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Year-round trap capture of the spotted-wing drosophila, *Drosophila suzukii* (Diptera: Drosophilidae), in Korean strawberry greenhouses

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ABSTRACT

Korean greenhouse strawberries are mostly cultivated from October to May, which includes the cold winter season. During this time, the population size of the spotted-wing drosophila (SWD), *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), is expected to decrease in the wild, and is also expected to decrease inside the greenhouses, as long as SWD are not already present inside. Field surveys of SWD have been extensively carried out for field-grown agricultural fruits, but no study has been conducted for greenhouse fruits, such as strawberries. In this study, SWD capture patterns were examined inside and outside of the greenhouse blocks, and in the nearby woodlands in a southwestern locality of Korea using selected traps and attractants for nearly 19 months—in addition to several greenhouse blocks—during the strawberry cultivating periods. The highest capture period was observed from October to mid-December in woodlands, whereas capture number subsequently and sharply decreased up to mid-April, resulting in mostly zero-captures or low captures (≤10). During this period, a zero-capture period was observed inside the greenhouse that lasted for nearly three months (late December to late February). An incubation of the fallen strawberries supported the results of trap capture from inside the greenhouses. Taken together, the occurrence of SWD in the strawberry greenhouses is likely to be highly dependent on that of the nearby woodlands. Thus, a sharp winter drop and the subsequent zero- or low-capture periods in the woodland areas were likely responsible for the observed zero-capture periods inside the greenhouses.

Introduction

Drosophila suzukii (SWD) Matsumura (Diptera: Drosophilidae) is endemic to Asia and has invaded multiple countries, resulting a significant damage to agricultural crops, so studies on the species—with diverse perspectives—especially damage to agricultural crops have been investigated (Kanzawa, 1935, 1939; Bolda et al., 2010; Isaacs, 2011; Lee et al., 2011; Calabria et al., 2012; Cini et al., 2012; Tait et al., 2018). In particular, SWD field monitoring has been implemented in both cultivated areas and in regions outside agricultural areas to understand SWD population dynamics from the perspective of the relationships between agricultural fields and natural environments like woodlands (Pelton et al., 2016; Cahenzli et al., 2018). For example, SWD captures in agricultural crops have been reported to be heavily influenced by the distance from the woodlands as well as woodland size (Pelton et al., 2016; Cahenzli et al., 2018).

Overwintering capacity and winter population dynamics of SWD have also been studied to understand the changes in population under cold temperature conditions (Dalton et al., 2011; Jakobs et al., 2015; Plantamp et al., 2016; Ryan et al., 2016; Aly et al., 2017). For example, it has been found that both the pupae and adults of SWD reached 100% mortality by day 17 at 1 °C, suggesting that the cold winter season can serve to create population bottlenecks (Dalton et al., 2011). In fact, year-round SWD monitoring in Italy has shown that severe winter-associated decline in SWD abundance—beginning in December after the abundance peaks in the fall and continues until at least March—was strongly correlated with the number of consecutive days with temperatures below 0 °C (Rossi-Stacconi et al., 2016). In addition, similar winter declines in SWD abundance caused by exposure to low temperatures below 0 °C have also been reported in other studies, although

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the exact times of the abundance peaks and declines differed by region (Dalton et al., 2011; Jakobs et al., 2015; Stephens et al., 2015; Zerulla et al., 2015).

In contrast to the abundant monitoring studies that have been carried out at field sites for outdoor-grown agricultural fruits and in woodland environments, no monitoring studies have been conducted for greenhouse fruits, such as strawberries. In Korea, several strawberry (*Fragaria* × *ananassa*; Rosales: Rosaceae) cultivars are grown in greenhouses for domestic and foreign consumption—as seasonal winter fruits—typically from the end of October to early or late May. Korea-grown strawberries need to be free of SWD in order for them to be exported to other countries, but strawberries are one of the most favored ovipositional media for SWD in both laboratory and agricultural field settings (Cini et al., 2012; Walse et al., 2012). However, the cultivation period of the greenhouse strawberries partially overlaps with the winter season (December to February), during which the daily mean temperature often drops to below 0 °C (Korea Meteorological Administration; https://data.kma.go.kr). Thus, the decline or absence of SWD populations would be expected in the wild (Rossi-Stacconi et al., 2016). Furthermore, incidence of SWD inside greenhouses would be minimal during winter season if SWD are not already the living inside greenhouses, and if the nearby woodlands serve as sources that provides dispersers to the agricultural environment as per the metapopulation concept (Hanski and Gilpin, 1991).

In this study, two strawberry greenhouse blocks located in Southwest Korea were monitored for approximately 19 and 15 months, respectively, after the selection of attractants and traps. Greenhouse block refers to a series of greenhouses composed of ~3–5 individual greenhouses. The traps were installed inside and just outside of the strawberry greenhouses, as well as in the nearby woodlands to evaluate the year-round SWD occurrence patterns. In Korea, the strawberry greenhouses are mostly located in plain fields that are often adjacent to rice paddies or cultivated crops, and mountainous hills are located at varying distances from the greenhouses. Additionally, greenhouse blocks that were located in three other regions were also monitored for one or two greenhouse strawberry cultivating periods. Furthermore, the fallen strawberries inside the greenhouses were collected and examined to see if any SWD emerged to complement the trap monitoring data.

Materials and methods

Selection of attractants and traps

A literature survey to select attractants and traps that had been previously assessed led us to two homemade baits, an apple cider vinegar + wine (ACV + W) mixture and an ACV + ground apple (ACV + GA) mixture (Landolt et al., 2012a, 2012b; Kang, 2013); the Scentry and Trécé commercial chemical lures (Cha et al., 2013, 2014, 2017; Burrack et al., 2015; Kirkpatrick et al., 2017); and the Haviland and Dreves homemade plastic traps (Lee et al., 2012, 2013; Fig. 1). The "Fuji" apple cultivar, which is one of the most popular apple cultivars in Korea, was ground after the skin was removed on the trap installation day. The homemade Haviland and Dreves traps (Lee et al., 2013) were difficult to find, and so similar-looking plastic containers were selected and then slightly modified. Consequently, the modified Haviland trap was a round-bottomed polypropylene container measuring 15 × 15 × 6 cm (width × depth × height) that could hold a maximum of 500 ml of attractant. After cutting off the majority of the lid but leaving the frame intact (8.5 cm in diameter), a black-colored polyvinyl chloride (PVC) net (0.3 cm mesh) was attached with glue to the lid frame. The Dreves trap was a 32-oz deli-cup trap. The upper portion of both sides of the cup was cut in a semicircle (8.5 cm in diameter), and a black PVC net (0.3 cm mesh) was attached. Both traps were covered with a plastic dish that was turned upside down to prevent the inflow of rainwater.

