Phytophagous Arthropods Associated with *Parthenium hysterophorus* (Asteraceae) in North America

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ABSTRACT A faunal survey was conducted to find possible biological control agents for *Parthenium hysterophorus* L. (Asteraceae), a serious annual weed in many parts of the world, particularly Queensland, Australia, and India. Between 1977 and 1991, most of the plant's native range in North America was surveyed from bases at Monterrey and Cuernavaca, Mexico, and Temple, TX. Two hundred and sixty-two phytophagous arthropod species were collected on *P. hysterophorus* by various methods including hand picking, dissection, rearing, and sweeping; 144 of these species were found to feed on the plant at some stage of their life cycle. The orders represented most abundantly were Coleoptera (33.2%), Homoptera (22.9%), Lepidoptera (20.2%), and Hemiptera (18.3%). Two fungal pathogens, *Puccinia abrupta* Dietel and Holway variety *partheniicola* (Jackson) Parmelee and *Puccinia melampodii* Dietel and Holway, were also observed. An index of similarity was used to make pairwise comparisons between the phytophagous arthropod communities on different plant taxa. These comparisons showed that the fauna of *P. hysterophorus* is most similar to that of ragweeds (*Ambrosia* spp.). Six insect species that were shown to be stenophagous were shipped to Australia for further testing and possible field release. One of the fungal pathogens underwent host-range testing in the United Kingdom and was released in Australia.

KEY WORDS *Parthenium hysterophorus*, Asteraceae, biological control, phytophagous, arthropod fauna, North America

Parthenium hysterophorus L. (Asteraceae) is a herbaceous annual weed native to the neotropics, from the southern United States to Argentina, which has become widely naturalized in other tropical and subtropical regions. It has become a particularly serious problem in Queensland, Australia (Haseler 1976) and in India (Towers et al. 1977). It also occurs in Taiwan, southern China, Vietnam, Vanuatu, New Caledonia, Kenya, Madagascar, Mozambique, South Africa, the Mascarenes and Seychelles, and Ethiopia. In Queensland, thousands of square kilometers of rangeland are infested, and pure stands of *P. hysterophorus* have excluded beneficial pasture species over large areas (McFadyen 1992). All parts of the plant contain parthenin, a bitter, toxic sesquiterpene lactone, which makes the plant unpalatable to cattle and has caused many cases of severe contact dermatitis in susceptible people (Towers et al. 1977). Its profuse seed production enables it to spread rapidly. The plant is reported to be allelopathic (Dharmaraj et al. 1988).

The center of diversification of the genus *Parthenium* is considered to be in northeastern Mexico, where at least 8 of the 16 described species occur (Rollins 1950). The general climatic characteristics of this area are similar to those of the infested areas of Queensland (McClay 1985).

The cost of chemical and cultural control of large stands of *P. hysterophorus* on low-value pasture is prohibitive (McFadyen 1992). In an attempt to identify alternative control measures for this serious rangeland weed, the Queensland Department of Lands (QDL) started a biological control program in 1975. As part of this program, scientists of the Department of Lands and of the Commonwealth (now International) Institute of Biological Control (CIBC, now IIBC) undertook exploration in North and South America. These staff were responsible for conducting faunal studies of *P. hysterophorus* and selecting appropriate stenophagous species for host specificity and biological studies. If these tests indicated that a species was a potential biological control agent, it was shipped to the Sir Alan Fletcher Research Station of the Queensland Department of Lands in Sherwood, Australia, for further testing, approval, and eventual release.

This article reports the phytophagous insects and mites found in North America during these investigations. A preliminary list of 159 phytophagous insects associated with the plant in Mexico

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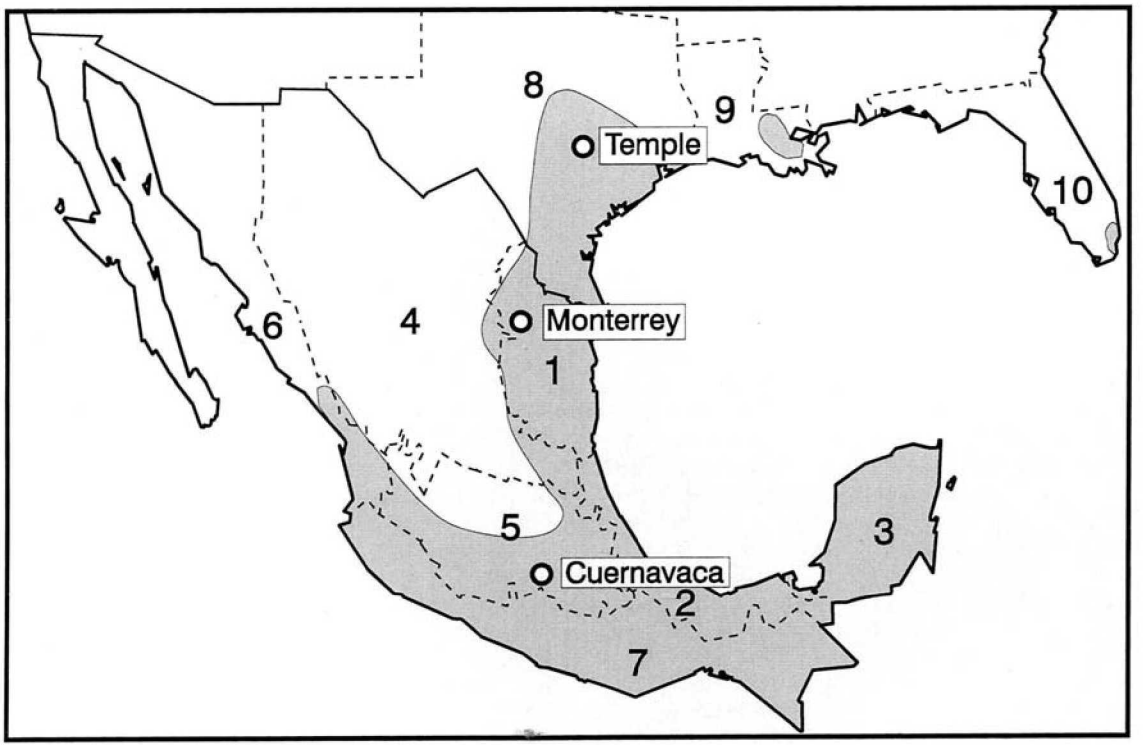

Fig. 1. Search area for natural enemies of *P. hysterophorus* in the United States and Mexico (shaded). Numbers identify the regions used to indicate geographical distribution in Table 1.

has been published (McClay 1981) and the species sent to Australia for further testing were discussed by McClay (1985). In addition to the surveys reported here, QDL staff conducted surveys of South American populations of *P. hysterophorus* in Brazil and Argentina (McFadyen 1976; QDL, unpublished data), and some collections were made in the Caribbean by F.D.B. and other CIBC staff. The biological control program for *P. hysterophorus* was reviewed by McFadyen (1992).

