A review of fruiting plant species as potential dead-end hosts of *Drosophila suzukii*

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1. Objective of the review

Drosophila suzukii, commonly known as spotted wing drosophila (SWD) is an invasive pest that lays its eggs in healthy soft fruit and cherries, rendering them unmarketable. SWD has a very wide host range, including many non-crop plant species; however, there is evidence to suggest variation in host suitability, with some hosts slowing or preventing the development of SWD eggs [1, 2, 3].

The objective of this review was to identify plant species that may act as dead-end hosts for the eggs/larvae of SWD. The review was undertaken by Sam Ardin who worked with the AHDB as an intern in 2017. She examined a number of scientific papers on the subject, identified a list of potential dead-end hosts which could be grown in the UK and ranked their potential efficacy using a method promoted by one of the paper authors.

Fruit of these plants should:

- Be attractive to female *D. suzukii* (preferably more so than the crop fruit)
- Prevent the development of *D. suzukii* eggs to adulthood, either through toxicity or lack of resources
- Have a suitable hardiness and growth habit in the UK
- Have a suitable phenology, such that the fruiting period overlaps with that of the crop

2. Identifying potential UK hosts

127 plant species across 57 genera were identified as SWD hosts either in field or laboratory studies across Japan [4, 5, 6, 7, 8], North America [1, 9, 10] and Europe [11, 12, 13].

3. Combining evidence to give an overall score

3.1. Method

Numerous studies have considered SWD host properties but each study has a different scope and method. A challenge when trying to combine such studies is finding a way to consolidate the evidence so different hosts can be objectively compared. To this end, a method was adopted similar to Bellamy et al. (2013) [14]. For each piece of available evidence on host attractiveness and/or development, plants were given a score based on the rank of the plant within the specific trial and the number of plants scoring in the trial (see Table 1).

Table 1. A simplified guide to the scoring system used. Please see [14] for details

		Plant's rank in study	
		Low	High
Host plants in study	Few	Low to medium Score	Medium to high score
	Many	Low score	High score

This scoring was repeated for each piece of evidence (note that a single study can contain multiple pieces of evidence) and averaged the appropriate scores to form a single 'attractiveness' score, a single 'development' score and a single 'emergence' score (Table 2).

Table 2. Overview of the three summary scores

Score	**Evidence type**	**Dead-end host=**
Attractiveness	Evidence that directly evaluates host attractiveness to gravid SWD females	As high as possible
Development	Evidence that directly evaluates SWD egg development in the host	As high as possible
Emergence	Evidence that evaluates rates of SWD emergence without an idea of initial infestation	As high as possible

3.2. Results

There was variation in the attractiveness of hosts and their suitability as SWD hosts. The hosts pictured in Figure 1 below all demonstrated high attractiveness and low egg development.

Figure 1. Hosts which demonstrate high attractiveness and low egg development

Figures 2 and 3 chart the relative attractiveness of a range of host plant berry species against the development of SWD in the berry. Those species in the shaded box have greatest potential to contribute towards SWD control. In Figure 3, the size of the point is proportional to the rate of SWD emergence from the berry. The species with the small points have lower emergence, therefore offering better potential for controlling SWD.

Figure 2. The attractiveness and development scores for each host plant. Each attribute is scored based on the host's ranking across all available literature (see section 3 for details). The shaded box highlights hosts in the upper quartile of SWD attractiveness and the lower quartile of SWD development; these plants have the greatest potential to contribute towards SWD control. The size of the point is proportional to the amount of evidence available for that host, such that the positioning of larger points is more certain

