Native				Rare	Stem/vine, foliage
Family Coccinellidae - lady beetles						
Epilachna borealis F., squash beetle	Native				Rare	Foliage
Epilachna varivestris Mulsant, Mexican bean beetle	Invader	Central America, Mexico, Caribbean		Before 1800	Frequent	Foliage
Family Elateridae - click beetles and wireworms						
Agriotes mancus (Say), wheat wireworm	Native				Rare	Tuber, root/ seed/bulb
Conoderus amplicollis (Gyllenhal),	Invader	South America		1900-1950	Periodic	Stem/vine,

Appendix continued on next page

Appendix 1. (continued)

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
Order Coleoptera - beetles, weevils, white grubs, and wireworms (continued)						
Gulf wireworm						tuber, root/ seed/bulb
Conoderus falli Lane, southern potato wireworm	Invader	South America		1900-1950	Periodic	Stem/vine, tuber, root/ seed/bulb
Conoderus vespertinus (F.), tobacco wireworm	Native				Periodic	Stem/vine, tuber, root /seed/bulb
Ctenicera aeripennis aeripennis (Kirby), Puget Sound wireworm	Native				Rare	Tuber, root/ seed/bulb
Ctenicera aeripennis destructor (Brown), prairie grain wireworm	Native				Rare	Tuber, root/ seed/bulb
Ctenicera glauca (Germar), dryland wireworm	Native				Rare	Tuber, root/ seed/bulb
Ctenicera pruinina (Horn), Great Basin wireworm	Native				Rare	Tuber, root/ seed/bulb
Limonius agonus (Say), eastern field wireworm	Native				Periodic	Tuber, root/ seed/bulb
Limonius californicus (Mannerheim), sugarbeet wireworm	Native				Periodic	Tuber, root/ seed/bulb
Limonius canus LeConte, Pacific Coast wireworm	Native				Periodic	Tuber, root/ seed/bulb
Melanotus communis (Gyllenhal), corn wireworm	Native				Periodic	Root/seed/ bulb
Melanotus longulus oregonensis (LeConte), Oregon wireworm	Native				Rare	Root/seed/ bulb
Family Meloidae - blister beetles						
Epicauta immaculata (Say), immaculate blister beetle	Native				Rare	Blossom, foliage
Epicauta maculata (Say), spotted blister beetle	Native				Rare	Blossom, foliage
Epicauta pensylvanica (De Geer), black blister beetle	Native				Periodic	Blossom, foliage
Epicauta vittata (F.), striped blister beetle	Native				Periodic	Blossom, foliage
Family Nitidulidae - sap beetles						
Carpophilus lugubris Murray, dusky sap beetle	Native				Rare	Fruit
Glischrochilus quadrisignatus (Say), fourspotted sap beetle	Native				Periodic	Fruit
Family Scarabaeidae - scarab beetles and white grubs						
Adoretus sinicus Burmeister, Chinese rose beetle	Invader	Asia		1850-1900	Rare	Foliage
Anomala orientalis Waterhouse, oriental beetle	Invader	Asia		1900-1950	Rare	Foliage, root/ seed/bulb
Bothynus gibbosus (De Geer), carrot beetle	Native				Rare	Root/seed/ bulb
Cotinis nitida (L.), green June beetle	Native				Rare	Foliage, root/ seed/bulb
Macrodactylus subspinosus (F.), rose chafer	Native				Rare	Blossom, fruit, foliage
Macrodactylus uniformis Horn, western rose chafer	Native				Rare	Blossom, fruit, foliage
Maladera castanea (Arrow), Asiatic garden beetle	Invader	Asia		1900-1950	Rare	Foliage, root/ seed/bulb
Phyllophaga and others, white grubs	Native				Periodic	Root/seed/bulb
Popillia japonica Newman, Japanese beetle	Invader	Asia		1900-1950	Frequent	Fruit, foliage, root/seed/ bulb
Strigoderma arboricola (F.), spring rose beetle	Native				Rare	Root/seed/ bulb
Family Tenebrionidae - darking beetles and false wireworms						
Blapstinus, *Coniontis*, *Eleodes*, and *Ulus* spp., false wireworms	Native				Rare	Stem/vine, tuber, root/ seed/bulb

