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Development of *Rhagoletis pomonella* and *Rhagoletis indifferens* (Diptera: Tephritidae) in mango and other tropical and temperate fruit in the laboratory

Wee L. Yee^{1,*} and Robert B. Goughnour²

Abstract

Temperate fruit flies in the genus *Rhagoletis* (Diptera: Tephritidae) have narrow host ranges relative to those of tropical fruit flies, suggesting they will not attack or are incapable of developing in most novel fruit. We tested the hypothesis that apple maggot fly, *Rhagoletis pomonella* (Walsh), and western cherry fruit fly, *Rhagoletis indifferens* Curran, whose normal hosts belong to the Rosaceae, will not attack or develop in mango (*Mangifera indica* L.; Anacardiaceae) and other non-rosaceous tropical fruit. Of fruits hung in infested apple trees, at least 49% of apples ($n = 77$) produced *R. pomonella* puparia, whereas only 1% of mangoes ($n = 291$) and 0% of papayas (*Carica papaya* L.; Caricaceae) and 8 other tropical fruit produced puparia. In laboratory tests in 1.9 L containers, 33% of apples ($n = 131$), 7% of mangoes ($n = 118$), and 7% of papayas ($n = 14$) produced *R. pomonella* puparia; adult flies also eclosed from puparia from mango and papaya. Females of *R. pomonella* landed approximately 4 to 9 times more often on apple than mango. When exposed to *R. indifferens* in laboratory tests in 1.9 L containers, 6% of mangoes ($n = 32$) and 0% of papayas ($n = 23$) versus 33 to 73% of sweet cherry, plum, and nectarine, and 0% of peach (all *Prunus* species; Rosaceae) produced puparia; no eggs were detected in mango and papaya. Contrary to our hypothesis, larvae of *R. pomonella* and *R. indifferens* were capable of developing in some tropical fruit under laboratory conditions. How findings here relate to fly quarantines versus basic fly biology is unknown and needs further study.

Key Words: apple maggot fly; western cherry fruit fly; *Mangifera indica*; *Carica papaya*

Resumen

Las moscas de la fruta en el género *Rhagoletis* (Diptera: Tephritidae) en la región templada tienen un rango de hospederos estrecho en relación con las de las moscas de la fruta tropical, lo que sugiere que no atacarán o son incapaces de desarrollar en la mayoría de los frutos foráneos. Se probó la hipótesis de que la mosca de la fruta de manzana, *Rhagoletis pomonella* (Walsh) y la mosca de la fruta de la cereza occidental, *Rhagoletis indifferens* Curran, cuyos hospederos normales pertenecen a las Rosaceae, no atacarán ni se desarrollarán en el mango (*Mangifera indica* L. Anacardiaceae) y otras frutas tropicales que no pertenecen a la familia Rosáceae. De las frutas colgadas en los manzanos infestados, por lo menos el 49% de las manzanas ($n = 77$) produjeron pupas de *R. pomonella*, mientras que sólo el 1% de los mangos ($n = 291$) y el 0% de las papayas (*Carica papaya* L.; Caricaceae) y 8 otras frutas tropicales produjeron pupas. En pruebas de laboratorio en recipientes de 1,9 L, 33% de manzanas ($n = 131$), 7% de mangos ($n = 118$) y 7% de papayas ($n = 14$) produjeron pupas de *R. pomonella*; moscas adultas también se emergieron de pupas en mango y papaya. Las hembras de *R. pomonella* aterrizaron ~ 4 a 9 veces más a menudo en manzana que mango. Cuando se expusieron las frutas a *R. indifferens* en pruebas de laboratorio en recipientes de 1,9 L, el 6% de mangos ($n = 32$) y el 0% de papayas ($n = 23$) frente a el 33 a 73% de cerezas dulces, ciruelas y nectarinas y el 0% de melocotón (todas especies de *Prunus*, Rosaceae) produjeron puparia; no se detectaron huevos en mango y papaya. Al contrario a nuestra hipótesis, las larvas de *R. pomonella* y *R. indifferens* fueron capaces de desarrollarse en algunas frutas tropicales en condiciones de laboratorio. No se sabe si estos hallazgos aquí se relacionan con la cuarentena de moscas versus la biología básica de la mosca por lo que más estudios son necesarios.

