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INVASION NOTE

Invasive aphids attack native Hawaiian plants

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Abstract Invasive species have had devastating impacts on the fauna and flora of the Hawaiian Islands. While the negative effects of some invasive species are obvious, other species are less visible, though no less important. Aphids (Homoptera: Aphididae) are not native to Hawai'i but have thoroughly invaded the Island chain, largely as a result of anthropogenic influences. As aphids cause both direct plant feeding damage and transmit numerous pathogenic viruses, it is important to document aphid distributions and ranges throughout the archipelago. On the basis of an extensive survey of aphid diversity on the five largest Hawaiian Islands (Hawai'i, Kaua'i, O'ahu, Maui, and Moloka'i), we provide the first evidence that invasive aphids feed not just on agricultural crops, but also on native Hawaiian plants. To date, aphids have been observed feeding and reproducing on 64 native Hawaiian plants (16 indigenous species and 48 endemic species) in 32 families. As the majority of these plants are endangered, invasive aphids may have profound impacts on the island flora. To help protect unique island ecosystems, we propose that border vigilance be enhanced to prevent the incursion of new aphids, and that biological control efforts be renewed to mitigate the impact of existing species.

Keywords Aphid · Aphididae · Hawai'i · Indigenous plants · Invasive species · Endemic plants · Hawaiian Islands · Virus

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Introduction

The Hawaiian Islands have been, and continue to be, inundated with invasive species. The state is a principal hub for tourism, trade, and military transport (State of Hawaii 2005), so foreign species are constantly being introduced throughout the archipelago. Several plants (e.g., fire tree [*Myrica faya*], fountain grass [*Pennisetum setaceum*], velvet tree [*Miconia calvescen*]) and animals (e.g., feral pig [*Sus scrofa*], mosquito [*Culex quinquefasciatus*], rat [*Rattus* sp.]) that have invaded Hawai'i are classic examples of how exotic species can drastically, and irreversibly, alter

ecological processes in island ecosystems (Atkinson 1977; Aplet 1990; Vitousek 1990; Anderson and Stone 1993). In this respect Hawaii is a model of many island nations and territories in a broad swath across the southern Pacific Ocean from French Polynesia all the way to Asia, including the larger areas of Australia and New Zealand.

Other exotic species introductions, while more subtle, may be just as significant. Approximately 20 arthropod species invade and become established in Hawaii each year (Beardsley 1979). While the majority of these species appear to be non-injurious, others rapidly become serious economic and ecological pests (e.g., the two-spotted leafhopper [*Sophonia rufofascia*], the Erythrina gall wasp [*Quadrastichus erythrinae*], the Argentine ant [*Linepithema humilis*]) (Cole et al. 1992; Messing and Wright 2006).

Aphids (Homoptera: Aphididae) are particularly troublesome invasive species due to their small size, asexual reproduction, broad host range, and close association with horticultural commodities imported from abroad (Mondor et al. 2006). Nearly 100 aphid species are documented to occur in the islands; every one an exotic, inadvertently introduced species (Messing et al. unpublished). Aphids cause direct crop feeding damage, increase production costs (due to pesticide usage), are contamination and quarantine pests, and vector viral diseases that can cause 100% crop losses in some situations (Hollingsworth et al. 1994). Transmission of papaya ringspot virus by *Aphis gossypii* and *Myzus persicae*, and banana bunchy top virus by *Pentalonia nigronervosa*, are just two examples in which invasive aphids have altered crop production systems statewide (Gonsalves 1998; Hu et al. 1996). Again, this is equally true for a broad range of Pacific islands as small as Guam (Pike et al. 2000) and as large as New Zealand (Teulon 2002).

Research in Hawaii has focused on aphids as pests of agricultural and ornamental crops (Hollingsworth et al. 1994; Schenk and Lehrer 2000); however, there is good reason to be concerned about potential damage to native plants. The Islands have one of the highest rates of floral endemism in the world (Kim et al. 1998). Many of these endemic species have lost the defensive adaptations that their ancestors maintain in continental ecosystems. As a result, these species are particularly susceptible to exploitation by invasive species (Howarth and Ramsay 1991). Hawaii has more endangered species per square mile than any other place on Earth, and the islands have 10% of all the endangered animals and 44% of all the endangered plants in the United States (USFWS 2006).