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
Order Dermaptera - Earwigs						
Euborellia annulipes (Lucas), ringlegged earwig	Invader	Europe		1900-1950	Periodic	Fruit, foliage
Forficula auricularia L., European earwig	Invader	Europe		1850-1900	Rare	Foliage, tuber, root/ seed/bulb
Order Diptera - Flies and Maggots						
Family Agromyzidae - leafminer flies						
Agromyza parvicornis Loew, corn blotch leafminer	Native				Rare	Foliage
Liriomyza brassicae (Riley), cabbage leafminer	Invader	?		?	Rare	Foliage
Liriomyza huidobrensis (Blanchard), pea leafminer	Invader?	South America		?	Periodic	Foliage
Liriomyza sativae Blanchard, vegetable leafminer	Invader?	South America		?	Rare	Foliage
Liriomyza trifolii (Burgess), American serpentine leafminer	Native				Periodic	Foliage
Ophiomyia simplex (Loew), asparagus miner	Invader	Europe		1850-1900	Rare	Stem/vine
Family Anthomyiidae - root and seed maggots, leafminer flies						
Delia antiqua (Meigen), onion maggot	Invader	Europe		Before 1800	Frequent	Stem/vine, root/ seed/bulb
Delia floralis (Fallén), turnip maggot	Invader?	Europe		?	Periodic	Root/seed/ bulb
Delia florilega (Zetterstedt), bean seed maggot	Invader	Europe		?	Rare	Root/seed/ bulb
Delia planipalpis (Stein), radish root maggot	Native				Rare	Root/seed/ bulb
Delia platura (Meigen), seedcorn maggot	Invader	Europe		1850-1900	Periodic	Root/seed/ bulb
Delia radicum (L.), cabbage maggot	Invader	Europe		1800-1850	Frequent	Stem/vine, root/seed/ bulb
Pegomya betae Curtis, beet leafminer	Invader	Europe		1800-1850	Frequent	Foliage
Pegomya hyoscyami (Panzer), spinach leafminer	Invader	Europe		1800-1850	Frequent	Foliage
Family Drosophilidae - pomace flies						
Drosophila spp., small fruit flies	Invader?	South America		?	Rare	Fruit
Family Otididae - picturewing flies						
Euxesta stigmatias Loew, cornsilk fly	Invader	Central America, Mexico, Caribbean		?	Periodic	Fruit
Tetanops myopaeformis (Roeder), sugarbeet root maggot	Native				Rare	Root/seed/ bulb
Family Psilidae - rust flies						
Psila rosae (F.), carrot rust fly	Invader	Europe		1850-1900	Frequent	Root/seed/ bulb
Family Syrphidae - flower and bulb flies						
Eumerus strigatus (Fallén), onion bulb fly	Invader	Europe		1850-1900	Rare	Root/seed/ bulb
Eumerus tuberculatus Rondani, lesser bulb fly	Invader	Europe		1850-1900	Rare	Root/seed/ bulb
Family Tephritidae - fruit flies						
Bactrocera cucurbitae Coquillett, melon fly	Invader	Asia		1850-1900	Frequent	Blossom, fruit, stem/ vine
Bactrocera dorsalis Hendel, oriental fruit fly	Invader	Asia		1900-1950	Frequent	Fruit
Euleia fratria (Loew), parsnip leafminer	Native				Rare	Foliage
Zonosemata electa (Say), pepper maggot	Native				Periodic	Fruit
Family Tipulidae - crane flies						
Tipula paludosa Meigen, European crane fly	Invader	Europe		1950-present		Stem/vine, foliage, root/ seed/bulb
Order Heteroptera - Bugs						
Family Coreidae - squash and leaffooted bugs						
Anasa armigera (Say), horned squash bug	Native?				Rare	Fruit, foliage
Anasa tristis (De Geer), squash bug	Native?				Frequent	Fruit, foliage

Appendix continued

Appendix 1. (continued)

