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Patterns among Host Plants of Potato Leafhopper, *Empoasca fabae* (Homoptera: Cicadellidae)

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ABSTRACT: Ecological characteristics of potato leafhopper, *Empoasca fabae* (Harris), including polyphagy, suggest that non-economic plant species in the landscape may be important to its population ecology. The objectives of this study were to compile a host list, to ascertain taxonomic and ecological patterns within the list, and to determine host utilization in non-crop habitats. The host plant list included 220 species in 100 genera and 26 families. Fabaceae represented 47% of the genera and 62% of the species. Yet, the list includes a diversity of taxonomic groups within the class Magnoliopsida, representing highly divergent chemistry and morphological types. Ecological classifications, based on such characteristics as habitat, growth form, and origin, were similarly diverse. Thus, the diversity of plant species suitable for reproduction suggests that non-crop habitats may be a significant source of potato leafhopper populations after spring migration into northern states. Also, the ability of leafhopper adults to utilize additional species (e.g., grasses, pines) as refugia provides a secondary role to non-crop habitats. Yet, our limited data suggest that utilization of non-crop habitats for reproduction is restricted to a relatively few naturalized hosts (e.g., deciduous trees). Host finding behavior, operating at a landscape or habitat level, as well as abiotic and biotic factors within habitats, may limit host utilization in non-crop habitats.

The potato leafhopper, *Empoasca fabae* (Harris) (Homoptera: Cicadellidae), has long been recognized as an economic pest of many crops including alfalfa, potato, bean, and soybean in the midwestern and eastern United States and Canada (DeLong, 1938). Research has concentrated on dynamics of this pest in crop systems, yet three ecological characteristics of the species suggest that non-economic plant species outside of crop systems may be important in its population ecology. First, it is highly polyphagous, reproducing on a wide range of plant species and families (Poos and Wheeler, 1943, 1949). Second, adults are highly mobile, traversing both long (interregional) and short (interhabitat) distances (Medler, 1957; Poston and Pedigo, 1975; Flanders and Radcliffe, 1989). Third, it is multivoltine, with three to five overlapping generations per year, and individuals have a life span of up to six months (DeLong, 1938). Adults have been collected in several habitats outside of crop systems, including deciduous forest, forest understory, old field, and newly-disturbed habitats (Lamp et al., 1989 and unpubl. data; Taylor, 1993). As a result, non-crop habitats are believed to contribute significantly to potato leafhopper population dynamics (Poos, 1935; Hogg and Hoffman, 1989).

As a group, leafhoppers have restrictive host ranges (Putnam, 1941; DeLong, 1965). Part of the reason for the wide host range of potato leafhopper may lie in its ability to vary feeding behaviors in response to its host plant. For example,

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Backus and Hunter (1989) found that adults on alfalfa fed on vascular tissues, whereas on beans they fed on mesophyll tissues. Furthermore, adults settle on different portions of the two hosts (Backus et al., 1990). Artificial plant breeding and plant introductions into North America may have enhanced the host range of the leafhopper. For example, plant resistance workers have long noted an association of susceptibility to this leafhopper species with lack of pubescence and other physical characteristics in original germplasm lines of soybean, potato, and alfalfa (Broersma et al., 1972; Robbins et al., 1979; Tingey, 1985; Brewer et al., 1986a, b). In part, this physical resistance is because trichomes impede the normal attachment of individuals to the plant surface (Lee et al., 1986). A chemical basis for resistance to feeding is less frequently cited compared to a physical basis. For example, comparisons of closely-related *Solanum* species suggest that trichome presence and not glycoalkaloid content is associated with resistance (Tingey and Sinden, 1982). Alternatively, Raman et al. (1979) found interrupted feeding behavior in response to feeding on glycoalkaloid within artificial diet in the absence of physical resistance factors, and that increased glycoalkaloid content was associated with greater resistance among potato cultivars. A larger study of 100 species of *Solanum* found potato leafhopper resistance associated with both the glycoalkaloid tomatine and glandular trichomes, and that artificial selection led to increased susceptibility by potato leafhopper (Flanders et al., 1992).

