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Infestation of Wild and Ornamental Noncrop Fruits by *Drosophila suzukii* (Diptera: Drosophilidae)

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ABSTRACT *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) is a pest of small fruits and cherries, and has also been noted to infest a variety of wild, ornamental, and uncultivated hosts. Identifying alternative hosts is critical for pest management. Research objectives were to: 1) survey fruits in the field for natural infestation of *D. suzukii*, 2) determine the susceptibility of fruits in laboratory no-choice studies, and 3) evaluate short-range preference between simultaneously ripe alternative hosts and cultivated fruits in laboratory choice studies. Field surveys identified new hosts or confirmed previously reported hosts including: *Berberis aquifolium* Pursh, Oregon grape; *Cornus* spp., dogwood; *Cotoneaster lacteus* W.W. Smith, milkflower cotoneaster; *Elaeagnus umbellata* Thunberg, Autumn olive; *Frangula purshiana* (de Candolle) A. Gray, cascara buckthorn; *Lindera benzoin* (L.) Blume, spicebush; *Lonicera caerulea* L., blue honeysuckle; *Morus* sp., mulberry; *Phytolacca americana* L., pokeweed; *Prunus avium* (L.) L., wild cherry; *Prunus laurocerasus* L., cherry laurel; *Prunus lusitanica* L., Portuguese laurel; *Rubus armeniacus* Focke, Himalaya blackberry; *Rubus spectabilis* Pursh, salmonberry; *Sambucus nigra* L., black elderberry; *Sarcococca confusa* Sealy, sweet box; *Solanum dulcamara* L., bittersweet nightshade; and *Symphoricarpos albus* (L.) S.F. Blake, snowberry. High fruit infestations were observed in *S. confusa* during April–May and *Lonicera* spp. in June before most commercial fruits ripen. From both field and laboratory studies, there was no evidence of susceptibility during the estimated ripe period *Crataegus* L. 'Autumn Glory,' hawthorn; *Ilex crenata* Thunberg, Japanese holly; *Nandina domestica* Thunberg, sacred bamboo; *Rhaphiolepis umbellata* (Thunberg) Makino, yeddo hawthorne; *Rosa acicularis* Lindley, prickly rose; *Skimmia japonica* Thunberg, Japanese skimmia; and *Viburnum davidii* Franchet, David's viburnum. Lastly, laboratory choice tests identified that several fall-ripening alternative hosts were more susceptible than 'Pinot noir' or 'Pinot gris' wine grapes. By understanding host use, growers can identify high-risk areas where coordinated action may reduce infestation of *D. suzukii* in crops.

KEY WORDS alternative host, fruit host, host range, invasive pest, spotted wing drosophila

Introduction

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae) is an invasive pest from Asia causing significant damage in commercial crops such as blackberry, blueberry, cherry, raspberry, and strawberry (*Rubus* subg. *Rubus* Watson, *Vaccinium corymbosum* L., *Prunus avium* (L.) L., *Rubus idaeus* L., *Fragaria × ananassa* Duchesne ex Rozier, respectively). Substantial economic losses occur as a consequence of reduced yield, increased management costs with insecticides (Goodhue et al. 2011), and potential rejection of exported fruit if the fruit exceed maximum pesticide residue limits (Haviland and Beers 2012). Economic losses and infestation are especially pronounced on late season crops when pest densities increase greatly. Moreover, *D. suzukii* can infest other wild, ornamental, and uncultivated fruits (collectively referred to as alternative hosts). The preference for alternative hosts has not yet been fully determined because *D. suzukii* arrived recently in North America (Hauser 2011). A variety of ornamental/wild fruit and other cultivated fruit have been described as hosts in the literature mostly from Japan and more recently in North America and Europe (Table 1), and this study has expanded the known host list for two major regions of perennial fruit production. We recognize that knowledge about the host associations of this pest is growing rapidly, and will be updated from studies underway in other regions where *D. suzukii* is also expanding its range.

Identifying alternative hosts for *D. suzukii* is a priority for developing pest management programs because reducing source populations may also reduce

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Table 1. Host species where fruit were found infested by *D. suzukii* in the field based on the literature and this field survey (Michigan, Oregon); list does not include common cultivated hosts, hosts from sources where collection details are not described, and laboratory-only observations, and the list is subject to expand as new information becomes available

Family	Scientific name	Common name	Location	Reference
Adoxaceae	*Sambucus* sp.	Elderberry	Michigan	This field survey
	Sambucus nigra L.	Black elderberry	Italy, Oregon	Grassi et al. 2011, this field survey
	Viburnum dilatatum Thunberg	Linden viburnum	Japan	Mitsui et al. 2010
Beberidaceae	*Berberis aquifolium* Pursh	Oregon grape	Oregon	This field survey
Buxaceae	*Sarcococca confusa* Sealy	Sweet box	Oregon	This field survey
Caprifoliaceae	*Lonicera* spp.	Honeysuckle	Italy, Michigan	Grassi et al. 2011, this field survey
	Lonicera caerulea L.	Blue honeysuckle	Oregon	This field survey
	Symphoricarpos albus (L.) S.F. Blake	Common snowberry	Oregon	This field survey
Cornaceae	*Alangium platanifolium* (Siebold & Zuccarini) Harms	None	Japan	Mitsui et al. 2010
	Aucuba japonica Thunberg	Japanese aucuba	Japan	Mitsui et al. 2010
	Cornus amomum Miller	Silky dogwood	Michigan	This field survey
	Cornus controversa Hemsl. ex Prain	Giant dogwood	Japan	Mitsui et al. 2010
	Cornus foemina Miller	Stiff dogwood	Michigan	This field survey
	Cornus kousa Hance	Japanese dogwood	Japan, Oregon	Mitsui et al. 2010, this field survey
	Cornus sericea L.	Red osier dogwood	Oregon	This field survey
Ebenaceae	*Diospyros kaki* Thunberg	Persimmon (damaged)	Japan	Kanzawa 1935, 1939, Mitsui et al. 2010
Elaeagnaceae	*Elaeagnus multiflora* Thunberg	Cherry silverberry	Japan	Kanzawa 1939, Sasaki and Sato 1995
	Elaeagnus umbellata Thunberg	Autumn olive	Michigan	This field survey
Ericaceae	*Arbutus unedo* L.	Strawberry tree	Spain	Arnó et al. 2012
	Gaultheria adenothrix (Miquel) Maximovich	Akamono	Japan	Mitsui et al. 2010
Lauraceae	*Lindera benzoin* (L.) Blume	Spicebush	Michigan	this field survey
Moraceae	*Ficus carica* (L.)	Common fig, 'Brown Turkey' and 'Mission'	California	Yu et al. 2013
	Morus sp.	Mulberry	Japan	Kanzawa 1935, Sasaki and Sato 1995
	Morus alba L.	White mulberry	Japan	Kanzawa 1939
	Morus alba x *rubra*	'Illinois Everbearing'	California	Yu et al. 2013
	Morus australis Poiret (=*bombycis*)	Wild Korean mulberry	Japan	Mitsui et al. 2010
	Morus nigra L.	Black mulberry	Oregon	This field survey
	Morus rubra L.	Red mulberry	Florida	Plant Inspection Advisory 2010
Myricaceae	*Morella rubra* Loureiro (=*Myrica rubra*)	Chinese bayberry	Japan	Yukinari 1988
Myrtaceae	*Eugenia uniflora* L.	Surinam cherry	Florida	Plant Inspection Advisory 2010
Phytolaccaceae	*Phytolacca americana* L.	Pokeweed	Japan	Sasaki and Sato 1995
			Michigan	This field survey
Rhamnaceae	*Frangula alnus* Miller	Glossy buckthorn	Italy	Grassi et al. 2011
	Frangula purshiana (de Candolle) A. Gray	Cascara buckthorn	Oregon	This field survey
Rosaceae	*Cotoneaster lacteus* W.W. Smith	Milkflower cotoneaster	Oregon	This field survey
	Eriobotrya japonica (Thunbergerg) Lindley	Loquat (Damaged)	Japan, Florida	Kanzawa 1935, Plant Inspection Advisory 2010
	Malus pumila Miller,	Paradise apple (Damaged)	Japan	Kanzawa 1939
	Prunus armeniaca, L.	Apricot (Damaged)	Japan	Kanzawa 1935, 1939
	Prunus avium (L.) L.	Various ornamental and wild cherries	Japan, Oregon	Kanzawa 1939, this field survey
	Prunus buergeriana Miquel		Japan	Sasaki and Sato 1995
	Prunus cerasus L.		Japan	Kanzawa 1939
	Prunus donarium Siebold		Japan	Kanzawa 1939, Mitsui et al. 2006
	Prunus japonica Thunberg		Japan	Kanzawa 1935, 1939
	Prunus mahaleb L.		Japan	Kanzawa 1935, 1939
	Prunus nipponica Matsumura		Japan	Mitsui et al. 2010
	Prunus sargentii Rehder		Japan	Kanzawa 1935
	Prunus serotina Ehrhart		France	Poyet et al. 2014
	Prunus yedoensis Matsumura		Japan	Kanzawa 1935, 1939, Sasaki and Sato 1995
	Prunus laurocerasus L.	Cherry laurel	Oregon	This field survey
	Prunus lusitanica L.	Portuguese-laurel	Oregon	This field survey
	Prunus persica (L.) Batsch	Peach (Damaged)	Japan	Kanzawa 1935, 1939, Sasaki and Sato 1995

