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ARTICLE

Comparisons of apple cultivar suitability for *Rhagoletis pomonella* (Diptera: Tephritidae) from Washington State, United States of America

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Abstract

It is unclear whether larval infestations of *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae) in earlier (softer) apple (Rosaceae) cultivars are greater than in later (firmer) apple cultivars in Washington State, United States of America, where flies were introduced and are quarantine pests of apple. Here, a field survey of apples in a noncommercial setting in Washington and experiments testing whether earlier apples are more suitable than later apples for Washington-origin *R. pomonella* were conducted. Early season 'Gala' and 'Golden Delicious', midseason 'Red Delicious', and late-season 'Granny Smith' and 'Fuji' were exposed to flies reared from early and midseason apples in laboratory experiments and to wild flies in apple trees in field experiments. The field survey provided evidence for softer apples being more infested and suitable. Likewise, most of the laboratory and field experimental data showed that 'Gala' and 'Golden Delicious', two of the softer apples tested, produced the most larvae and were most suitable, regardless of whether test apples were conventional or organic and ripe or unripe. To optimise fly trapping protocols in Washington, trapping in early apple trees near 'Gala' and 'Golden Delicious' orchards should be prioritised over trapping near mid- or late-season apple cultivar orchards.

Introduction

The apple maggot fly, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae), evolved in eastern North America on hawthorns, *Crataegus* spp. (Rosaceae), but shifted to cultivated apples, *Malus domestica* Borkhausen (Rosaceae), in the mid-1800s (Bush 1966). Not all apples are equally infested by *R. pomonella*: early maturing, soft-fleshed apple cultivars tend to be more infested than later and firmer apple cultivars (Illingworth 1912; Porter 1928; Dean and Chapman 1973; Neilson 1976; Cameron and Morrison 1977; Reissig 1979).

Rhagoletis pomonella was first detected in western North America in 1979 in Portland, Oregon, United States of America (AliNiazee and Penrose 1981) and in 1980 in Washington State (Washington), United States of America (Brunner 1987), where it attacks apples and hawthorns (Tracewski *et al.* 1987; Hood *et al.* 2013).

Rhagoletis pomonella is a major quarantine pest of apples in the Pacific Northwest of the United States of America, where apples were valued at US$2.14 billion in 2021 (Washington State Department of Agriculture 2023; Northwest Horticultural Council 2023). Although the ecology of

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R. pomonella in the region has been well studied, it is unclear whether flies in Washington infest early apples more than later apples as the flies do in eastern North America. Data from one field site suggested flies in Washington also infest early apples more than later apples, but apples from only a few trees were sampled and the cultivars were not identified (Mattsson *et al.* 2015). Washington and eastern *R. pomonella* prefer different apple volatile blends (Cha *et al.* 2012), so eastern and western flies may have diverged in their ability to develop in early *versus* late apple cultivars.

In central Washington, where the state's commercial apple orchards are concentrated, the Washington State Department of Agriculture deploys traps in apple and hawthorn trees outside orchards to detect *R. pomonella*. By Washington State law, capture of one fly 0.8 km from an orchard prevents the movement of apples from the orchard if apples are not inspected or if they have not undergone 40 or 90 days of chilling (Legal Information Institute 2024) to kill immature fly stages. *Rhagoletis pomonella* occurs at low densities in central Washington, and although no commercial apples there have been reported to be infested (Washington State Department of Agriculture 2023), flies do infest apples of noncommercial trees in that region (Yee 2008), prompting quarantines. Apple trees in backyards, near orchards, and in riparian zones, and apples in unpicked or abandoned orchards (Bush *et al.* 2005; Millman 2012; Brun and Bush 2016; Gross 2020; King 2020; Courtney and Mullinax 2023) are potential fly sources. Predicting whether early or late cultivar trees outside orchards are more likely to be infested could improve efficiency of fly-detection programmes, including decisions on which trees to pay particular attention to and on prioritising protection of the most susceptible apple cultivars. Deploying traps for *R. pomonella* detection purposes only in apple trees that are likely to be infested by flies has been proposed in California, United States of America (Murphy *et al.* 1991) and could be extended to Washington, but identifying the apple cultivars most susceptible to the flies is needed.

Here, a survey was conducted to determine if earlier, softer apples are more heavily infested than later, firmer apples by *R. pomonella* in a noncommercial apple setting in Washington. Experiments were then conducted to test whether commercial, earlier apple cultivars are more suitable (more able to support viable larvae) than later cultivars for Washington-origin *R. pomonella*. Possible proximate causes for results and practical applications of findings are presented.