The best attractant was selected after two baits and two lures were respectively tested using the same Dreves trap. For the trap test, the selected attractant was used. Every experiment took place over 24 h and was repeated six times. For the bait, 75 ml of ACV was mixed with either 75 ml of wine or ground apple and 1 ml of unscented soap was added to eliminate surface tension. For every experiment, the positions of the two attractants and traps were exchanged. Attractant-baited traps were hung at a height of 1–1.5 m from the ground and placed at a distance of 4 m from one another.

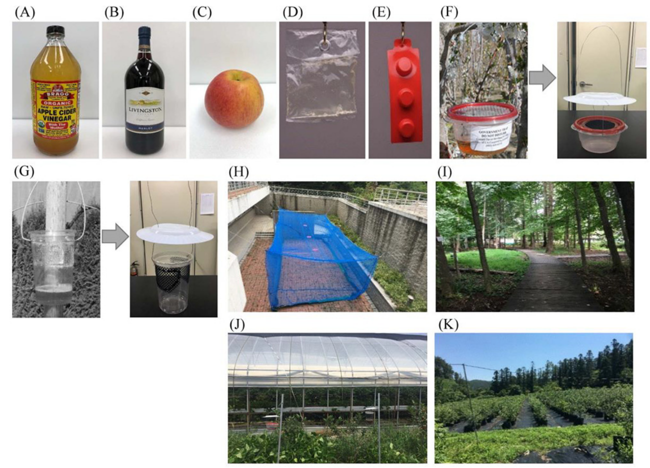

Fig. 1. Ingredients of the homemade bait, commercial lures, and sites for testing baits, lures, and traps. (A) Apple cider vinegar (BRAGG, Santa Barbara, CA, USA), (B) Merlot wine (Livingston Cellars, Modesto, CA, USA), (C) "Fuji" apple cultivar, (D) Scentry lure (Scentry Biologicals. Inc., Billings, MT, USA), (E) Trécé lure (Trécé Inc., Adair, OK, USA), (F) Haviland trap (left) and modified Haviland trap (right), (G) Dreves trap (left) and modified Dreves trap (right), (H) manufactured net installed in Chonnam National University (CNU), (I) an arboretum at CNU, (J) strawberry greenhouse located in Hwasun, Jeollanam-do Province, and (K) blueberry field located in Hwasun, Jeollanam-do Province.

The trap and attractant efficacy experiments were conducted from July to September 2017 and during October 2018. In 2017, each bait pair and each lure pair was tested only in the manufactured mesh cage that was installed outdoors at the Chonnam National University (CNU) in Gwangju (Fig. 1H). A 10 × 4 × 3 m (width × length × height) blue-colored nylon mesh cage with a mesh size smaller than 1 × 1 mm and a zippered entrance was manufactured, and approximately 1,000 adult SWD that had been maintained at CNU (Kim et al., 2015) were released in the middle of the mesh cage. A 10-m distance was maintained between the two baits or two lures, and the experiment was run for 24 h. The final selection test of the best attractant between the baits and lures was performed at four different sites, including outside a strawberry greenhouse, a blueberry field, an arboretum at CNU, and the mesh cage (Fig. 1H, 1I, 1J, and 1K). The trap test was also performed at the four sites. Two baits, two lures, and two traps were tested again in October 2018—a period during which more SWD are present than during the July-September period, based on our monitoring results—although the experiment was performed only at the arboretum at CNU. The results of the SWD attraction experiment for attractants and traps were evaluated in terms of total SWD, male SWD, and female SWD. One-tailed *t*-tests were carried out to evaluate the significant differences between the comparisons using JMP v. 13 (SAS Institute Inc., Cary, NC, USA).

SWD identification

The attractants collected from the field were poured into 15-cm diameter glass jars, the bottom of which was attached to a 0.5 mm mesh. The samples were washed with double-distilled water, and spread with a slight shaking motion to avoid the overlap of individuals and to facilitate the evaluation of the major morphological characteristics of the trapped flies. Non-Drosophilidae individuals were separated from the Drosophilidae ones, and only SWD were individually counted. In addition, males and females were identified with a magnifying glass. Consequently, the captures were divided into total SWD, male SWD, and female SWD.

SWD were identified using the major keys that have been reported in previous studies (Kanzawa, 1939; Vlach, 2010; Hauser, 2011; Walsh et al., 2011; Calabria et al., 2012). When the ovipositor of SWD females did not extrude from the abdomen, the middle part of the abdominal area was gently pressed and examined under the magnifying glass. If clear identification was not obtained due to damage, the sample was examined in detail under a SZ51 microscope (Olympus, Tokyo, Japan), and photographs of the body and ovipositor were taken for future reference. When necessary, SWD were further distinguished from other *Drosophila* species using field guide books, which described the morphological features of the dominant *Drosophila* species that were captured in the attractant-baited traps (Kim et al., 2019). Furthermore, molecular identification was performed by sequencing the DNA barcoding region (658 bp) when necessary. Detailed experimental procedures have been presented in our previous study (Choi et al., 2018), which had analyzed global samples of SWD barcoding sequences.

Study areas

SWD trap capture was performed inside and outside of the strawberry greenhouses as well as in the nearby woodland areas. One strawberry greenhouse block (G1), located in Gokseong, Jeollanam-do Province, in Southwest Korea was selected due to availability (Table 1; Fig. 2). This block is composed of four individual greenhouses, each measuring ~2000 m^2 and surrounded by paddy fields. This block hydroponically cultivates the 'Seolhyang' strawberry cultivar. Toward the northwestern side of the block, a woodland (GW) comprising mainly of pine trees and occasionally of raspberry (*Rubus crataegifolius* Bunge), baby brier (*Rosa multiflora*), bracken (*Pteridium aquilinum* var. latiusculum), and oriental white oak (*Quercus aliena*) was located at a distance of 150 m from G1 (Fig. 2). These two sites were continuously trapped for 19 months from November 2017 to May 2019. Four months later, another greenhouse block (G2), which cultivates the same cultivar, but in a soil-based system, was included and trap capture was commenced.