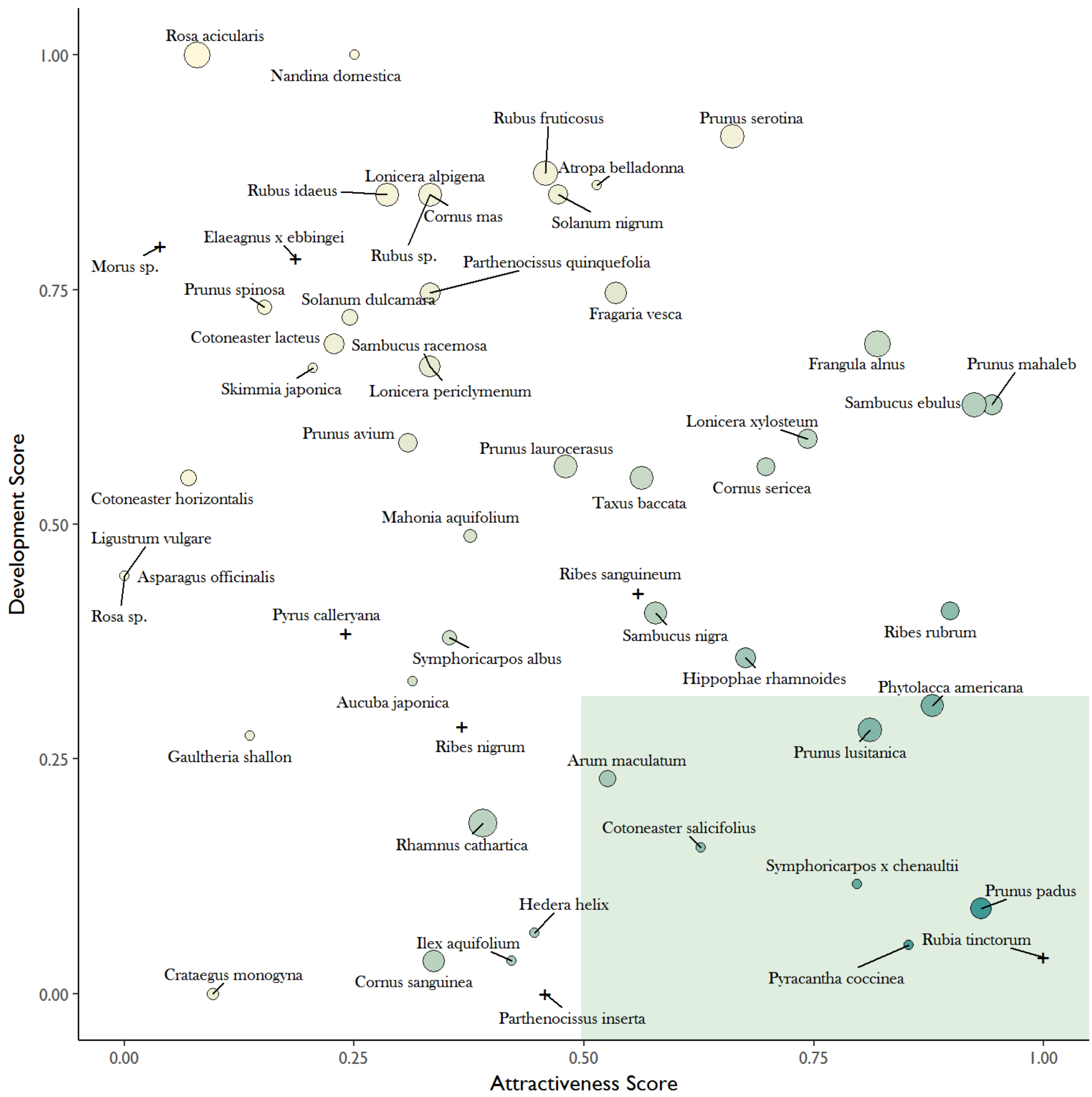

Figure 3. As for Figure 2, except the size of the point illustrates the emergence score for each plant. The bigger the point, the more adult SWD emerge from fruits exposed to SWD either in the field or lab (+ symbols indicate that no such data is available)

4. A review of key studies

This section reviews the potential of the eight most promising dead-end hosts. It describes the most informative studies before summarising all the available evidence for each shortlisted host.

4.1. Host attractiveness

These lab-based studies measure how readily SWD females oviposit in the host with no alternative host present (eg [2, 3]). Typically, these studies comprise a series of trials in which picked fruits of an individual host plant are exposed to a given number of gravid SWD females for a set time. With the use of a microscope and/or fruit dissection, the number of egg filaments can be counted.