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
Order Heteroptera - Bugs (continued)						
Leptoglossus spp., leaffooted bugs	Native				Frequent	Fruit, foliage
Family Cydnidae - burrower bugs						
Pangaeus bilineatus (Say), burrowing bug	Native				Rare	Fruit, foliage
Family Lygaeidae - seed bugs						
Blissus leucopterus (Say), chinch bugs	Native				Rare	Foliage
Nysius niger Baker, false chinch bug	Native				Periodic	Foliage
Nysius raphanus Howard, false chinch bug	Native				Periodic	Foliage
Family Miridae - plant bugs						
Adelphocoris lineolatus (Goeze), alfalfa plant bug	Invader	Europe		1900-1950	Rare	Blossom, foliage
Adelphocoris rapidus (Say), rapid plant bug	Native				Rare	Blossom, foliage
Adelphocoris superbus (Uhler), superb plant bug	Native				Rare	Blossom, foliage
Halticus bractatus (Say), garden fleahopper	Native				Periodic	Foliage
Lygus elisus Van Duzee, pale legume bug	Native				Rare	Blossom, fruit, stem/ vine, foliage
Lygus hesperus Knight, western tarnished plant bug	Native				Periodic	Blossom, fruit, stem/ vine, foliage
Lygus lineolaris (Palisot de Beauvois), tarnished plant bug	Native				Frequent	Blossom, fruit, stem/ vine, foliage
Orthops scutellatus Uhler, carrot plant bug	Invader	Europe		1900-1950	Rare	Blossom, fruit, foliage
Family Pentatomidae - stink bugs						
Acrosternum hilare (Say), green stink bug	Native				Rare	Fruit, foliage
Chlorochroa sayi (Stål), Say stink bug	Native				Rare	Blossom, fruit, stem/vine
Chlorochroa uhler (Stol), Uhler stink bug	Native				Rare	
Euschistus conspersus Uhler, consperse stink bug	Native				Periodic	Fruit
Euschistus servus (Say), brown stink bug	Native?				Rare	Blossom, fruit, stem/ vine
Euschistus variolaris (Palisot de Beauvois), onespotted stink bug	Native				Rare	Blossom, fruit, foliage
Murgantia histrionica (Hahn), harlequin bug	Invader	Central America, Mexico, Caribbean		1850-1900	Periodic	Foliage
Nezara viridula (L.), southern green stink bug	Invader	Africa		Before 1800	Frequent	Blossom, fruit, stem/ vine, tuber
Family Thyreocoridae - Negro bugs						
Corimelaena pulicaria (Germar), little black bug	Native				Rare	Stem/ vine, foliage
Family Tingidae - lace bugs						
Gargaphia solani Heideman, eggplant lace bug	Native				Rare	Foliage
Order Homoptera - Aphids, Leaf- and Planthoppers, Psyllids and Whiteflies						
Family Aleyrodidae - whiteflies						
Bemisia argentifolii Bellows & Perring, silverleaf whitefly	Invader	?		1950-present	Frequent	Foliage
Bemisia tabaci (Gennadius), sweetpotato whitefly	Invader	?		1900-1950	Rare	Foliage
Trialeurodes vaporariorum (Westwood), greenhouse whitefly	Invader	Central America, Mexico, Caribbean			Periodic	Foliage
Family Aphididae - aphids						
Acyrthosiphon kondoi Shinji, blue alfalfa aphid	Invader	Asia		1950-present	Rare	Blossom, fruit, stem/ vine, foliage
Acyrthosiphon pisum (Harris), pea aphid	Invader	Europe		1850-1900	Periodic	Blossom, fruit, stem/ vine, foliage
Aphis craccivora Koch, cowpea aphid	Invader	Africa?		?	Periodic	Fruit, stem/