In addition to the Gokseong (i.e., G1, G2, and GW) sites, three other regions were selected in this study. Two regions are located in other districts in the Jeollanam-do Province (Damyang and Hwasun), while the third region, Jinju, is located in the Gyeongsangnam-do province, towards the mid-southern region of Korea. Detailed information regarding the greenhouse blocks and trap capture schemes is presented in Table 1, and the views of monitoring sites are presented in Figs. S1, S2, and S3 for Damyang, Hwasun, and Jinju, respectively. Damyang trap captures were performed at three greenhouse blocks (D1, D2, and D3) and in one woodland area (DW; Fig. S1). Unlike in the other regions, fruit-cultivating sites were selected as an alternative to woodlands in Hwasun because of the difficulty involved in accessing the nearby woodlands (Fig. S2). Thus, trap capture was performed at one greenhouse block (H1), vineyard (HV), and peach farm (HP) in Hwasun. The greenhouse blocks at Jinju were located within the strawberry complex, which grows different cultivars with different methods, and this complex was surrounded on three sides by the artificial Jinyang lake while the fourth side was connected to the adjacent woodlands (Fig. S3). Given that the strawberry export complex is located in Jinju, different cultivars and culture systems were available, allowing us to test different factors with the potential to affect SWD occurrence. Thus, trap capture was performed at four greenhouse blocks (J1, J2, J3, and J4; Table 1). At ~100 m distance from J1, a woodland (JW) was located at a distance of ~0.8–1.6 km from other greenhouse blocks (Fig. S3). For these three regions (i.e., Damyang, Hwasun, and Jinju), trap capture was conducted for one or two greenhouse strawberry culture periods (October to May), with extra periods included for preliminary monitoring (e.g., from April 2018 to June 2018 for Jinju). The start of the trap capture period varied among regions and greenhouse blocks due to differences in cultivation start times, variable dates permitted to access to strawberry greenhouses, and a limited labor force. The exact dates are presented in Table 1.

Table 1
Summary of trap capture schemes.

Region	Coordinates	Trap sites (inside/ outside trap no.)	Environment	Distance from woodland (m)	Cultivar	Cultivation method	Export	Duration
Gokseong	35°17′07″ N, 127°20′14″ E	GW (3)	Pine trees, Raspberry, Chestnut	–	–	–	–	20 Nov 2017–20 May 2019
		G1 (6/6)	Rice paddy	150	Seolhyang	Hydroponics	Y	
		G2 (6/6)	Rice paddy	160	Seolhyang	Soil system	N	22 Mar 2018–20 May 2019
Damyang	35°14′30″ N, 126°58′11″ E	DW (3)	Pine trees, Persimmon, Bamboo	–	–	–	–	29 Jan 2018–26 May 20185 Oct 2018–23 May 2019
		D1 (6/6)	Blueberry, Rice paddy, Cabbage	700	Seolhyang	Hydroponics	Y	27 Nov 2017–26 May 20185 Oct 2018–23 May 2019
		D2 (6/6)	Rice paddy, Cabbage, Strawberry	750	Jughyang	Hydroponics	Y	
		D3 (3/6)	Strawberry	730	Seolhyang	Soil system	N	2 Apr 2018–26 May 20185 Oct 2018–23 May 2019
Hwasun	35°00′12″ N, 126°56′16″ E	HV (3)	Strawberry	–	–	–	–	27 Nov 2017–26 May 2018
		HP (3)	Strawberry	–	–	–	–	
		D1 (3/3)	Grape, Peach	–	Seolhyang	Hydroponics	N	
Jinju	35°14′30″ N, 127°57′27″ E	JW (3)	Pine trees, Bamboo Mulan magnolia	–	–	–	–	30 Apr 2018–2 Jun 201828 Sep 2018–20 May 2019
		J1 (6/6)	Strawberry	100	Seolhyang	Soil system	Y	
		J2 (6/6)	Strawberry	800	Seolhyang	Hydroponics	Y	
		J3 (6/6)	Strawberry	1600	Maehyang	Hydroponics	Y	
		J4 (6/6)	Strawberry	1100	Maehyang	Soil system	Y	

Greenhouse block refers to a series of greenhouses composed of ~ 3–5 individual greenhouses, which were separated from one another by more than 1 m. The size of greenhouses ranged from 2,148 (18 × 90 m) to 3,966 m^2 (38 × 100 m). Numbers in parentheses indicate the number of traps hung at each greenhouse block or woodland. G1, G2, D1, D2, D3, H1, J1, J2, J3, and J4 are the names of the greenhouse blocks, and comprise a letter from region name and a serial number. GW, DW, and JW are the names of the woodlands, with the first letter referring to the region name. HV and HP are the vineyard and peach farm, respectively in Hwasun. Y, yes; N, no; and -, not applicable.

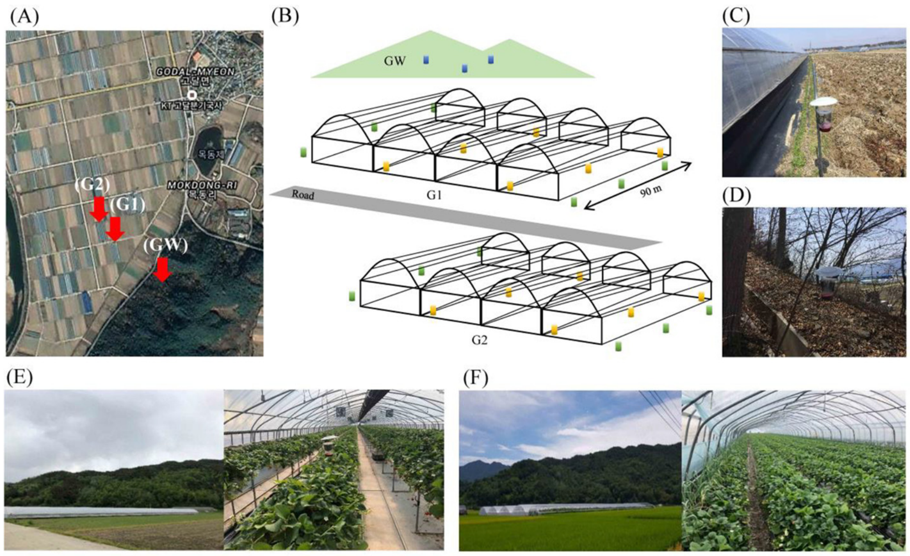

Fig. 2. Monitoring sites in Gokseong, Jeollanam-do Province, which is located in the southwestern portion of Korea. (A) The GPS map (https://www.google.co.kr/maps) indicates the greenhouse blocks (G1 and G2) and woodland (GW); (B) a schematic of the monitoring sites, showing trap positions inside greenhouses, outside greenhouses, and in woodland; (C) view of the outside of a greenhouse, (D) view of woodland, (E) overview of G1 and GW (left) and inside G1 (right); and (F) overview of G2 and GW (left) and inside G2 (right).

Trap capture

At each individual greenhouse block, three traps were placed diagonally in two greenhouses 10 cm above the strawberries. Outside, three traps were placed at each side of a greenhouse block at a height of 1 m above the ground in a straight line. In the woodland areas, tree traps were placed at a distance of ~5 m and 1.5 m above the ground, where wild fruits (e.g. raspberries) grew nearby. The Dreves traps were filled with 75 ml of ACV + W, along with a small amount of unscented soap. Capture collection and bait refills were conducted weekly for the regions of the Jeollanam-do Province, and three times per month in Jinju.