Key study

Poyet et al. (2015) [3] sampled fleshy fruit of 67 plant species in France before counting the eggs laid in each fruit after a 24 hour period of exposure to 3 gravid SWD females. Per fruit volume, most eggs were laid in Prunus padus, Phytolacca americana, Prunus mahaleb, Rubia tinctorum, Ribes rubrum and Sambucus ebulus. Figure 3 illustrates the performance of the shortlisted dead-end hosts, relative to blackberry and raspberry.

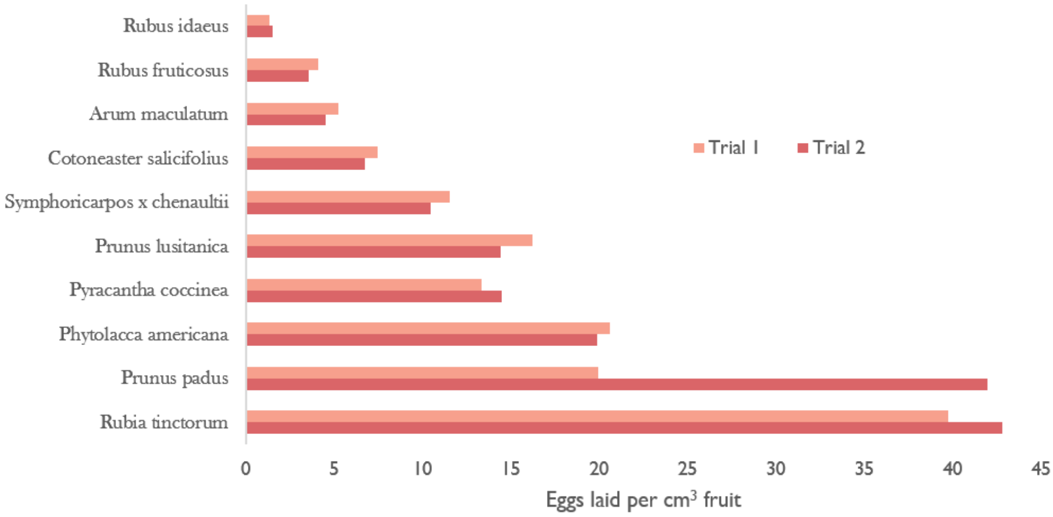

Figure 4. The average number of SWD eggs laid per cm^3 of fruit after exposure to 3 mated SWD females for 24 hours [3]

Limitations

These studies can only evaluate the preference of SWD under very specific conditions. It is not possible to tell how attractiveness might vary over different geographical scales, against different backgrounds or when multiple hosts are present. Furthermore, some evidence suggests that female SWD host preference is influenced by the host in which that SWD developed [15].

4.2. SWD development in the host

These studies capture some measure of how well SWD eggs can develop in different hosts. Typically, these studies comprise two phases: the number of eggs in a fruit are counted then, after a period of development in the lab, a count of the number of developing larvae or emerged SWD adults can be used to calculate percentage SWD survival.

Key study

Poyet et al. (2015) [3] counted the number of eggs laid in a range of lab-infested hosts before tracking the number of eggs that developed into larvae and adults. Several species had low or zero levels of SWD development (Figure 5).