(Continued)

Table 1. (continued)

Family	Scientific name	Common name	Location	Reference
	Prunus salicina Lindley (=*triflora*)	Asian plum (Damaged)	Japan	Kanzawa 1935, 1939
	Rubus crataegifolius Bunge	Various wild raspberries	Japan	Mitsui et al. 2010
	Rubus microphyllus L.f.		Japan	Kanzawa 1939, Mitsui et al. 2010
	Rubus parvifolius L. (=*triphyllus*)		Japan	Kanzawa 1939, Sasaki and Sato 1995
	Rubus armeniacus Focke	Himalaya blackberry	Oregon	This field survey
	Rubus spectabilis Pursh	Salmonberry	Oregon	This field survey
Rutaceae	*Murraya paniculata* (L.) Jack	Orange jasmine	Florida	Plant Inspection Advisory 2010
Solanaceae	*Solanum dulcamara* L.	Bittersweet nightshade	Michigan and Oregon	This field survey
	Solanum villosum Miller (=*luteum*)	Hairy nightshade	Spain	Arnó et al. 2012
	Solanum lycopersicum L.	Tomato (Damaged)	Japan, Florida	Kanzawa 1935, Plant Inspection Advisory 2010
Taxaceae	*Torreya nucifera* (L.) Siebold & Zuccarini	Japanese torreya	Japan	Mitsui et al. 2010

infestation of nearby fruit crops. First, noncrop hosts such as *Rubus armeniacus* Focke, Himalaya blackberry, present in field margins may contribute to higher densities and patchy distribution in the adjacent crop, as suggested by a protein marking study with *D. suzukii* and spatial statistics (J. Klick unpublished data). Second, alternate hosts may enable fly development when crop hosts are not available, particularly in late fall to spring. In temperate climates, *D. suzukii* would be expected to develop on small fruits and stone fruits from May to October when fruits are ripening and become susceptible to infestation (Lee et al. 2011). Third, alternative hosts can provide sugar sources to sustain adult *D. suzukii*, particularly in the winter. Sugar from split fruit, floral nectar, extrafloral nectar, sap, yeast, and insect honeydew have been shown to maintain tephritid flies (Drew and Yuval 2000). The same might be expected for drosophilid flies, as it has been shown that adult *D. suzukii* can feed on sap from wounded oak trees (Kanzawa 1939) or have extended longevity with access to blueberry or cherry flowers (S. Tochen, unpublished data). Also, overwintering adult *D. suzukii* have been observed feeding on overripe and damaged persimmons, figs, and fallen rotting apples from October to January in 2012 and 2013 in Oregon (A.J.D., unpublished data). Fourth, nearby alternative hosts may serve as a refuge for pest survival and continued reproduction while crop fields are sprayed with insecticides to protect fruit from *D. suzukii*. Insecticide sprays may occur repeatedly given that insecticides have a 10–14-d residual period (Bruck et al. 2011) and rainfall reduces insecticidal effectiveness (Van Timmeren and Isaacs 2013). On the other hand, the presence of alternative hosts may also have benefits as shown in other pest–crop systems. A nontreated refuge could potentially delay the development of insecticide resistance (Huang et al. 2011). Alternative hosts can also serve as a refuge for natural enemy populations that will likely not survive in treated crop fields (Lee et al. 2001).

Given the importance of alternative hosts and its implications for pest management, an important first step is to identify host plant species on which *D. suzukii* can complete their life-cycle on. The objectives of this study were to: 1) survey wild, ornamental, uncultivated, and noncommercial fruits (collectively referred to as alternative hosts) in the field for host use by naturally occurring *D. suzukii*; 2) determine the susceptibility of alternative hosts to the development of *D. suzukii* in laboratory no-choice studies; and 3) evaluate short-range preference between simultaneously ripe alternative hosts and cultivated fruits in laboratory choice studies. A field survey of hosts begins to confirm what *D. suzukii* will do under natural conditions in the areas studied. No-choice laboratory tests can determine the physiological capability of *D. suzukii* to oviposit and develop on a host, establishing what they can do, but not necessarily what they will do in the field. When possible, results from both studies are discussed together as the laboratory tests can overestimate susceptibility and the field surveys can underestimate susceptibility.

Materials and Methods

Plant Identification. Plants were identified with the assistance of plant taxonomists and reference guides (Newcomb 1977, Barnes and Wagner 1981). Latin names and common names are used according to the GRIN Taxonomy for Plants (U.S. Department of Agriculture–Agricultural Research Services [USDA-ARS] National Genetic Resources Program, 2014) whenever possible.

Field Surveys. Fruits were collected from field sites in Michigan and Oregon and reared in the laboratory to determine rates of natural infestation by *D. suzukii*. All sites were known to have *D. suzukii* within 50-m radius of the given host type by the fact that other infested fruits were collected or alt *D. suzukii* were trapped in the area. Multiple sites were defined as being >400 m apart. If sampling of one host type occurred at multiple sites, it was done on the same day or within a week. During collection, we recorded the date, location, and number of fruits collected per species, and condition of the fruit (i.e., ripe or overripe).

In Michigan, fruits were collected in and around blueberry and grape fields in Berrien, Van Buren, Allegan, and Ottawa counties in 2011 and 2012. In 2011, fruit were collected once a week throughout the summer during the entire ripening period for each species. In 2012, fruit were collected once per month per site during the midpoint of the ripening period for

Table 2. Field-collected fruits checked for the presence of *D. suzukii* during 2011–2013 expressed as the percentage of fruit (Oregon) or percentage of samples (Michigan) with emerging *D. suzukii*, number of fruits or samples collected and sites visited; collections were made of ripe fruit and sometimes overripe fruit (indicated by *)