Materials and Methods

The area covered by this survey (Fig. 1) comprised most of Mexico and parts of the southeastern United States. Two preliminary surveys were conducted over a total of 40 d in June, October, and November 1976 by F.D.B. (unpublished data, 1977). During these surveys, collections were made in the states of Veracruz, Yucatán, Campeche, Quintana Roo, Puebla, and Nuevo León, Mexico, and in the areas of Houston and College Station, TX, Baton Rouge, LA, and Miami and Homestead, FL. More detailed studies were then conducted by A.S.M. from 1978 to 1983 from a base at the Instituto Tecnológico y de Estudios Superiores de Monterrey (ITESM) at Monterrey, Nuevo León. During this period, extensive collections were made in northeastern Mexico, particularly the states of Nuevo León, Tamaulipas, and eastern Coahuila. Some collections were also made along the Gulf coastal areas of Veracruz and Tabasco, and on the Pacific coast from Sinaloa to Nayarit and from Oaxaca to Chiapas. From 1983 to 1993, surveys were conducted in Texas by W.A.P. from a base at the Queensland Department of Lands North American Field Station (NAFS) in Temple, TX. From 1988, W.A.P and K.R.P. made additional surveys in southern Mexico, particularly the state of Morelos, from a substation at Cuernavaca, Morelos.

Collections were made on natural stands of *P. hysterophorus* on roadsides, wasteland, neglected fields, and similar sites at frequent intervals throughout the year. Arthropods resting on the plant were captured directly by hand or with an aspirator, or by sweeping pure stands of *P. hysterophorus* with a sweep net. All parts of the plant were dissected for endophagous species. Adults of root-feeding species were obtained by keeping roots in emergence boxes with glass vials fitted over the exit holes or in large glass jars covered with nylon gauze. Other plant parts were usually too perishable to be held in the laboratory long enough for emergence of adult stages of endophages. Some stem and root-feeding insects were reared to the adult stage in the laboratory by feeding field-collected larvae on an artificial diet (Harley and Willson 1968).

In addition to these collections on natural stands, a series of plots (5 m by 5 m) were sown with *P. hysterophorus* at the ITESM field station, Apodaca, Nuevo León, and allowed to become infested with arthropods. Samples were taken from the plots at 2-wk intervals from 1978 to 1982 by selecting 25 plants at random and collecting all arthropods resting on them or feeding internally in them.

Most specimens were initially submitted for identification either to the United States Department of Agriculture Systematic Entomology Laboratory, Beltsville, MD, or to the Commonwealth (now International) Institute of Entomology, London. Specimens that could not be identified to species by these laboratories were later forwarded to other taxonomists. Many submitted specimens were identified only to genus because of inadequate material, unavailability of type specimens, or lack of satisfactory taxonomic revisions. These are reported here only if they represent a genus not otherwise reported or if the taxonomist explicitly stated that they are distinct from the other named species of the genus reported here.

The probable level of host specificity of each species was assessed using information from the literature, specialists, and field observations. Species that appeared likely to be host specific, at least the subtribe level, were selected for preliminary host-specificity studies conducted in Mexico and Texas. Test plants were selected from the subtribe Ambrosiinae and tribe Heliantheae, to which the genus *Parthenium* belongs (Stuessy 1977), with the addition of some economic species from other tribes of the Asteraceae. Sunflower, *Helianthus annuus* L., is the most important crop species closely related to *Parthenium* and was considered a critical test plant (Wapshere 1975). Experimental details depended on the biology of each species tested, but many tests were conducted in multiple-choice cages as described by McClay (1987). Field observations of the insects' host plant associations were also made.

If our investigations indicated that the host range of an insect was within the subtribe Ambrosiinae, the insect was recommended for further study and shipped to Australia after quarantine approval had been received.

In our field surveys, it was not always possible to determine whether a captured insect was actually feeding on *P. hysterophorus*. Published faunal lists for many plants frequently do not indicate whether the species listed are known to feed on the plant in question or were simply collected on it. We report here all the species belonging to known phytophagous taxa that we collected on *P. hysterophorus*, with the exceptions of pollen or nectar gatherers, adult Lepidoptera and Diptera, species shown in laboratory tests not to feed on *P. hysterophorus*, and species whose known biology clearly indicates that *P. hysterophorus* is an unlikely host. Where any life stage of an insect species has been observed to feed on *P. hysterophorus*, this fact is indicated in Table 1. Records where feeding is not indicated refer only to collections of adults on the plant; this category undoubtedly includes some species which are casual visitors on *P. hysterophorus*.

Specimens of many of the species identified were retained by the taxonomists responsible for identification, and were deposited mainly in the National Museum of Natural History in Washington, DC, and the Natural History Museum in London. Material of all species collected from 1978 to 1983 was deposited in the collection of the IIBC Caribbean and Latin American Station, Trinidad, and at NAFS. Additional material from the years 1978 to 1983 was deposited in the collection at ITESM. Material collected in 1983 and afterward was placed in the NAFS collection, now held at the Tropical Weeds Research Centre (TWRC), Charters Towers, Queensland. Inquiries concerning the location of particular material collected during the project may be directed to W.A.P. or A.S.M. Relevant information about each species was also entered into a computer database now maintained at TWRC (Palmer 1995); detailed database records for particular species may be obtained from W.A.P.