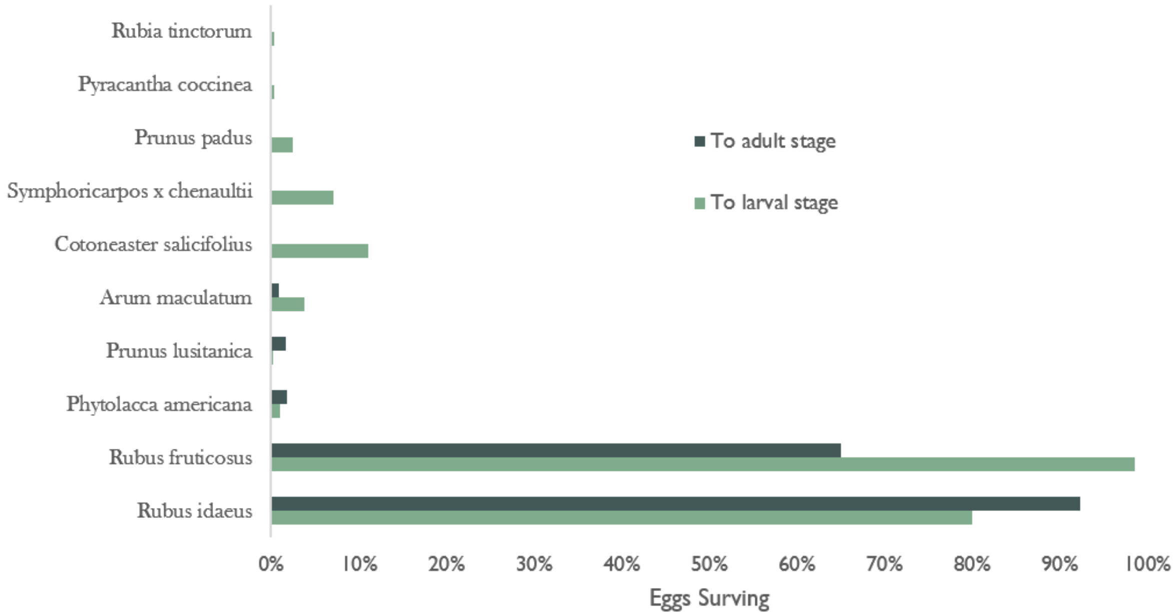

Figure 5. The percentage of SWD eggs surviving to larval and adult stages in different potential dead-end hosts [3]

Limitations

The rate at which fruits lose their vitality once removed from the plant is likely to vary based on fruit properties such as firmness, size and ripeness. This variability might have influenced the survival of SWD eggs reared under lab conditions, with the quality of some hosts degrading more rapidly.

4.3. Adult emergence from wild-collected hosts

In these studies, the fruit of potential host plants are collected from regions with active SWD populations in order to count the number of emerging SWD adults [12, 13], without taking any measure of the number of eggs laid in the host. These studies typically screen large numbers of plants for their suitability as hosts and hence provide an important overview of SWD host use.

Key study

Kenis et al. (2016) [13], reared SWD adults from wild host fruit collected from sites with known SWD presence. No SWD adult emerged from *C.salicifolius*, *S.x chenaultii* or *P.coccinea* whilst SWD adults did emerge from *P.padus*, *P.americana* and *P.lusitanica* (Figure 6). *R.tinctorum* and *A.maculatum* were not included in the study.