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
						vine, foliage
Aphis fabae Scopoli, bean aphid	Invader	Europe		?	Periodic	Foliage
Aphis gossypii Glover, melon aphid	Invader?	?		?	Frequent	Foliage
Aphis maidiradicis Forbes, corn root aphid	Native				Rare	Root/seed/ bulb
Aphis nasturtii Kaltenbach, buckthorn aphid	Invader	Europe?		?	Periodic	Foliage
Aulacorthum solani (Kaltenbach), foxglove aphid	Invader	Europe?		?	Rare	Foliage
Brachycorynella asparagi (Mordvilko), asparagus aphid	Invader	Europe		1950-present	Frequent	Foliage
Brevicoryne brassicae (L.), cabbage aphid	Invader	Europe?		Before 1800	Frequent	Foliage
Capitophorus elaeagni (del Guercio), artichoke aphid	Invader	Europe		?	Periodic	Foliage
Cavariella aegopodii Scopoli, willow-carrot aphid	Invader	?		?	Frequent	Foliage
Dysaphis crataegi (Kaltenbach), carrot root aphid	Invader	Europe		?	Rare	Stem/vine, root/seed/ bulb
Dysaphis foeniculus (Theobald), carrot root aphid	Invader	Europe		?	Rare	Stem/vine, root/seed/ bulb
Hyadaphis coriandri (Das), coriander aphid	Invader	Europe		1950-present	Rare	Foliage
Hyadaphis foeniculi (Passerini), honeysuckle aphid	Invader	Europe		1900-1950	Rare	Foliage
Lipaphis erysimi (Kaltenbach), turnip aphid	?				Periodic	Foliage
Macrosiphum euphorbiae (Thomas), potato aphid	Native				Frequent	Stem/vine, foliage
Myzus persicae (Sulzer), green peach aphid	Invader	?		?	Frequent	Foliage
Nasonovia ribisnigri (Mosley), lettuce aphid	Invader	Europe		1950-present	Periodic	Foliage
Pemphigus betae Doane, sugarbeet root aphid	Native				Rare	Root/seed/ bulb
Pemphigus bursarius (L.), lettuce root aphid	Invader	Europe		?	Periodic	Root/seed/ bulb
Pemphigus populivenae Fitch, sugarbeet root aphid	Native				Rare	Root/seed/ bulb
Rhopalosiphum maidis (Fitch), corn leaf aphid	Invader	Asia?		?	Rare	Blossom, fruit, foliage
Rhopalosiphum padi (L.), bird cherry-oat aphid	Native				Periodic	Foliage
Rhopalosiphum rufiabdominalis (Saaki), rice root aphid	Invader	Asia		?	Rare	Root/seed/ bulb
Smynthurodes betae Westwood, bean root aphid	Invader	Europe		?	Rare	Root/seed/ bulb
Family Cicadellidae - leafhoppers						
Circulifer tenellus (Baker), beet leafhopper	Invader	Europe		Before 1800	Frequent	Foliage
Dalbulus maidis (DeLong & Wolcott), corn leafhopper	Invader	Central America, Mexico, Caribbean		?	Periodic	Foliage
Empoasca abrupta Delong, western potato leafhopper	Native				Rare	Foliage
Empoasca fabae (Harris), potato leafhopper	Native				Periodic	Foliage
Macrosteles quadrilineatus Forbes, aster leafhopper	Native				Frequent	Foliage
Family Delphacidae - planthoppers						
Peregrinus maidis (Ashmead), corn delphacid	Invader	Africa		?	Rare	Foliage
Family Psyllidae - psyllids						
Paratrioza cockerelli (Sulc), potato psyllid	Native			Periodic	Foliage	
Order Hymenopters - Ants and Sawflies						
Family Argidae - sawflies						
Sterictiphora cellularis (Say), sweetpotato sawfly	Native				Rare	Foliage
Family Formicidae - ants						
Solenopsis invicta Buren, red imported fire ant	Invader	South America		1900-1950	Periodic	Fruit, stem/ vine, foliage, tuber, root/ seed/bulb
Order Lepidoptera - Caterpillars, Moths and Butterflies						
Family Arctiidae - woollybear caterpillars and tiger moths						
Estigmene acrea (Drury), saltmarsh caterpillar	Native				Periodic	Foliage
Pyrrharctia isabella (J.E. Smith), banded woollybear	Native				Rare	Foliage
Spilosoma virginica (F.), yellow woollybear	Native				Rare	Foliage