We assessed the degree of similarity between the fauna of *P. hysterophorus* and those of 1 other *Parthenium* species, 6 other native North American genera of Asteraceae, and 4 native North American genera in other families. A pairwise index of percentage similarity I_s was defined by

$$I_S = 100 \times (n_{shared}/n_{pooled})$$

where n_{shared} is the number of arthropod species in common between the 2 plant taxa and n_{pooled} is the total number of species in the pooled faunas of both taxa.

Results and Discussion

Phytophagous arthropods associated with *P. hysterophorus* in Mexico and the United States are listed in Table 1. Information on host specificity and pest status in this table is a synthesis of the results of feeding tests carried out during the program, field observations, literature records, and information from specialists who identified the insects. Species that were subjected to host range tests during the project are indicated. The numbered regions used to identify geographic distribution are shown in Fig. 1. Distribution records in Table 1 represent only data from our surveys and do not include information from the literature. Many species may, therefore, have wider distributions than indicated in the table.

Table 1 also indicates frequency of collection for each species. Because collections were not quantitative, the assessment of whether a given species is common, occasional, or rare is based on a subjective assessment of the collecting experience of

Table 1. Phytophagous arthropods associated with *P. hysterophorus*

Species	Frequency[a]	Stages feeding[b]	Feeding site[c]	Feeding type[d]	Host specificity[e]	Tested[f]	Distribution[g]	Pest status[h]
			Acari					
Eriophyidae								
Eriophyes nr. *parthenii* Keifer	O	N, A	F	ECT	*****	T	1	
Tetranychidae								
Tetranychus nr. *ludeni* Zacher	G	N, A	L	ECT	**		1	
			Orthoptera					
Gryllidae								
Oecanthus nr. *celerinictus* T. Walker	O	N, A	L	ECT			1	
Tettigoniidae								
Conocephalus fasciatus (DeGeer)	R				*		8	
			Thysanoptera					
Thripidae								
Caliothrips phaseoli (Hood)	G	N, A	L	ECT	*		1	P
Microcephalothrips abdominalis (Crawford)	O	N, A	F	ECT	**		1	
			Hemiptera					
Alydidae								
Burtinus femoralis (Distant)	R						1	
Berytidae								
Jalysus reductus Barber	R						5	
Coreidae								
Chariesterus moestus Burmeister	R						5	
Nirvoecus claviger Stål	R						1	
Phthia picta (Drury)	R						5	
Sagotylus confluens (Say)	C	N, A	S	ECT	*	T	1, 3, 5	P
Lygaeidae								
Acroleucus sp.	R						5	
Blissus leucopterus (Say)	R				*		7	P
Neopamera bilobata (Say)	R				*		5	
Nysius senecionis (Schilling)	C	A	F	ECT	***		1	
Nysius sp.	C	A	F	ECT			1	
Xyonysius californicus (Stål)	C	A	F	ECT			1, 5	
Miridae								
Collaria oleosa (Distant)	O				*		5	
Cyrtopeltis sp.	O						5	
Halticus bractatus (Say)	R				*		12	P
Ilnacora inusta (Distant)	O				**		5	
Lygus lineolaris (Palisot de Beauvois)	O				*		5, 8	P
Neurocolpus prob. *mexicanus* Distant	R						5	
Phytocoris sp.	R						5	
Poecilocapsus nigriger (Stål)	R	N, A	L	ECT	*		1	
Polymerus basalis (Reuter)	R				*		12	
Polymerus testaceipes (Stål)	O				*		5	
Proba distanti (Atkinson)	C	N, A	F, L, S	ECT	**	T	1, 2, 4, 5, 7	
Proba sallei (Stål)	R				**		5	
Reuteroscopus ornatus (Reuter)	C	N, A	F, L, S	ECT	**	T	1, 2, 4, 8, 10	
Rhinacloa forticornis (Reuter)	R				*		5	P
Sixeonotus sp.	R						5	
Taedia sp.	R						5	
Taylorilygus pallidulus (Blanchard)	C	N, A	F, L, S	ECT	*		1, 5, 7, 8, 10	
Pentatomidae								
Chlorochroa ligata (Say)	R				*		12	P
Dendrocoris sp.	R						12	
Euschistus quadrator Rolston	O	N, A	L, S	ECT	*		1, 7	
Euschistus sp.	R						2, 7	
Mormidea notulata (Herrich-Schaffer)	R				*		7	
Thyanta accerra McAtee	R				*		8	P
Thyanta perditor (F.)	R				*		5	P
Piesmatidae								
Piesma cinereum (Say)	O				*		1	P