Family Scientific name, common name	State	Date[a]	% Fruit	% Samples	Total no. fruits (no. samples)	Sites[b]
Adoxaceae						
Sambucus sp., Elderberry	Michigan	Aug. 2012		100%	200 (8)	1
Sambucus nigra L., Black elderberry	Oregon	Sept. 2010	0%		375	2
""		Nov. 2010	17%		150	1
""		July 2011	0%		200	1
""		Aug. 2012	8%		100	1
""		June, Aug. 2013	3%		300	1
Viburnum sp., Viburnum	Michigan	July–Oct. 2011		0%	4,100 (20)	2
""		July–Aug. 2012		0%	375 (15)	2
Viburnum davidii Franchet, David's viburnum	Oregon	April* 2013	0%		100	1
Viburnum ellipticum Hook., Common viburnum	Oregon	Aug. 2012	0%		100	1
Viburnum lantana L., Wayfaring tree	Oregon	Aug. 2012	0%		100	1
Viburnum tinus L., Laurustinus	Oregon	April* 2012	0%		100	1
Viburnum opulus L. var. *americanum* Aiton, American cranberry-bush	Michigan	Aug.-Oct. 2011		0%	918 (9)	2
Aquifoliaceae						
Ilex aquifolium L., English holly	Oregon	Feb.*, June 2011	0%		200	1
""		June 2012	0%		100	1
Ilex glabra (L.) A. Gray, Inkberry	Oregon	Feb.* 2011	0%		200	1
""		Feb.-Mar.* 2012	0%		125	1
Ilex verticillata (L.) A. Gray, Winterberry	Michigan	Sept.–Oct. 2011		0%[c]	2,624 (16)	3
Ilex crenata Thunberg, Japanese holly	Oregon	June 2011	0%		100	1
""		Feb.* 2013	0%		75	1
Araceae						
Arisaema triphyllum (L.) Schott, Jack-in-the-pulpit	Michigan	Oct. 2011		0%	83 (1)	1
Asparagaceae						
Asparagus officinalis L., Garden asparagus	Michigan	Oct. 2011		0%	356 (2)	1
Maianthemum stellatum (L.) Link, False Solomon's seal	Michigan	Sept.-Oct. 2011		0%	1,386 (14)	2
Beberidaceae						
Berberis aquifolium Pursh, Oregon grape	Oregon	Sept. 2010	0%		500	1
""		Sept. 2011	0%		300	1
""		Sept. 2012	4%		200	1
Berberis thunbergii DC., Japanese barberry	Michigan	Sept.–Oct. 2011		0%	952 (7)	2
Nandina domestica Thunberg, Sacred bamboo	Oregon	June 2011	0%		75 (3)	1
""		May 2012	0%		200	1
""		May 2013	0%		100	1
Buxaceae						
Sarcococca confusa Sealy, Sweet box	Oregon	May–June 2011	10%		400	1
""		May–June 2012	80%		400	1
""		May–June 2013	30%		400	1
Caprifoliaceae						
Lonicera spp., Honeysuckle	Michigan	July–Oct. 2011		20%	4,200 (50)	6
""		June–Aug. 2012		28%	625 (25)	4
Lonicera caerulea L., Blue honeysuckle	Oregon	June 2013	27%		200	1
Lonicera ciliosa (Pursh) Poir. ex DC., Orange	Oregon	Sept. 2010	0%		50	1
honeysuckle		Oct. 2011	0%		100	1
Lonicera utahensis S. Watson, Utah honeysuckle	Oregon	Sept. 2010	0%		125	1
Symphoricarpos albus (L.) S.F. Blake, Snowberry	Oregon	Sept. 2010	1%		375	1
""		Oct. 2011	1%		200	2
""		Aug.–Sept. 2012	0%		250	3
""		April* 2013	0%		200	2
Clusiaceae						
Hypericum androsaemum L., Sweet amber	Oregon	Aug. 2012	0%		100	1
Cornaceae						
Cornus amomum Miller, Silky dogwood	Michigan	Aug. 2012		100%	125 (5)	1
""		Aug.–Oct. 2011		33%	183 (3)	1
Cornus foemina Miller, Stiff dogwood	Michigan	Aug.–Oct. 2011		6%	2,346 (17)	3
Cornus kousa Hance, Japanese dogwood	Oregon	Aug. 2011	5%		250	1
Cornus sericea L., Red osier dogwood	Oregon	Sept. 2010	10%		100	1
""		Sept. 2011	5%		175	1
""		Aug. 2012	8%		200	2
Elaeagnaceae						
Elaeagnus umbellata Thunberg, Autumn olive	Michigan	Aug.–Oct. 2011		37%	7,056 (49)	6
""		Aug.–Sept. 2012		13%	200 (8)	1
Ericaceae						
Vaccinium ovatum Pursh, Evergreen huckleberry	Oregon	Oct. 2013	0%		100	1
Arbutus unedo L., Strawberry tree	Oregon	June*, Nov. 2011	0%		400	2

(*Continued*)

Table 2. (continued)

Family Scientific name, common name	State	Date[a]	% Fruit	% Samples	Total no. fruits (no. samples)	Sites[b]
“”		July*, Oct. 2012	0%		200	2
Garryaceae						
Aucuba japonica Thunberg, Japanese aucuba	Oregon	Feb.*, May–June 2011	0%		400	1
Grossulariaceae						
Ribes sanguineum Pursh, Flowering currant	Oregon	May 2011	0%		100	1
Lauraceae						
Lindera benzoin (L.) Blume, Spicebush	Michigan	Aug.–Oct. 2011		7%	798 (14)	2
“”		Aug. 2012		0%	150 (6)	2
Moraceae						
Morus nigra L., Black mulberry	Oregon	Aug.–Sept. 2010	49%		250	1
“”		July–Aug. 2011	40%		250	1
“”		June–Aug. 2012	52%		350	1
“”		June–Aug. 2013	89%		150	1
Oleaceae						
Ligustrum vulgare L., European privet	Michigan	Oct. 2011		0%	955 (5)	2
Phytolaccaceae						
Phytolacca americana L., American pokeweed	Michigan	Aug.–Oct. 2011		91%	1,419 (11)	4
Ranunculaceae		Aug. 2012		57%	175 (7)	2
“”						
Actaea pachypoda Elliot, White baneberry	Michigan	Aug. 2011		0%	9 (1)	1
Rhamnaceae						
Frangula purshiana (de Candolle) A. Gray, Cascara buckthorn	Oregon	Aug. 2010	0%		25	1
“”		Aug. 2013	52%		100	1
Rosaceae						
Amelanchier sp., Serviceberry	Michigan	July 2011		0%	166 (2)	1
Amelanchier lamarckii F.G. Schroed., Juneberry	Oregon	May 2012	0%		100	1
Aronia x *prunifolia* (Marshall) Rehder, Purple chokeberry	Michigan	Aug.–Oct. 2011		0%	2,223 (13)	1
Cotoneaster lacteus W.W. Smith, Milkflower cotoneaster	Oregon	June 2011	0%		200	1
“”		May 2012	23%		250	1
Crataegus douglasii Lindl., Black hawthorn	Oregon	Mar. 2013	0%		275	2
Crataegus L.‘Autumn Glory,’ hawthorn	Oregon	Sept. 2010	0%		75	1
“”		Feb.*, June 2011	0%		100	1
“”		Feb.–Mar.* 2012	0%		200	1
“”		April* 2013	0%		200	1
Malus sp., Crabapple	Oregon	Sept. 2010	0%		200	1
“”		Oct. 2011	0%		100	1
“”		Feb. 2012	0%		100	1
Prunus avium (L.) L., Sweet cherry (wild)	Oregon	Aug. 2011	46%		75	1
“”		Aug. 2012	68%		400	3
“”		July 2013	100%		50	1
Prunus laurocerasus L., Cherry laurel	Oregon	Sept. 2010	2%		100	1
“”		Oct. 2011	20%		100	1
“”		Sept. 2012	20%		300	1
“”		Aug. 2013	8%		500	3
“”		Oct. 2013	39 %		100	2
Prunus lusitanica L., Portuguese laurel	Oregon	Sept. 2010	1%		25	1
“”		Sept. 2011	49%		100	1
“”		Aug. 2012	8%		100	1
Prunus serotina Ehrhart, Black cherry	Michigan	July 2012		0%	50 (2)	1
Prunus virginiana L., Choke cherry	Oregon	Oct. 2011	0%		200	2
“”		Aug. 2012	0%		200	1
Rhaphiolepis indica (L.) Lindley, Indian hawthorne	Oregon	May–June 2011	0%		100	1
“”		June 2012	0%		100	1
Rhaphiolepis umbellata (Thunberg) Makino, Yeddo hawthorne	Oregon	June 2011	0%		100	1
“”		April* 2013	0%		100	1
Rosa multiflora Thunberg, Multiflora rose	Michigan	Sept.–Oct. 2011		0%	4,446 (26)	5
“”		Aug. 2012		0%	25	1
Rosa acicularis Lindl., Prickly rose	Oregon	Sept. 2010	0%		375	1
“”		Feb. 2011	0%		250	1
Rubus sp., Blackberry (wild)	Michigan	July–Sept 2011		65%	1395 (31)	3
“”		July–Aug. 2012		54%	325 (13)	3
Rubus sp., Red raspberry (wild)	Michigan	July–Sept. 2011		13%	88 (8)	1
“”		July 2012		100%	25 (1)	1
Rubus armeniacus Focke, Himalaya blackberry	Oregon	Sept.–Oct. 2010	85%		800	4
“”		Aug.–Sept. 2011	67%		450	4
“”		Aug.–Sept. 2012	83%		500	6

(*Continued*)

Table 2. (continued)

Family Scientific name, common name	State	Date[a]	% Fruit	% Samples	Total no. fruits (no. samples)	Sites[b]
“”		July–Sept. 2013	85%		400	4
Rubus spectabilis Pursh, Salmonberry	Oregon	July 2012	8%		100	1
“”		July 2013	12%		200	1
Sorbus americana Marshall, American mountain ash	Oregon	Aug. 2012	0%		200	1
Sorbus sitchensis M. Roemer, Western mountain ash	Oregon	Sept. 2010	0%		150	1
Rutaceae						
Skimmia japonica Thunberg, Japanese skimmia	Oregon	Feb.*, May–June 2011	0%		300	2
“”		Feb.*, July 2012	0%		200	1
“”		Mar.* 2013	0%		200	1
Similacaceae						
Smilax tamnoides L., Bristly greenbriar	Michigan	Oct. 2011		0%	502 (2)	1
Solanaceae						
Solanum carolinense L., Carolina horse nettle	Michigan	Oct. 2011		0%	222 (6)	2
Solanum dulcamara L., Bittersweet nightshade	Michigan	July–Oct. 2011		16%	1349 (19)	2
“”		Aug. 2012		33%	75 (3)	1
“”	Oregon	Sept. 2010	0%		300	2
“”		Sept. 2011	2%		200	1
“”		Sept. 2012	1%		200	1
Solanum nigrum L., Black nightshade	Oregon	Aug. 2011	0%		200	2
“”		Sept. 2012	0%		200	2
Theaceae						
Camellia sp., Camelia (buds)	Oregon	Feb. 2011	0%		100	2
“”		Mar. 2012	0%		150	2
Thymelaeaceae						
Daphne sp., Daphne	Oregon	Feb. 2011	0%		50	1
“”		Mar. 2012	0%		50	1
Vitaceae						
Parthenocissus quinquefolia (L.) Planch., Virginia-creeper	Michigan	Aug. 2012		0%	50 (2)	1
Vitis riparia Michaux, Riverbank grape	Michigan	Aug.–Oct. 2011		0%	4312 (28)	4
“”		Aug. 2012		0%	75 (3)	2

[a]Fruit collections were made once per month except for weekly collections in 2011 and in *Lonicera* sp. in 2012 in Michigan; and *Sarcococca confusa* (2012–2013), *Morus nigra* (2010–2013), and *Rubus armeniacus* (2010–2013) in Oregon.