These studies suggest that potato leafhopper is able to feed as an adult on a wide range of plant species, although certain morphological and chemical factors limit their host utilization for reproduction. Fewer plants serve as hosts for female oviposition as well as survival of small nymphs in comparison to those that serve as hosts for adult feeding (Lamp et al., 1984b). As a consequence, nymphs develop on fewer species compared to species suitable for adult survivorship. Furthermore, potato leafhopper response to genetically diverse and phenotypically variable plant populations within species shows considerable variation. The list of plants suitable for reproduction (hosts), other plant taxa not suitable for reproduction (non-hosts), and actual utilization of hosts in nature may suggest patterns in host plant selection by potato leafhopper.

Although the host plant lists published by Poos and Wheeler (1943, 1949) are extensive, they are not conducive to the analysis of patterns because the species were not grouped by taxonomic classification or ecological characteristics. Also, additional host plants have been discovered since their publications. A more complete listing and its analysis was desired toward the goal of greater understanding of the role of non-economic plant species in the population ecology of potato leafhopper and the relationship between plant characteristics and acceptability by potato leafhopper. The objectives of this study were to compile a complete host list for this leafhopper, to determine taxonomic and ecological patterns within the host list, and to determine major groups of non-host plants. Furthermore, we compared the compiled host list to actual utilization of hosts at two disparate sites.

Methods

Host plant species were determined by literature search on the basis of suitability for nymphal development, i.e., if nymphs were observed or collected from the plant in the field and reared to adult. Research of *Solanum* species has received

considerable emphasis in the search for resistant germplasm. Rather than list all species (which are primarily exotic to North America and not used as cultivated plants), we cited these species only as genus in the table. A major problem in the study of this leafhopper is species determination. DeLong (1931) first recognized that many *Empoasca* species are superficially identical and cannot be separated without careful examination of male genitalia. Therefore, only studies published and specimens identified after this discovery were included.

Plant species (including common names and authorities) and families were determined by consulting Gleason (1952), Radford et al. (1964), Fernald (1970), Hitchcock and Cronquist (1973), and Bailey (1976). Higher classification (order, subclass, and class) was based on Smith (1977). Ecological classification was determined by consulting the ecological and morphological information found in the taxonomic references listed above. Analysis of ecological trends among the host plants was based on genera instead of species because some genera were over-represented by species (e.g., *Solanum* as discussed above), and also because the genus is generally indicative of ecological type. Five ecological classes were used. First, habitats of host genera were categorized by the level of human disturbance either as occupants of habitats subjected to disturbance by humans (including that caused by grazing livestock) or of "natural" habitats (i.e., rarely or never subjected to human disturbance). Two, habitats associated with genera were further categorized by the level and frequency of disturbance. Three habitat types were recognized: annually-tilled cropland (land that is cultivated at least once a year); fields, pastures, and waste places (land that is disturbed on average once every five years and may be grazed by livestock); and woodlands, shrublands, and park-like settings where long-lived perennial plants (e.g., trees and shrubs) have been naturalized or planted. Third, genera were categorized by growth form (i.e., woody versus herbaceous and if herbaceous then annual, biennial, or perennial life history). Fourth, genera were categorized as native or introduced to the region coincident with the leafhopper's range. Occasionally, a genus included both native and introduced species (e.g., *Medicago*). In such cases, the majority of species was used to classify the genus. Fifth, hosts were categorized as "competitive," "ruderal," or "stress tolerant" according to the autecological scheme by Grime (1979). Briefly, this scheme is defined by the role of stress and disturbance factors on limiting the distribution of plants. Competitors are plant species that exploit conditions of low stress and low disturbance, ruderals exploit low stress and high disturbance, and stress tolerants exploit high stress and low disturbance.

To determine actual host utilization, Nebraska sites were identified during 1989 and 1990 in Lancaster Co. that provided a number of plant species that were considered potential hosts for potato leafhopper (based on an early draft of Table 1). The sites were adjacent to established alfalfa fields, and were sampled once each week during the growing season from June 6 to August 30 in 1989 and from June 11 to August 15 in 1990. The non-crop species that were sampled at the 1989 site were American elm [*Ulmus americana* L.], red mulberry [*Morus rubra* L.], wild four o'clock [*Mirabilis nyctaginea* (Michx.) MacM.], motherwort [*Leonurus cardiaca* L.], catnip [*Nepeta cataria* L.], common milkweed [*Asclepias syriaca* L.], Siberian elm [*Ulmus pumila* L.], narrowleaf dock [*Rumex crispus* L.], English walnut [*Juglans regia* L.], hackberry [*Celtis occidentalis* L.], and sunflower [*Helianthus annuus* L.]. Species sampled at the 1990 site were smooth sumac [*Rhus*