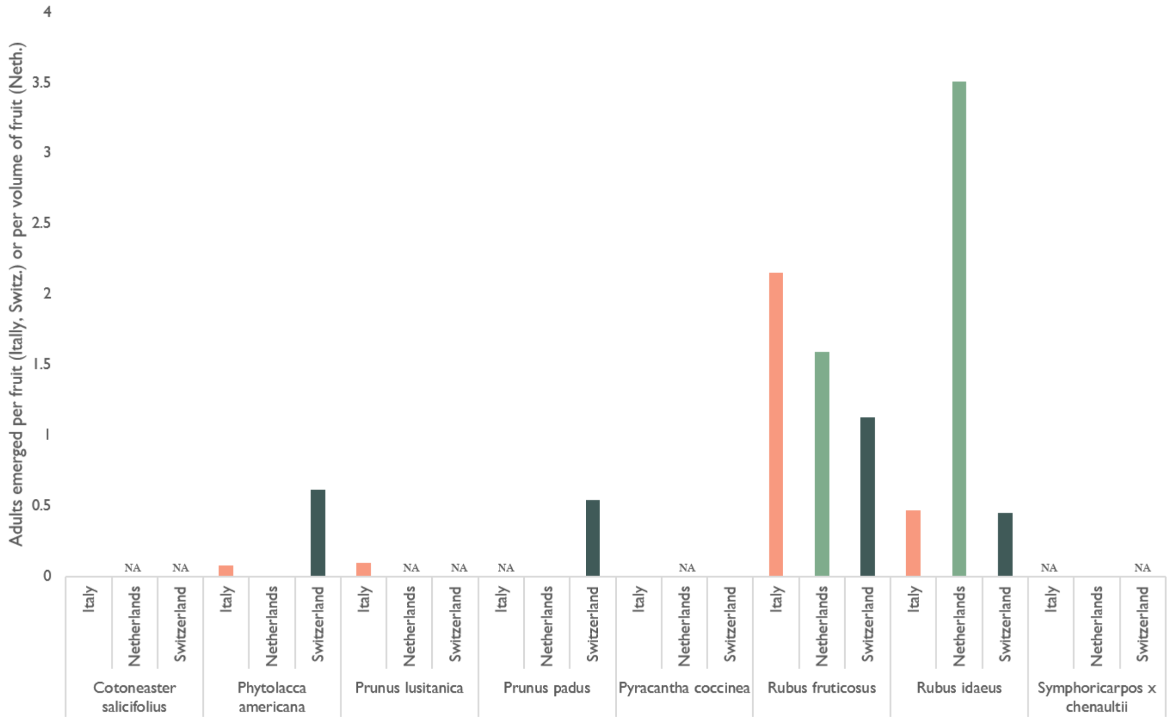

Figure 6. The number of SWD emerged per number (Italy and Switzerland) or volume (Nether- lands) of fruit collected from sites with SWD present [13]. 'NA' indicates that the plant was not surveyed in that country

Limitations

Collecting such a wide breadth of plant species necessitates a wide range of sample sites, both within and across studies. Differences in the size and activity of SWD populations across the different sites may have greatly influenced the initial infestation rate, and hence the number of emerging SWD. Furthermore, it is impossible to disentangle the effects of host attractiveness and SWD development in the host (ie a host with very few emerging SWD could either be very unattractive to SWD, such that very few eggs were laid in that host, or could be highly attractive but very poor for SWD development).

4.4. Adult emergence from lab-infested hosts

In these studies [16, 1, 12], fruit are exposed to controlled infestation regimes in the lab in order to count the number of developing SWD larvae and/or SWD adults for each host.

Key study

These studies did not include many of the shortlisted plants. However, the SF 145 project trials [17] found that no SWD adults emerged from Pyracantha sp. infested in the lab (however, the specific Pyracantha species tested is not detailed).

Limitations

Whilst this approach ensures consistent SWD exposure, in a way that is impossible when rearing SWD from wild-collected hosts, these studies are still unable to disentangle the relative effects of host attractiveness and SWD development success.

5. Summary of evidence for shortlisted plants

Table 3 lists notes on the suitability of the most promising dead-end hosts.

Table 3. Evidence for the suitability of the eight most promising dead-end hosts

Plant	Notes on suitability		
Pyracantha coccinea (Scarlet firethorn)	Attractiveness	[3]	Mean number of eggs per fruit was 2.5 after 24 hours of exposure to 3 mated females. This is equivalent to 14 eggs per cm^3 of fruit (approx), 10 and 4 times more than was laid in raspberry and blackberry, respectively.
	Development	[3]	In two separate lab trials, < 1% of eggs reached larval stage and 0% of eggs reached adult stage, compared to 99% and 65% in blackberry.
	Emergence	[13]	SWD did not emerge from *P. coccinea* collected from sites in Italy or the Netherlands where SWD populations were present.
Prunus padus (Bird cherry)	Attractiveness	[3]	Mean number of eggs per fruit was 6.1 after 24 hours of exposure to 3 mated females. This is equivalent to 31 eggs per cm^3 of fruit (approx), 22 and 8 times more than was laid in raspberry and blackberry, respectively.
	Development	[3]	In two separate lab trials, 2.4% of eggs reached larval stage and 0% of eggs reached adult stage, compared to 99% and 65% in blackberry.
	Emergence	[13]	SWD emerged from 67% of samples collected. From samples collect adults emerged per cm^3 compared to 0.4 and 0.2 adults from blackberry and raspberry, respectively. From samples collected in the Netherlands, an average of < 0.001 SWD adults emerged per cm^3 compared to 1.6 and 3.5 adults from blackberry and raspberry, respectively.

Continued...