Materials and methods

Field survey of apples for firmness and larval infestations

Apples of various cultivars fallen from trees within approximately one week at a 0.320-km^2 unsprayed demonstration and educational farm in Hazel Dell in Clark County (45.677029, −122.651332, 73 m above sea level), southwestern Washington State, were collected on 17–19 August 2015 to relate apple firmness to larval infestation levels. Fallen apples produce more larvae than unpicked apples on trees (Illingworth 1912; O'Kane 1914; Dean and Chapman 1973; Bower 1977; Reissig 1979). A batch of 18–46 (mean 32.1) apples under each of 17 replicate trees was collected. Cultivars were 'Gala' (four trees), 'Cider' (one tree), 'Tompkins King' (two trees), 'Golden Delicious' (one tree), 'Gravenstein' (one tree), 'Cox's Orange Pippin' (one tree), 'Winter Banana' (one tree), 'Pacific Rose' (one tree), and unidentified yellow (one tree), red (two trees), and yellow/red (two trees) apples. The weight and firmness of 10 randomly selected apples per batch were recorded. Firmness indicated softness/firmness (Volz *et al.* 2003) and/or skin toughness (Messina and Jones 1990) and was measured using a handheld fruit pressure tester with an 8-mm probe (FT327, Alfonsine, Italy) inserted into the skin. One reading was made on each of the 10 apples, and the readings per batch were averaged. Apples were placed on metal screens in tubs for larvae to emerge over a 30-day period outdoors under shade.

Table 1. Laboratory no-choice experiments (Exp.) conducted to determine suitability of five apple cultivars to Washington State, United States of America-origin *Rhagoletis pomonella*. 'Gala', 'Golden Delicious', 'Red Delicious', 'Granny Smith', and 'Fuji' cultivars were tested, except in Lab Exp. 2, where there was no 'Golden Delicious'. N, replicates or numbers of apples per cultivar; F, female; M, male

Exp.	Apple type, source	Apple cultivar stages	Set up dates	Days exposed	No. flies	No. apples
1	Conventional, store	All ripe	17 Dec 2015 to 1 Feb 2016	31–47 d*	5F, 5M	6
2	Organic, packinghouse	All ripe	10 April to 8 July 2018	37–131 d*	2F, 1M	17, 18
3	Organic; store + research orchard	All ripe†	1 Oct 2018 to 4 April 2019	30 d	2F, 1M	25–30
4	Organic, research orchard	Ripe and unripe‡	18 Aug to 17 Sep 2020	30 d	2F, 1M	31
5	Organic, research orchard	Ripe, unripe§	18 Sep 2023	3 d	3F, 3M	20‖

*Replaced with new apple approximately every 30 days.
†Commercial organic 'Gala', 'Granny Smith', apples from Walmart; 'Golden Delicious', 'Fuji', and 'Red Delicious' picked in season from the United States Department of Agriculture, Agricultural Research Service farm (USDA farm), Moxee, Washington, United States of America; chilled before testing.
‡Picked from the USDA farm in August and September; chilled before testing.
§Picked from the USDA farm on 18 September 2023, not chilled.
‖Half of the replicates were used for larval emergence, and the other half were used for examination of eggs laid.

Table 2. Field choice experiments (Exp) to determine suitability of five apple cultivars to *Rhagoletis pomonella* in noncommercial apple trees in southwestern Washington State, United States of America. 'Gala', 'Golden Delicious', 'Red Delicious', 'Granny Smith', and 'Fuji' cultivars were tested, except in Field Exps. 2 and 7, where 'Red Delicious' and 'Granny Smith', respectively, were not tested. N, replicates or numbers of apples per cultivar

Exp.	Apple type, source	Apple cultivar stages	Dates apples picked	Set up dates	Days exposed	N
1	Conventional, store	All ripe	—	9 July to 1 Aug 2016	20–24	16
2	Conventional, store	All ripe	—	25 July to 8 Aug 2017	17–28	19
3	Conventional, commercial orchard	All ripe	10, 11 July 2018	17 July to 2 Aug 2018	16	25
4	Conventional, commercial orchard	Ripe, unripe	17 July 2018	3 Aug to 4 Sep 2018	32	14
5	Conventional, commercial orchard	Ripe, unripe	27 Aug 2018	5 to 26 Sep 2018	21	25
6	Organic, research orchard	All unripe	28 July 2020	2 to 16 Aug 2020	14	20
7	Organic, research orchard	All unripe	15 Aug 2022	17 to 28 Aug 2022	11	20
8	Organic, research orchard	All unripe	7 Aug 2023	8 to 15 Aug 2023	7	20

Unripe apples are a combination of green colour, small, hard, Brix of roughly < 9%.; others were considered ripe.