During the course of an extensive survey of aphid diversity throughout the Hawaiian Islands, we observed many instances in which invasive aphids were feeding and reproducing on native Hawaiian plants. While quantification of feeding and virus damage was beyond the scope of this project, documenting the colonization of native plant species serves as a useful starting point for further investigations on the exploitation of native Hawaiian plant populations, many of which are threatened or endangered. It also serves as an early warning system for aphid invasions of other Pacific Island territories.

Methods

The aphid survey was conducted over a period of three years (March 2003–March 2006) on the five largest Hawaiian Islands (Hawai'i, Kaua'i, O'ahu, Maui, and Moloka'i). Plants on local, state, federal and private lands, botanical gardens, and commercial nurseries were visually examined for the presence of aphids. On these plants we recorded aphid incidence on leaf, stem and, when the plant was known to be susceptible, root tissues. To be recorded as an infestation, a plant had to have several (>10) individuals of mixed instars on the same plant part. We established this criterion to distinguish between legitimate aphid colonies and those few cases where an aphid(s) might have been accidentally transported to the plant (e.g., wind-blown), but was not feeding or reproducing. The absence of a species record on a given island or host plant does not necessarily indicate that the aphid does not occur there, only that it was not documented during our survey.

We differentiate between indigenous plants (those that occur naturally in Hawai'i, but also occur elsewhere) and endemic host plants (those that occur naturally only in Hawai'i). We consider

both indigenous and endemic species to be native. The conservation status of Hawaiian plants is assessed by several organizations, including the Hawai'i Biodiversity and Mapping Program (HBMP 2006), the International Union for the Conservation of Nature and Natural Resources (IUCN 2004), and the U.S. Fish and Wildlife Service (USFWS 2006). Here we determine native plant status according to the USFWS (2006). In some cases, only subspecies of plants are endangered, and we could not discriminate among subspecies in our field collections. However, given the polyphagy of most aphid species in Hawai'i (Mondor et al. in press), it is unlikely that aphid host-specificity would be restricted to the subspecies level. Thus, the plant status listed in Table 2 represents that of any subspecies or variety within the listed species.

Live aphid specimens were transported to the laboratory, photographed and subsequently slide mounted. Specimens were identified using the most recent and widely accepted nomenclature (Remaudière and Remaudière 1997; Halbert 2004). Voucher specimens are maintained in the Canadian National Collection of Insects and in the reference collection of the Kaua'i Agricultural Research Station, University of Hawai'i at Manoa. Records labeled as "unidentified" in Tables 1 and 2 refer to those few instances in which adults were not available for slide mounting and identification. We present each unique aphid/plant/island association once, though the same association may have been documented on subsequent occasions.

Results

In Hawai'i, one or more aphid species were found feeding on 16 indigenous plant species in 13 families (Table 1). Aphids feeding on indigenous plants are polyphagous species that are common