Palabras Clave: mosca de la fruta de manzana; mosca de la fruta de la cereza occidental; *Mangifera indica*; *Carica papaya*

Temperate fruit flies in the genus *Rhagoletis* (Diptera: Tephritidae) include some of the major quarantine pests of tree fruit in North America, but the threat these flies pose to orchard crops as a whole is unclear because their natural host ranges tend to be narrow relative to those of tropical or subtropical fruit flies. Typically, the host plants of any one *Rhagoletis* species are confined to a specific family, within which only plants in 1 genus or in related genera are utilized (Bush 1969). This contrasts with, for example, the melon fly, *Bactrocera cu-*

curbitae (Coquillett), and Mediterranean fruit fly, *Ceratitidis capitata* (Wiedemann), which attack approximately 136 plants from 62 genera in 30 families (McQuate et al. 2017) and approximately 321 plants from 157 genera in 62 families (Liquido et al. 2014), respectively.

The utilization by temperate *Rhagoletis* flies of plants mostly within specific families suggests the flies will not attack or are incapable of developing in novel fruit evolutionarily distant from them. Such fruit include those of economically important tropical plants. This hypoth-

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esis could have implications for fly quarantines. The non-use of these fruit by flies would reduce the threat of the flies establishing in tropical countries even if they were accidentally introduced and some could tolerate the climates there.

Two *Rhagoletis* species in the western USA that have adapted to cultivated host plants but still have relatively narrow host ranges within the Rosaceae are apple maggot fly, *Rhagoletis pomonella* (Walsh), and western cherry fruit fly, *Rhagoletis indifferens* Curran, which are quarantine pests of apple (*Malus pumila* Miller) and cherries (*Prunus* species), respectively. *Rhagoletis pomonella* is native to eastern North America and the highlands of Mexico (Bush 1969; Rull et al. 2006) and was introduced into the western USA sometime in the mid-1900s. It is not found outside North America. Its ancestral hosts are hawthorns (*Crataegus* species; Rosaceae), but it adapted to cultivated apple in the eastern USA about 150 yr ago (Bush 1969). *Rhagoletis pomonella* infests about 54 plant species in nature, but all in the Rosaceae; furthermore, 28 are *Crataegus* species and another 25 species are rarely infested (Yee et al. 2014). *Rhagoletis indifferens* is native to the western USA and British Columbia, Canada (Foote et al. 1993); it is found nowhere else. Its ancestral host is bitter cherry (*Prunus emarginata* [Douglas ex Hook.] Walp.), but the fly has adapted to cultivated sweet cherry (*Prunus avium* [L.] L.) and tart cherry (*Prunus cerasus* L.) throughout its range. *Rhagoletis indifferens* infests 15 plant species in nature (Yee et al. 2014), but only 4 of them are commonly used.

The main objective here was to test the hypothesis that *R. pomonella* and *R. indifferens* will not attack or develop in tropical fruit. We focused on mango (*Mangifera indica* L.; Anacardiaceae) because it is economically important (Shah et al. 2010), is taxonomically distant from Rosaceae (Angiosperm Phylogeny Group 2016), and has qualities (e.g., smooth and soft skin) that make it a candidate for attack by these flies, thus presenting a challenge for our hypothesis. We also determined the use of various temperate fruit by these flies as a basis for comparison with tropical fruit.