Apple cultivars for experiments

Five laboratory no-choice experiments (Lab Exps. 1–5; Table 1) and eight field choice experiments (Field Exps. 1–8; Table 2) were conducted to compare five apple cultivars or a subset of them. The five cultivars, grown commercially in Washington, are (1) early season 'Gala' and 'Golden Delicious' (picked late July to early September); (2) midseason 'Red Delicious' (picked mid to late September); and (3) late-season 'Granny Smith' and 'Fuji' (picked mid to late October).

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Classifications of seasonality vary; here, they are based on Benivia, LLC (2020) and Washington State University (2023). In the Pacific Northwest in 2021/2022, 'Gala' comprised 19.5% of the fresh apple crop; 'Red Delicious', 15.9%; 'Granny Smith', 14.0%; 'Fuji', 12.5 %; and 'Golden Delicious', 3.7 % (Northwest Horticultural Council 2023).

Depending on the experiment, conventional apples, grown commercially for market presumably with use of synthetic pesticides, or organic apples were used (Tables 1 and 2). Conventional apples were store-bought or collected from commercial orchards around Wapato, Washington. Organic apples were obtained from commercial cold storage or stores or were collected off trees from unsprayed orchards at the United States Department of Agriculture, Agricultural Research Service research farm in Moxee, Washington (46.495533, –120.176528, 473 m above sea level), a site with no *R. pomonella*. All five cultivars at the farm were grown within an approximately 0.008-km^2 block or separately in blocks 0.43 ('Gala') km or 0.26 ('Golden Delicious' and 'Red Delicious') km away. No residues of 76 insecticides (analysed by Pacific Agricultural Laboratory, Sherwood, Oregon) were detected in the store-bought organic 'Gala' and 'Granny Smith' used in Lab Exp. 3. Whether conventional or organic, apples were washed with water and dried before testing.

Laboratory no-choice experiments

Flies used in the experiments originated as larvae infesting noncommercial backyard or wild apples in early (late July) to midseason (August) from four sites in Clark and Cowlitz Counties in southwestern Washington (survey site above in Hazel Dell; Vancouver, Clark County: 45.632033, –122.617658, 55 m above sea level; two Woodland sites: 45.940686, –122.672006, 51 m above sea level, and 45.887944, –122.765275, 6 m above sea level). Fly populations in central Washington are too low (Yee 2008; Yee *et al.* 2012, 2023) to provide enough flies for experiments.

Apples were held on hardware mesh screens for larvae to emerge. Puparia were chilled at 3–4 °C for approximately six months and then held at 21–25 °C for adult eclosion. Flies were held at about 20 females to 20 males inside 10.2-cm-high × 16.2-cm-wide paper containers with dry food (20% yeast extract and 80% sucrose) and water and covered with white tulle. Flies were aged for at least two weeks after eclosion before testing.

Five laboratory experiments (Table 1) were conducted over five years to determine if results were repeatable over time. Multiple-year testing resulted in variability in apple sources (see previous section) among experiments. Flies for two laboratory experiments eclosed in the winter and spring, when no field apples were available. In three experiments, puparia were held in chill conditions longer into summer and fall, so that fly eclosion occurred when field apples could be collected for testing.

All laboratory experiments followed the same general protocol and were conducted at a 16:8 hours light:dark photoperiod, 22–27 °C, and approximately 20–70% relative humidity. Aged flies were removed from their holding containers and placed in new containers (same type) that were provisioned with food and water. Female and male flies (see Table 1 for exact numbers) were transferred to test containers. One apple was introduced into each container, except in Lab Exp. 5, where there were two apples. Apple(s) were exposed to flies inside containers for at least 30 days in most experiments (Table 1). Variability in experimental durations was due to amount of time available to monitor experiments. In addition, in Lab Exp. 5, exposure was only three days in order to count eggs laid in apples before they hatched. When all females died, a replicate ended. In Lab Exps. 1 and 2, where exposure was protracted, apples were replaced after approximately 30 days, as long as one female was alive. No differences in female mortality among treatments were observed. For example, in Lab Exp. 5, the percentage of females that had died across the five cultivars 17 days into the experiment ranged from 4.8 to 9.7% and did not differ (test of multiple proportions: $\chi^2 = 2.25$; $df = 4$; $P = 0.6898$).

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Apples were removed from containers after exposure to flies (Table 1). Apples were placed in pails and checked for larval emergence over 42–60 days at 22–27 °C. Apple suitability was measured by numbers of emerged larvae (puparia). In Lab Exp. 5, where there were two apples, larval emergence from one apple and eggs laid into the other (observed by examining the undersides of apple skin under a microscope) were recorded.