The trap capture results were compared to test (1) the differences among the monitoring sites (i.e., inside the greenhouse, outside the greenhouse, and in woodland), (2) the differences between export varieties (e.g., Seolhyang, Jughyang, and Maehyang), (3) the differences between cultivation methods (i.e., hydroponics or soil-based systems), and (4) the differences between regions (e.g., Gokseong and Damyang) using equivalent data that included overlapping periods. For the Jinju trap capture data, which was collected three times per month, only the first three tests were performed. Weekly mean capture numbers were categorized into LL for 0.1–5 individuals, L for 5.1–10, M for 10.1–50, H for 50.1–100, and HH for 100.1–600. Significance between comparisons was tested by a one-tailed *t*-test using JMP v. 13 (SAS Institute Inc., Cary, NC, USA). The temperature information for each trap capture region was obtained from the within-district official temperature station in Korea (https://data.kma.go.kr).

Emergence check for fallen strawberries

In order to supplement the trap capture data, fallen strawberries were collected and monitored to detect adult emergence to confirm the presence or absence of SWD. Due to the limited access to individual fallen strawberries, a total of six greenhouse blocks in three regions were used to collect a total of 6,448 individuals from December 2018 to May 2019: G1 (Seolhyang, hydroponics), G2 (Seolhyang, soil system), D1 (Seolhyang, hydroponics), D2 (Jukhyang, hydroponics), J1 (Seolhyang, hydroponics), and S2 (Seolhyang, soil system). The fallen strawberries in the greenhouses were collected on the days the trapped flies were collected. In addition, we asked the greenhouse owners to collect the fallen strawberries whenever possible. For this, one 4-L basket with a lid was provided per greenhouse. Nevertheless, the complete and consistent collection of SWD was unsuccessful due to the time constraints of the farmers, a dislike for leaving rotting strawberries inside the greenhouses, and the casual practice of removing fallen strawberries. Therefore, the number of collected strawberries varied weekly and among the greenhouse blocks.

Once the fallen strawberries were brought to the laboratory, they were individually placed in a 120-ml plastic specimen cup (SPL Life Sciences, Pocheon, Korea), and incubated in a culture chamber at 24 ± 1 °C (70–80% relative humidity and a 16:8h light:dark photoperiod cycle), and outward changes in the strawberries and signs of fly growth were evaluated once a day for 14 days. Species identification was performed as previously explained.

Results

Molecular identification

Sixty-one SWD individuals that could not be casually distinguished due to damaged morphology were identified via DNA barcoding (including one *D. melanogaster* obtained for morphological examination from Gwangju Institute of Science and Technology, Korea). Six *Drosophila* species and one non-*Drosophila* species were identified, including *D. immigrans*, *D. simulans*, *D. melanogaster*, *D. rufa*, *D. lutescens*, and *Leucophenga maculata* (Drosophilidae), and a species complex group consisting of *D. auraria*, *D. triauraria*, and *D. quadraria* (Table S1). Seventeen SWD individuals presented five haplotypes, with the sequence divergence ranging from 1 to 4 bp (0.15–0.46%) and were well differentiated from other species, and presented the least divergence compared to *D. lutescens* at 48 nucleotide residues (7.3%; Table S2). Further phylogenetic analysis also differentiated the SWD haplotypes from other species, forming a strong monophyletic group (data not shown). Additional, phylogenetic analysis with the inclusion of several previously reported SWD haplotypes also resulted in well separated SWD haplotypes from other species with high nodal support (data not shown; Choi et al., 2018), indicating that sequencing of the DNA barcoding region is a powerful tool to distinguish SWD from other similar-looking species.

Selection of attractants and traps

In 2017, an experiment to select the better fermentation and chemical attractants in the mesh cage resulted in higher capture with the ACV + W mixture than that with the ACV + GA mixture, and with the Scentry lure than the Trécé lure; all categories were supported by statistical significance (i.e., total SWD, male SWD, and female SWD; Tables S3 and S4). After the effective bait and lure were selected, the final

Table 2
Comparison of the trapping efficiency of chemical lures, baits, and traps from the 2018 arboretum test.

Type	Comparison	Total SWD	SWD ♂	SWD ♀
Bait	ACV + W	55.83 ± 45.16**	51.02 ± 51.65	55.92 ± 56.13*
	ACV + GA	44.17 ± 54.84	48.98 ± 48.35	44.08 ± 43.87
Chemical lure	Scentry lure	87.36 ± 88.43***	88.35 ± 88.32***	93.75 ± 82.09***
	Trécé lure	12.64 ± 11.57	11.65 ± 11.68	6.25 ± 17.91
Selected attractants	ACV + W	80.27 ± 82.87***	83.69 ± 82.89***	91.84 ± 79.67***
	Scentry lure	19.73 ± 17.13	16.31 ± 17.11	8.16 ± 20.33
Traps	Dreves	62.29 ± 53.02***	58.46 ± 56.43**	58.70 ± 66.18
	Haviland	37.71 ± 46.98	41.54 ± 43.57	41.30 ± 33.82

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. ACV, apple cider vinegar; W, wine; and GA, ground apple

selection for the best attractant was performed at four different sites. In the attractant test, the ACV + W mixture resulted in higher captures than the Scentry lure in all categories and all sites, with statistical data being available for most comparisons (Table S5). In strawberry fields, only the results for total SWD were statistically significant (T = 5.349193; P = 0.0003), although both male and female SWD captures were numerically higher with the ACV + W mixture. Comparisons between the Dreves and Haviland traps in the four different sites, including the mesh cage, showed that the use of Dreve traps resulted in more captures numerically than with the Haviland trap for all categories and all sites, including the strawberry fields, although statistical significance was obtained in a limited number of categories and sites (Table S6).

In 2018, numerically higher captures were obtained with the ACV + W mixture than with ACV + GA mixture and with the Scentry lures than with the Trécés lures in the arboretum at CNU, although statistical significance was obtained in a limited number of categories (Table 2). In addition, comparisons between captures with the ACV + W mixture and Scentry lures also showed higher SWD captures in the ACV + W mixture with the statistical significance only in a limited number of categories. Higher SWD captures were also obtained with the Dreves trap with some statistical significance (Table 2). Therefore, experiments of the attractant and trap comparisons that were conducted in 2017 and 2018 showed overall consistent results.