Materials and Methods

Tropical fruit were chosen based on a list of major fruit produced in Indonesia (World Bank 2007). For *R. pomonella*, the only fruit tested known to be a host for the fly was apple; for *R. indifferens*, it was sweet cherry. Fruit were purchased in local markets in western and central Washington. Tropical fruit originated mostly from Mexico, Chile, and Peru. Temperate fruit used in field tests originated from the USA, Chile, and Peru. In all experiments, smooth-skinned fruit were rubbed under water by hand and air dried before testing.

INFESTATION OF FRUIT HUNG IN APPLE TREES BY *R. POMONELLA*

Tests to measure whether flies attack and larvae can develop in apple and tropical fruit in the field were conducted by hanging fruit in fly-infested apple trees at sites in Woodland (Cowlitz County), Vancouver (Clark County), and in Skamania County in western Washington State in 2013 and in Woodland in 2014. A 0.64 cm wide beige strip of hook-and-loop fastener was wrapped around the center of each fruit. Green floral wire was attached to the strip on opposite sides. The wires were attached to 1 office binder clip, which was clipped onto a branch approximately 1.5 m above ground.

At the Woodland site in 2013, fruit were exposed in 13 trees during 10 to 31 Jul: 30 apples (10 'Gala'; 20 'Golden Delicious'), 49 mangoes (20 'Ataulfo'; 29 'Kent'), 11 Mexican papayas (*Carica papaya* L.; Caricaceae), 9 plantains (*Musa acuminata* Colla; Musaceae), 18

bananas (*M. acuminata*), 9 kumquats (*Citrus japonica* Thunberg; Rutaceae), 10 oranges (*Citrus × sinensis* (L.) Osbeck; Rutaceae), 10 mandarin oranges (*Citrus reticulata* Blanco; Rutaceae), 10 lemons (*Citrus × limon* [L.] Burm. f.; Rutaceae), 5 pineapples (*Ananas comosus* (L.) Merrill; Bromeliaceae), and 10 kiwifruit (*Actinidia deliciosa* C. F. Liang & A. R. Ferguson; Actinidiaceae) were tested. At the Vancouver site in 2013, fruit were exposed in 10 trees during 28 Jun to 19 Aug: 7 apples, 70 mangoes (32 Ataulfo; 38 Kent), 3 Mexican papayas, 20 bananas, 12 oranges, 9 lemons, 6 pineapples, and 10 kiwifruit were tested. At the Skamania site in 2013, 78 mangoes (30 Ataulfo; 48 Kent) were exposed in 4 trees during 8 to 29 Aug. At the Woodland site in 2014, fruit were exposed in 10 of 14 trees during 20 Jul to 2 Aug: 20 Gala apples, 50 Kent mangoes, and 5 Hawaiian papayas were tested; all fruit were removed on 27 Jul and replaced with a second set of fruit comprising 20 Gala apples and 44 Ataulfo mangoes. At all sites in both years, fruit were removed after exposure and held in tubs for larvae to emerge in an outdoor shed for 30 to 45 d, depending on when fruit deteriorated. Puparia in tubs were then counted.

Fallen apples were collected under test trees to confirm that *R. pomonella* was present at the sites during exposures. In 2013, 1,648 apples were collected under 8 and 10 test trees at Woodland and Vancouver sites, respectively. In 2014, 892 apples were collected under the 14 trees at the Woodland site. Larvae were reared from apples as described above.

INFESTATION OF FRUIT BY *R. POMONELLA* IN THE LABORATORY

Four tests to measure whether *R. pomonella* can develop in tropical and temperate fruit in the laboratory were conducted in 2013 to 2015. *Rhagoletis pomonella* originated from puparia from infested apples or black hawthorns (*Crataegus douglasii* Lindley) collected in Aug or Sep 2012 to 2014 in western Washington. Puparia were chilled at 4 to 5 °C for approximately 6 mo and then transferred to 23 to 26 °C for fly eclosion. Groups of 10 to 20 flies were maintained inside a 1.9 L (16 cm high × 10 cm wide) paper container with dry yeast extract and sucrose food on a paper towel and water on a wick and aged 10 d before testing. Then, 1 female and 1 male or 3 females and 3 males were transferred to another 1.9 L container with 1 fruit. Fruit were replaced every 10 to 15 d over 30 to 45 d, for 2 or 3 fruit per replicate. Any dead flies were replaced with similarly aged live flies (mortality was <20%). After exposures, fruit were placed individually in tubs for 30 to 45 d for larvae to emerge. Tests were conducted at 23 to 26 °C, a 16:8 h L:D photoperiod, and 35 to 45% relative humidity. Fruit in each container comprised a replicate.