Table 1. Continued

Species	Frequency[a]	Stages feeding[b]	Feeding site[c]	Feeding type[d]	Host specificity[e]	Tested[f]	Distribution[g]	Pest status[h]
Pyrrhocoridae								
Dysdercus mimulus Hussey	R				*		1	P
Rhopalidae								
Harmostes nebulosus Stål	R				**		1, 5	
Harmostes reflexulus (Say)	O				**		1	
Harmostes serratus (F.)	R				*		3	
Liorhyssus sp.	R						1	
Scutelleridae								
Chelysomidea variabilis (Herrich-Schaffer)	R	N, A	L, S	ECT	*		1	
Homaemus proteus Stål	O						1, 5	
Sphyrocoris obliquus (Germar)	O						1	
Tingidae								
Corythucha morrilli Osborn & Drake	C	N, A	L, S	ECT	*	T	1, 2, 5, 8	P
Dictyla monotropidia (Stål)	R				*		11	
Leptodictya tabida (Herrich-Schaffer)	R				*		5	
		Homoptera						
Aleyrodidae								
Trialeurodes abutilonea (Haldeman)	G	N	L	ECT	*		1	P
Aphididae								
Aphis gossypii Glover	G	N, A	L, S	ECT	*		1	P
Geopemphigus floccosus (Moreira)	C	N, A	R	ECT	*		1	
Uroleucon ambrosiae (Thomas)	C	N, A	S, L	ECT	*****	T	1, 2, 3, 4, 7, 8, 9	
Cercopidae								
Aeneolamia sp.	R						3	
Clastoptera xanthocephala Germar	C	A	L	ECT			8	
Prosapia sp.	R						3	
Cicadellidae								
Aceratagallia gillettei (Osborn & Ball)	C	N, A	L, S	ECT	*	T	1	
Agallia barretti Ball	R				*		5	
Agallia quadripunctata excavata Oman	C				*		5	
Agrosoma pulchella (Guérin)	R				*		2, 5	
Egidemia inflata Young	R						3	
Empoasca abrupta DeLong	C	N, A	L, S	ECT	*		1	P
Empoasca nr. *crocostigmata* Davidson & DeLong	O						5	P
Empoasca nigra var. *typhlocyboides* Gillette & Baker	C	N, A	L, S	ECT	**		1	
Graphocephala rufimargo (Walker)	C	A	L	ECT	*		5, 7	
Gyponana sp.	R						1, 2, 3	
Homalodisca coagulata (Say)	O	A	S	ECT	*		1	P
Homalodisca insolita (Walker)	R	A	L, S	ECT	*		5	P
Macrosteles sp.	R						5	
Momoria misella (Ball)	R				**		7	
Oncometopia clarior Walker	O				*		1, 3	
Penestragania robusta (Uhler)	C	N, A	L, S	ECT	*	T	1, 2, 4, 5, 8	P
Phera lanei Young	R						5	
Phera obtusifrons (Fowler)	R				*		5	
Scaphytopius frontalis (Van Duzee)	R				*		8	
Scaphytopius fuliginosus (Osborn & Ball)	O	N, A	L, S	ECT	*	T	1, 5	P
Sibovia compta (Fowler)	R				*		5	
Texananus ovatus (Van Duzee)	O				*		1	
Xerophloea viridis (F.)	O	N, A	L, S	ECT	*	T	1	
Coccidae								
Ceroplastes cirripediformis Comstock	R	N, A	S	ECT	*		3	P
Lecanium sp.	R	N, A	L	ECT			5	
Parasaissetia nigra (Nietner)	R	N, A	S	ECT	*		2, 3	P
Saissetia miranda (Cockerell & Parrot)	R	N, A	S	ECT	*		3	P
Delphacidae								
Stobaera concinna (Stål)	C	N, A	L, S	ECT	****	T	1, 4, 5	
Dictyopharidae								
Scolops sp.	C	N, A	L, S	ECT			1	

Table 1. Continued

Species	Frequency[a]	Stages feeding[b]	Feeding site[c]	Feeding type[d]	Host specificity[e]	Tested[f]	Distribution[g]	Pest status[h]
Eriococcidae								
Acanthococcus dubius (Cockerell)	R	N, A	S	ECT	*		3	
Flatidae								
Flatormenis sp.	O						5	
Issidae								
Colpoptera albavenosa Caldwell	R						2	
Margarodidae								
Icerya nr. *littoralis* Cockerell	R	N, A	L	ECT			3	
Icerya purchasi Maskell	R	N, A	S	ECT	*		3	P
Membracidae								
Acutalis tartarea (Say)	R						12	
Entylia carinata (Forster)	C	N, A	S, L	ECT	**		1, 5, 12	
Micrutalis sp.	C						1, 2, 5	
Polyglypta sp.	R						5	
Publilia sp.	O						1, 4, 5	
Spissistilus festinus (Say)	R				*		1, 2, 12	P
Stictocephala sp.	O						1	
Umbonia prob. *crassicornis* Amyot & Serville	O				*		5	
Vanduzea segmentata (Fowler)	R				*		1	
Ortheziidae								
Orthezia praelonga Douglas	R	N, A	L, S	ECT	*		11	
Orthezia pseudinsignis Morrison	R				*		3	
Pseudococcidae								
Ferrisia virgata (Cockerell)	C	N, A	L, R, S, M	ECT	*		1, 2, 3, 5	P
Paracoccus sp.	R	N, A	S	ECT			2	
Phenacoccus nr. *defectus* Ferris	G	N, A	S, M	ECT			1	
Phenacoccus gossypii Townsend & Cockerell	O	N, A	S	ECT	*		3	P
Phenacoccus solani Ferris	O	N, A	R	ECT	*		1, 2	P
Pseudococcus affinis (Maskell)	O	N, A	S	ECT	*		11	P
Spilococcus sp.	R	N, A	F	ECT	*		2, 3	
Putoidae								
Puto barberi (Cockerell)	R	N, A	S	ECT	*		11	P
		Coleoptera						
Anthribidae								
Trigonorhinus limbatus (Say)	R						1	
Apionidae								
Chrysapion auctum (Sharp)	R						5	
Bruchidae								
Acanthoscelides sp.	R						5	
Cerambycidae								
Dectes nigripilus Chemsak & Linsley	R						4	
Dectes sayi Dillon & Dillon	C	L, A	S, L	END	**		1	
Dectes texanus LeConte	O	L, A	S, L	END	*		4, 5	P
Dorcasta cinerea (Horn)	R				*		1	P
Hippopsis lemniscata (F.)	O	L, A	S, L	END	*		1, 2, 3, 10	P
Phaea tenuata Bates	R						5	
Pseudocanidia cuernavacae Dillon	O	L	S	END	***	T	5	
Chrysomelidae								
Acalymma blomorum Munroe & Smith	R				*		3	P
Agathomerus rufus Klug	R						5	
Anoplitis sp.	R	L	L	END			2	
Chaetocnema horni Jacoby	R						11	
Chalepus nr. *contiguus* Baly	R	A	L	ECT			1	
Chrysodina sp.	R						5	
Crepidodera sp.	R						5	
Cryptocephalus irroratus Suffrian	O	L, A	L	ECT	****	T	1	
Cryptocephalus prob. *nigrovittatus* Jacoby	O	L, A	L	ECT			1	
Cryptocephalus sp.	O	L, A	L	ECT			1	