Trap capture

Gokseong

The G1 and GW trap capture results in Gokseong—over 19 months (November 2017 to May 2019) —and the G2 trap capture results—over 15 months (March 2017 to May 2019)—are collectively presented in Fig. 3. Weekly mean capture numbers were categorized into LL, L, H, and HH classes (see Methods section class definitions). From December 2017 to November 2018 at GW, two high capture periods were observed. The first began in the first week of June 2018 (2018JUN1; the date code follows the following format: YearMonthWeek) and ended in the second week of July 2018 (2018JUL2), with M to HH class captures. The second began from the third week in September 2018 (2018SEP3) and ended on the first week of December 2018 (2018DEC1), and HH class captures were recorded most weeks. The mean capture per trap during 2018SEP3-2018DEC1 was 346, ranging from 206 to 449 individuals (Fig. S4). After excluding these two periods from the year-round capture data, the captures at GW were classified as either LL, L, or zero. From January-December 2018, a zero-capture period at GW that spanned three months (2018JAN3-2018APR2) was observed. A comparison of the overlapping periods between 2017 and 2018 and 2018–2019 at GW indicated that zero capture period recorded during December 2017 – April 2018 was occasionally changed to LL, L, and M class during December 2018 – April 2019, indicating higher captures during the 2018–2019 period than those during the 2017–2018 period. Outside of the greenhouses, the overall trap captures were substantially lower compared to that of GW, with the highest captures ranked as class M captures during the entire monitoring period, and the zero capture period was 20 weeks longer than that of GW (Fig. 3). Inside the greenhouses, captures were of the classes LL and L categories, and six zero-capture periods were recorded that ranged from one week to 24 weeks, with the longest period spanning the fourth week of November 2017 to the second week of May 2018. This zero-capture period was 10 weeks longer than the zero-capture period outside of the greenhouses. The comparison of the overlapping period between 2017–2018 and 2018–2019 inside the greenhouses showed that the zero-capture period recorded during December 2017 to May 2018 changed to three LL class captures (i.e., 2018NOV4, 2018DEC2, and 2019MAY1). Nonetheless, the remaining zero-capture periods were

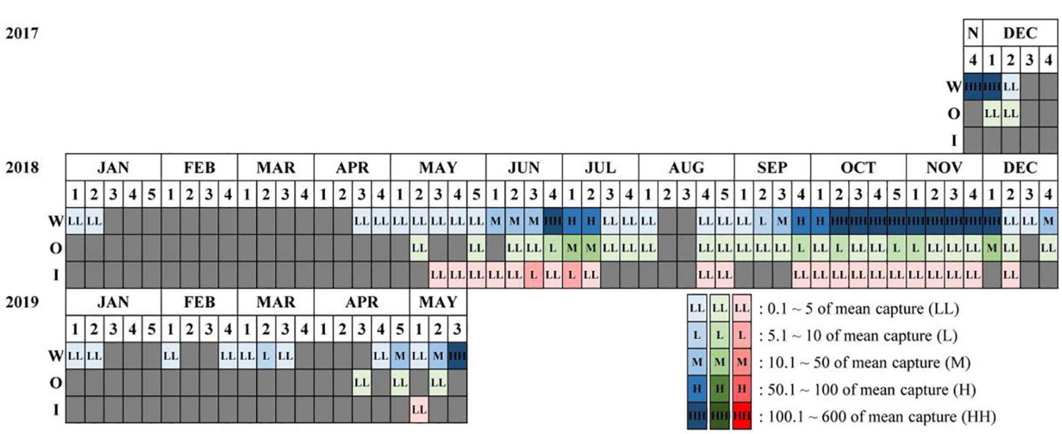

Fig. 3. Monitoring results in Gokseong, Jeollanam-do Province. W, woodland; O, outside greenhouse; and I, inside greenhouse. Dark grey color indicates the absence of SWD. Capture numbers were categorized as LL (0.1–5 individuals), L (5.1–10 individuals), M (10.1–50 individuals), H (50.1–100 individuals), and HH (100.1–600 individuals). The numbers below the months indicate each week.

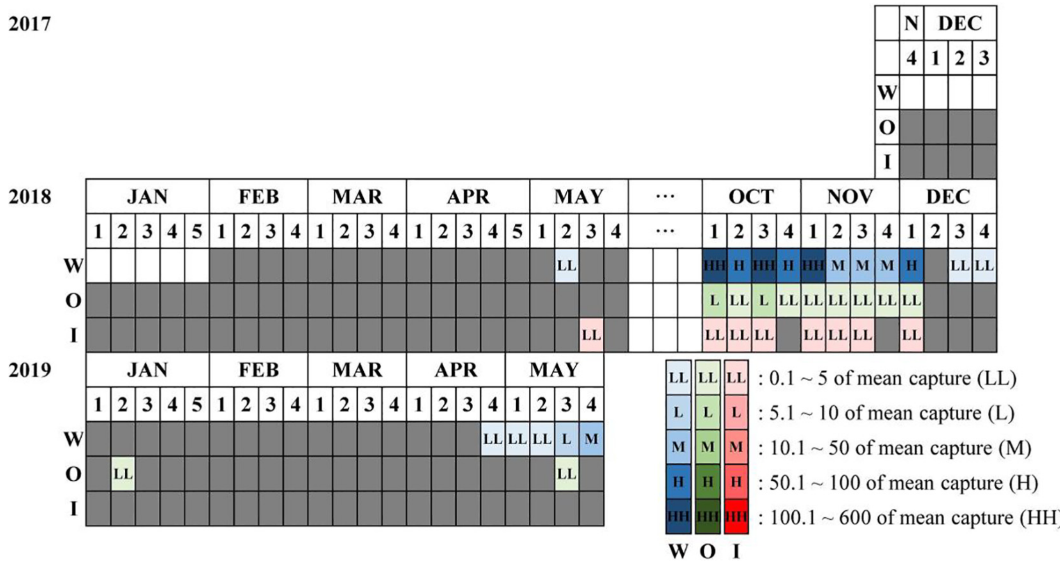

Fig. 4. Monitoring results in Damyang, Jeollanam-do Province. W, woodland; O, outside greenhouse; and I, inside greenhouse. Dark grey color indicates an absence of SWD. Capture numbers were categorized as LL (0.1–5 individuals), L (5.1–10 individuals), M (10.1–50 individuals), H (50.1–100 individuals), and HH (100.1–600 individuals). The numbers below the months indicate each week.

consistent between years.