Tests 1 to 3 used flies from apples and test 4 used flies from black hawthorns. In test 1 in 2013, 6 replicates of apple (Gala, Golden Delicious, 'Fuji', 'Red Delicious', 'Pink Lady', 'Honey Crisp') and 1 each of mango, Hawaiian papaya, orange, avocado (*Persea americana* Miller; Lauraceae), and green grape (*Vitis vinifera* L.; Vitaceae) (10 fruit) were set up with 3 females and 3 males each. In test 2 in 2014 to 2015, 67 replicates of apple, 67 of mango (mix of Kent and Ataulfo), 7 of Hawaiian papaya, 12 of 'Hass' avocado, 5 of kiwifruit, and 5 of mandarin orange were set up with 1 female and 1 male each. In test 3 in 2014, 10 replicates of apple, 10 of Kent mango, 15 of lemon, 10 of Hass avocado, and 15 of kiwifruit were set up with 3 males and 3 females each. In test 4, 48 replicates of apple, 40 of Kent mango, 6 of Hawaiian papaya, 13 of kiwifruit, and 4 of persimmon (*Diospyros kaki* L. f.; Ebenaceae) were set up with 1 female and 1 male each. Puparia of *R. pomonella* from tropical fruit were chilled for approximately 6 mo and then transferred to 23 to 24 °C for fly eclosion.

LANDINGS ON APPLE VERSUS OTHER FRUIT BY *R. POMONELLA* IN THE LABORATORY

To measure relative acceptance by female and male flies of different fruit within tests 2 and 3 (tests described in previous section), numbers of fly landings on fruit were counted. In test 2, instantaneous counts of flies resting on, mating on, or stinging apple and mango at 1100, 1130, 1300, and 1330 h (6 to 8.5 h after lights-on in a 16 h photophase) were recorded on 10 to 18 d. In test 3, numbers of flies seen on apple and the 4 other fruit types at 1400 h (9 h after lights-on in a 16 h photophase) were counted on 5 d; here, numbers of dead flies were also recorded at each check to obtain a number of fly landings per live fly per day measure. In test 2, observations were made in 30 and 24 replicates of apple and mango, respectively; in test 3, observations were made in all 10 or 15 replicates of apple, mango, avocado, lemon, and kiwifruit.

INFESTATION OF FRUIT BY *R. INDIFFERENS* IN THE LABORATORY

Tests to measure relative development in or attack of cherries and tropical and temperate fruit by *R. indifferens* were conducted in 2014 to 2015. *Rhagoletis indifferens* originated from field-infested sweet cherries collected in Jul 2013 and 2014 in central Washington. Puparia were chilled at 3 to 4 °C for approximately 6 mo and transferred to 22 to 24 °C for fly eclosion. Fly age, containers used, and ambient conditions before and during tests were the same as in *R. pomonella* tests. As before, each container comprised a replicate; for sweet cherries, there were 10 fruits per replicate.