Table 1. Continued

Species	Frequency[a]	Stages feeding[b]	Feeding site[c]	Feeding type[d]	Host specificity[e]	Tested[f]	Distribution[g]	Pest status[h]
Derocrepis sp.	R						5	
Diabrotica balteata LeConte	O				*		1, 3, 5, 7	P
Diabrotica undecimpunctata Jacoby	R				*		11	
Diachus auratus (F.)	C	L, A	L	ECT	**	T	1, 5, 8	
Disonycha knabi Blake	R						5	
Durangoita chrysodinoides (Jacoby)	R						1	
Epitrix sp.	R						1	
Exema prob. *conspersa* (Mannerheim)	C	L, A	L	ECT	**	T	1, 2, 5, 7	
Exema nr. *dispar* Lacordaire	O				**		5	
Glyptina sp.	R						1	
Glyptoscelis nr. *mexicana* Jacoby	R						11	
nr. *Hippuriphila* sp.	R						5	
Labidomera sp.	R						1	
Lexiphanes guerini (Perbosc)	C				*		5	
Lupraea sp.	R						7	
Microrhopala pulchella Baly	R				*		3	
Microrhopala prob. *sallei* Baly	R						5	
Nodonota nr. *atra* Harold	R						11	
Omophoita aequinoctialis (L.)	R				*		1	
Ophraella communa LeSage	O	L, A	L	ECT	***	T	1, 2, 5	
Ophraella prob. *slobodkini* Futuyma	O	L, A	F	ECT	***	T	2	
Pachybrachis nr. *femorata* Olivier	R						11	
Pachybrachis immaculatus Jacoby	O	L, A	L	ECT	***	T	1, 4	
Pachybrachis nr. *vestigialis* Fall	O						5	
Pachybrachis sp.	O	L, A	L	ECT	***	T	1	
Psylliodes sp.	R						11	
Systena blanda Melsheimer	C				*		11	P
Systena nigroplagiata Jacoby	R						5	
Systena nr. *pectoralis* Clark	O						1, 2	
Systena nr. *semivittata* Jacoby	R						3	
Systena sp.	C	A	L	ECT			1	
Zygogramma bicolorata Pallister	C	L, A	L	ECT	****	T	1, 2, 4, 5	
Zygogramma malvae Stål	R	A	L	ECT			5	
Coccinellidae								
Epilachna mexicana (Guérin)	R				*		7	P
Curculionidae								
Baris prob. *aerea* Boheman	C	L, A	R	END	**	T	1, 2, 5, 6, 7	
Baris prob. *interstitialis* Say	O	L, A	R	END	**		1, 2, 6	
Baris sulcipennis (Brisout)	R						5	
Chalcodermus sp.	R	L	S	END			1	
Compsus auricephalus (Say)	O	A	L	ECT	*		1	
Cylindrocopturus armatus Champion	O	L, A	R, S	END	***	T	1, 2, 7	
Cylindrocopturus nr. *mammillatus* (LeConte)	R						5	
Cylindrocopturus tetralobus Champion	R						5	
Epicaerus aurifer Boheman	R				*		5	P
Epicaerus prob. *texanus* Casey	O						1	
Geraeus picumnus (Herbst)	R						1, 5	
Geraeus senilis (Boheman)	R						5	
Linogeraeus sp.	R						5	
Listroderes costirostris obliquus Klug	R	L, A	L		*		1	P
Lixus prob. *scrobicollis* Boheman	C	L, A	S, L	END	***	T	1, 2, 4	
Mitostylus setosus (Sharp)	O	A	L	ECT	**		1, 4	
Onychobaris sp.	O						1	
Pandeleteius sp.	R						1	
Rhodobaenus quinquepunctatus (Say)	O	L, A	S	END	**		8	
Rhodobaenus sanguineus (Gyllenhal)	C	L, A	S	END	**		2, 5	
Rhodobaenus tredecimpunctatus (Illiger)	R	L, A	S	END	***		1, 2	
Sciadrusus propheticus Sharp	R						5	
Sibinia sp.	R				*		1, 5	
Smicronyx lutulentus Dietz	C	L, A	F	END	*****	T	1, 2, 4, 8	
Smicronyx sordidus LeConte	R				***		1	
Thecesternus hirsutus Pierce	O	L, A	R	ECT	*****	T	1, 8	
Trepobaris inornata Champion	R						5	
Languriidae								
Dasydactylus sp.	R	L	S	END			2	
Languria mozardi Latreille	O	L	S	END	*		1	P
Languria nr. *laeta* Leconte	R	L	S	END			2	
Langurites lineatus (Castelnau)	R	L	S	END	**		1	