[b]All collection sites were known to have *D. suzukii* within 50 m of the given host type by the fact that other infested fruits were collected or adult *D. suzukii* were trapped in the area.

Multiple sites were defined as being >400 m radius apart. If sampling of one host type occurred at multiple sites, it was done on the same day or within a week.

[c]0% of samples also means that 0% of fruit had *D. suzukii*.

each species, except for six weekly collections of *Lonicera* spp. The ripe stage was chosen based on the fact that various cultivated fruits are highly susceptible at the ripe stage (Lee et al. 2011). Fruits collected in Michigan were grouped together into one or more samples and monitored for *D. suzukii* on a per sample basis. In 2011, a volume of 118.3 ml of fruit was collected per sample, and in 2012, samples were standardized to 25 fruit per sample. Samples in both years were placed in 0.47 l plastic containers, either on clean sand (2011; Quikrete brand, Atlanta, GA) or in a wire basket made of hardware cloth (6.4 mm in diameter) on top of a piece of yellow cellulose sponge to absorb liquid and reduce fungal growth. Containers were placed in the laboratory at $24 \pm 3°C$, and emerging vinegar flies were either aspirated out of containers weekly or caught using a yellow sticky insert (Great Lakes IPM, Inc., Vestaburg, MI) in the container that was replaced weekly. Vinegar flies emerging in the first 21 d were identified as *D. suzukii* males, females, or other *Drosophila* species. The percent of samples ([number of infested samples/total number of samples] × 100) with emerging *D. suzukii* is presented in Table 2.

In Oregon, fruits were collected from one to eight different sites located in Benton, Dalles, Hood River, Linn, and Marion counties from 2010 to 2013. Fruits were collected once a month during the ripe period for all species, except for several weekly collections made in *Sarcococca confusa* Sealy (2012–2013), *Morus nigra* L. (2010–2013), and *R. armeniacus* (2010–2013). Fruits collected in Oregon were monitored on an individual basis. Individual fruits were placed in 30- to 89-ml plastic cups depending on fruit size. Cups were sealed with a screened lid to reduce fungal growth. In some cases, a small cotton swab or sand layer was added to the bottom of the container to absorb moisture. Cups were placed in the laboratory at $21 \pm 1°C$. Fruits remained in cups for a maximum of 18 d, and were examined for presence of adults. The percent of fruit with emerging *D. suzukii* ([number of infested fruit/total number of fruit] × 100) is presented in Table 2 as a separate column from the Michigan data.

Lastly, two highly susceptible hosts were studied in more detail: *Lonicera* spp. in Michigan, and *S. confusa* in Oregon. Both plants are commonly grown as ornamentals in urban areas. *S. confusa* is native to Southeast Asia. Both species were collected often on a weekly basis: *Lonicera* spp. from June to August–October in 2011–2012 in Michigan, and *S. confusa* from March to June in 2012–2013 in Oregon. Also, adult *D. suzukii* were monitored in the plant canopy with a clear 946-ml plastic container trap containing 10 holes and baited with either with yeast sugar water (Michigan) or apple cider vinegar with a drop of soap (Oregon). Traps deployed in Michigan also contained a yellow sticky insert (7.6 by 8.9 cm, Great Lakes IPM Inc., Vestaburg, MI) hung from the lid of the trap.

Laboratory Studies. *D. suzukii* were obtained from a laboratory colony at the USDA-ARS Horticultural Crops Research Unit in Corvallis, Oregon with yearly introduction of wild flies. Fruits were collected in Benton and Linn counties a few days before each trial with the exception of purchased grape tomatoes. Prior to testing, fruits were washed, weighed, and checked under the microscope to be free of wounds and *D. suzukii* eggs.

In no-choice and choice tests, *D. suzukii* were exposed to fruits for 24 h at 22°C, a photoperiod of 16:8 (L:D) h, and ~70% relative humidity. In no-choice tests, five female and four male *D. suzukii* about 2 wk old were used, whereas 10 females and 8 males were used in choice tests to keep the fly-to-fruit type ratio equal in the different studies. Fruits were presented on the bottom of a 22.9 by 22.9 by 25.4 cm white homemade plastic cage with a clear top and sides and a mesh sleeve on one side. Each cage contained a cotton wick inserted in a tube containing 20% sucrose, and a sponge soaked with distilled water in a container. The number of fruits varied depending on fruit size to provide flies with sufficient ovipositional substrate (though not equal masses across fruit types), with a maximum of 20 fruits per cage. Concurrent positive controls were run in cages separate from the fruits, with three 2.0-g diet cups, five females and four males in no-choice cages, and six diet cups, 10 females and 8 males in choice cages to keep the fly-to-diet ratios constant in the different studies. The diet was composed of 45 g of agar, 125 g of cornmeal, 200 g of sugar, 70 g of nutritional yeast, 4.7 liter of dH_2O, 17.7 ml of propionic acid, 3.3 g of methyl paraben, and 33.3 ml of 95% ethanol. Flies exposed to diet only during both no-choice and choice trial periods served as a positive control confirming that *D. suzukii* laid viable eggs. Each no-choice test and concurrent positive controls were replicated 7 or 8 times (cages), and choice tests and concurrent positive controls were replicated 9 or 10 times.

After 24 h of exposure to *D. suzukii*, fruits were removed from cages, and the number of eggs laid by *D. suzukii* was counted under a microscope by searching for egg filaments. The same fruit were transferred to rearing cups with mesh lids, and then kept at ~22°C with natural daylight. After 2 wk, fruits were dissected and flies at the larval, pupal, and adult stages were counted. All three life stages were combined and referred to as "developing *D. suzukii*." Given that the life stages present at 2 wk may reflect effects from fruit quality, size of fruit (resource), or number of eggs (competitors), the development rate on hosts was not evaluated because the number of eggs laid would need to be controlled per unit fruit size to eliminate confounding factors. Eggs were more difficult to see on fleshy or textured fruit, and the development count at 2 wk was only made for caneberries and *Duchesnea indica* (Andrews) Focke. Lastly, pH and brix (% soluble solids) readings require destructive sampling by macerating fruit, and were taken on a subset of fruit that were not exposed to flies. For some plant species, readings were not taken because the macerated fruit did not produce sufficient liquid for readings, or no remaining fruit was available after the exposure assays.

No-choice studies confirmed whether fruits were potentially suitable for egg laying and development of *D. suzukii*. Fruits were grouped by observed presence or absence of host use, and not analyzed statistically: 1) fruits with no eggs laid and no development; 2) fruits with eggs laid but no development or minimal development of less than one *D. suzukii* per replicate cage; and 3) fruits with development. Choice studies were analyzed by testing whether the proportion of eggs laid in the alternative host per cage (number of eggs in alternative fruit/[number of eggs in alternative fruit + number of eggs in cultivated fruit]), or the proportion of *D. suzukii* developing in the alternative host per cage (number of larvae, pupae and adults from alternative fruit/[number from alternative fruit + number from cultivated fruit]) was significantly different from 0.5 using *t*-tests in JMP 8.0 (SAS Institute Inc. 2007, Cary, NC). Data are presented as the percent of eggs laid in the given hosts (Fig. 2).