Table 1 Summary of aphids feeding on indigenous Hawaiian plants

Aphid(s)[a]	Plant family[b]	Host plant[b]	Hawaiian name(s)[b]	Island[c]
Aphis craccivora	Fabaceae	*Senna gaudichaudii*	kolomona, kalamona, uhiuhi	M
Aphis craccivora	Fabaceae	*Vigna marina*	mohihihi, nanea, pulihilihi	H
Aphis craccivora	Malvaceae	*Sida fallax*	'ilima	H
Aphis fabae	Solanaceae	*Solanum americanum*	popolo, 'olohua, polopolo	M, O
Aphis gossypii	Boraginaceae	*Heliotropium anomalum*	hinahina, hinahina ku kahakai	M
Aphis gossypii	Fabaceae	*Vigna marina*	mohihihi, nanea, pulihilihi	H
Aphis gossypii	Goodeniaceae	*Scaevola taccada*	naupaka kahakai, naupaka kai, huahekili	H
Aphis gossypii	Malvaceae	*Hibiscus furcellatus*	akiohala, 'akiahala, hau hele, hau hele wai	O
Aphis gossypii	Malvaceae	*Sida fallax*	'ilima	H, K, M, Mo
Aphis gossypii	Malvaceae	*Thespesia populnea*	milo	Mo
Aphis gossypii	Myoporaceae	*Myoporum sandwicense*	naio, naeo, naieo	K, O
Aphis gossypii	Nyctaginaceae	*Boerhavia* sp.	alena	Mo
Aphis gossypii	Verbanaceae	*Vitex rotundifolia*	kolokolo kahakai, pohinahina	H, K, M
Aphis spiraecola	Goodeniaceae	*Scaevola taccada*	naupaka kahakai, naupaka kai, huahekili	H
Aphis spiraecola	Rosaceae	*Osteomeles anthyllidifolia*	'ulei, eluehe, u'ulei	M
Aphis sp.	Rosaceae	*Osteomeles anthyllidifolia*	'ulei, eluehe, u'ulei	K
Hysteroneura setariae	Goodeniaceae	*Scaevola taccada*	naupaka kahakai, naupaka kai, huahekili	K
Myzus persicae	Malvaceae	*Sida fallax*	'ilima	M
Rhopalosiphum maidis	Malvaceae	*Sida fallax*	'ilima	Mo
Rhopalosiphum maidis	Primulaceae	*Lysimachia mauritiana*		M
Toxoptera aurantii	Sapotaceae	*Nesoluma polynesicum*	keahi	O
Unidentified	Capparaceae	*Cleome spinosa*	honohino, 'ili'ohu	K
Unidentified	Rosaceae	*Osteomeles anthyllidifolia*	'ulei, eluehe, u'ulei	K
Unidentified	Rubiaceae	*Psydrax odorata*	alahe'e, 'ohe'e, walahe'e	M
Unidentified	Verbanaceae	*Vitex rotundifolia*	kolokolo kahakai, pohinahina	H

[a] Aphid taxonomy: Remaudière and Remaudière (1997) and Halbert (2004)

[b] Plant taxonomy: Wagner et al. (1990), Staples and Herbst (2005), and USDA, NRCS (2006)