Appendix continued

Appendix. (continued)

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
Order Lepidoptera - Caterpillars, Moths and Butterflies (continued)						
Family Gelechiidae - leafminer moths						
Keiferia lycopersicella (Walsingham), tomato pinworm	Invader	Central America, Mexico, Caribbean		1900-1950	Frequent	Fruit, foliage
Phthorimaea operculella (Zeller), potato tuberworm	Native				Periodic	Foliage, tuber
Tildenia inconspicuella (Murtfeldt), eggplant leafminer	Native				Rare	Foliage
Family Hesperiidae - skipper butterflies						
Urbanus proteus (L.), bean leafroller	Native				Periodic	Foliage
Family Lycaenidae - hairstreak butterflies						
Strymon melinus (Hübner), cotton square borer	Native				Rare	Fruit, foliage
Family Lyonetiidae - lyonetiid moths						
Bedellia orchilella Walsingham, sweetpotato leafminer	Invader	Asia		?	Rare	Foliage
Bedellia somnulentella (Zeller), morningglory leafminer	Invader	Asia		?	Rare	Foliage
Family Noctuidae - armyworms, cutworms, loopers, stalk borers, and nocutid moths						
Agrotis ipsilon (Hufnagel), black cutworm	Native				Periodic	Foliage
Agrotis orthogonia Morrison, pale western cutworm	Native				Rare	Stem/vine
Agrotis subterranea (F.), granulate cutworm	Native				Periodic	Stem/vine, foliage
Anagrapha falcifera (Kirby), celery looper	Native				Rare	Foliage
Anomis erosa Hübner, okra caterpillar	Invader?	?		?	Rare	Foliage
Apamea devastator (Brace), glassy cutworm	Native				Rare	Stem/vine, root/seed/bulb
Autographa californica (Speyer), alfalfa looper	Native				Periodic	Foliage
Autographa precationis (Guenée), plantain looper	Native				Rare	Foliage
Autoplusia egena (Guenée), bean leafskeletonizer	Native				Rare	Foliage
Dicestra trifolii (Hufnagel), clover cutworm	Native				Periodic	Foliage
Euxoa auxiliaris (Grote), army cutworm	Native				Rare	Stem/vine, foliage
Euxoa messoria (Harris), darksided cutworm	Native				Rare	Foliage
Euxoa ochrogaster (Guenée), redbacked cutworm	Native				Periodic	Stem/vine, foliage
Feltia jaculifera (Guenée), dingy cutworm	Native				Rare	Foliage
Feltia subgothica (Haworth), dingy cutworm	Native				Rare	Foliage
Helicoverpa zea (Boddie), corn earworm	Native				Frequent	Fruit, foliage
Heliothis virescens (F.), tobacco budworm	Native				Rare	Blossom, fruit, stem/vine
Hydraecia immanis (Guenée), hop vine borer	Native				Periodic	Stem/vine, foliage, root/seed/bulb
Hydraecia micacea (Esper), potato stem borer	Invader	Europe		1900-1950	Periodic	Stem/vine, foliage, root/seed/bulb
Loxagrotis albicosta (Smith), western bean cutworm	Native				Rare	Fruit
Mamestra configurata Walker, bertha armyworm	Native				Periodic	Foliage
Megalographa biloba (Stephens), bilobed looper	Native				Rare	Foliage
Melanchra picta (Harris), zebra caterpillar	Native				Rare	Foliage
Mocis latipes Guenée, striped grass looper	Native				Rare	Foliage
Nephelodes minians Guenée, bronzed cutworm	Native				Rare	Foliage
Papaipema nebris (Guenée), stalk borer	Native				Rare	stem/vine
Peridroma saucia (Hübner), variegated cutworm	Invader	Europe?		1800-1850	Periodic	Stem/vine, foliage
Plathypena scabra (F.), green cloverworm	Native				Rare	Foliage
Pseudaletia unipunctata (Haworth), armyworm	Native				Periodic	Foliage
Pseudoplusia includens (Walker), soybean looper	Native				Rare	Fruit, foliage
Spodoptera dolichos (F.), sweetpotato armyworm	Native				Rare	Stem/vine, foliage
Spodoptera eridania (Stoll), southern armyworm	Native				Frequent	Fruit, foliage, tuber
Spodoptera exigua (Hübner), beet armyworm	Invader	Asia		1850-1900	Frequent	Foliage
Spodoptera frugiperda (J.E. Smith), fall armyworm	Native				Frequent	Fruit, foliage