glabra L.], willow [*Salix* sp.], Arkansas rose [*Rosa arkansana*], bird's foot trefoil [*Lotus corniculatus* L.], Siberian elm, hemp [*Cannabis sativa* L.], box elder [*Acer negundo* L.], bur clover [*Medicago hispida* Gaertn.], red bud [*Cercis canadensis* L.], and hackberry. Five individual plants of each species were sampled in 1989 and three plants per species were sampled in 1990.

Similarly, sites at the Western Maryland Research and Education Center, Washington Co., Maryland, were sampled for host utilization by potato leafhopper. Sites were sampled each week from June 7 in 1989, June 11 in 1990, and May 28 in 1991 until mid-July. Sampling consisted of approximately three man-hours each week of inspecting leaves of various plants in non-crop habitats near alfalfa. Primary species sampled were black locust [*Robinia pseudoacacia* L.], chestnut oak [*Quercus prinus* L.], hackberry, redbud, slippery elm [*Ulmus rubra* Muhl.], black nightshade [*Solanum nigrum* L.], bitternut hickory [*Carya cordiformis* (Wang.) K. Koch.], blackberry [*Rubus* sp.], and red maple [*Acer rubrum* L.]. Other less common species were also inspected, but no nymphs were successfully reared to adulthood.

In both states, large nymphs found on plants were collected in vials and returned to the laboratory. The nymphs were reared in one dram vials. A second screw-cap vial, filled with 5% sucrose in water and covered with Parafilm 'M,' was set top-down on the vial containing the nymph. Large nymphs were allowed to feed on the solution until molting to the adult stage. Adults were frozen and later identified to species.

Results and Discussion

The list of known species of plants that were suitable for potato leafhopper reproduction and development was composed of 220 species, in 100 genera and 26 families (Table 1). In spite of the species diversity, the majority of host species are represented by the family Fabaceae (=Leguminosae, 61.8% of the species, 47% of the genera). This fact, plus the fact that the leafhopper was originally described from a specimen collected on 'Windsor' bean, *Vicia faba* L. (Harris, 1841), contradicts the use of the common name, potato leafhopper. The following five families represent over 75% of the species on the list: Fabaceae (61.8%), Asteraceae (5.0%), Fagaceae (4.5%), Rosaceae (3.6%), and Cucurbitaceae (3.6%).

The families of known potato leafhopper hosts include 16 orders which represent all six North American subclasses of the class Magnoliopsida (=dicotyledonous plants, Table 2), and include a range of relatively ancestral families (e.g., Berberidaceae) to more derived families (e.g., Asteraceae). Furthermore, the families represent species with highly divergent chemistry and morphological types.

The diversity in the taxonomic classification is reflected in the diversity within the ecological classification (Table 3). Within the leafhopper's range, 73% of its host genera occur exclusively in manmade habitats. Although the remaining 27% of the host genera are members of natural communities, they are often used as ornamentals or pasture/forage crops. The habitats these plants occupy can be divided into three types depending on the level and frequency of anthropomorphic disturbance. About one-third (32%) are commonly associated with annually tilled crop land, another third (32%) inhabit fields, pastures, and waste places, and the final third (36%) reside in woodlands, shrubland, and park-like settings. Herbs represent almost two-thirds (64%) of the host genera, most of which are perennial.

Table 1. Plant species suitable for potato leafhopper nymphal development as discovered during field studies.