[c] Island legend: H = Hawai'i, K = Kaua'i, M = Maui, Mo = Moloka'i, O = O'ahu

Table 2 Summary of aphids feeding on endemic Hawaiian plants

Aphid(s)[a]	Plant family[b]	Host plant[b]	Hawaiian name(s)[b]	Status[c]	Island[d]
Aphis craccivora	Fabaceae	*Sesbania tomentosa*	‘ohai	E	K, M, Mo, O
Aphis fabae	Araliaceae	*Tetraplasandra hawaiensis*	‘ohe, ‘ohe ‘ohe		O
Aphis gossypii	Amaranthaceae	*Charpentiera* sp.	papala	C (1 spp.)	O
Aphis gossypii	Asteraceae	*Bidens menziesii*	ko’oko’olau, ko’olau		M, Mo
Aphis gossypii	Asteraceae	*Bidens micrantha*	ko’oko’olau	E (1 spp.), C (1 ssp.)	M
Aphis gossypii	Asteraceae	*Lipochaeta lavarum*	nehe		M
Aphis gossypii	Asteraceae	*Pseudognaphalium sandwicensium*	‘ena’ena, puheu	C	M
Aphis gossypii	Capparaceae	*Capparis sandwichiana*	maiapilo, pua pilo		O
Aphis gossypii	Euphorbiaceae	*Chamaesyce* sp.	akoko, kokomalei	E (5 sp., 1 ssp.), C (1 sp., 2 spp.)	M
Aphis gossypii	Fabaceae	*Erythrina sandwicensis*	wiliwili		O
Aphis gossypii	Fabaceae	*Strongylodon ruber*	nuku ‘i’iwi, ka ‘i’iwi, nuku		M
Aphis gossypii	Goodeniaceae	*Scaevola coriacea*	naupaka	E	M
Aphis gossypii	Malvaceae	*Abutilon menziesii*	ko’oloa’ula	E	O
Aphis gossypii	Malvaceae	*Gossypium tomentosum*	ma’o, huluhulu		H, K
Aphis gossypii	Malvaceae	*Hibiscus arnottianus*	koki’o ke’oke’o, pamakani, pua aloalo	E (1 spp.)	H, M, O
Aphis gossypii	Malvaceae	*Hibiscus brackenridgei*	ma’o hau hele	E	H, K, M, O
Aphis gossypii	Malvaceae	*Hibiscus clayi*	aloalo	E	M
Aphis gossypii	Malvaceae	*Hibiscus kokio*	koki’o ‘ula’ula		K, M
Aphis gossypii	Malvaceae	*Hibiscus waimeae*	koki’o ke’oke’o, koki’o kea		H, M
Aphis gossypii	Malvaceae	*Kokia drynaroides*	koki’o, hau hele ‘ula	E	H
Aphis gossypii	Myrsinaceae	*Myrsine lessertiana*	kolea lau nui		H
Aphis gossypii	Myrtaceae	*Metrosideros polymorpha*	‘ohi’a lehua, ‘ohi’a, lehua		K, M
Aphis gossypii	Rubiaceae	*Gardenia brighamii*	na’u, nanu	E	K, M, O
Aphis gossypii	Rubiaceae	*Hedyotis formosa*	au, pilo, ‘awiwi, kio’ele		M
Aphis gossypii	Rubiaceae	*Hedyotis littoralis*			M
Aphis gossypii	Urticaceae	*Pipturus albidus*	mamaki, mamake		M
Aphis spiraecola	Apiaceae	*Peucedanum sandwicense*	makou	T	K
Aphis spiraecola	Araliaceae	*Tetraplasandra oahuensis*	‘ohe mauka		O
Aphis spiraecola	Araliaceae	*Munroidendron racemosum*		E	K
Aphis spiraecola	Asteraceae	*Artemisia mauiensis*	ahinahina, hinahina		H, K
Aphis spiraecola	Malvaceae	*Hibiscus kokio*	koki’o ‘ula’ula		H
Aphis spiraecola	Rubiaceae	*Gardenia brighamii*	na’u, nanu	E	K
Aulacorthum circumflexum	Hydrangeaceae	*Broussaisia arguta*	kanawao		Mo
Coloradoa rufomaculata	Asteraceae	*Artemisia mauiensis*	ahinahina, hinahina		K
Ericaphis fimbriata	Ericaceae	*Vaccinium reticulatum*	‘ohelo, ‘ohelo ‘ai		M
Greenidea psidii	Myrtaceae	*Metrosideros macropus*	‘ohi’a lehua, ‘ohi’a, lehua		O
Greenidea psidii	Myrtaceae	*Metrosideros polymorpha*	‘ohi’a lehua, ‘ohi’a, lehua		K, M, O
Hayhurstia atriplicis	Chenopodiaceae	*Chenopodium oahuense*	aheahea, ‘aweoweo, kahai’ihai		Mo
Hysteroneura setariae	Poaceae	*Deschampsia nubigena*			M
Hysteroneura setariae	Cyperaceae	*Carex wahuensis*			K
Myzus persicae	Asteraceae	*Bidens menziesii*	ko’oko’olau, ko’olau		M
Myzus persicae	Thymelaeceae	*Wikstroemia uva-ursi*	akia		H
Rhopalosiphum padi	Pittosporaceae	*Pittosporum hawaiiense*	ho’awa, ha’awa		K
Sitobion fragariae	Juncaceae	*Luzula hawaiiensis*			M
Sitobion fragariae	Poaceae	*Deschampsia nubigena*			M
Toxoptera aurantii	Apocynaceae	*Alyxia oliviformis*	maile		K