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
Spodoptera latifascia (Walker), velvet armyworm	Native				Rare	Stem/vine, foliage
Spodoptera ornithogalli (Guenée), yellowstriped armyworm	Native				Periodic	Fruit, foliage
Spodoptera praefica (Grote), western yellowstriped armyworm	Native				Periodic	Fruit, foliage
Trichoplusia ni (Hübner), cabbage looper	?				Frequent	Foliage
Xestia adela Franclemont, spotted cutworm	Invader	Europe		?	Periodic	Fruit, stem/vine, foliage
Xestia dolosa Franclemont, spotted cutworm	Invader	Europe		?	Periodic	Fruit, stem/vine, foliage
Family Oecophoridae - oecophorid moths						
Depressaria pastinacella (Duponchel), parsnip webworm	Invader	Europe		1850-1900	Rare	Blossom
Family Papilionidae - celeryworms and swallowtail butterflies						
Papilio polyxenes F., black swallowtail	Native				Rare	Foliage
Papilio zelicaon Lucas, anise swallowtail	Native				Rare	Foliage
Family Pieridae - cabbageworms, white, and sulfur butterflies						
Ascia monuste (L.), southern white	Native				Rare	Foliage
Colias eurytheme Boisduval, alfalfa caterpillar	Native				Rare	Foliage
Pieris napi (L.), mustard white	Native				Rare	Foliage
Pieris rapae (L.), imported cabbageworm	Invader	Europe		1850-1900	Frequent	Foliage
Pontia protodice (Boisduval & LeConte), southern cabbageworm	Native				Rare	Fruit, foliage
Family Pterophoridae - plume moths						
Platyptilia carduidactyla (Riley), artichoke plume moth	Native				Frequent	Blossom, fruit, stem/vine, foliage
Family Pyralidae - borers, budworms, leaftiers, webworms, and snout moths						
Achyra rantalis (Guenée), garden webworm	Native				Rare	Foliage
Crambus and others, sod and root webworms	Native				Rare	Stem/vine, foliage, root/seed/bulb
Diaphania hyalinata (L.), melonworm	Native				Periodic	Fruit, foliage
Diaphania nitidalis (Stoll), pickleworm	Native				Frequent	Blossom, fruit
Diatraea crambidoides (Grote), southern cornstalk borer	Native					Stem/vine, foliage
Diatraea grandiosella Dyar, southern corn borer	Invader	Central America, Mexico, Caribbean		1850-1900	Rare	Fruit, stem/vine, foliage
Diatraea saccharalis (F.), sugarcane borer	Invader	Central America, Mexico, Caribbean		1850-1900	Rare	Fruit, stem/vine, foliage
Elasmopalpus lignosellus (Zeller), lesser cornstalk borer	Native				Rare	stem/vine
Etiella zinckenella (Treitschke), limabean pod borer	Invader	?		1850-1900	Rare	Fruit
Evergestis pallidata (Hufnagel), purplebacked cabbageworm	Invader	Europe		1850-1900	Rare	Stem/vine, foliage, Root/seed/bulb
Evergestis rimosalis (Guenée),	Native				Periodic	Foliage
Hellula phidilealis (Walker), cabbage budworm cross-striped cabbageworm	Invader?	Central America, Mexico, Caribbean		?	Rare	Stem/vine
Hellula rogatalis (Hulst), cabbage webworm	Native				Rare	Foliage
Hellula undalis (F.), oriental cabbage webworm	Invader?	?		?	Rare	Foliage
Herpetogramma bipunctalis (F.), southern beet webworm	?				Rare	Foliage
Hymenia perspectalis (Hübner), spotted beet webworm	?				Rare	Foliage
Loxostege cereralis (Zeller), alfalfa webworm	Native				Rare	Foliage
Loxostege sticticalis (L.), beet webworm	Invader	Europe		?	Rare	Foliage
Omphisa anastomosalis (Guenée), sweetpotato vine borer	Invader	Asia		1850-1900	Rare	Stem/vine, tuber
Ostrinia nubilalis (Hübner), European corn borer	Invader	Europe		1900-1950	Frequent	Blossom, fruit, stem/