For Lab Exp. 4, percent larval emergence from the different cultivars by 30 days *versus* over the entire 90-day period was determined. For Lab Exp. 5, percent larval emergence within the first 31 days of a 45-day larval monitoring period was determined.

Field choice experiments

Aiming for repeatability of results as for laboratory experiments, eight field choice experiments (Table 2) in which apples were exposed to wild flies in the field were conducted over six seasons. Three field experiments were run from July to September 2018 because apples ripened over the course of the approximately two months when flies were present in the field, possibly affecting relative fly responses to them. Test apples were hung in 3- to 8-m-tall and 3- to 9-m-wide wild or backyard apple trees (cultivars unknown except for 'Gravenstein') infested with *R. pomonella* in southwestern Washington. Field Exps. 1 and 2 were conducted in Hazel Dell, Woodland, and Vancouver. Field Exp. 5 was conducted at Saint Cloud Ranch in Skamania County (45.600153, –122.111511, 12 m above sea level). The remaining experiments, Field Exps. 3, 4, and 6–8, were conducted in Woodland.

Apples were hung using green floral wires attached on opposite sides to a 1-cm-wide strip of Velcro wrapped around the middle of each apple. The wires were tied to a binder clip that was secured to a tree branch. Groups of test apples consisted of the five cultivars spaced approximately 10–15 cm apart and were hung within trees, with each group a replicate separated more than 1 m apart from others around a tree's periphery in partial shade. Positions of cultivars within a group were random. One to five replicates were placed in each of 5–14 trees. After a 7- to 28-day exposure, depending on the experiment (Table 2), apples were removed and transported to the laboratory for larval emergence. Exposure durations varied due to labour availability and were longer for Field Exps. 1–4 than for later experiments (Field Exps. 5–8) because it was unclear in the beginning whether flies would attack apples hung in trees in numbers high enough to generate analysable data. It was thought that exposure times needed to be at least a few weeks to increase chances flies would attack the apples. For Field Exp. 1, numbers of unhatched eggs and larvae inside apples rather than larval emergence were recorded.

Apple cultivar traits

Selected traits of representative apples from test batches for Lab Exps. 3, 4, and 5 and Field Exps. 6, 7, and 8 were measured. For all experiments, colour, diameter, and weight were recorded. In addition, except in Field Exp. 6, firmness and Brix of apples were recorded. Firmness was measured as for field survey apples, except up to three recordings (averaged) were taken per apple. Percent Brix was recorded using a handheld refractometer (ATAGO N1, Tokyo, Japan). Depending on the experiment, from 5 to 20 apples were measured.

Statistical analysis

For the field survey to examine apple firmness and larval infestation, correlations between apple firmness (kg/cm^2) and numbers of larvae per apple and gram of apple were calculated using each batch of apples under a tree as one replicate. Apple traits for experiments were analysed using unreplicated block (each experiment) design analysis of variance, followed by Tukey's honestly significant difference test for pairwise comparisons ($P < 0.05$). Data were checked for normality

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using the Kolmogorov–Smirnov D test statistic and for equal variances using the Brown and Forsythe's test of homogeneity of variances in Statistical Analysis System (SAS) software (SAS Institute, Inc. 2009). In one experiment where diameter data for 'Fuji' were not normal, log transformation was applied to normalise the data. All variances were equal. Apple suitability data for Lab Exps. 1, 3, 4, and 5 were analysed using two-way analysis of variance, with experiment and apple cultivar as fixed factors because it was of interest to know whether experiments differed due to differences in apple sources and slight differences in methodologies in each experiment (Table 1), followed by the Tukey test. Data were converted to puparia/apple/female/day (square rooting counts of puparia and females) of exposure before the analysis of variance using SAS software. Field Exp. 2 had four cultivars, so data were analysed separately using the Kruskal–Wallis (rank) test, followed by the Tukey test, on the ranks (not the data themselves; Conover 1980). The test of multiple proportions, followed by Tukey-type comparisons (Zar 1999), was used to determine if there were differences among cultivars in percentages of larvae that emerged during the first 30 days out of a 90-day period (Lab Exp. 4) or during the first 31 days out of a 45-day period (Lab Exp. 5). Means ± standard errors of the means of untransformed data are presented for clarity.

For larval infestation data from the field choice experiments, data from replicates in each experiment were combined to generate enough numbers to compare proportions from each cultivar out of total puparia emerged from all cultivars or out of total eggs and larvae in all cultivars (in Field Exp. 1 only). Data across Field Exps. 1, 3, 4, 5, 6, and 8 were combined and subjected to preference analysis (Sauro and Lewis 2016; Sauro 2023). Proportions of puparia from each of the five cultivars out of total puparia were analysed by computing 95% adjusted (modified) Wald confidence intervals (Lewis and Sauro 2006) around each apple cultivar choice. Overlap in confidence intervals was the criterion for nonsignificance between cultivars. Field Exps. 2 and 7 were missing 'Red Delicious' and 'Granny Smith', respectively, so data from those field experiments were analysed separately, using the same method.