Table 1. Continued

Species	Frequency[a]	Stages feeding[b]	Feeding site[c]	Feeding type[d]	Host specificity[e]	Tested[f]	Distribution[g]	Pest status[h]
Scarabaeidae								
Euphoria sp.	R						5	
Scolytidae								
Hypothenemus nr. *beameri* Wood	R	L	S	END			1	
		Lepidoptera						
Arctiidae								
Estigmene acrea (Drury)	O	L	L	ECT	*		1	P
Halisidota catenulata Hübner	R	L	L	ECT	*		2	
Gelechiidae								
Dichomeris nr. *aenigmatica* (Clarke)	R	L	L	ECT	**		2	
Dichomeris simpliciella (Busck) or nr.	O	L	L	ECT			1	
Glyphidocera sp.	R	L	L	ECT			2	
Gnorimoschaema saphirinella Chambers	R	L	L	ECT	****		1	
Helcystogramma chambersella (Murtfeldt)	O	L	L	ECT	****		1	
Geometridae								
Anacamptodes prob. *herse* (Schaus)	R	L	L	ECT			5	
Anacamptodes perfectaria McDunnough	C	L	L	ECT	***	T	1	
Anavitrinella pampinaria (Guenée)	R	L	L	ECT	*		1	P
Chlorochlamys chloroleucaria (Guenée)	C	L	L	ECT	*		1	
Cyclophora nanaria Walker	C	L	F, L	ECT	**		1	
Eupithecia miserulata (Grote) or near	R	L	L	ECT	*		1, 8	
Hypomecis nr. *umbrosaria* Hübner	R	L	L	ECT	*		8	
Pleuroprucha asthenaria (Walker)	R	L	F	ECT	*		5	P
Pleuroprucha insulsaria (Guenée)	R	L	F	ECT	*		3, 8	P
Sabulodes arga Druce	R	L	L	ECT			5	
Synchlora frondaria Guenée	C	L	F, L	ECT	*		1, 8	
Tornos abjectarius Guenée	R	L	L	ECT	****		1	
Gracillariidae								
Phyllonorycter sp.	R	L	L	END			1	
Lyonetiidae								
Bucculatrix ambrosiaefoliella Chambers	C	L	L	END	***		1	
Bucculatrix nr. *criticopa* Meyrick	R	L	L	END	***		1	
Bucculatrix parthenica Bradley	O	L	L	END	*****	T	1, 4	
Noctuidae								
Condica sutor (Guenée)	R	L	L	ECT	*		8	
Helicoverpa zea (Boddie)	C	L	F	ECT	*		1	P
Lophoceramica pyrrha Druce	R	L	L	ECT	*		5	
Ogdoconta cinereola (Guenée)	O	L	L	ECT	*		1, 8	
Pseudoplusia includens (Walker	R	L	L	ECT	*		1, 8	P
Spodoptera latifascia (Walker)	R	L	L	ECT	*		2	P
Spragueia guttata Grote	O	L	L	ECT			1	
Nymphalidae								
Chlosyne lacinia Geyer	C	L	L	ECT	***	T	1, 2, 4	P
Pterophoridae								
Oidaematophorus fumiventris (Zeller)	R	L					5	
Oidaematophorus inquinatus (Zeller)	O	L	L	ECT	***		1, 2	
Oidaematophorus stramineus (Walsingham)	R	L	S	END			1	
Pyralidae								
Achyra rantalis (Guenée)	R	L	L	ECT	*		1, 8	P
Conchylodes ovulalis (Guenée)	O	L	L	ECT	**		1	
Riodinidae								
Calephelis laverna Godman & Salvin or nr.	R	L	L	ECT	**		1	
Saturniidae								
Hylesia sp.	R	L	L	ECT			2	
Sesiidae								
Carmenta ithacae (Beutenmüller)	C	L	R	END	***		1, 2	
Tineidae								
Acrolophus sp.	R	L	R	END			2	
Tinea sp.	R	L	M	END			7	

Table 1. Continued

Species	Frequency[a]	Stages feeding[b]	Feeding site[c]	Feeding type[d]	Host specificity[e]	Tested[f]	Distribution[g]	Pest status[h]
Tortricidae								
Aethesoides distigmatana Walsingham or near	R	L	R	END			2, 5	
Amorbia emigratella Busck	O	L	L	ECT	*		5	P
Amorbia nr. *rectangularis* Meyrick	R	L	L	ECT			2	
Argyrotaenia montezumae (Walsingham)	O	L	L	ECT	*		2, 3, 5	
Carolella nr. *buscana* Comstock	O	L	R, S	END			1, 4	
Cochylis subolivacea Walsingham	R	L	M	END			7	
Epiblema strenuana (Walker)	C	L	S	END	****	T	1, 2, 3, 4, 5, 8, 10	
Platynota labiosana Zeller or near	C	L	L	ECT			1, 2, 7	
Platynota nigrocervina Walsingham	O	L	L	ECT	*		8	
Platynota rostrana (Walker)	R	L	L	ECT	*		8	P
Platynota stultana Walsingham	C	L	L, F	ECT	*		1	P
Suleima skinnerana Heinrich	O	L	S	END	***		5	
		Diptera						
Agromyzidae								
Agromyza sp.	R	L	L	END			1	
Amauromyza maculosa (Malloch)	O	L	L, M	END	*		1	P
Liriomyza sp.	O	L	L	END			1	
Melanagromyza sp.	C	L	S	END			1, 2, 4, 5	
Cecidomyiidae								
Contarinia sp.	R	L	F	END			1	
Lasioptera sp.	C	L	S	END	*****		1	
Tephritidae								
Euarestoides acutangulus Thomson	C	L	F	END	**		1	
Eutreta angusta Banks	R	L	S	END	**		1	

[a] C, common; O, occasional; R, rare; G, found in greenhouse but not in field.
[b] N, nymph; L, larva; A, adult.
[c] L, leaves; R, roots; S, stems; F, flowers/seeds; M, apical/axillary meristems.
[d] END, endophagous; ECT, ectophagous.
[e] *****, genus *Parthenium*; ****, subtribe Ambrosiinae; ***, tribe Heliantheae; **, family Asteraceae; *, other families.
[f] T, species subjected to laboratory host-range tests.
[g] 1, NE Mexico (Nuevo León, Tamaulipas); 2, Mexico Gulf Coast (Veracruz, Tabasco); 3, Mexico Yucatan (Campeche, Yucatán, Quintana Roo); 4, N Central Mexico (Chihuahua, Coahuila, Durango, Zacatecas, San Luís Potosí); 5, S Central Mexico (Aguascalientes, Guanajuato, Querétaro, Hidalgo, México, Puebla, Morelos, Distrito Federal, Michoacán (inland), Jalisco (inland)); 6, N Pacific Mexico (Sonora, Sinaloa, Nayarit, Baja California Norte, Baja California Sur); 7, S Pacific Mexico (Chiapas, Guerrero, Oaxaca, Colima, Michoacán (coastal), Jalisco (coastal); 8, Texas; 9, Louisiana; 10, Florida; 11, Mexico, unspecified; 12, United States, unspecified.
[h] P, known economic pest species.

the authors. Species listed as common can be easily found at a high proportion of collection sites within their geographic range, often in large numbers, and appear to be regularly associated with *P. hysterophorus*. Species listed as occasional require greater searching effort or a knowledge of particular sites at which they occur; they were found only at a limited number of sites or occasions, but still show a consistent pattern of association with the plant. Species listed as rare were collected only on one or a few occasions, usually in small numbers or as single individuals, and may not be consistently associated with the plant.