Plant family, species	Common name	Source[1]
Aceraceae		
Acer sp.	maple	d
Acer negundo L.	boxelder	d, l
Acer saccharum Marshall	sugar maple	j
Amaranthaceae		
Amaranthus retroflexus L.	pigweed	d
Anacardiaceae		
Rhus chinensis Mill.	nutgall tree	e
Rhus copallina L.	shining sumac	d
Rhus glabra L.	smooth sumac	d
Rhus typhina L.	staghorn sumac	d
Asteraceae (=Compositae)		
Artemisia absinthium L.	wormwood	d
Carthamus tinctorius L.	safflower	e
Dahlia sp.	dahlia	a, d
Guizotia abyssinica (L.f.) Cass.	ramtilla	d
Helianthus annuus L.	sunflower	d
Helianthus tuberosus L.	Jerusalem artichoke	d
Helichrysum sp.	strawflower	d
Inula helenium L.	inula	d
Tagetes erecta L.	African marigold	d
Xanthium sp.	cocklebur	d
Zinnia sp.	zinnia	d
Berberidaceae		
Berberis aquifolium Pursh	barberry	d
Betulaceae		
Betula sp.	birch	d
Betula nigra L.	river birch	e
Cannabinaceae		
Cannabis sativa L.	hemp	d
Caricaceae		
Carica papaya L.	papaya	d
Chenopodiaceae		
Beta vulgaris L.	sugar beet	d
Convolvulaceae		
Ipomoea batatas Poir.	sweet potato	d
Cucurbitaceae		
Cucurbita ficifolia Bouche	fig leaf gourd	h
Cucurbita lundelliana Bailey	wild squash	h
Cucurbita maxima Duchesne	pumpkin	h
Cucurbita mixta Pangalo	winter squash	h
Cucurbita moschata Duchesne	butternut squash	h
Cucurbita pepo L.	acorn squash	h
Cucurbita sororia Bailey	wild squash	h
Cucumis sativus L.	cucumber	d

Table 1. Continued.

Plant family, species	Common name	Source[1]
Euphorbiaceae		
Croton capitatus Michx.	hogwort	e
Ricinus communis L.	castor-bean	d
Fabaceae (=Leguminosae)		
Amorpha glabra Poir.	false indigo	d
Amorpha herbacea Walt.	herbaceous false indigo	e
Arachis hypogaea L.	peanut	d, l
Astragalus canadensis L.	milk vetch	e
Astragalus cicer L.	milk vetch	e
Astragalus falcatus Lam.	milk vetch	d
Astragalus glycyphylla L.	milk vetch	d
Astragalus uliginosus L.	milk vetch	e
Caragana arborescens Lam.	Siberian pea tree	e
Cassia fasciculata Michx.	partridge pea	e
Cassia fasciculata var. *robusta* (Pollard) Macb.	partridge pea	e
Cassia nictitans L.	wild sensitive plant	e
Centrosema sp.	butterfly-pea	d
Cercis canadensis L.	redbud	d, m
Cladrastis lutea (Michx.) K. Koch	yellow-wood	d
Clitoria laurifolia Poir.	butterfly-pea	e
Colutea arborescens L.	bladder senna	e
Coronilla varia L.	crown vetch	d, l
Coronilla cretica L.		e
Crotalaria incana L.	rattlebox	d
Crotalaria intermedia Kotschy	rattlebox	d
Crotalaria lanceolata E. Mey.	rattlebox	d
Crotalaria usaramoensis Baker f.	rattlebox	d
Dalea alopecuroides Willd.	foxtail dalea	e
Dalea frutescens A. Gray	black dalea	e
Dalea lumholtzii Robins and Fern.	indigo dalea	e
Dalea ordiae A. Gray	indigo bush	e
Desmodium batacaulon A. Gray	tick trefoil	e
Desmodium paniculatum (L.) DC	tick trefoil	e
Desmodium strictum DC	tick trefoil	e
Dolichos lablab L.	bonavist bean	d
Galactia texana A. Gray	milk pea	e
Galactia volubilis (L.) Britton	milk pea	e
Galactia wrightii A. Gray	milk pea	e
Galega officinalis L.	goat's rue	e
Gleditsia triacanthos L.	honey locust	e
Glycine max (Merrill)	soybean	d
Glycyrrhiza glabra L.	licorice	d
Glycyrrhiza lepidota (Nutt.) Pursh	licorice	d
Glycyrrhiza uralensis Fisch.	licorice	e
Indigofera sp.	indigo	d
Indigofera arrecta Benth.	indigo	e
Indigofera farichildii E. G. Baker	indigo	e
Indigofera kirilowi Maxim.	indigo	e
Indigofera lindheimeriana Scheele	indigo	e
Indigofera linifolia Retz.	flax-leaved indigo	e
Indigofera macrostachys Vent.	indigo	e

Table 1. Continued.