Table 2 continued

Aphid(s)[a]	Plant family[b]	Host plant[b]	Hawaiian name(s)[b]	Status[c]	Island[d]
Toxoptera aurantii	Araliaceae	*Cheirodendron* sp.	olapa, lapalapa		K
Toxoptera aurantii	Brassicaceae	*Lepidium serra*	anaunau		K
Toxoptera aurantii	Campanulaceae	*Clermontia oblongifolia*	‘oha wai	E (1 spp.)	O
Toxoptera aurantii	Myrsinaceae	*Myrsine lessertiana*	kolea lau nui		O
Toxoptera aurantii	Myrsinaceae	*Myrsine sandwicensis*	kolea lau li’i		O
Toxoptera aurantii	Myrtaceae	*Metrosideros polymorpha*	‘ohi’a lehua, ‘ohi’a, lehua		K
Toxoptera aurantii	Pittosporaceae	*Pittosporum hosmeri*	ho’awa, ‘a’awa hua kukui		O
Unidentified	Malvaceae	*Abutilon menziesii*	ko’oloa’ula	E	M
Unidentified	Malvaceae	*Gossypium tomentosum*	ma’o, huluhulu		O
Unidentified	Malvaceae	*Gossypium tomentosum*	ma’o, huluhulu		M
Unidentified	Malvaceae	*Gossypium tomentosum*	ma’o, huluhulu		Mo
Unidentified	Malvaceae	*Hibiscus waimeae*	koki’o ke’oke’o, koki’o kea	E (1 spp.)	H
Unidentified	Pittosporaceae	*Pittosporum glabrum*	ho’awa, papahekili		O
Unidentified	Rubiaceae	*Gardenia brighamii*	na’u, nanu	E	M
Unidentified	Rubiaceae	*Hedyotis coriacea*	kio’ele	E	M
Unidentified	Solanaceae	*Solanum sandwicense*	‘aiakeakua, popolo	E	K

[a] Aphid taxonomy: Remaudière and Remaudière (1997) and Halbert (2004)

[b] Plant taxonomy: Wagner et al. (1990), Staples and Herbst (2005), and USDA, NRCS (2006)

[c] Conservation status: USFWS (2006), as designated under the U.S. Endangered Species Act; E = endangered, T = threatened, C = candidate

[d] Island legend: H = Hawai’i, K = Kaua’i, M = Maui, Mo = Moloka’i, O = O’ahu

and abundant on agricultural, ornamental, and weedy host plants throughout the Islands. On endemic Hawaiian plants, 48 species in 25 plant families were successfully attacked by invasive aphids (Table 2). For the most part, aphids on endemic plants are also polyphagous species, common on cultivated plants and weeds.

The most commonly encountered aphid on both endemic and indigenous plants was *Aphis gossypii* (9 of 16 indigenous plants, and 24 of 48 endemic plants). *Aphis gossypii* is one of the most polyphagous and invasive aphids in the world, feeding on hosts in over 50 plant families. Other highly polyphagous aphids collected on native Hawaiian plants include *Aphis craccivora* (three indigenous and one endemic plant), *Aphis spiraecola* (two indigenous and six endemic plants), and *Toxoptera aurantii* (one indigenous and eight endemic plants).

Polyphagous aphids, however, were not always associated with a broad range of native host plants. For example, *Myzus persicae*, with a previously recorded host range almost as broad as *A. gossypii*, was recorded from only one indigenous and two endemic plants. *Aphis fabae*, another very polyphagous aphid, was also found on only one indigenous and one endemic plant. Similarly, the corn leaf aphid, *Rhopalosiphum maidis*, which feeds on over 30 genera of grasses, including several important crop species, was found on only two indigenous species.

Several aphids with more restricted feeding ranges were also found feeding on native plants. For example, *Greenidea psidii*, which feeds almost exclusively on plants in the Myrtaceae (e.g., guava, *Psidium guajava*) was found colonizing two endemic plants. *Hayhurstia atriplicis* was found colonizing one endemic plant and *Sitobion fragariae* was found on two endemic species.