Results

Field Studies. The following hosts were infested with *D. suzukii* in the field from both Michigan and Oregon: *Cornus* spp., *Lonicera* spp., *Rubus* spp., *Sambucus* spp., and *Solanum dulcamara* L. (Table 2 for this paragraph). Hosts infested when collected in Michigan include *Elaeagnus umbellata* Thunberg, *Lindera benzoin* (L.) Blume, and *Phytolacca americana* L. Hosts infested when collected in Oregon include *Berberis aquifolium* Pursh, *Frangula purshiana* (de Candolle) A. Gray, *Morus nigra* L., *P. avium*, *Prunus laurocerasus* L., *Prunus lusitanica* L., *Rubus spectabilis* Pursh, *S. confusa*, and *Symphoricarpos albus* (L.) S.F. Blake. In summary, plants within the families of Adoxaceae, Beberidaceae, Buxaceae, Caprifoliaceae, Cornaceae, Elaeagnaceae, Lauraceae, Moraceae, Phytolaccaceae, Thamnaceae, Rosaceae, and Solanaceae were hosts for developing *D. suzukii* in Michigan and Oregon landscapes. From the detailed survey, more frequent collections of *Lonicera* spp. revealed up to 100% of samples infested with *D. suzukii* in 2011 during August (Fig. 1a). The first detection of oviposition was from fruit collected on 24 June 2012. Traps captured between 0 and 82 *D. suzukii* per week in 2011, and 5 and 205 in 2012. In Oregon, weekly collections of *S. confusa* in Oregon revealed up to 92 and 42% of berries infested with *D. suzukii* in 2012 and 2013, respectively (Fig. 1b). The first detection of oviposition was from fruit collected on 22 April 2012 and 1 April 2013.

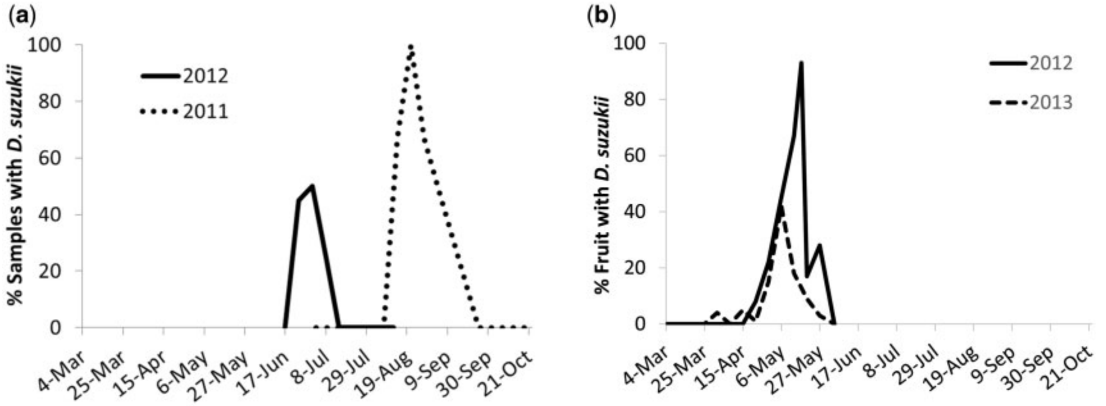

Fig. 1. Percentage of *Lonicera* sp. samples in Michigan (a) and *S. confusa* fruit in Oregon (b) that were infested with *D. suzukii* based on weekly field collections from one to four sites in Michigan and one site in Oregon.

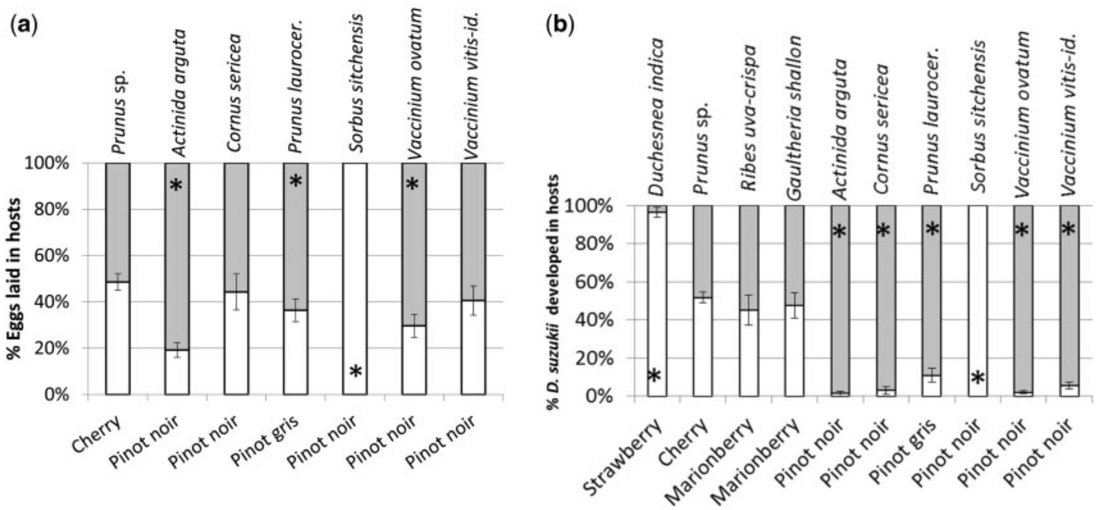

Fig. 2. In choice tests, the mean percent (± SE) of eggs laid within a replicate cage that were on the alternate host (top grey bar) or on the cultivated host (bottom white bar) (a). Mean percent (± SE) of developing *D. suzukii* within a cage that were from the alternate host or cultivated host (b). Asterisk denotes a significant difference from 50% by *t*-test ($n = 9$ or 10).

The trap placed in the canopy of *S. confusa* captured between 54 and 126 *D. suzukii* per week in 2012, and between 108 and 729 in 2013 during the ripening period.

Forty-six fruiting species did not show evidence of infestation during the field survey, indicating no egg laying or no surviving larvae during the period of this study. Absence of infestation in the field does not necessarily indicate that a fruit is not susceptible to *D. suzukii*; therefore, fruits with no observed infestation in the field nor in the laboratory study are emphasized which include: *Aucuba japonica* Thunberg, *Crataegus* L. 'Autumn Glory', *Ilex crenata* Thunberg, *Nandina domestica* Thunberg, *Rhaphiolepis umbellata* (Thunberg) Makino, *Rosa acicularis* Lindley, *Sk. japonica* Thunberg, and *Viburnum davidii* Franchet.

Laboratory Studies. In no-choice cages, *D. suzukii* did not lay eggs on *Callicarpa* sp. *Ilex cornuta* Lindley & Paxton, *I. crenata*, *Sk. japonica* (white fruit), or *V. davidii* (Table 3). These five fruits were purple, red, black, white, and blue colors, respectively. The pH of these fruits that were measured was 5.0–5.7, and brix levels were 10.2–19.5%. Flies laid eggs but had no observed development or minimal development with less than one *D. suzukii* developing per replicate cage on *A. japonica*, *Cotoneaster lacteus* W.W. Smith, *Crataegus* 'Autumn Glory', *Ginkgo biloba* L., *N. domestica*, *R. umbellata*, *P. lusitanica*, *Ro. acicularis*, *Sk. japonica* (red fruit), *So. dulcamara*, and *Solanum lycopersicum* L. These 11 fruits were colored peach, orange, red, purple, or black. The pH of fruits that were measured was 3.3–5.2, and the brix levels were 11.0–21.0%. For *P. lusitanica*, the flesh was notably dried out after 2 wk. Lastly, flies laid eggs and developed on *Actinidia arguta* (Siebold & Zuccarini) Planchon ex Miquel (tested at soft ripe stage, but this

Table 3. Mean number (± SE) of eggs laid, and developing *D. suzukii* from fruit in laboratory no-choice assays conducted in Corvallis, Oregon, during 2011–2012, and experimental details