Plant family, species	Common name	Source[1]
Indigofera pseudotinctoria Mats.	indigo	e
Indigofera reticulata Franch.	indigo	e
Indigofera sphaerocarpa A. Gray	indigo	e
Indigofera suffruticosa Mill.	indigo	e
Laburnum sp.	golden chain	d
Lathyrus hirsutus L.	singletary pea	l
Lathyrus latifolius L.	everlasting pea	e
Lathyrus ornatus Nutt.	wild pea	e
Lathyrus sylvester L.	perennial pea	e
Lathyrus venosus Muhl.	wild pea	e
Lebeckia sericea Thunb.		e
Lespedeza sp.	bush clover	d
Lespedeza angustifolia Ell.	bush clover	e
Lespedeza bicolor Turez.	bush clover	e
Lespedeza capitata Michx.	bush clover	e
Lespedeza cuneata (Dumont) G. Don	bush clover	d
Lespedeza cyrtobotrya Miq.	bush clover	e
Lespedeza daurica v. *shimadae* (Masam.) Masam. and Hosak	bush clover	e
Lespedeza frutescens (L.) Hornem.	bush clover	e
Lespedeza hirta (L.) Hornem.	bush clover	e
Lespedeza japonica L. H. Bailey	bush clover	e
Lespedeza juncea (L.f.) Pers.	bush clover	e
Lespedeza latissima Nakai	bush clover	e
Lespedeza maximowiczi C. K. Schneider	bush clover	e
Lespedeza procumbens Michx.	bush clover	e
Lespedeza seiboldi Miq.	bush clover	e
Lespedeza stuvei Nutt.	bush clover	e
Lespedeza thunbergii (DC.) Nakai	bush clover	e
Lespedeza virginica (L.) Britt.	bush clover	e
Lotus corniculatus L.	bird's-foot trefoil	e
Lotus grandiflorus (Benth.) Greene	large-flowered trefoil	e
Lotus humistratus Greene	trefoil	e
Lotus purshianus (Benth.) Clements and Clements	deer vetch	e
Lotus salsuginosus Greene	deer vetch	e
Lotus scoparius (Nutt.) Ottley	deer vetch	e
Lupinus nanus Dougl.	lupine	d
Medicago arabica (L.) Huds.	spotted medic	l
Medicago denticulata Willd.	toothed bur clover	e
Medicago hemicycla Grossheim	bur clover	e
Medicago hispida Gaertn.	bur clover	e
Medicago lupulina L.	black medic	e, l
Medicago polymorpha L.	bur clover	l
Medicago sativa L.	alfalfa	a, d, l
Medicago scutellata (L.) All.	bur clover	e
Melilotus alba Desr.	white sweet clover	d, f, l
Melilotus indica (L.) All.	yellow sour clover	l
Melilotus officinalis (L.) Lam.	yellow sweet clover	d, f
Mimosa sp.	mimosa	d
Nissolia schottii A. Gray	Schott's nissolia	e
Onobrychis arenaria DC.	onobrychis	d
Onobrychis sativa Lam.	onobrychis	e
Petalostemun prostratum Woot. and Standl.	prairie clover	e

Table 1. Continued.