Damyang

Trap capture at Damyang was conducted for three greenhouse blocks (D1, D2, and D3) and one woodland (DW) for one complete strawberry cultivating period (October 2018 to May 2019) and one incomplete cultivating period with different start dates during 2017–2018 (Table 1). From October 2018 to May 2019, one high-capture period (2018OCT1 to 2018DEC1) was detected at DW, with the capture classes spanning M-HH (Fig. 4; Fig. S5). Excluding this period, the captures were classified into LL, L, M, or zero-capture classes. There was a more than three month period (2019JAN1 to 2019APR3) during which no captures were recorded at DW. Similar to the Gokseong data, captures were highest in woodlands, followed by captures outside the greenhouses and captures inside the greenhouses. The zero-capture period was longest inside the greenhouses, followed by the zero-capture period outside the greenhouses and the zero-capture period in the woodlands. The 2018–2019 period presented both higher captures and a longer capture period than that of 2017–2018 period.

Hwasun

Trap captures in Hwasun were conducted for only one greenhouse block (H1), a vineyard (HV), and a peach farm (HP) instead of woodlands for one incomplete cultivating period (November 2017 to May 2018; Table 1; Fig. 5). For only one week (2018NOV4) a mean capture of 0.3 individuals (LL) per trap was recorded each at HV and HP, while no SWD were trapped inside and outside the greenhouses during the entire monitoring period at Hwasun. Thus, inferable information, such as potential preferences between the two fruits, was not obtained. However, many *D. immigrans* were captured from April to May (~60 individuals per trap; data not shown).

Jinju

Unlike in other regions, a specialized strawberry complex that cultivates strawberries primarily for export is located in Jinju. Thus, four greenhouse blocks (J1, J2, J3, and J4) growing two different cultivars using different cultivation methods were selected for trap capture, along with one woodland (JW; Fig. S3). Trap capture was conducted mainly during one complete cultivating period (September 2018 to May 2019), along with a short period of preliminary trap capture (Table 1; Fig. 6). Unlike in other regions, such as Gokseong and Damyang, SWD were captured during the whole monitoring period at SW at HH-LL levels, and the highest capture corresponded to 566 individuals (2018OCT3; Fig. 6; Fig. S6). Nevertheless, the woodland capture pattern was similar to that observed in Gokseong and Damyang in that one period of HH capture (beginning of October to the middle of December) was observed. However, during the subsequent zero-capture periods observed in other regions, LL capture was observed in Jinju. Thus, nearly no woodland zero-capture periods were recorded. Outside of the greenhouses, the highest capture levels corresponded to the L class while the zero-capture period was reduced compared to that in other regions (2019FEB4 to 2019MAR4). Inside the greenhouses, the highest captures corresponded to the LL class and the zero-capture period increased compared to that observed outside of the greenhouses from 8 to 13 weeks, resulting in one continuous zero-capture period (2018DEC2 to 2019FEB4; Fig. 6).

In summary, the number of SWD captured and capture period were the highest and lasted the longest in the woodland area. When comparing captures outside and inside the greenhouses, the outside greenhouse captures were higher. The zero-capture period inside the greenhouses in Jinju lasted for a substantially shorter period (~3 months) than that of Gokseong (4.5 months) and Damyang (~6 months). Due to a few SWD that were continuously captured inside the greenhouses in Sansheong (LL), the zero-capture period during the entire monitoring regions was low. Nevertheless, a nearly three-month zero-capture period was observed, which continued from 2018DEC2 to 2019FEB4 concordantly in all greenhouse blocks.

Comparison of SWD capture between cultivating environments

In order to see if any differences in SWD captures were present among the different cultivating environments, captures of overlapping periods were compared between regions, between varieties, between cultivation methods, and between trap sites. This comparison was conducted for the Gokseong and Damyang regions and separately for the Jinju region, due to differences in the trap collection cycle.

Between the different cultivation methods (hydroponics vs. soil-based systems), cultivars (Seolhyang vs. Jughyang), and regions (Gokseong vs. Damyang), statistically significant differences were not detected in nearly all comparisons. However, the differences between woodland and inside greenhouse captures and between woodland and outside greenhouse captures were statistically significant (Table 3).

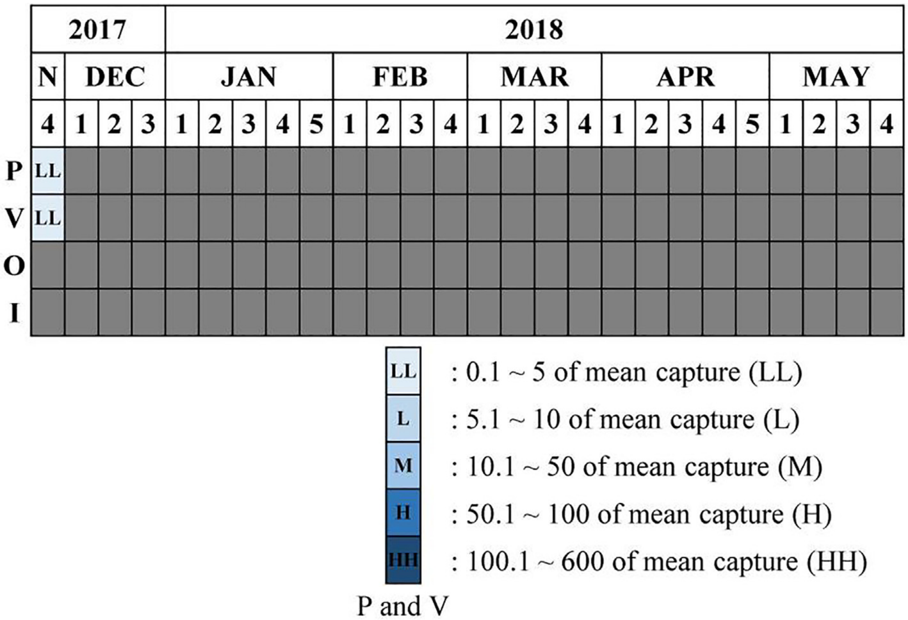

Fig. 5. Monitoring results in Hwasun, Jeollanam-do Province. P, peach farm; V, vineyard; O, outside greenhouse; and I, inside greenhouse. Dark grey color indicates an absence of SWD. Capture numbers were categorized as LL (0.1–5 individuals). The numbers below months indicate each week.

Only one comparison between regions for captures inside the greenhouse blocks (G1 and D1) showed a significant difference, but it was marginal ($P = 0.482$), and the mean trap capture for Gokseong and Damyang was 0.03 and 0, respectively (Table 3). This suggests that overall there was no statistically significant difference in SWD capture between regions, cultivars, or cultivation methods, but a significant difference was always observed for comparisons between woodlands and captures both outside and inside the greenhouse blocks.