Two tests were done to measure larval development in different fruit. In a test in 2014, 1 Kent mango was exposed to 1 female and 1 male fly in each of 12 replicate containers for 30 d. Dead flies were replaced with similarly aged live flies as before. Containers were checked for puparia after 30 d. In test 1 in 2015, 1 fruit was exposed to 5 female and 5 male flies per container. Fifteen sweet cherry, 20 Kent mango, 23 Hawaiian papaya, 26 black plum (*Prunus domestica* L.; Rosaceae), 23 nectarine (*Prunus persica* [L.] Batsch var. *nuciper-sica* [Suckow] C. K. Schneid.; Rosaceae), 32 peach (*Prunus persica* (L.) Stokes; Rosaceae), and 23 Asian pear (*Pyrus pyrifolia* (Burm.) Nakai; Rosaceae) replicates were set up. After 2 wk, fruit were removed and set aside in 473 mL containers for larval emergence. Puparia in containers were collected at the end of 30 d, chilled in moist soil at 3 to 4 °C for 6 mo, and then transferred to 27 °C for fly eclosion.

Test 2 in 2015 was conducted to measure oviposition and larval development responses in all fruit. Twenty-nine sweet cherry, 21 mango, 16 papaya, 26 black plum, 23 nectarine, 21 peach, and 24 Asian pear replicates were set up. Methods were the same as in test 1 of 2015, except fruit at 2 wk were preserved in 70% ethanol. Fruit were dissected ≥ 1 mo later under a stereomicroscope and numbers of eggs just under the skin and larvae in the pulp were counted. The white eggs were laid approximately 1 mm below the fruit skin surface and were visible under the skin after preservation in ethanol.

STATISTICAL ANALYSES

Numbers of *R. pomonella* puparia per fruit in field and laboratory tests, *R. pomonella* landings on fruit, and numbers of *R. indifferens* puparia, eggs, and larvae across fruit types were analyzed using the Kruskal–Wallis test, as data were not normally distributed due to many zeroes, followed by LSD tests on ranks if needed (Conover 1980). For *R. indifferens* data in tests 1 and 2 of 2015, proportions of fruit infested were also analyzed and Tukey-type multiple comparisons between all fruit pairs were made (Zar 1999).

Results

INFESTATION OF FRUIT HUNG IN APPLE TREES BY *R. POMONELLA*

Combined data from Woodland, Vancouver, and Skamania in 2013 and 2014 showed that only apples and mangoes produced *R. pomonella* puparia (Table 1). At least 49% of 77 apples (“at least” because the group of 10 apples in Woodland was inadvertently combined) but only 1% of 291 mangoes were positive (2% of Ataulfo, 0% of Kent) and none of the other fruit were positive. The number of puparia per fruit was greater in apple (mean \pm SE, 2.64 \pm 0.25) than in mango (0.03 \pm 0.02), papaya (Mexican and Hawaiian), plantain, banana, kumquat, orange, mandarin orange, lemon, pineapple, and kiwifruit (all zeroes); the only significant difference was between apple and all other fruit ($\chi^2 = 295.37$; $df = 10$; $P < 0.0001$). In 2013 and 2014, all apple trees in which fruits were hung in Woodland and Vancouver had infested apples (Table 2).

INFESTATION OF FRUIT BY *R. POMONELLA* IN THE LABORATORY

Across the 4 laboratory tests, 33% of 131 apples, 7% of 118 mangoes, and 7% of 14 papayas produced puparia, whereas no avocado ($n = 23$ fruit), kiwifruit ($n = 33$), orange or mandarin orange ($n = 6$), lemon ($n = 5$), persimmon ($n = 4$), and grape ($n = 10$) produced puparia. The number of puparia per fruit was greater in apple (mean \pm SE, 3.57 \pm 0.47) than in mango (0.41 \pm 0.15), papaya (0.46 \pm 0.33), avocado, kiwifruit, orange, mandarin orange, lemon, persimmon, and grape (all zeroes); the only significant difference was between apple and all other fruit ($\chi^2 = 60.17$; $df = 8$; $P < 0.0001$). From the 48 puparia from mango, 20 *R. pomonella* adults (7 females and 7 males; sex of others not recorded) eclosed. From the 4 puparia from papaya, 3 *R. pomonella* adults (2 females and 1 male) eclosed.