Results

Field survey to examine apple firmness and larval infestation

The mean number of larvae emerged per fallen apple from the Hazel Dell farm was 1.163 ± 0.307 ($n = 17$, all infested). Significant negative correlations occurred between apple firmness (mean: 17.18 ± 1.15 kg/cm^2; range: 9.71–24.40 kg/cm^2) and larvae per apple ($r = -0.7533$; $P = 0.0005$) and larvae per gram of apple ($r = -0.7652$; $P = 0.0003$).

Differences in apple cultivar traits

Apples included in the analysis ranged from unripe and green to ripe and red. Of the four quantified traits, only firmness differed significantly among the five apple cultivars (Table 3). Specifically, 'Granny Smith' was significantly firmer than 'Gala', 'Golden Delicious', and 'Red Delicious' but not firmer than 'Fuji'. 'Gala', 'Golden Delicious', and 'Red Delicious' were the softest cultivars and did not differ.

Laboratory no-choice experiments

Numbers of puparia/apple/female/exposure day in Lab Exps. 1, 3, 4, and 5 differed, but no significant interaction between experiment and apple cultivars (Table 4) was detected, suggesting that experimental details, including year and apple sources, affected numbers of puparia from apples but not trends among apple cultivars across experiments. 'Gala' produced significantly more puparia than 'Red Delicious' did but not significantly more than the other three cultivars

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Table 3. Mean traits ± standard error of mean of five apple cultivars of different ripeness (green, unripe; yellow/red, or red, ripe) representative of apples tested in Lab Exps. 3, 4, and 5 and Field Exps. 6, 7, and 8 for suitability to Washington State, United States of America-origin *Rhagoletis pomonella*

Cultivar	Colour	Diameter (mm)	Weight (g)	Firmness (kg/cm^2)	Brix
'Gala'	Green, red	64.82 ± 2.78	114.23 ± 12.02	15.29 ± 1.61c	11.46 ± 1.32
'Golden Delicious'	Green, yellow/green	65.00 ± 2.88	119.08 ± 12.79	15.43 ± 1.06c	11.51 ± 0.93
'Red Delicious'	Green, red	64.56 ± 3.27	112.66 ± 13.65	17.45 ± 1.78bc	10.90 ± 0.75
'Granny Smith'	Green	63.76 ± 4.09	102.34 ± 12.95	20.01 ± 1.14a	10.51 ± 0.36
'Fuji'	Green, yellow/red	62.06 ± 4.84	106.96 ± 23.13	18.98 ± 1.60ab	11.21 ± 0.91
	ANOVA	$F = 0.84$; $df = 4,20$; $P = 0.5148$	$F = 0.61$; $df = 4,20$; $P = 0.6632$	$F = 10.43$; $df = 4,16$; $P < 0.0001$	$F = 0.93$; $df = 4,16$; $P = 0.4696$

Data were analysed using unreplicated block (= experiment) design analysis of variance (ANOVA), followed by Tukey's honestly significant difference test. Means followed by the same letter are not significantly different ($P > 0.05$). Significant experiment effects occurred ($P < 0.05$).

Table 4. Results of laboratory no-choice experiments, Lab Exps. 1–5, testing the suitability of five apple cultivars to Washington State, United States of America-origin *Rhagoletis pomonella*. N, replicates or numbers of apples per cultivar

Cultivar	N (total)	Apples with larvae (%)	Puparia/apple/female/day ± standard error of the mean	% fewer puparia than highest ranked apple
Lab Exps. 1, 3, 4, 5				
'Gala'	6–31 (77)	88.3a	0.478 ± 0.172a	—
'Golden Delicious'	6–31 (72)	66.7b	0.446 ± 0.2437ab	6.7
'Fuji'	6–31 (76)	77.6ab	0.328 ± 0.140ab	31.4
'Red Delicious'	6–31 (77)	68.8b	0.305 ± 0.164b	36.1
'Granny Smith'	6–31 (77)	70.1b	0.293 ± 0.126ab	38.7
Lab Exp 2				
'Gala'	18	88.9a	0.192 ± 0.031 (49.4a)	—
'Granny Smith'	17	82.4ab	0.102 ± 0.021 (38.9ab)	46.9
'Fuji'	17	47.1b	0.067 ± 0.034 (26.0b)	65.1
'Red Delicious'	18	55.6ab	0.052 ± 0.017 (27.3b)	72.9