Plant	Notes on suitability		
Rubia tinctorum (Dyer's madder)	Attractiveness	[3]	Mean number of eggs per fruit was 2.7 after 24 hours of exposure to 3 mated females. This is equivalent to 41 eggs per cm^3 of fruit (approx), 29 and 11 times more than was laid in raspberry and blackberry, respectively.
	Development	[3]	In two separate lab trials, < 1% of eggs reached larval stage and 0% of eggs reached adult stage, compared to 99% and 65% in blackberry.
Symphorica-rpos* x *chenaultii (Chenault coralberry)	Attractiveness	[3]	Mean number of eggs per fruit was 3.0 after 24 hours of exposure to 3 mated females. This is equivalent to 11 eggs per cm^3 of fruit (approx), 8 and 3 times more than was laid in raspberry and blackberry, respectively.
	Development	[3]	In two separate lab trials, 7% of eggs reached larval stage and 0% of eggs reached adult stage, compared to 99% and 65% in blackberry.
	Emergence	[13]	SWD did not emerge from *S.* x *chenaultii* collected from sites in the Netherlands where SWD populations were present.
Cotoneaster salicifolius (Willowleaf cotoneaster)	Attractiveness	[3]	Mean number of eggs per fruit was 1.9 after 24 hours of exposure to 3 mated females. This is equivalent to 7 eggs per cm^3 of fruit (approx), 5 and 2 times more than was laid in raspberry and blackberry, respectively.
	Development	3]	In two separate lab trials, 11.1% of eggs reached larval stage and 0% of eggs reached adult stage, compared to 99% and 65% in blackberry.
	Emergence	[13]	SWD was not found in *C. salicifolia* across two years in a site where 0.7 and 0.2 SWD emerged per cm^3 of blackberry and raspberry collected, respectively.
Arum maculatum (Lords and ladies)	Attractiveness	[3]	Mean number of eggs per fruit was 5.6 after 24 hours of exposure to 3 mated females. This is equivalent to 4.9 eggs per cm^3 of fruit (approx), 3.4 and 1.3 times more than was laid in raspberry and blackberry, respectively.
	Development	[3]	In two separate lab trials, 4% of eggs reached larval stage and 0.8% of eggs reached adult stage, compared to 99% and 65% in blackberry.
	Emergence	[2] [16]	*A. maculatum* is ranked as a 'poor'' host (1 on a scale of 0-4) following lab infestation. A single individual emerged from samples of *A. maculatum*, although the total number of fruit collected is not stated.

Continued...

Plant	Notes on suitability		
Prunus lusitanica (Portugal laurel)	Attractiveness	[1]	In lab trials, > 2 times as many eggs were laid per cm^3 of fruit than the average across all hosts.
		[3]	Mean number of eggs per fruit was 5.9 after 24 hours of exposure to 3 mated females. This is equivalent to 15 eggs per cm^3 of fruit (approx), 11 and 4 times more than was laid in raspberry and blackberry, respectively.
	Development	[1]	0% of eggs developed to larvae after lab infestation (the presence of eggs was confirmed).
		[3]	In two separate lab trials, < 1% of eggs reached larval stage and 2% of eggs reached adult stage, compared to 99% and 65% in blackberry.
	Emergence	[1]	SWD adults emerged from 19% of fruits collected from areas with SWD present.
		[13]	SWD emerged from 100% of samples collected in Italy. An average of 0.16 SWD adults emerged per cm^3 of fruit versus 0.7 and 0.2 adults from blackberry and raspberry, respectively.
Phytolacca Americana (Pokeberry)	Attractiveness	[2]	*P. Americana* is ranked as 'very attractive' (2 on a scale of 0-2), but no method is given so it is unclear what this means.
		[3]	Mean number of eggs per fruit was 10.6 after 24 hours of exposure to 3 mated females. This is equivalent to 20 eggs per cm^3 of fruit (approx), 14 and 5 times more than was laid in raspberry and blackberry, respectively.
	Development	[3]	In two separate lab trials, 1% of eggs reached larval stage and 2% of eggs reached adult stage, compared to 99% and 65% in blackberry.
	Emergence	[1]	SWD emerged from 74% of fruits collected from areas with SWD present.
		[2]	*P. americana* is ranked as an 'adequate' host (2 on a scale of 0-4) following lab infestation.
		[13]	SWD emerged from 100% of samples collected in Italy and Switzerland in 2014. No SWD adults emerged from samples collected from Italy in 2015 or the Netherlands in 2014. An average of 0.15 and1.2 SWD adults emerged per cm^3 of fruit collected in Italy and Switzerland, respectively (compared to 0.7/0.4 from blackberry and 0.2/0.21 from raspberry).
		[15]	SWD females emerging from *P. americana* preferred to oviposit into blackberries, while females emerging from blackberry had no preference. SWD that developed in *P. americana* berries were less fit than those developed in blackberries (based on several measures).
		[16]	*P. americana* is ranked as an 'adequate' host (2 on a scale of 0-4) as only small numbers of SWD adults emerged from lab infested hosts (not quantified).