Scientific name	Common name	Eggs	Development[a]	*n* (rep = cage)	No. fruit per cage	Mean weight (g)	Color	Mean pH	Mean Brix%	Assay group () and date[b]
No eggs laid										
Callicarpa sp.	Beautyberry	0 ± 0	0 ± 0	7	20	0.8	Purple	5.5	19.5	(7) 12–15 Dec. 2011
Ilex cornuta Lind. & Paxton	Chinese holly	0 ± 0	0 ± 0	7	20	3.9	Red	5.0	na	(1) 15–28 June 2011
Ilex crenata Thunberg	Japanese holly	0 ± 0	0 ± 0	7	20	2.1	Black	5.3	na	(1) 15–28 June 2011
Skimmia japonica Thunberg	Japanese skimmia (white)	0 ± 0	0 ± 0	7	15	5.7	White	5.7	10.2	(1) 15–28 June 2011
Viburnum davidii Franchet	David's viburnum	0 ± 0	0 ± 0	7	20	2.0	Blue	na	na	(1) 15–28 June 2011
Eggs laid, no/low development										
Aucuba japonica Thunberg	Japanese aucuba	1.5 ± 5.0	0.6 ± 0.6	8	10	15.0	Red	5.0	17.0	(1) 15–28 June 2011
Cotoneaster lacteus W.W. Smith	Milkflower cotoneaster	6.9 ± 4.5	0.13 ± 0.13	8	20	3.8	Red	4.6	16.3	(1) 15–28 June 2011
Crataegus 'Autumn Glory'	Hawthorne	13.4 ± 2.8	0 ± 0	7	6	16.7	Red	3.3	15.6	(7) 12–15 Dec. 2011
Ginkgo biloba L.	Ginkgo	3.0 ± 1.5	0 ± 0	7	4	33.4	Peach	4.4	21.0	(7) 12–15 Dec. 2011
Nandina domestica Thunberg	Sacred bamboo	7.5 ± 4.1	0 ± 0	8	20	3.0	Red	4.4	13.0	(1) 15–28 June 2011
Prunus lusitanica L.	Portuguese laurel	55.1 ± 8.1	0 ± 0 dried	7	10	9.3	Black	4.2	na	(6) 24–27 Oct. 2011
Rhaphiolepis umbellata Makino	Yeddo hawthorne	0.5 ± 0.4	0 ± 0	7	10	6.8	Purple	5.2	16.6	(7) 12–15 Dec. 2011
Rosa acicularis Lindley	Prickly rose (red)	0.9 ± 0.6	0 ± 0	7	8	14.4	Red	3.7	na	(6) 24–27 Oct. 2011
Rosa acicularis Lindley	Prickly rose (orange)	1.1 ± 0.7	0 ± 0	7	5	19.8	Orange	3.9	na	(6) 24–27 Oct. 2011
Skimmia japonica Thunberg	Japanese skimmia (red)	6.8 ± 3.3	0.25 ± 0.25	8	15	7.2	Red	5.9	11.0	(1) 15–28 June 2011
Solanum dulcamara L.	Climbing nightshade	0.9 ± 0.6	0 ± 0	7	15	6.4	Red	4.1	16.3	(4) 27–28 July 2011
Solanum lycopersicum L.	Grape tomato	4.1 ± 2.0	0.3 ± 0.3	7	4	25.5	Red	na	na	(6) 24–27 Oct. 2011
Development										
Actinidia arguta (Siebold & Zuccarini) Planchon ex Miquel	Hardy kiwi (soft[c])	32.4 ± 3.8	16.3 ± 2.1	7	4	29.0	Green	4.4	9.1	(6) 24–27 Oct. 2011
Arbutus unedo L.	Strawberry tree	Na	25 ± 2.4	7	3	29.8	Red	2.8	18.0	(11) 19 Oct. 2012
Berberis aquifolium Pursh	Oregon grape	48.6 ± 4.4	30 ± 2.4	7	20	9.0	Blue	2.4	16.1	(9) 16 July 2012
Cornus sericea L.	Red osier dogwwod	30.9 ± 3.2	23.0 ± 5.2	7	20	4.3	White	2.5	na	(6) 24–27 Oct. 2011
Duchesnea indica (Andrews) Teschem.	Indian strawberry	Na	2.4 ± 1.7	7	15	7.5	Red	5.5	6.2	(2) 11 July 2011
Gaultheria shallon Pursh	Salal	2.6 ± 7.6	18.3 ± 3.7	7	12	3.9	Black	3.0	13.4	(5) 15 Aug. 2011
Prunus avium (L.) L.	Sweet cherry (wild)	23.4 ± 7.1	24.3 ± 4.3	7	10	15.5	Purple	3.5	23.6	(3) 21 July 2011
Prunus laurocerasus L.	Cherry laurel	41.4 ± 6.6	13.7 ± 2.1	7	10	10.3	Black	4.4	na	(6) 24–27 Oct. 2011
Ribes uva-crispa L.	Gooseberry	49.6 ± 8.8	19.7 ± 5.6	7	12	10.3	Blue	3.7	16.6	(4) 27–28 July 2011
Rubus spectabilis Pursh	Salmonberry	Na	38.7 ± 7.3	6	5	7.6	Pink	2.5	4.3	(8) 6 June 2012
Sambucus nigra L.	Black elderberry	48.3 ± 5.3	30.3 ± 4.4	7	20	3.1	Black	3.9	13.5	(10) 12 Sept. 2012
Sarcococca confusa Sealy	Sweet box	33.8 ± 7.6	10.6 ± 2.4	7	20	6.9	Black	5.4	13.8	(7) 12–15 Dec. 2011
Sorbus sitchensis M. Roemer	Western mountain ash	12.1 ± 1.7	3.1 ± 1.7	7	10	7.6	Red	2.9	na	(6) 24–27 Oct. 2011
Symphoricarpos albus (L.) S.F. Blake	Snowberry	17.4 ± 4.3	12 ± 3.1	7	10	9.5	White	5.2	6.2	(7) 12–15 Dec. 2011
Vaccinium ovatum Pursh	Evergreen huckleberry	30.0 ± 10.6	23.7 ± 6.9	7	20	6.6	Black	1.9	16.3	(6) 24–27 Oct. 2011
Vaccinium vitis-idaea L.	Lingonberry	15.7 ± 2.0	8.7 ± 2.0	7	20	7.9	Red	2.2	14.1	(6) 24–27 Oct. 2011

[a] In each cage, a set of fruits or three diet cups were exposed to five female and four male *D. suzukii* for 24 h, eggs were counted afterwards, and fruit were reared for 2 wk to count developing larvae, pupae, and adults.

[b] Separate cages with diet (control) were also simultaneously exposed to *D. suzukii* to confirm that flies laid viable eggs, a mean of 15.6 *D. suzukii* developed from the diet per cage. Control cages were replicated six to eight times as the host being tested.

[c] *A. arguta* was soft and ripe, but fruit are typically harvested while hard and unripe. Susceptibility of harvested fruit is not known.

Table 4. Experimental description of laboratory choice assays conducted in Corvallis, Oregon, during 2011–2012, results in Fig. 2

Alternate host scientific name	Common name	No. fruit, mean weight	Mean pH, Brix%	Cultivated host	No. Fruit, mean weight	Mean pH, Brix%	*n*	Assay group () and date[a]
Duchesnea indica	Indian strawberry	20, 5.1 g	4.7, 5.0	Totem strawberry	1, 5.0 g	2.7, 10.5	9	(2) 21 June 2012
Prunus avium	Sweet cherry (wild)	8, 15.3 g	4.3, 17.4	Royal Anne cherry	3, 15.1 g	3.4, 17.3	10	(3) 28 June 2012
Gaultheria shallon	Salal	18, 6.2 g	2.6, 14.3	Marionberry	1, 6.2 g	3.1, 11.4	10	(4) 19–20 July 2012
Ribes uva-crispa	Gooseberry	15, 8.1 g	5.1, 15.7	Marionberry	1, 8.0 g	3.1, 11.4	10	(4) 19–20 July 2012
Actinida arguta[b]	Hardy kiwi	2, 13.8 g	na	Pinot noir wine grape	10–14, 13.7 g	2.8, 19.8	10	(5) 3–8 Oct. 2012
Cornus sericea	Red osier dogwood	20, 3.5 g	2.5, na	Pinot noir wine grape	2, 3.4 g	2.8, 19.8	10	(5) 3–8 Oct. 2012
Prunus laurocerasus	Cherry laurel	10, 11.3 g	4.3, na	Pinot gris wine grape	10, 11.3 g	na	10	(1) 1–4 Nov. 2011
Sorbus sitchensis	W. mountain ash	15, 8.8 g	2.9, na	Pinot noir wine grape	6–8, 8.8 g	2.8, 19.8	10	(5) 3–8 Oct. 2012
Vaccinium ovatum	Evergreen huckleberry	20, 8.2 g	1.9, 16.3	Pinot noir wine grape	6–7, 8.2 g	2.8, 19.8	10	(5) 3–8 Oct. 2012
Vaccinium vitis-idaea	Lingonberry	20, 7.2 g	2.2, 14.1	Pinot noir wine grape	5–8, 7.2 g	2.8, 19.8	10	(5) 3–8 Oct. 2012

[a]Separate cages with diet (control) were also simultaneously exposed to *D. suzukii* to confirm that flies were laying eggs that would develop. Control cages were replicated 9–10 times as the choice tests (see "*n*" column). A mean of 45.4 *D. suzukii* developed from the diet per cage.
[b]*A. arguta* was soft and ripe, but fruit are typically harvested while hard and unripe.

fruit is harvested at hard stage before full ripeness), *Arbutus unedo* L., *B. aquifolium* Pursh, *Cornus sericea* L., *D. indica*, *Gaultheria shallon* Pursh, *P. avium*, *P. laurocerasus*, *Ribes uva-crispa* L., *R. spectabilis*, *Sambucus nigra* L., *S. confusa*, *Sorbus sitchensis* M. Roemer, *Sy. albus*, *Vaccinium ovatum* Pursh, and *Vaccinium vitis-idaea* L. These 15 fruits ranged in color from white, green, pink, red, blue, purple, and black. The pH of fruits that was measured was 1.9–5.5, and brix was 4.3–23.6%. Susceptible fruits that shared similar ripening times as cultivated fruits were further tested in close-range choice studies.