Lab Exps. 1, 3, 4, 5: apples with larvae: $\chi^2 = 12.49$; $df = 4$; $P = 0.0140$; puparia/apple/female/day: overall analysis of variance: $F = 36.88$; $df = 19, 359$; $P < 0.0001$; experiment effect: $F = 223.24$; $df = 3, 359$; $P < 0.0001$; puparia/apple/female/day from all except two experiments differed ($P < 0.05$); apple cultivar: $F = 2.88$; $df = 4, 359$; $P = 0.0226$; experiment × apple cultivar: $F = 1.63$; $df = 12, 359$; $P = 0.0817$. Lab Exp 2 apples with larvae: $\chi^2 = 10.01$; $df = 3$; $P = 0.0185$; puparia/apple/female/day: Kruskal–Wallis test: $\chi^2 = 15.965$; $df = 3$; $P = 0.0012$. Apples with larvae (%) or mean puparia/apple/female/day or their ranks (inside parentheses) in Lab Exp. 2 followed by the same letter are not significantly different based on Tukey's honestly significant difference test ($P > 0.05$).

(Table 4). In Lab Exp. 2, where there was no 'Golden Delicious', 'Gala' produced more puparia than 'Fuji' and 'Red Delicious' did but not more than 'Granny Smith' did (Table 4).

In Lab Exps. 4 and 5, larvae from 'Golden Delicious' and 'Gala' emerged earlier than from 'Fuji' and 'Granny Smith'. The timing of larval emergence from 'Red Delicious' occurred in between those of the two sets of cultivars (Table 5). In addition, in Lab Exp. 5, mortality of late-emerging larvae was high. During the last seven days of the 45-day period, 35 of 36 larvae that emerged from 'Red Delicious' (three), 'Granny Smith' (19), and 'Fuji' (13) were dead and shrivelled, measuring

Table 5. Emergence periods of Washington State, United States of America–origin *Rhagoletis pomonella* larvae from different apple cultivars in Lab Exps. 4 and 5

Lab Exp. 4			Lab Exp. 5		
Cultivar	% larvae emerged by 30 days after 30-day exposure	Total larvae emerged over 90 days after first exposure	Cultivar	% larvae emerged by 31 days after 3-day exposure	Total larvae emerged over 45 days after first exposure
'Gala'	43.2a	956	'Golden Delicious'	98.9a	95
'Golden Delicious'	36.9b	1178	'Gala'	98.8a	84
'Red Delicious'	33.3bc	642	'Red Delicious'	88.2b	68
'Granny Smith'	28.4c	721	'Fuji'	33.9c	59
'Fuji'	25.4c	852	'Granny Smith'	27.8c	54
Statistics*	$\chi^2 = 78.91$; $df = 4$; $P < 0.0001$		Statistics*	$\chi^2 = 180.84$; $df = 4$; $P < 0.0001$	

*Test of multiple proportions followed by Tukey-type multiple comparisons. Percentages within experiments followed by the same letter are not significantly different.

Table 6. Lab Exp. 5 – Mean number of eggs laid ± standard error of mean by Washington State-origin *Rhagoletis pomonella* flies (three females; mean ranks from Kruskall–Wallis test inside parentheses) into different apple cultivars over a 3-day exposure under no-choice conditions. N, replicates or numbers of apples per cultivar

Cultivar	N	Apples with eggs (%)	Eggs/apple	% fewer than highest
'Gala'	10	90	20.900 ± 3.831 (31.4)	—
'Fuji'	10	80	19.300 ± 5.445 (27.4)	7.7
'Golden' Delicious'	10	90	17.600 ± 3.670 (28.2)	15.8
'Red Delicious'	10	100	12.20 ± 3.258 (21.3)	41.6
'Granny Smith'	10	90	10.900 ± 2.693 (19.3)	47.8

$\chi^2 = 4.81$; $df = 4$; $P = 0.3074$.

Table 7. Results of field choice experiments (Field Exps.) 1, 3, 4, 5, 6, and 8 (combined data) testing the suitability of five apple cultivars to wild *Rhagoletis pomonella* in noncommercial apple trees in southwestern Washington State, United States of America

Cultivar	No. apples	% of total puparia (95% confidence interval)*	% fewer puparia than highest ranked apple
'Gala'	120	45.5a (41.0, 50.2)	—
'Golden Delicious'	120	22.2b (18.6, 26.3)	51.2
'Fuji'	120	11.7c (9.0, 15.0)	74.3
'Granny Smith'	120	11.2c (8.6, 14.5)	75.4
'Red Delicious'	120	9.4c (7.0, 12.5)	79.3
Total puparia		446	

*% of total eggs and larvae in apples was determined in Field Exp. 1; equated to percentage of total puparia as a measure of fly preference in this analysis. Percentages followed by the same letter are not significantly different ($P > 0.05$), based on overlap of 95% adjusted Wald confidence intervals (Sauro and Lewis 2016) shown inside parentheses.

only 3–3.5 mm long (normal larvae are ~7 mm long). Only one larva, from 'Granny Smith', pupariated. Dead/shrivelled larvae were not seen among earlier emergers. Live and dead larvae in other experiments were not recorded.