Appendix continued

Appendix 1. (continued)

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
Order Lepidoptera - Caterpillars, Moths and Butterflies (continued)						
						vine, foliage
Plutella xylostella (L.), diamondback moth	Invader	Europe		1850-1900	Frequent	Foliage
Spoladea recurvalis (F.), Hawaiian beet webworm	Invader	?		?	Rare	Foliage
Udea profundalis (Packard), false celery leaftier	Native				Rare	Stem/vine, foliage
Udea rubigalis (Guenée), celery leaftier	Native				Rare	Stem/vine, foliage
Family Sesiidae - vine borers and clearwing moths						
Melittia calabaza Duckworth & Eichlin, southwestern squash vine borer	Native				Rare	Stem/vine
Melittia cucurbitae (Harris), squash vine borer	Native				Frequent	Stem/vine
Family Sphingidae - hornworms and sphinx moths						
Agrius cingulatus (F.), sweetpotato hornworm	Native				Rare	Foliage
Hyles lineata (F.), whitelined sphinx	Native				Rare	Foliage
Manduca quinquemaculata (Haworth), tomato hornworm	Native				Periodic	Fruit, foliage
Manduca sexta (L.), tobacco hornworm	Native				Periodic	Fruit, foliage
Family Tortricidae - leafroller moths						
Cydia nigricana (F.), pea moth	Invader	Europe		1850-1900	Rare	Fruit
Order Orthoptera - Grasshoppers and Crickets						
Family Acrididae - grasshoppers						
Melanoplus bivittatus (Say), twostriped grasshopper	Native				Periodic	Foliage
Melanoplus differentialis (Thomas), differential grasshopper	Native				Periodic	Foliage
Melanoplus femurrubrum (De Geer), redlegged grasshopper	Native				Rare	Foliage
Melanoplus propinquus Scudder, southern redlegged grasshopper	Native				Rare	Foliage
Melanoplus sanguinipes (F.), migratory grasshopper	Native				Periodic	Foliage
Romalea microptera (Beauvois), eastern lubber grasshopper	Native				Periodic	Foliage
Schistocerca americana (Drury), American grasshopper	Native				Rare	Foliage
Family Gryllidae - field crickets						
Gryllus pennsylvanicus Burmeister, fall field cricket	Native				Rare	Blossom, fruit, stem/vine, foliage, root/seed/bulb
Gryllus rubens Scudder, southeastern field cricket	Native				Rare	Blossom, fruit, stem/vine, foliage, root/seed/bulb
Gryllus veletis (Alexander & Bigelow), spring field cricket	Native				Rare	Blossom, fruit, stem/vine, foliage, root/seed/bulb
Family Gryllotalpidae - mole crickets						
Scapteriscus abbreviatus Scudder, shortwinged mole cricket	Invader	South America		1850-1900	Rare	Stem/vine, foliage, tuber, root/seed/bulb
Scapteriscus borellii Giglio-Tos, southern mole cricket	Invader	South America		1850-1900	Rare	Stem/vine, foliage, tuber, root/seed/bulb
Scapteriscus vicinus Scudder, tawny mole cricket	Invader	South America		1850-1900	Rare	Stem/vine,