For Jinju, comparisons between cultivation methods and between cultivars also did not show any statistical differences in captures both outside or inside the greenhouse blocks, with the exception of one comparison between cultivars the inside the greenhouses [(Seolhyang (J1) vs. Maehyang (J3); $P = 0.0038$], with 0.07 and 0 captures in Seolhyang and Maehyang, respectively (Table 4). Similar to Gokseong and Damyang, the comparisons between woodland and outside and inside the greenhouse blocks always showed statistically significant differences. However, unlike Gokseong and Damyang, the comparisons between captures outside and inside the greenhouse blocks showed a significant difference in some comparisons, such as between captures outside and inside J1 ($P = 0.006$) and between captures outside and inside J3 ($P = 0.0466$), although differences in capture numbers outside and inside the greenhouse blocks were not that substantial (0.27 vs. 0.07 mean capture outside and inside J1; 0.53 vs. 0 mean capture outside and inside J3; Table 4). These results appear to support the conclusion that the environments inside the greenhouses are not appropriate habitats for SWD and that the greenhouses themselves serve as a physical barrier against SWD invasion to some degree.

Fallen strawberry evaluations

In order to supplement the trap capture results, fallen strawberries were collected inside the greenhouses and incubated in the insectarium to identify emerging individuals. Due to the restrictions imposed by greenhouse owners, only a limited number of greenhouse blocks participated in data collection [i.e., two greenhouse blocks in Gokseong (G1 and G2), two out of three greenhouse blocks in Damyang (D1 and D2), and two out of four greenhouse blocks in Jinju; J1 and J2; Table S7)]. A total of 6,448 fallen strawberries were collected during

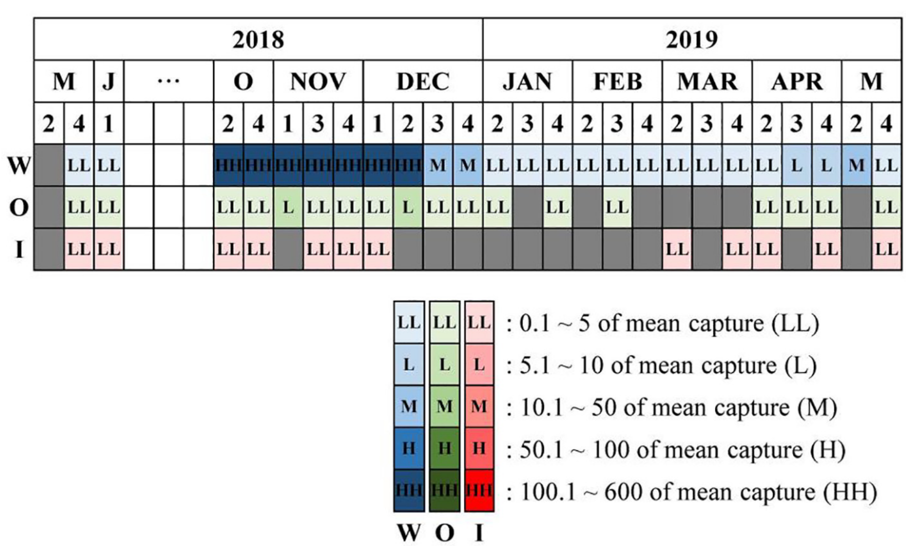

Fig. 6. Monitoring results in Jinju, Gyeongsangnam-do Province. W, woodland; O, outside greenhouse; and I, inside greenhouse. Dark grey color indicates an absence of SWD. Capture numbers were categorized as LL (0.1–5 individuals), L (5.1–10 individuals), M (10.1–50 individuals), H (50.1–100 individuals), and HH (100.1–600 individuals). The numbers below months indicate each week.

Table 3
Comparison of trap captures between trap sites, cultivating methods, strawberry cultivars, and regions (Gokseong and Damyang).

Categories	Sites	Comparison	Mean capture per trap	P
Trap sites (woodland, outside, and inside greenhouse blocks)	GW/G1	GW vs. Outside	69.20 vs. 0.85	0.0072**
		GW vs. Inside	69.20 vs. 0.03	0.0066**
		G1 Outside vs. G1 Inside	0.85 vs. 0.03	0.1006
	GW/G2	GW vs. Outside	69.20 vs. 0.52	0.0070**
		GW vs. Inside	69.20 vs. 0.07	0.0066**
		G2 Outside vs. G2 Inside	0.52 vs. 0.07	0.115
Cultivation methods (hydroponics and soil system)	Inside	Hydroponics (G1) vs. Soil system (G2)	0.03 vs. 0.07	0.3552
	Outside	Hydroponics (G1) vs. Soil system (G2)	0.85 vs. 0.52	0.5624
	Inside	Hydroponics (D1) vs. Soil system (D3)	0.00 vs. 0.02	0.1554
	Outside	Hydroponics (D1) vs. Soil system (D3)	0.15 vs. 0.04	0.0888
Strawberry cultivars (Seolhyang and Jughyang)	Inside	Seolhyang (D1) vs. Jughyang (D2)	0.00 vs. 0.03	0.1426
	Outside	Seolhyang (D1) vs. Jughyang (D2)	0.15 vs. 0.16	0.9501
Regions (Gokseong and Damyang)	Inside	Gokseong (G1) vs. Damyang (D1)	0.03 vs. 0.00	0.0428*
	Outside	Gokseong (G1) vs. Damyang (D1)	0.85 vs. 0.15	0.1658
	Inside	Gokseong (G2) vs. Damyang (D3)	0.07 vs. 0.02	0.2467
	Outside	Gokseong (G2) vs. Damyang (D3)	0.52 vs. 0.04	0.0873

GW, woodland at Gokseong; G1 and G2, greenhouse blocks 1 and 2 at Gokseong; D1, D2, and D3, greenhouse blocks 1, 2, and 3 at Damyang.
*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

December 2018 to May 2019, and flies were observed to emerge from 132 strawberries (2.047%), but no SWD were present among the emerging individuals. The identification of fly species returned four species [*D. melanogaster*, a species complex group comprised of *D. auraria*, *D. triauraria*, and *D. quadraria*, *D. immigrans*, and *Bradysia impatiens* (Diptera: Sciaridae)]. In the 26 fallen strawberry collection dates, the most common species to emerge was *D. melanogaster* (during 9 collection dates, 658 emerging adults), followed by *B. impatiens* (during 8 collection dates, 125 emerging adults), and both the species complex group and *B. impatiens* were detected during six collection dates. Infrequently, *B. impatiens*, which had long been present in the trap captures, was detected as masses of larvae prior to emergence (125 individuals).