We collected 262 phytophagous arthropod species, representing 108 genera and 58 families in 8 orders. The orders represented were Acari (2 species, 0.8% of species), Orthoptera (2, 0.8%), Thysanoptera (2, 0.8%), Hemiptera (48, 18.3%), Homoptera (60, 22.9%), Coleoptera (87, 33.2%), Lepidoptera (53, 20.2%), and Diptera (8, 3.1%). The percentage representation of the main insect orders in the fauna of *P. hysterophorus* is broadly similar to those reported for other herbaceous composites in their native ranges, such as *Ambrosia psilostachya* DC (Goeden and Ricker 1976c), *Cirsium californicum* Gray (Goeden and Ricker 1986), and for the woody perennial composite *Baccharis halimifolia* L. (Palmer 1987), although the percentage of Diptera is lower than reported for these other composites. Fifty-three species were known agricultural pests.

Of the species collected, 144 were confirmed to feed on *P. hysterophorus* at some stage of their life cycle. Because little has been published on the insect fauna of *P. hysterophorus*, many of these are new host records. In a comparable series of faunal surveys on ragweeds (*Ambrosia* spp.), none of 9 ragweed species had an arthropod fauna of more than 130 species (Goeden and Ricker 1974a, b; 1975; 1976 a–c). Of the 144 species known to feed on *P. hysterophorus*, 29 (20.1%) were stenophagous as defined by Goeden and Teerink (1993), feeding on species within the tribe Heliantheae; of these 6 (4.2%) were considered to be monopha-

gous, feeding only on species within the genus *Parthenium*. In comparison, the insect faunas of Ambrosiinae in California reviewed by Goeden and Teerink (1993) included 27.0% stenophagous and 18.2% monophagous species. The insect fauna of *P. hysterophorus* thus appears to be in general less host specific than for other species of North American Ambrosiinae, being particularly deficient in monophagous species. This may be related to the status of *P. hysterophorus* as an annual species whose abundance fluctuates strongly in response to rainfall and habitat disturbance, thus providing a relatively unreliable food resource and discouraging the evolution of specialized phytophages (Bernays and Chapman 1994).

Forty (27.8%) of the species feeding on *P. hysterophorus* were endophagous, a similar value to that observed by Goeden and Teerink (1993) for Californian Ambrosiinae. Internally feeding species tended to be more host specific; 30.0% of endophagous species and only 16.3% of ectophagous species were restricted to the tribe Heliantheae.

Thirteen species were considered to be restricted to the subtribe Ambrosiinae. This level of specificity was considered sufficient to qualify a species as a potential biological control agent for use in Australia, because the only members of this subtribe occurring in Australia are introduced weeds in the genera *Ambrosia, Parthenium, Xanthium,* and *Iva*. Six species were shipped to Australia for further testing. These were a defoliating beetle, *Zygogramma bicolorata* Pallister, a stem-galling moth, *Epiblema strenuana* (Walker) (McClay 1987), a leaf-mining moth, *Bucculatrix parthenica* Bradley (McClay et al. 1990), a sap-sucking planthopper, *Stobaera concinna* (Stål) (McClay 1983), a seed-feeding weevil, *Smicronyx lutulentus* Dietz, and a root-galling weevil, *Thecesternus hirsutus* Pierce (McClay and Anderson 1985). All except *T. hirsutus* were subsequently released (McFadyen 1992). *Zygogramma bicolorata* also has been released and established in India (Jayanth 1987, Jayanth and Bali 1990). *Epiblema strenuana* has been introduced to China for the biological control of annual ragweed, *Ambrosia artemisiifolia* L. (Wan and Wang 1995).

Two rust fungi were also found on *P. hysterophorus*. *Puccinia abrupta* Dietel and Holway var. *partheniicola* (Jackson) Parmelee was found on the stems and abaxial leaf surfaces, most commonly in Coahuila and other areas of Mexico at altitudes of 1500 m or higher. It was subsequently screened under quarantine in the United Kingdom and released in Queensland (Evans 1987, Parker 1990, McFadyen 1992, Parker et al. 1994). *Puccinia melampodii* Dietel and Holway was found on the adaxial leaf surfaces on plants in south Texas and Nuevo León.

The 6 insect species shipped to Australia for further testing covered a range of feeding niches on *P. hysterophorus*. Although a root-mining insect would have been a desirable addition to this list, no suitable candidates were identified. The 2 most common root-feeding species were *Baris* prob. *aerea* Boheman, which was tested and found to be insufficiently specific, and *Carmenta ithacae* (Beutenmüller). Larvae of *C. ithacae* were common in the roots of *P. hysterophorus* in Mexico and were reared to the adult stage on many occasions. *Carmenta ithacae* is found on species of *Helenium* and *Heliopsis* (Asteraceae) in the United States (Eichlin and Duckworth 1988). However, because no fertile eggs were ever laid in the laboratory, we were unable to conduct host-specificity tests to determine whether *C. ithacae* from *P. hysterophorus* would also accept these host plants.

Other species that may have a narrow host range on *P. hysterophorus* include the leaf-rolling moth *Helcystogramma chambersella* (Murtfeldt) and the aphid *Uroleucon ambrosiae* (Thomas). The only other host records for *H. chambersella* are from *Ambrosia* spp. (Hodges 1986). It was never obtained in sufficient numbers for host-specificity tests to be conducted. *Uroleucon ambrosiae* is recorded from many species of Asteraceae (Robinson 1985), but material collected from *P. hysterophorus* in Mexico would breed only on *P. hysterophorus* and *P. confertum* Gray in cage tests, suggesting the existence of sibling species or host races. This bears out the suggestion of Robinson (1985) that the host range of *U. ambrosiae* may be more limited than appears from literature records.

Numerous species of Cicadellidae (Homoptera) and Miridae (Hemiptera) were collected. Few feeding tests were conducted with these species, because most did not appear sufficiently damaging to be useful as biological control agents. Many of these species are therefore indicated in Table 1 as collection records only. With further tests, it is likely that some of these could be shown to feed and develop on *P. hysterophorus*.