Plant family, species	Common name	Source[1]
Phaseolus aconitifolius Jacq.	moth bean	e
Phaseolus acutifolius v. *latifolius* Freeman	tepary bean	e
Phaseolus aureus Roxb.	mung	d
Phaseolus calcaratus Roxb.	rice bean	d
Phaseolus lunatus var. *macrocarpus* Benth.	lima bean	d
Phaseolus metcalfii Woot. Standl.	Metcalf's bean	e
Phaseolus vulgaris L.	garden bean, kidney bean	a, d
Piptanthus nepalensis (Hook.) Sweet	piptanthus	e
Pueraria thunbergiana Benth.	kudzu	d
Rhynchosia difformis (Ell.) DC.	rhynchosia	e
Rhynchosia rariflora Standl.	rhynchosia	e
Rhynchosia texana Torr. and Gray	Texas rhynchosia	e
Robinia pseudoacacia L.	black locust	d, m
Sesbania exaltata (Raf.) Cory	Colorado river hemp	e
Sesbania vesicaria Ell.		e
Sophora japonica L.	Japanese pagoda-tree	d
Strophostyles helvola (L.) Britt.	wild bean	e
Tephrosia spicata (Walt.) Torr. and Gray	goat's rue	e
Tephrosia tenella A. Gray	hoary pea	e
Tephrosia toxicaria (L.) Pers.	cracca	d
Tephrosia vivginiana (L.) Pers.	cracca	d
Trifolium sp.	clover	a
Trifolium hybridum L.	alsike clover	d
Trifolium medium L.	zigzag clover	d
Trifolium pratense L.	red clover	d, m
Trifolium repens L.	white clover	d, l
Trifolium resupinatum L.	Persian clover	d, l
Trigonella corniculata L.	trigonella	e
Trigonella foenum-grecum L.	trigonella	e
Vicia amoena v. *oblongifolia* Regel	vetch	e
Vicia angustifolia L.	narrow-leaved vetch	l
Vicia cracca L.	cow vetch	d
Vicia dasycarpa Ten.	winter vetch	l
Vicia faba L.	broadbean	d
Vicia ludoviciana Nutt.	deer-pea vetch	l
Vicia minutiflora Dietr.	pygmy-flowered vetch	l
Vicia variabilis Freyn and Sint.	vetch	e
Vigna capensis Walp.	cowpea	e
Vigna sinensis (L.) Endl.	cowpea	d
Wisteria floribunda f. *rosea* (Bean) Rehd. and Wils.	American wisteria	d
Wisteria sinensis (Sims) Sweet	Chinese wisteria	d
Fagaceae		
Castanea sp.	Chinese chestnut	d
Castanea dentata (Marsh.) Borkh.	American chestnut	d
Castanea pumila (L.) Mill.	chinquapin	d
Quercus alba L.	white oak	d
Quercus ilicifolia Wang.	scrub oak	d
Quercus marilandica Muench.	blackjack oak	d
Quercus muhlenbergii Engelm.	yellow chestnut oak	d
Quercus palustris Muench.	pin oak	j
Quercus phellos L.	willow oak	d
Quercus rubra (Marsh.) Ashe	northern red oak	d

Table 1. Continued.

Plant family, species	Common name	Source[1]
Quercus stellata Wang.	post oak	d
Junglandaceae		
Carya sp.	hickory	d, j
Juglans regia L.	English walnut	d
Lamiaceae (=Labiatae)		
Lallemantia iberica Fisch. & Mey.		d
Leonurus cardiaca L.	motherwort	i
Satureja hortensis L.	savory	e
Malvaceae		
Althaea sp.	hollyhock	d
Althaea officinalis L.	marshmallow	d
Gossypium sp.	cotton	a, d
Hibiscus cannabinus L.	rose-mallow	d
Hibiscus roseus Thore	hibiscus	e
Hibiscus sabdariffa L.	roselle	d
Malva sp.	mallow	d
Moraceae		
Humulus lupulus L. *americanus* Nutt.	hop	e
Phytolaccaceae		
Phytolacca sp.	pokeweed	d
Polygonaceae		
Polygonum pensylvanicum L.	smartweed	d
Rheum rhaponticum L.	rhubarb	a, d
Rumex crispus L.	narrow leaf dock	d, m
Rumex obtusifolius L.	broadleaf dock	d
Rhamnaceae		
Rhamnus Frangula L.	alder buckthorn	d
Rosaceae		
Fallugia paradoxa (Don) Endl.	Apache plume	e
Fragaria sp.	strawberry	d
Malus sp.	apple	a, d
Prunus sp.	cherry	d, j
Prunus americana Marsh.	plum	d
Prunus cerasus L.	sour cherry	d
Rosa spp.	rose	d
Rubus sp.	blackberry	d, m
Sanguisorba minor Scop.	salad burnet	e
Salicaceae		
Salix sp.	willow	d
Salix exigua Nutt.	willow	e
Salix hookeriana Barratt	Hooker's willow	e
Solanaceae		
Atropa belladonna L.	belladonna	d
Solanum spp.		c, g, k
Solanum carolinense L.	horsenettle	d
Solanum melongena L.	eggplant	a, b, d
Solanum onigerum		b

Table 1. Continued.