LANDINGS ON APPLE VERSUS OTHER FRUIT BY *R. POMONELLA* IN THE LABORATORY

In test 2, female flies landed approximately 4 times more often on apple than mango (Fig. 1A). In test 3, female flies landed approximately 9 times more often on apple than mango, and more than on all tropical fruit (Fig. 1B). In test 2, stinging was seen 7.8 times more often on apple than mango when adjusted for numbers of female flies and observations. However, in test 3, stinging was rarely seen, with 1 event each on apple, kiwifruit, and lemon.

Table 1. Infestation by *Rhagoletis pomonella* of apple versus other fruit hung in apple trees, combined from Woodland, Vancouver, and Skamania sites in Washington State in 2013 and 2014.

| Fruit hung in apple trees | No. of fruit hung in trees | Fruit positive (%) | No. of puparia |
|---------------------------|----------------------------|--------------------|----------------|
| Apple ^a | 77 | 49 | 203 |
| Mango ^b | 291 | 1 | 9 |
| Papaya ^c | 19 | 0 | 0 |
| Plantain | 9 | 0 | 0 |
| Banana | 38 | 0 | 0 |
| Kumquat | 9 | 0 | 0 |
| Orange | 22 | 0 | 0 |
| Mandarin orange | 10 | 0 | 0 |
| Lemon | 19 | 0 | 0 |
| Pineapple | 11 | 0 | 0 |
| Kiwifruit | 20 | 0 | 0 |

^aGala and Golden Delicious. ^bAtaulfo and Kent. ^cMexican and Hawaiian.

Table 2. Infestation by *Rhagoletis pomonella* of apples from apple trees in which fruit were hung at 2 sites in 2013 and 1 site in 2014.

| Year | Site | No. of apple trees | No. of fruit | No. of puparia |
|------|-----------|--------------------|--------------|----------------|
| 2013 | Woodland | 8 | 293 | 1,648 |
| | Vancouver | 10 | 415 | 1,331 |
| 2014 | Woodland | 14 | 892 | 2,617 |

INFESTATION OF FRUIT BY *R. INDIFFERENS* IN THE LABORATORY

In the test in 2014, 2 of the 12 Kent mangoes produced 44 *R. indifferens* puparia, but in test 1 in 2015, none of 20 Kent mangoes produced puparia (Table 3), i.e., 6% of 32 mangoes were positive for the 2 yr combined. In addition to mango in test 1 in 2015, papaya, peach, and Asian pear did not produce puparia, whereas sweet cherry, black plum, and nectarine all produced puparia (Table 3). In test 2 in 2015, there were no eggs found in mango and papaya, although 1 larva was found inside a mango; nectarine had the greatest numbers of eggs and black plum had the greatest numbers of larvae (Table 3). Twenty-four adults eclosed from 45 puparia from sweet cherry, 27 from 231 puparia from black plum, and 4 from 143 puparia from nectarine.