In choice tests, where an equal weight of two fruits was provided in cages (Table 4), the susceptibility varied between alternate and commercial hosts. More *D. suzukii* developed on 'Totem' strawberry than *D. indica*, and more on Pinot noir wine grape than *So. sitchensis* (Fig. 2b). *Ac. arguta*, *C. sericea*, *P. laurocerasus*, *V. ovatum*, and *V. vitis-idaea* were more susceptible than Pinot noir or Pinot gris wine grapes. More eggs were laid on and subsequently more flies developed in *A. arguta*, *P. laurocerasus*, and *V. ovatum* (Fig. 2a and b), suggesting a preference of *D. suzukii* as ovipositional substrates. In contrast, a similar proportion of eggs were laid among *C. sericea* and *V. vitis-idaea* (Fig. 2a), but significantly more developed from these hosts than the wine grapes (Fig. 2b). In this case, *D. suzukii* may not prefer either fruit as an ovipositional substrate but the eggs and larvae might experience differential survival.

Fruiting species included in both the field survey and no-choice laboratory assay were summarized in the following groups: 1) infestation in the field and laboratory; 2) no infestation in either study; 3) infestation in the laboratory but not in the field; and 4) infestation in the field but not in the laboratory. Eight fruits were infested both in the field and during laboratory assays: *B. aquifolium*, *C. sericea*, *P. avium*, *P. laurocerasus*, *R. spectabilis*, *Sa. nigra*, *S. confusa*, and *Sy. albus*. Seven fruits were neither infested in the field nor during laboratory assays: *A. japonica*, *Crataegus* 'Autumn Glory', *I. crenata*, *N. domestica*, *R. umbellata*, *Ro. acicularis*, *Sk. japonica*, and *V. davidii*. Three fruit were infested in the laboratory but not in the field: *Ar. unedo*, *So. sitchensis*, and *V. ovatum*. Lastly, three fruit were infested in the field but had low or no infestation during the laboratory assays: *C. lacteus* (low infestation in lab), *P. lusitanica* (dried out in laboratory), and *So. dulcamara*.

Discussion

Our field surveys identified several newly reported hosts for *D. suzukii*: *B. aquifolium*, *Cornus amomum* Miller, *Cornus foemina* Miller, *C. sericea*, *C. lacteus*, *E. umbellata*, *F. purshiana*, *L. benzoin*, *Lonicera caerulea* L., *M. nigra*, *P. laurocerasus*, *P. lusitanica*, *R. spectabilis*, *S. confusa*, *So. dulcamara*, and *Sy. albus*. This study also confirms previous reports of host-use by *D. suzukii* for the species *Cornus kousa* (Hance), *Ph. americana*, *P. avium* (wild), and *Sa. nigra* (see references in Table 1), and *R. armeniacus* (host list by European and Mediterranean Plant Protection Organization [EPPO] 2010), and within the genera *Cornus*, *Elaeagnus*, *Frangula*, *Lonicera*, *Morus*, *Prunus*, *Sambucus*, and *Solanum*. Observed infestation rates were >10% of collected fruits or in >25% of the samples among the following hosts: *C. amomum*, *C. sericea*, *C. lacteus*, *E. umbellata*, *F. purshiana*, *Lonicera* sp., *Lonicera caerulea*, *M. nigra*, *Ph. americana*, *P. avium*, *P. laurocerasus*, *P. lusitanica*, unspecified *Rubus* spp., *R. armeniacus*, *R. spectabilis*, *Sambucus* sp., *Sa. nigra*, and *S. confusa*.

The field survey identified potential hosts of concern. The spring-bearing fruit of *S. confusa* may serve as an early season host allowing *D. suzukii* populations to increase. Initial infestations were observed during April, and up to 92% of collected berries were infested during May 2012 in Oregon. This common ornamental plant may be in close proximity to backyard fruits, enabling further population growth and spread to nearby commercial fields. In Michigan, *Lonicera* sp. likewise may be an early season host that ripens before most commercial crops as infestations were observed in June 2012. Other hosts of concern include *P. laurocerasus* and *P. lusitanica* that are often grown as a hedgerow border, and *R. armeniacus* is a prevalent weed surrounding agricultural landscapes in the Pacific

Northwest (U.S. Department of Agriculture–Natural Resources Conservation Service [USDA-NRCS] 2014). Moreover, laboratory studies were consistent with our field surveys showing that *D. suzukii* oviposited and developed on *B. aquifolium*, *C. sericea*, *P. avium*, *P. laurocerasus*, *R. spectabilis*, *Sa. nigra*, *S. confusa*, and *Sy. albus*.

Results of the laboratory no-choice tests and field surveys were not always consistent with respect to either both studies showing susceptibility to *D. suzukii* or both studies not showing susceptibility. *D. suzukii* developed on *Ar. unedo*, *So. sitchensis*, and *V. ovatum* in no-choice laboratory tests, but no infestation was detected among these fruits when they were field-collected. This might be expected if *D. suzukii* populations were low at the site of collection, or more attractive hosts were nearby. Also, *D. suzukii* is more likely to oviposit on a given host under no-choice conditions compared to having multiple choices in the field. In contrast, for three other hosts, *D. suzukii* performed poorly in the laboratory while field-collected hosts were infested. In laboratory no-choice tests, females oviposited but progeny had very low development in *C. lacteus*, and no development in *P. lusitanica* and *So. dulcamara.* Meanwhile, field-collected fruit were infested among 23% of individual fruits of *C. lacteus*, 49% of *P. lusitanica*, 2% of *S. dulcamara* in Oregon, and 33% of *S. dulcamara* samples in Michigan. These discrepancies may be due to differences in fruit suitability among picked (laboratory) versus hanging (field) fruit and the timing of sampling. In the laboratory, picked *P. lusitanica* were oviposited on but the fruits dried out, which probably prevented development of *D. suzukii.* In the field, *P. lusitanica* fruit that remained hanging on the shrub for some time after oviposition was suitable for development. In the laboratory study, *C. lacteus* was picked later than in the field survey in Oregon (June vs. May), and *S. dulcamara* was picked earlier than when field samples started showing infestation in Oregon and Michigan (July vs. August–September). While flies laid eggs on *S. dulcamara* picked in July, it is possible that *S. dulcamara* becomes more suitable for development as it ripens further. In summary, while laboratory studies offer a quick way to screen many fruits under controlled conditions, this method can identify potential hosts but is not a definitive measure of host range potential.

Absence of infestation among the other 46 fruiting species surveyed in the field does not necessarily indicate that they are unsuitable fruits even though *D. suzukii* were found within 50 m of these host plants. Rather, infestations in the field will depend on the level of *D. suzukii* populations, timing of collection (ripe and overripe), age and architecture of the host plant, and relative attractiveness of other hosts in surrounding vicinity (adjacent crop and riparian zone). For instance, *Prunus serotina* Ehrhart was not infested when collected at one site in Michigan in July 2012, but 70% of *P. serotina* was infested at a site in France (Poyet et al. 2014). From both field surveys and laboratory study, *A. japonica*, *Crataegus* 'Autumn Glory', *I. crenata*, *N. domestica*, *R. umbellata*, *Ro. acicularis* (rosehips), *Sk. japonica*, and *V. davidii* showed no evidence of being susceptible to *D. suzukii*, or supported very low development of *D. suzukii*, during the dates of our field survey and laboratory assay. To our knowledge, none of these species have been reported as hosts elsewhere. One exception is *A. japonica*, where field collections made in Japan from April to June were infested with *D. suzukii* (Mitsui et al. 2010). In our no-choice laboratory study, some eggs were laid in *A. japonica*, *R. acicularis*, and *S. japonica*, but very few flies were observed to develop after 2 wk. Interestingly, eggs were laid in red *S. japonica* fruits but not white fruits from another variety of *S. japonica*. However, the color, pH, and brix range overlapped between hosts categorized as having no eggs laid, no or low development, or substantial development. Therefore, no general trends were identified in terms of the color, pH, or brix of the tested fruits. This suggests that other fruit quality characteristics are affecting oviposition and development of *D. suzukii*. In past studies, when comparisons were made within a fruit type with commercial fruit, fruit with higher pH and brix levels had higher numbers of eggs laid, and more developing *D. suzukii* (Lee et al. 2011). Higher skin firmness also corresponded with lower levels of oviposition (Burrack et al. 2013, Kinjo et al. 2013), so these factors likely interact to affect host suitability.