6. Other considerations

6.1. Phenology

Figure 7 illustrates the relative timing of berry production of the eight most promising dead-end hosts compared to the highly susceptible commercial fruit crops.

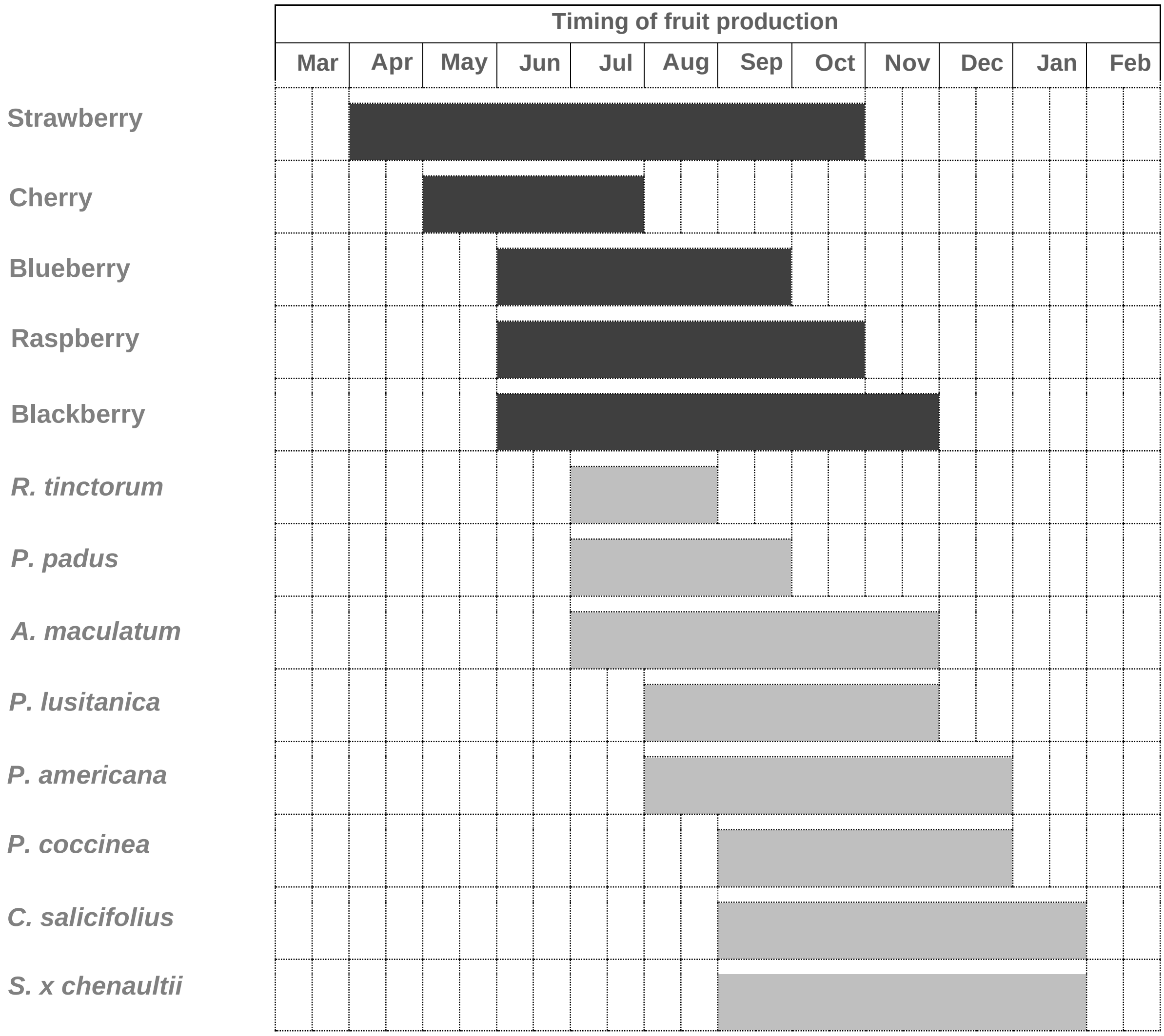

Figure 7. The fruiting phenology of potential dead-end host plants (pale grey) relative to common crops (dark grey). Note that several factors will affect the persistence of host fruits through the winter, including the popularity of the fruit with birds and mammals, pruning regimes and the weather

6.2. Growing in the UK

Table 4 provides guidance on the host plant's suitability for growing in the UK.

Table 4. The suitability of growing the eight most promising dead-end hosts in the UK

Plant	Native to	UK Status	Hardiness
A. maculatum	Europe	Native	Hardy in the severest European continental climates (< -20^{o}C)
P. padus	Europe Parts of Asia		Hardy in all of UK and northern Europe (-20 to -15^{o}C)
P. lusitanica	Iberian peninsula		
P. coccinea	Asia-Temperate S and E Europe	Non-native	Hardy in the severest European continental climates (< -20^{o}C)
P. Americana	USA		
S. x chenaultii	N and C America		
C. salicifolius	China		Hardy in all of UK and northern Europe (-20 to -15^{o}C)
R. tinctorum	Asia-Temperate		

6.3. Birds: the double-edged sword

It is important to note that the introduction of additional fruiting plants into a habitat may promote bird populations. Of the above shortlisted plants, *P. coccinea, P. lusitanica* and *P. padus* are popular with birds. *P. americana* is popular with American birds, which might extrapolate to UK birds. For many fruit growers, increasing bird populations would be highly undesirable, as birds can steal and damage the crop. In this case, it might be prudent to focus on potential dead-end hosts that are not desirable to birds, such as *R. tinctorum, A. maculatum* and, possibly, *C. salicifolius, P. laurocerasus* and *S. x chenaultii* (although these are sometimes eaten by birds).