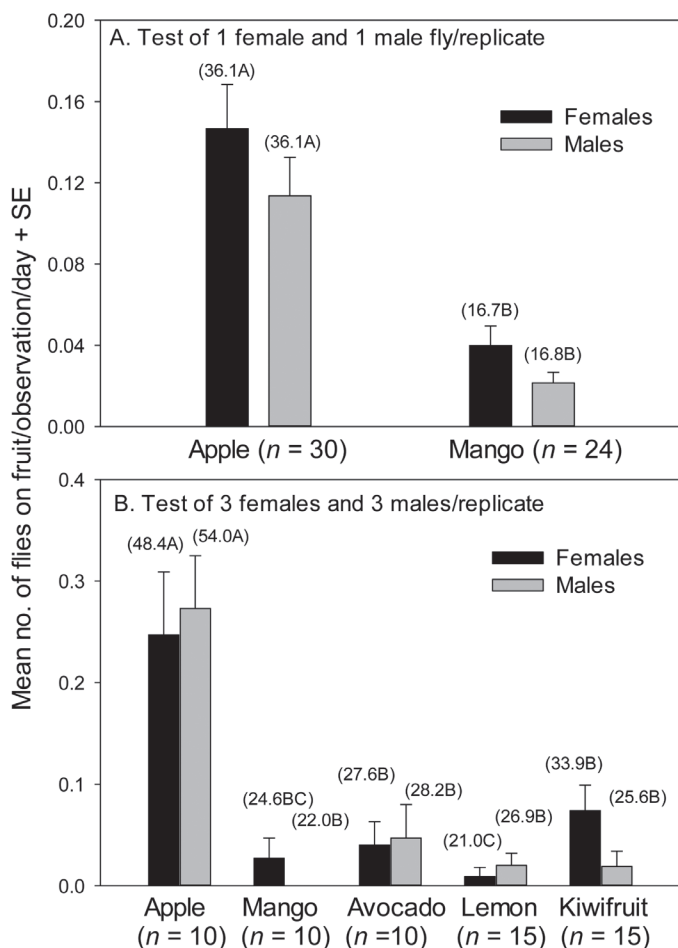


Fig. 1. Mean numbers of apple-origin female and male adults of *Rhagoletis pomonella* that landed on apple and tropical fruit in the laboratory in 2014. (A) Test using 1 female and 1 male per replicate; (B) test using 3 females and 3 males per replicate; n = number of replicates. Error bars represent SE. Ranks inside parentheses above bars with the same letter within sexes are not significantly different ($P > 0.05$; LSD test after Kruskal–Wallis test). Females in (A): $\chi^2 = 20.46$; $df = 1$; $P < 0.0001$; males in (A): $\chi^2 = 20.37$; $df = 1$; $P < 0.0001$; females in (B): $\chi^2 = 22.18$; $df = 4$; $P = 0.0002$; males in (B): $\chi^2 = 35.54$; $df = 4$; $P < 0.0001$.

Discussion

Contrary to our hypothesis, *R. pomonella* attacked mango exposed in apple trees and was capable of producing viable larvae from mango and papaya under laboratory conditions. Mango and papaya are hosts for tropical tephritids (e.g., Mwatawala et al. 2009; Verghese et al. 2012; Martinez-Barrera et al. 2015), so these fruit appear suitable for a wide range of fly species. Despite this finding, acceptance of these fruit by *R. pomonella* seems low, as evidenced by the fewer fly landings on mango and other tropical fruit than on apple in the laboratory. Whether *R. pomonella* larvae can survive at the same rates in apple, mango, and papaya is unknown. The fecundity of females from larvae in mango and papaya that produce adults also is unknown.

Tests were conducted using commercial fruit, so there is a possibility that insecticides in fruit affected results. However, test apples, mangoes, and papayas were not organic and all produced *R. pomonella* larvae. Also, although some insecticides applied on cherries and apples with fly eggs and larvae can reduce emergence of *Rhagoletis* larvae, none eliminated them (Yee & Alston 2006; Wise et al. 2009). In orchards, insecticide sprays do not target fruit, so any insecticides in flesh of fruit in our tests probably occurred in lower amounts than in those studies.

Whereas ripe mangoes may be a suitable host for *R. pomonella* in the laboratory, some of the other fruit may not have been because they were ripe or overripe. At the stage they are sold in stores, some fruit may already be poor hosts because they have overly high water content or other unfavorable properties. These same fruit may be suitable hosts if exposed to flies at an earlier stage in fruit ripening. *Rhagoletis pomonella* puparia were not produced from firm, immature hawthorn fruit, and less mature hawthorns or cherries were less likely attacked than riper fruit (Messina & Jones 1990).

Our hypothesis as it pertains to *R. indifferens* was not fully supported, as puparia were produced in low numbers from mango. As suggested for *R. pomonella*, acceptance of fruit by adult *R. indifferens* was probably low, as indicated by the lack of eggs in mango in test 2 in 2015. Averages of about 4 of the 5 females were alive in mango and papaya treatments at the end of the tests (data not shown), so high mortality was not a factor in low responses to tropical fruit.