Beyond confirming that certain plant species are susceptible hosts or not, understanding the timing and relative attractiveness of hosts compared to the surrounding landscape will be important for incorporating host plant management into integrated pest management programs for *D. suzukii*. For instance, the alternative host might be susceptible to flies earlier in the season, but less preferred than the commercial crop, so it might harbor pests that would move to infest the crop as it becomes susceptible. In short-range choice tests, cultivated strawberry was more susceptible than the ornamental *D. indica*, and Pinot noir was more susceptible than *So. sitchensis*. On the other hand, if the alternative host is preferred over the commercial crop, it may serve as a "sink," pulling the pest away from the crop. However, the alternative host may also recruit more *D. suzukii* into the area, thereby increasing local pest density. Whether the first, second, or both scenarios occur will depend on the distance to which the alternative host may attract *D. suzukii* from surrounding areas, and the timing of their ripening. Interestingly, *Ac. arguta* (soft and ripe, typical postharvest stage), *P. laurocerasus*, and *V. vitis-idaea* were preferred ovipositional hosts over Pinot wine grapes. Lastly, the no-choice laboratory study identified several fruits that *D. suzukii* oviposit in but develop minimally. If these hosts are attractive to flies in the field, these hosts may serve as an egg "sink" reducing pest pressure in the crop. However, this requires future testing under field conditions.

In summary, a combination of field surveys and laboratory assays have identified wild, ornamental, and uncultivated hosts of *D. suzukii* in two major regions of production of fruit crops susceptible to this pest. Once these hosts are known, further studies can elucidate the extent *D. suzukii* may use a given host. Removal of the entire plant or fruit may be necessary to manage pest populations in the landscape, but there is currently little published information on the efficacy of this cultural control tactic for reducing populations of *D. suzukii*. Choice studies reported in this article start to address the relative susceptibility of alternative hosts compared with cultivated hosts. Further understanding of the relative host suitability of various plant species could lead to spatial mapping that combines host quality with host distribution and phenology to predict pest risk across landscapes. These spatial analyses and host lists could help guide management investment decisions across regions of production of crops susceptible to *D. suzukii* and also potentially identify areas where coordinated action should be focused to remove reservoirs of wild hosts if it is shown that they drive infestation in nearby crops.

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References Cited

Arnó, J., J. Riudavets, and R. Gabarra. 2012. Survey of host plants and natural enemies of *Drosophila suzukii* in an area of strawberry production in Catalonia (northeast Spain). IOBC/WPRS Bull. 80: 29–34.

Barnes, B. V., and W. H. Wagner. 1981. Michigan trees: a guide to trees of Michigan and the Great Lakes region. University of Michigan Press, Ann Arbor, MI.

Bruck, D. J., M. Bolda, L. Tanigoshi, J. Klick, J. Kleiber, J. DeFrancesco, B. Gerdeman, and H. Spitler. 2011. Laboratory and field comparisons of insecticides to reduce infestation of *Drosophila suzukii* in berry crops. Pest Manage. Sci. 67: 1375–1385.

Burrack, H. J., G. E. Fernandez, T. Spivey, and D. A. Kraus. 2013. Variation in selection and utilization of host crops in the field and laboratory by *Drosophila suzukii* Matsumara (Diptera: Drosophilidae), an invasive frugivore. Pest Manage. Sci. 69: 1173–1180.

Drew, R.A.I., and B. Yuval. 2000. The evolution of fruit fly feeding behavior, pp. 731–749. In M. Aluja and A. L. Norrbom (eds.), Fruit flies (Tephritidae): phylogeny and evolution of behavior. CRC, Boca Raton, FL.

(EPPO) European and Mediterranean Plant Protection Organization. 2010. *Drosophila suzukii* (Diptera: Drosophilae). (http://www.eppo.org/Quarantine/Alert_List/insects/drosophila_suzukii.htm) (accessed February. 2012).

Goodhue, R. E., M. Bolda, D. Farnsworth, J. C. Williams, and F. G. Zalom. 2011. Spotted wing drosophila infestation of California strawberries and raspberries: economic analysis of potential revenue losses and control costs. Pest Manage. Sci. 67: 1396–1402.

Grassi, A., L. Giongo, and L. Palmieri. 2011. *Drosophila suzukii* (Matsumura), new pest of soft fruits in Trentino (North-Italy) and in Europe. IOBC/WPRS Bull. 70: 121–128.

Haviland, D. R., and E. H. Beers. 2012. Chemical control programs for *Drosphila suzukii* that comply with international limitations on pesticide residues for exported sweet cherries. J. Integr. Pest Manage. 3: 1–6.

Huang, F. N., D. A. Andow, and L. L. Buschman. 2011. Success of the high-dose/refuge resistance management strategy after 15 years of *Bt* crop use in North America. Entomol. Exp. Appl. 141: 262–262.

Hauser, M. 2011. A historic account of the invasion of *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) in the continental United States, with remarks on their identification. Pest Manage. Sci. 67: 1352–1357.

Kanzawa, T. 1935. Research into the fruit-fly *Drosophila suzukii* Matsumura (Preliminary Report). *In* S. Kawai (Ed), Yamanashi Prefecture Agricultural Experiment Station Report. In Japanese.

Kanzawa, T. 1939. Studies on *Drosophila suzukii* Mats, p. 49. *In* S. Kawai (Ed), Kofu, Yamanashi Agricultural Experiment Station, In Japanese.

Kinjo, H., Y. Kunimi, T. Ban, and M. Nakai. 2013. Oviposition Efficacy of *Drosophila suzukii* (Diptera: Drosophilidae) on Different Cultivars of Blueberry. J. Econ. Entomol. 106: 1767–1771.

Lee, J. C., D. J. Bruck, H. Curry, D. Edwards, D. R. Haviland, R. A. Van Steenwyk, and B. M. Yorgey. 2011. The susceptibility of small fruits and cherries to the spotted-wing drosophila, *Drosophila suzukii*. Pest Manage. Sci. 67: 1358–1367.

Lee, J. C., F. D. Menalled, and D. A. Landis. 2001. Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. J. Appl. Ecol. 38: 472–483.

Mitsui, H., K. H. Takahashi, and M. T. Kimura. 2006. Spatial distributions and clutch sizes of *Drosophila* species ovipositing on cherry fruits of different stages. Popul. Ecol. 48: 233–237.

Mitsui, H., K. Beppu, and M. T. Kimura. 2010. Seasonal life cycles and resource uses of flower- and fruit-feeding drosophilid flies (Diptera: Drosophilidae) in central Japan. Entomol. Sci. 13: 60–67.

Newcomb, L. 1977. Newcomb's wildflower guide. Little, Brown and Co., Boston, MA.

Plant Inspection Advisory. 2010. Update for spotted wing drosophila, *Drosophila suzukii* and potential on blueberries. Memo to: Bureau of Plant & Apiary Inspectors and Supervisors, Florida, May 6, 2010.

Poyet, M., P. Eslin, M. Heraude, V. Le Roux, G. Prevost, P. Gibert, and O. Chabrerie. 2014. Invasive host for invasive pest: when the Asiatic cherry fly (*Drosophila suzukii*) meets the American black cherry (*Prunus serotina*) in Europe. Agric. For. Entomol. 16: 251–259.

SAS. 2007. JMP® Statistics and Graphics Guide, Version 7.0.1. SAS Institute, Cary, NC.

Sasaki, M., and R. Sato. 1995. Bionomics of the cherry drosophila, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae) in Fukushima Prefecture. Annual Report Plant Protection Northern Japan 46: 170–172.

(USDA-ARS) U.S. Department of Agriculture–Agricultural Research Service National Genetic Resources Program. 2014. The plants database. National Plant Data Team, Greensboro, NC. (http://plants.usda.gov) (accessed 18 December 2014).

Van Timmeren, S. and R. Isaacs. 2013. Control of spotted wing Drosophila, *Drosophila suzukii*, by specific insecticides and by conventional and organic crop protection programs. Crop Prot. 54: 126–133.

Yu, D., F. G. Zalom, and K. A. Hamby. 2013. Host status and fruit odor response of *Drosophila suzukii* (Diptera: Drosophilidae) to figs and mulberries. J. Econ. Entomol. 106: 1932–1937.

Yukinari, M. 1988. Drosophilid flies injurious to the fruits of wax-myrtle, *Myrica rubra*. Japan J. Appl. Entomol. Zool. 32: 146–148.

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