	Status	Origin	Host range	Period of detection	Damage frequency	Site damaged
Order Orthoptera - Grasshoppers and Crickets (continued)						
						foliage, tuber, root/ seed/bulb
Family Tettigoniidae - shield-backed crickets						
Anabrus simplex Haldeman, Mormon cricket	Native				Rare	Foliage
Peranabrus scabricollis (Thomas), coulee cricket	Native				Rare	Foliage
Order Thysanoptera - Thrips						
Anaphothrips obscurus (Müller), grass thrips	Native				Rare	Foliage
Caliothrips fasciatus (Pergande), bean thrips	Native				Rare	Foliage
Frankliniella fusca (Hinds), tobacco thrips	Native				Frequent	Blossom, foliage
Frankliniella occidentalis (Pergande), western flower thrips	Native				Frequent	Blossom
Thrips palmi Karny, melon thrips	Invader	Asia		1950-present	Frequent	Blossom, fruit, foliage
Thrips tabaci Lindeman, onion thrips	Invader	Asia		1850-1900	Frequent	Fruit, foliage
Other Invertebrate Pests						
Class Acari - mites						
Aculops lycopersici (Massee), tomato russet mite	Invader	?		1800-1850	Periodic	Stem/vine, foliage
Oligonychus pratensis (Banks), Banks grass mite	Native				Rare	Foliage
Polyphagotarsonemus latus (Banks), broad mite	Invader	Asia		?	Periodic	Blossom, fruit, foliage
Rhizoglyphus echinopus (Fumouze & Robin), bulb mite	Invader	?		?	Rare	Root/seed/ bulb
Rhizoglyphus robini Claparede, bulb mite	Invader	?		?	Rare	Root/seed/ bulb
Tetranychus tumidus Banks, tumid spider mite	Native				Rare	Foliage
Tetranychus turkestani Ugarov & Nikolski, strawberry spider mite	Native	Asia			Rare	Foliage
Tetranychus urticae Koch, twospotted spider mite	Invaver	Europe		1850-1900	Frequent	Foliage
Class Collembola - springtails						
Bourletiella hortensis Fitch, garden springtail	Invader	Europe		?	Rare	Stem/vine, foliage
Class Diplopoda - millipedes						
Oxidus gracilis Koch, garden millipede	Invader	?		?	Rare	Fruit, stem/ vine, tuber
Class Isopoda - pillbugs and sowbugs						
Armadillidium vulgare (Latreille), common pillbug	Invader	Europe		?	Rare	Fruit, stem/ vine, foliage
Porcellio scaber Latreille, dooryard sowbug	Invader	Europe		?	Rare	Fruit, stem/ vine, foliage
Class Gastropoda - slugs and snails						
Arionater rufus (L.), black slug	Invader	Europe		1850-1900	Rare	Foliage
Cepaea, *Helix*, *Rumina* spp. and others, snails						
Cepaea hortensis (Müller), white-lipped snail	Invader	Europe		1850-1900	Rare	Foliage
Cepaea nemoralis (L.), brown-lipped snail	Invader	Europe		1850-1900	Rare	Foliage
Deroceras, *Limax*, *Milax* spp. and others, slugs						
Deroceras laeve (Müller), marsh slug	Native				Rare	Foliage
Deroceras reticulatum (Müller), gray garden slug	Invader	Europe		1850-1900	Periodic	Root/seed/ bulb
Helix aperta Born, singing snail	Invader	Europe		1850-1900	Rare	Foliage
Helix aspera Müller, brown garden snail	Invader	Europe		1850-1900	Periodic	Foliage
Helix pomatia L., Roman snail	Invader	Europe		1850-1900	Rare	Foliage
Limax flavus (L.), tawny garden slug	Invader	Europe		1850-1900	Periodic	Foliage
Limax maximus L., spotted garden slug	Invader	Europe		1850-1900	Periodic	Foliage
Milax gagates (Draparnand), greenhouse slug	Invader	Europe		1850-1900	Periodic	Foliage
Otala lactea (Müller), milk snail	Invader	Europe		?	Rare	Foliage
Rumina decollata (L.), decollate snail	Invader	Europe		?	Rare	Foliage
Theba pisana (Müller), white garden snail	Invader	Europe		1900-1950	Rare	Foliage
Class Symphyla - symphylans						
Scutigerella immaculata (Newport), garden symphylan	Invader	Europe		?	Periodic	Root/seed/ bulb