How findings here relate to fly quarantines versus basic fly biology is unknown and needs further study. Mango is a host of *R. pomonella* (supporting adult eclosion) and *R. indifferens* (supporting at least pupa formation) under laboratory conditions, but based on published climatic requirements of the 2 fly species, the flies are highly unlikely to survive in tropical environments where mangoes grow (Kumar et al. 2014, 2016). For *R. pomonella*, a maximum entropy model predicted no suitable areas in southern Thailand, Cambodia, Indonesia, and Malaysia; a climate matching model predicted marginally suitable habitats in northern Laos and Vietnam but no suitability in southern Thailand, Cambodia, Indonesia, and Malaysia (Kumar et al. 2016). For *R. indifferens*, maximum entropy and climate matching models predicted no suitable habitats in Indonesia, Malaysia, and Thailand (Kumar et al. 2014). Models that predict climatic conditions suitable for both flies and tropical fruit, and studies of fruit ripeness effects on fly responses are needed to further assess the relevance of current findings to fly quarantines.

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Table 3. Mean numbers \pm SE (ranks) of *Rhagoletis indifferens* puparia produced from fruit and mean numbers of eggs and larvae inside fruit \pm SE (ranks) after 2 wk exposure to 5 female and 5 male flies in 2015.

| Fruit | Test 1: puparia produced | | | Test 2: eggs and larvae in fruit | | | |
|---------------------------|--------------------------|-----------------|--------------------------|----------------------------------|----------------------------------|-------------------------|-------------------------|
| | N ^a | Positive (%) | No. of puparia per fruit | N ^a | Positive for eggs and larvae (%) | No. of eggs per fruit | No. of larvae per fruit |
| Sweet cherry ^b | 15 | 33 ^c | 0.3 \pm 0.1 (86.7B) | 29 | 100A | 8.5 \pm 1.2 (108.2B) | 0.5 \pm 0.2 (89.1B) |
| Kent mango | 20 | 0B | 0 (64.0C) | 21 | 5C | 0 (38.0D) | 0.1 \pm 0.1 (56.3C) |
| Papaya | 23 | 0B | 0 (64.0C) | 16 | 0 ^c | 0 (38.0D) | 0 (53.5C) |
| Black plum | 26 | 73A | 8.9 \pm 1.9 (125.9A) | 26 | 96A | 18.0 \pm 6.0 (104.1B) | 26.6 \pm 7.4 (123.4A) |
| Nectarine | 23 | 48A | 6.2 \pm 3.1 (102.5B) | 23 | 100A | 23.4 \pm 3.9 (132.6A) | 8.9 \pm 4.2 (92.5B) |
| Peach | 32 | 0B | 0 (64.0C) | 21 | 57B | 4.6 \pm 1.9 (73.3C) | 0.9 \pm 0.4 (70.3C) |
| Asian pear | 23 | 0B | 0 (64.0C) | 24 | 12C | 0.6 \pm 0.6 (43.4D) | 1.0 \pm 0.9 (60.2C) |
| χ^2 statistics; df | | 80.51; 5 | 80.55; 6 | | 192.36; 5 | 103.92; 6 | 58.77; 6 |
| Critical χ^2 | | 11.070 | 12.59 | | 11.070 | 12.59 | 12.59 |
| P value | | <0.05 | <0.0001 | | <0.05 | 0.0001 | 0.0001 |

Percentages or ranks inside parentheses within columns followed by the same letter are not significantly different ($P > 0.05$; for % positive, Tukey-type test after test of proportions; for ranks of numbers of puparia and numbers of eggs and larvae, LSD test after Kruskal–Wallis test).

^aN, Number of replicates = containers with 1 fruit each.

^bCherries, 10 per replicate, converted to no. per cherry.

^cNot included in analysis because $n < 20$.

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