In Lab Exp. 5, high variability in number of eggs laid across the 10 replicates within each cultivar was observed (*e.g.*, 0–36 eggs per 'Gala' replicate), and no significant differences were detected among cultivars (Table 6).

Field choice experiments

In Field Exps. 1, 3, 4, 5, 6, and 8, percentage of total puparia was greatest from 'Gala', followed by 'Golden Delicious' and then by the other three cultivars, which did not differ from each other (Table 7). In Field Exp. 2, where there was no 'Red Delicious', percentage of total puparia was greatest from 'Gala', followed by 'Granny Smith' and then by 'Golden Delicious' and 'Fuji' (Table 8). In Field Exp. 7, where there was no 'Granny Smith', percentage of total puparia was again greatest from 'Gala', followed by 'Golden Delicious' and then by 'Red Delicious' and 'Fuji' (Table 8).

Table 8. Results of field choice experiments (Field Exp) 2 and 7 testing the suitability of apple cultivars to wild *Rhagoletis pomonella* in noncommercial apple trees in southwestern Washington State, United States of America

Cultivar	No. apples	% of total puparia (95% confidence intervals)	% fewer puparia than highest ranked apple
Field Exp. 2			
'Gala'	19	62.8a (57.4, 67.9)	–
'Granny Smith'	19	17.7b (13.8, 22.3)	71.8
'Golden Delicious'	19	9.8c (6.9, 13.6)	84.4
'Fuji'	19	9.8c (6.9, 13.6)	84.4
Total puparia		317	
Field Exp. 7			
'Gala'	20	41.8a (35.6, 48.2)	–
'Golden Delicious'	20	29.3b (23.8, 35.5)	29.9
'Red Delicious'	20	16.4c (12.1, 21.7)	60.8
'Fuji'	20	12.5c (8.8, 17.4)	70.1
Total puparia		232	

Percentages followed by the same letter are not significantly different ($P > 0.05$), based on overlap of 95% adjusted Wald confidence intervals (Sauro and Lewis 2016) shown inside parentheses.

Discussion

Significant negative correlations between apple firmness and infestations (per apple and per gram of apple) by *R. pomonella* were detected in the field survey, suggesting that at at least one southwestern Washington site, early apples are more infested than later apples. This supports findings from early and late apples picked off trees (18 July to 14 August) at a nearby site (Mattsson *et al.* 2015). Apples here were picked up to a week after their falling, so some larvae may have left fruit before collections. However, larvae would have emerged from softer apples sooner than they did from the firmer apples (*e.g.*, the correlation between number of days in fruit and apple firmness was $r = 0.647$, $P < 0.01$; Dean and Chapman 1973), making our negative correlations even stronger. Also, all apples had fallen by 17–19 August, so apples were mostly early to midseason cultivars, other than 'Winter Banana' and 'Pacific Rose'. Inclusion of more late cultivars might have strengthened correlations between apple firmness and infestations.

Despite the differences in apple sources and variations in methodologies within laboratory and field studies, trends observed across the experiments in the present study did not differ, validating the results. Consistent with the field survey, laboratory and field experimental results suggest that softer, earlier apple cultivars are more suitable than later apples for Washington-origin *R. pomonella*. Results were clearer when flies chose which cultivars to attack in the field than when exposures to apples were forced in the laboratory, because, as Fitt (1986) reported, under confined conditions, tephritid flies may attack fruit that they do not attack in nature. Results imply early/midseason phenotypes of Washington flies have not diverged from eastern North America and Utah flies (Illingworth 1912; Dean and Chapman 1973; Messina and Jones 1990) with respect to greater larval development in some early apple cultivars compared to midseason and late cultivars. The trait of developing better in softer than in firmer apples may be rigid across *R. pomonella* populations in North America, unlike the odour preference trait of adult apple-origin flies (Cha *et al.* 2012).

The flesh of 'Gala' (Volz *et al.* 2003; Ng *et al.* 2013) and 'Golden Delicious', two of the least-firm cultivars tested in the present study, softens rapidly during development, making it conducive to high larval survival (Porter 1928; Cameron and Morrison 1977). Larvae also developed more quickly and survived better in 'Gala' and 'Golden Delicious' than in firmer 'Granny Smith' and 'Fuji', consistent with other cultivars for eastern *R. pomonella*, in which percent larval survival and firmness of 20 apple cultivars was negatively correlated (Dean and Chapman 1973). The Queensland fruit fly, *Bactrocera tryoni* (Froggatt), also survived poorly (44.9–90.8% larval mortality) in 'Granny Smith' (Bower 1977).