Plant family, species	Common name	Source[1]
Solanum torvum Swartz	Mexican solanum	d
Solanum tuberosum L.	potato	a, c
Tiliaceae		
Tilia americana L.	American basswood	j
Ulmaceae		
Celtis occidentalis L.	hackberry	d, j, m
Celtis laevigata Willd.	sugarberry	l
Ulmus americana L.	American elm	d, j, l, m
Ulmus pumila L.	dwarf elm	d
Ulmus rubra Muhl.	slippery elm	m

[1] Sources are as follows: a, DeLong, 1931; b, Poos and Haenseler, 1931; c, Sleesman, 1940; d, Poos and Wheeler, 1943; e, Poos and Wheeler, 1949; f, Manglitz and Jarvis, 1966; g, Radcliffe and Lauer, 1967; h, Howe and Rhodes, 1976; i, Lamp et al., 1984; j, Lamp et al., 1989; k, Flanders and Radcliffe, 1992; l, Taylor, 1993; m, this first report.

Table 2. Summary of higher classification, based on Smith (1977), of hose plants listed in Table 1. All subclasses are within the class Magnoliopsida.

Subclass	Order	Family	Number of Genera	Number of Species
Magnoliidae	Ranunculales	Berberidaceae	1	1
Hamamelidae	Fagales	Betulaceae	1	1
		Fagaceae	2	10
	Uticales	Moraceae	1	1
		Cannabaceae	1	1
		Ulmaceae	2	5
	Juglandales	Juglandaceae	2	2
Caryophyllidae	Caryophyllales	Amaranthaceae	1	1
		Phytolaccaceae	1	1
		Chenopodiaceae	1	1
	Polygonales	Polygonaceae	3	4
Dilleniidae	Violales	Caricaceae	1	1
		Cucurbitaceae	2	8
	Malvales	Malvaceae	4	6
		Tiliaceae	1	1
	Salicales	Salicaceae	1	2
Rosidae	Rosales	Rosaceae	7	8
		Fabaceae	47	136
	Euphorbiales	Euphorbiaceae	2	2
	Rhamnales	Rhamaceae	1	1
	Sapindales	Aceraceae	1	2
		Anacardiaceae	1	4
Asteridae	Polemoniales	Solanaceae	2	6
		Convolvulaceae	1	1
	Asterales	Asteraceae	10	11
	Lamiales	Lamiaceae	3	3
		Total	100	220

Table 3. Ecological classification of plant genera suitable for potato leafhopper reproduction, from Table 1.

Class	Category	Genera within class (%)
Source of disturbance	Human	73
	Natural	27
Habitat disturbance	Annually-tilled cropland	32
	Field, pastures, waste places	32
	Woodlands, shrublands, parks	36
Growth form	Woody	36
	Herbaceous perennial	40
	Herbaceous biennial	2
	Herbaceous annual	22
Plant origin	Native	38
	Introduced	62
Plant autecology	Competitive	64
	Ruderal	36
	Stress tolerant	0

Annuals comprise 22% of the host genera and woody perennials 36%. Moreover, 62% of the genera represent species that have been introduced into the leafhopper's range. According to Grime's (1979) classification system, 36% are ruderals while the remaining genera are competitive. These competitive genera represent herbaceous or woody perennial species commonly associated with old fields, hay fields, and pastures that experience little below ground disturbance. The lack of stress tolerant hosts is likely a function of a number of factors, including few highly stressful environments over the leafhopper's range, our limited use of such plants for crop and ornamental plants, and limited observations.

The breadth of plant hosts alone, and especially when classified taxonomically and ecologically, demonstrated that this species has readily adopted hosts from most of the major and disparate dicotyledonous taxa within its range. Wherever it occurs, potato leafhopper utilizes native and introduced dicot crops, forages, weeds, shrubs, and trees. From its propensity for openings (fields, meadows, pastures) created by and shared with humans, it is not surprising that most of its hosts are found in anthropogenic habitats, most are herbaceous, and the majority have been introduced. A recent analysis of potato leafhopper resistance in *Solanum* clones suggest that ancestral types have resistant characteristics, while intermediate types derived from human selection lack resistance (Flanders et al., 1992). Yet, its use of human-derived plants does not occur without the use of native plants in natural landscapes, including trees and native legumes (Lamp et al., 1989; Taylor, 1993, and data discussed below). This observation suggests that although human modification of the landscape has enhanced the leafhopper's utilization of hosts, the leafhopper likely was able to utilize native hosts and habitats before the presence of agriculture in North America. Furthermore, the use of plant monocultures for agriculture and land management has likely led to increased leafhopper densities both during spring generations at overwintering sites (e.g., the use of legumes for erosion control, Taylor, 1993) as well as during

Table 4. Common non-crop hosts at two disparate sites within potato leafhopper summer range, determined by rearing of collected nymphs.