Adults of several species of Chlamisinae and Cryptocephalinae (Coleoptera: Chrysomelidae) were frequently collected. Larvae of these subfamilies live in a case constructed from fecal material. Some of these species, including *Cryptocephalus irroratus* Suffrian, *Pachybrachis immaculatus* Jacoby, *Exema conspersa* Mannerheim, and *Diachus auratus* F., could be reared from eggs to adults on living foliage of *P. hysterophorus*, but larvae were rarely encountered in the field. Other members of these subfamilies feed as larvae primarily on dead foliage and detritus (LeSage 1985).

The indices of percentage similarity between the fauna of *P. hysterophorus* and the 11 other plant taxa included in our comparisons ranged from 1.1 to 8.3% (Table 2). Although these are not high overall levels of similarity, the values appear to reflect the taxonomic relationships of the host plants, at least at the tribal level. The fauna of *P. hysterophorus* is most closely related to those of other genera within the tribe Heliantheae, such as *Ambrosia, Helianthus,* and *Xanthium*. Characteristic stenophagous insect genera shared among these

Table 2. Similarities between phytophagous arthropod faunas of *P. hysterophorus* and other plant taxa

Plant taxon (no. species included)	Total phytophagous insect species	Phytophagous species in common with *P. hysterophorus*	Index of similarity, % I_s
Ambrosia[a–g] (9)	274	41	8.28
Helianthus[b, h, i] (10)	224	37	8.24
Xanthium[a, j] (2)	197	32	7.49
Baccharis[k–p] (11)	577	44	5.53
Lantana[a, q] (4)	550	38	4.91
Parthenium argentatum[r, s, b](1)	194	20	4.59
Senna[a] (5)	121	11	2.96
Gutierrezia[t] (1)	149	11	2.75
Parkinsonia[a, u] (1)	120	10	2.69
Prosopis[v] (5)	433	13	1.91
Cirsium[w–y] (9)	117	4	1.07

[a] W.A.P., unpublished data.
[b] A.S.M., unpublished data.
[c] Harris and Piper (1970).
[d] Goeden and Ricker (1975).
[e] Goeden and Ricker (1976a).
[f] Goeden and Ricker (1976b).
[g] Goeden and Ricker (1976c).
[h] Hilgendorf and Goeden (1981).
[i] Rogers (1988).
[j] Hilgendorf and Goeden (1982).
[k] Boldt and Robbins (1987).
[l] Boldt and Robbins (1994).
[m] Palmer (1987).
[n] Palmer and Bennett (1988).
[o] Palmer and Pullen (1994).
[p] Tilden (1951).
[q] Perkins and Swezey (1924).
[r] Aguirre-Uribe et al. (1988).
[s] Stone and Fries 1986.
[t] Foster et al. (1981).
[u] Wood (1992).
[v] Ward et al. (1977).
[w] Goeden and Ricker (1986).
[x] Goeden and Ricker (1987a).
[y] Goeden and Ricker (1987b).

plant taxa include *Exema, Ophraella, Zygogramma, Cylindrocopturus, Smicronyx, Carolella, Helcystogramma,* and *Epiblema.* The relatively high overlap with *Ambrosia* occurs despite the fact that most of the faunal data on *Ambrosia* are from southern California, well outside the range of our survey and the native range of *P. hysterophorus.* There was a lower level of similarity between the fauna of *P. hysterophorus* and that of the congeneric species *Parthenium argentatum* Gray (guayule), with only 20 insect species in common. This may be because of the marked differences of plant architecture, secondary chemistry, and habitat between the 2 species. *P. argentatum* is a small rubber-producing shrub of xeric habitats in northern Mexico, and rarely co-occurs with *P. hysterophorus.* In contrast, the genera *Ambrosia, Xanthium,* and *Helianthus* include numerous herbaceous annual or perennial species occurring in ruderal habitats similar to those occupied by *P. hysterophorus.* Genera in the tribes Astereae (*Baccharis* and *Gutierrezia*) and Cynareae (*Cirsium*) and the families Caesalpiniaceae (*Parkinsonia, Senna*) and Mimosaceae (*Prosopis*) had lower similarities with the fauna of *P. hysterophorus,* reflecting their greater taxonomic distance from *Parthenium. Lantana camara* had a surprisingly high degree of similarity (4.91%) with *P. hysterophorus;* the reasons for this are unknown.

These faunal relationships are of importance to the practical aspects of selecting weed biological control agents. The relatively high degree of similarity between the faunas of *P. hysterophorus* and *Helianthus* validated the selection of *H. annuus* as a critical test plant. Thirty-nine species (14.8%) of the fauna of *P. hysterophorus* have also been recorded from *Helianthus,* making them ineligible for further consideration as biological control agents. This close association between the faunas of *P. hysterophorus* and *H. annuus* was probably the most important factor limiting the number of biological control agents obtained from this project.

The choice of Monterrey in northeastern Mexico as the main project base seems to have been fully justified. All 6 of the species sent to Australia were found in the immediate vicinity of Monterrey, whereas only *S. lutulentus, E. strenuana,* and *S. concinna* were found in proximity to the base at Temple, TX, and only *E. strenuana* and *S. concinna* were found near Cuernavaca.

One indicator of potentially good biological control agents is their effect on the host plant in its native range (Wapshere 1985, Crawley 1989). Severe insect damage on *P. hysterophorus* was rarely observed in our surveys. *Zygogramma bicolorata* occasionally became abundant enough to cause defoliation, and on one occasion a young stand was severely stunted by heavy *E. strenuana* infestation. These 2 species have been the most effective biological control agents when released in India and Australia (McFadyen 1992, Jayanth and Bali 1990). During the cooler winter months, plants were often coated with dense colonies of *U. ambrosiae.* Occasional defoliation by polyphagous Lepidoptera was seen in Texas.

The absence of native or economic species of Ambrosiinae in Australia facilitated the introduction of biological control agents into Queensland against *P. hysterophorus,* as it was possible to release several species which were oligophagous on *Parthenium, Ambrosia,* or *Xanthium,* rather than strictly monophagous. This implies, however, that caution should be exercised in releasing any of these agents in other countries where *P. hysterophorus* is a problem. Any such releases should be preceded by a careful review of the status of potential host plants present in the proposed area of introduction, and, if necessary, additional host specificity tests should be performed.

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