What factors other than firmness affect survival of larval *R. pomonella* remain unclear. Dean and Chapman (1973) showed that percent larval survival of eastern *R. pomonella* was negatively and significantly correlated with percent sucrose but was not significantly correlated with pH, percent reducing sugars, and percent total sugars. Other chemical factors may play a role in apple suitability. Although there are numerous compounds in apples (Arnold and Gramza-Michalowska 2023), secondary compounds could reduce growth rates of or are toxic to tephritid larvae (Fitt 1986). Specifically, differences in amounts of phenolic compounds could affect fruit suitability to fly larvae.

Phenolic compounds added to larval diet reduced survival of larval olive fruit fly *Bactrocera oleae* (Rossi) (Manoukas 1993), whereas high total phenolic content in apples was correlated with reduced egg or larval survival in the Mexican fruit fly, *Anastrepha ludens* (Loew) (Aluja *et al.* 2014). 'Gala' and 'Golden Delicious' had a total phenolic content of 1.21–1.25 g/kg, the lowest of 12 cultivars tested, whereas 'Fuji' had 1.39 g/kg. Correspondingly, 'Fuji' had 40 times fewer *A. ludens* larvae than 'Gala' and 'Golden Delicious' did (Aluja *et al.* 2014). 'Granny Smith' had a total phenolic content (mg GAE/100 g freeze-dried material) of 581.0 whereas 'Golden Delicious' had a content of 521.9 (Kschonsek *et al.* 2018). Whether the 11% additional phenolics in 'Granny Smith' is sufficient to reduce survival of *R. pomonella* larvae remains to be studied, but the phenolic content was only 11–15% greater in 'Fuji' than in 'Gala' and 'Golden Delicious' in the *A. ludens* study (Aluja *et al.* 2014). Fly egg hatch rates can also be reduced by polyphenolic extracts (Di Ilio and Cristofaro 2021).

Whether *R. pomonella* prefers softer, earlier apples because they are more suitable for larvae than firmer apples are is unclear because puncture frequency in early apple cultivars does not appear related to percent larval survival in eastern North America flies (Dean and Chapman 1973). Similarly, in the present study, albeit under no-choice conditions, there was no statistical difference in eggs laid in 'Gala' *versus* in the other cultivars, although this result is inconclusive due to low sample size. In choice tests, eastern North America *R. pomonella* accepted 'Gala' for boring in greater proportions than they did 'Red Delicious' and 'Fuji' (Rull and Prokopy 2004), indicating cultivar preferences may exist. *Anastrepha ludens* eggs per clutch laid in 'Gala' and 'Golden Delicious' did not differ from that in 'Fuji', but 'Fuji' produced fewer puparia (Aluja *et al.* 2014), implying no preference but lower egg and/or larval survival in 'Fuji'. Whether such an oviposition–larval development relationship exists for *R. pomonella* in 'Fuji' *versus* other cultivar remains to be seen.

The possibility that late-eclosing phenotype *R. pomonella* attacking late apples in western Washington (Mattsson *et al.* 2015; Yee *et al.* 2021) can develop equally well in early, mid-, and late-season apples was not explored. Because larvae develop in firm apples, fly populations may be able to adapt and specialise on these apples, leading to the formation of a late apple cultivar host race. However, there is currently no evidence that late-season phenotype flies exist in central Washington.

The results presented here have implications for management of *R. pomonella* in central Washington. The Washington State Department of Agriculture conducts *R. pomonella* trapping surveys to protect commercial apple orchards from fly infestation in central Washington at a cost of approximately $USD 800 thousand/year. In 2019–2022, the department deployed traps in 372–570 noncommercial apple trees, with fewer than 10% of trees having at least one fly caught

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(Yee *et al.* 2023). To optimise fly trapping protocols in central Washington given the low fly densities there, trapping in early apple cultivar trees should be prioritised over trapping in later apple cultivar trees, which are less likely to be infested by flies. In addition, trapping in early cultivar trees near orchards of 'Gala' and 'Golden Delicious' or other early cultivars should be prioritised over such trapping near orchards of midseason or late apple cultivars to reduce the numbers of traps needed. The exact trap numbers needed can be obtained by counting how many early *versus* late cultivar apple trees are near the orchards. Such a trapping approach by state and county regulatory agencies could help reduce labour and costs of apple pest management in central Washington.

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