Conversely, birds might be important natural enemies of SWD, consuming wild fruit in which SWD eggs and larvae are developing. In particular, they may act to reduce residual SWD populations in the cooler late-autumn and winter months in which berries form a predominant part of many birds' diets (although this relationship has not been studied). In situations where the crop is routinely protected by netting, the efficacy of dead-end hosts might be increased if they are desirable to both SWD and local bird populations. As such, planting bird-desirable dead-end hosts might be an effective strategy to use alongside SWD netting.

7. Conclusions

Several plant species have shown potential as dead-end hosts during mid- and late-season soft fruit production periods. In particular, *Rubia tinctorum* (Dyer's madder), *Prunus padus* (Bird cherry), *Arum maculatum* (Lords and ladies), *Prunus lusitanica* (Portugal laurel), *Phytolacca Americana* (Pokeberry), *Pyracantha coccinea* (Scarlet firethorn), *Cotoneaster salicifolius* (Willowleaf cotoneaster) and *Symphoricarpos x chenaultii* (Chenault coralberry) are attractive to SWD but do not offer suitable conditions for the development of SWD eggs. When used alongside SWD netting of the crop, the use of dead-end host planting could be further supported by natural bird populations which might consume ripe dead-end fruit.

However, it remains unclear how SWD preference and development might change in different contexts. Further research needs to be done to ascertain:

- How the environmental conditions and life history experienced by SWD, influences attraction towards and development in different hosts.
- How SWD preference is affected when there is a choice of hosts.
- How genetic variation between different SWD and host populations influences SWD:host interactions.

Without this understanding, it is hard to predict how the inclusion of a particular 'dead-end host' might influence long term dynamics of SWD populations.

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