Discussion

For a group that is so abundant, widespread, and economically important, the biology of most aphid species in Hawai’i is poorly known (Messing et al. 2006). Although inadvertent introductions are occasionally reported in the literature (e.g., Kumashiro et al. 2001), the aphid fauna of Hawai’i has not been reviewed in almost 30 years (Beardsley 1979). In our recent survey, we recorded nine aphid species not previously known to occur in the state (Messing et al. 2006), as well as numerous new host and island records.

Given the lack of information on aphid diversity on economically important plants in the Hawaiian Islands, it is perhaps not surprising that virtually nothing is known about aphid distributions on native plants.

Aphids attacking native Hawaiian plants are primarily polyphagous, cosmopolitan species that attack agricultural and weedy host species (e.g., *A. gossypii*). In Hawai'i, anholocyclic populations of *A. gossypii* are common on a wide variety of crop plants and weeds, both on windward and leeward sides of the islands, during all months of the year (Messing and Klungness 2002). It is also arguably the most common aphid on other Pacific islands such as Guam, American Samoa, and Micronesia (Johnson et al. 1989; Pike et al. 2000). The importance of polyphagy is not unexpected, as broad feeding range appears to be a key trait contributing to the invasiveness of the aphid fauna in Hawai'i (Mondor et al. 2006). It is highly likely that additional native host plants, besides those listed here, will be found to host one or more of these polyphagous aphid species. Continued and expanded monitoring is required to determine the distribution, abundance, and impact of these arthropods on native Hawaiian plants.

Aphids feeding on Hawaiian plants are also known to vector numerous plant viruses. For example, *A. craccivora, A. fabae*, and *A. gossypii* vector approximately 30, 30, and 50 plant viruses, respectively (Blackman and Eastop 2000). We did not establish the degree to which aphids on native plants carried either persistent or non-persistent viral particles, but given their notorious role as virus vectors in numerous Hawaiian crops such as banana and papaya (Hu et al. 1996; Gonsalves 1998), the proximity of agricultural to natural habitats (Juvik and Juvik 1998), and the fact that many non-persistent virus particles can be transmitted in just a few seconds (Ng and Perry 2004), it is likely that at least some of these viruses could be vectored to native plants. Not only could virus transmission directly impact native plant populations, but these plants may also serve as virus reservoirs, thereby complicating control efforts for commercially grown crops.

Hawaiian plants are under extraordinary pressure from habitat destruction, competition with invasive plants, and exploitation by invasive herbivores (i.e., Vitousek and Walker 1989). When native plant species are already under extreme pressure, the impact of a new invasive arthropod may be the final factor leading to an extinction event (e.g., the iconic Hawaiian wiliwili tree, *Erythrina sandwicensis*, is under severe threat of extinction from the newly invasive African gall wasp, *Quadrastichus erythrinae* (Hymenoptera: Eulophidae)) (Messing and Wright 2006). Even when it is not possible to pinpoint the exact cause of a species decline, there is little doubt that increased herbivory contributes to the environmental stress threatening the existence of many native plant species.

Hawaii serves as a harbinger of biological invasions for a broad range of Pacific island territories, as it is a major commercial and tourism gateway between the west (North America) and the east (Australasia). The precarious nature of many Pacific island ecosystems and the role of the Hawaiian archipelago as an ecological model have been well documented (i.e., Cox and Elmqvist 2000; Vitousek 2002). The broader aphid/plant relationships documented here can help focus efforts at detection and mitigation of these invasive pests in island systems across the Pacific.

To date, there is no evidence that invasive aphids are having major effects on the survival or reproduction of native Hawaiian plants. All too often, however, the effects of invasive species are not noticed until irreparable ecological damage has been done. Given what we know of aphid biology and the efficiency with which these insects vector devastating viral diseases, documentation of aphid feeding on endemic plants lends credence to calls for increased border vigilance to prevent the incursion of additional aphid species (Stone 1999), and renewed biological control efforts to mitigate the impacts of existing species (Messing and Wright 2006).

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