Site	Year	Minimum number of host species sampled	Host(s)
NE: Lancaster Co.	1989	11	*Rumex crispus, Ulmus americana, Trifolium pratense*
	1990	10	*Cercis canadensis, Celtis occidentalis*
MD: Washington Co.	1988	9	*Robinia psuedoacacia*
	1989	9	*Robinia pseudoacacia, Rubus* sp., *Celtis occidentalis, Ulmus rubra*
	1990	9	*Celtis occidentalis, Ulmus rubra*

the summer in northern agricultural landscapes (e.g., the use of alfalfa monocultures, Lamp, 1991; Lamp et al., 1984a).

We can only speculate why some plant taxa are not suitable hosts for this polyphagous insect. One of the more striking non-host groups is all of the species in the class Liliopsida (i.e., monocotyledonous plants such as grasses and sedges). Its inability to produce offspring on any member of this class may be a function of the relatively smaller vascular bundles or the inability of its nymphs to access them (Lamp et al., 1984b). Adults are frequently collected on grasses (e.g., corn, Poos and Wheeler, 1943), and in no choice tests adults will survive but will not oviposit on various weed and crop grasses (Lamp et al., 1984b, and unpubl. data). Another taxon not represented on the list is gymnosperms (Division Pinophyta). Potato leafhopper has been collected on eastern white pine, *Pinus strobus* L., loblolly pine, *Pinus taeda* L., and longleaf pine, *Pinus palustris* Mill (Poos and Wheeler, 1943; Taylor, 1993). Recent evidence using elemental markers has demonstrated that adults do ingest fluids from loblolly pine, a common site of overwintering potato leafhopper in southern U.S. (Taylor et al., 1993).

Among the class Magnoliopsida, eight major orders frequently encountered in the leafhopper's range have not been found as hosts: Ericales, Gentianales, Geraniales, Myrtales, Papaverales, Rubiales, Scrophulariales, and Umbellales. Some of these orders are well known for possessing prominent chemical defenses (e.g., Papaverales, Scrophulariales, and Umbellales), some have both chemical and physical defenses (e.g., Geraniales and Ericales), and for some we know little about their defensive strategies (e.g., Rubiales and Myrtales) (Harborne and Turner, 1984).

In spite of its inability to reproduce on these groups, non-host plants for potato leafhopper may contribute to its population ecology during times when hosts are unavailable. For example, studies during the winter have shown that the leafhopper uses non-host plant species as refugia (Decker and Cunningham, 1968; Taylor, 1993). Furthermore, increases in population densities in corn have been associated with the harvesting of adjacent alfalfa fields during the summer (Lamp, unpubl. data). Thus, these non-hosts may allow adults to survive during times when host plants are unavailable or are difficult to locate.

The nymph rearing technique, although successful with a laboratory culture (Lamp, unpubl. data), had varying success with field-collected nymphs. Approximately 20% of the Nebraska nymphs collected, and 48% of the Maryland nymphs collected, survived to adulthood. Also, the sex ratio was skewed to females: 72%

of the Nebraska nymphs and 80% of the Maryland nymphs surviving to adulthood were female. This may have been the result of the rearing procedure. All males that survived were identified as *E. fabae*. Of the 26 potential hosts sampled, potato leafhopper nymphs were verified on only one to four plant species per year and site (Table 4). Thus, in spite of the large list, host utilization under field conditions suggests that in fact the actual host range for reproduction at one location may consist of only a few species. DeLong (1965) further suggested that host utilization varies between years as a result of varying host phenology at the time of first spring migration.

In conclusion, the diversity of host plants suitable for reproduction suggests that non-crop habitats may be a significant source of potato leafhopper populations after spring migration into northern states. Also, the ability of leafhopper adults to utilize at least some non-host species as refugia contributes a secondary role to non-crop habitats. Yet, our limited data suggest that utilization of non-crop habitats is restricted to a relatively few naturalized hosts. Additional information on the role of these habitats is needed to better understand potato leafhopper population dynamics.

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