Discussion

Highest SWD captures in woodland

Recently, many studies have focused on the relationships between woodland landscapes and agricultural fields to understand SWD population dynamics and the significance of woodland areas to the presence of SWD in agricultural environments given that this information is critical for the development of an efficient and integrated pest management strategy (Harris et al., 2014; Pelton et al., 2016; Cahenzli et al., 2018). The current trap capture study found that woodland areas were a major source of SWD populations rather than the strawberry fields (Figs. 3–6). Cahenzli et al. (2018) evaluated the impact of forests on SWD incidence in nearby crops and found that higher SWD captures were recorded in the crop areas that were closer to the forests during the fruit-ripening period, highlighting the importance of forests in the perspective of SWD incidence and abundance. Furthermore, the areas outside the cultivated fields, including woodlands, have been found to be resource-rich and 84 plant species belonging to 19 families have been reported in these areas that serve as hosts for the emergence of SWD adults across Italy, the Netherlands, and Switzerland (Kenis et al., 2016). Haro-Barchin et al. (2018) evaluated the relationship between landscape complexity (forest cover) and SWD abundance by comparing SWD captures in landscapes with or without blueberry fields and found that the capture number of SWD individuals increased as the forest cover increased, regardless of the presence of blueberry fields. Thus, these studies support our findings that SWD captures were the highest in woodland areas for the longest

Table 4
Comparison of trap captures between trap sites, cultivating methods, and strawberry cultivars in the Jinju region.

Comparison criterion	Site	Comparison	Mean capture per trap	P
Trap locations (woodland, outside, and inside of greenhouse)	JW / J1	JW vs. Outside	86.09 vs. 0.27	0.0155*
		JW vs. Inside	86.09 vs. 0.07	0.0153*
		J1 Outside vs. J1 Inside	0.27 vs. 0.07	0.0060**
	JW / J2	JW vs. Outside	86.09 vs. 0.24	0.0155*
		JW vs. Inside	86.09 vs. 0.03	0.0153*
		J2 Outside vs. J2 Inside	0.24 vs. 0.03	0.0554
	JW / J3	JW vs. Outside	86.09 vs. 0.53	0.0158*
		JW vs. Inside	86.09 vs. 0.00	0.0152*
		J3 Outside vs. J3 Inside	0.53 vs. 0.00	0.0466*
	JW / J4	JW vs. Outside	86.09 vs. 0.18	0.0154*
		JW vs. Inside	86.09 vs. 0.02	0.0152*
		J4 Outside vs. J4 Inside	0.18 vs. 0.02	0.0504
Cultivation methods (hydroponic and soil system)	Inside	Hydroponic (J1) vs. Soil system (J2)	0.07 vs. 0.03	0.1404
	Outside	Hydroponic (J1) vs. Soil system (J2)	0.27 vs. 0.24	0.8186
	Inside	Hydroponic (J3) vs. Soil system (J4)	0.00 vs. 0.02	0.1546
	Outside	Hydroponic (J3) vs. Soil system (J4)	0.53 vs. 0.18	0.2018
Strawberry cultivars(Seolhyang and Maehyang)	Inside	Seolhyang (J1) vs. Maehyang (J3)	0.07 vs. 0.00	0.0038**
	Outside	Seolhyang (J1) vs. Maehyang (J3)	0.27 vs. 0.53	0.3328
	Inside	Seolhyang (J2) vs. Maehyang (J4)	0.03 vs. 0.02	0.6895
	Outside	Seolhyang (J2) vs. Maehyang (J4)	0.24 vs. 0.18	0.644

JW, woodland at Jinju; J1, J2, J3 and J4, greenhouse blocks 1, 2, 3 and 4 at Jinju.
*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

periods of time than either outside or inside the strawberry greenhouses (Figs. 3–6).

Occurrence pattern in Korea

Our year-round trap capture results that are based largely on Gokseong can be summarized as a first peak that occurred during June-July, a subsequent rapid decrease from middle of July to the beginning of September, the highest peak during September to mid-December, and a sharp and subsequent decrease and zero-captures until the middle of April (Figs. 3, 4, and 6). Although the exact mean year-round temperature may differ from region to region, available reports from the other side of the world have shown similar occurrence patterns among seasons. For example, Harris et al. (2014) showed that the greatest captures occurred during October to early December with another peak occurring in May in deciduous fruit blocks in Wolfskill, USA. In addition, low trap captures were observed during the hottest summer months (August to September) and the coldest winter months (December to April) in most of the deciduous fruit blocks. Similarly, Mazzetto et al. (2015) observed a few captures in early spring in northwestern Italy, while no adults were found again until June, although captures increased in late summer and reached peaks in October and November, which were followed by a severe population decrease with a few captures in winter.

Following the highest trap captures up to mid-December, the sharp winter drop in captures appears to be related to the drop in temperature during the winter season in Korea (December-February). Rossi-Stacconi et al. (2016) also found that captures declined at the end of December in Trentino, Italy, and a strong correlation between the drop in winter trap captures and the presence of average temperatures below 0 °C, even for non-successive days. During 2017–2018 in Gokseong, the number of days during which subzero daily minimum temperatures were recorded were 29, 29, and 25 days which corresponded to monthly mean minimum temperatures of −5.0, −7.0, and −6.0 °C during December, January, and February, respectively (Fig. S7A), suggesting a close relationship between cold temperatures and sudden winter drops in SWD captures.

A continual drop after the initial winter drop that continued until early spring has also been reported. Our collective trap capture results show low or zero-captures that were observed after the initial winter drop and that continued to mid-April (Figs. 3, 4, and 6). For Gokseong, the mean minimum temperature increased to 2.5 °C in March 2018 and was higher in April 2018, but the trap captures remained either low or zero. Rossi-Stacconi et al. (2016) also found a period of almost no captures in all monitored sites, which began at the end of February 2013 and continued to the end of June 2013. In San Joaquin County, California, no SWD were captured from the beginning of January to the beginning of April, but the average daily mean temperature during this period was 10.6 °C without the presence of daily mean subzero temperatures (Dalton et al., 2011). Thus, our year-round trap capture results show similar occurrence patterns to those found in other distant locations. It seems that the drop in winter captures was the result of lower temperatures, which appears to delay population recovery despite the mean minimum temperature rising to create adequate conditions for SWD survival and reproduction.

Differences between years

A comparison of the overlapping period of December to May between 2017 and 2018 and 2018–2019 in Gokseong showed a reduction in zero-captures during the 2018–2019 period in woodland areas (Fig. 3). This may have been the result of slightly higher temperatures during the 2018–2019 winter season. In particular, the monthly mean minimum temperature was −5.0, −7.0, and −6.0 °C in December, January, and February, respectively, during the 2017–2018 period, while these temperatures increased to −3.4, −5.2, and −2.7 °C, respectively, during the 2018–2019 period (Fig. S7A). For Damyang, temperature changes similar to those observed in Gokseong were present (Fig. S7B), which appeared to influence the observed reduction of the woodland zero-capture period during 2018–2019, although the change in the zero-capture period was slight.

Unlike other regions, woodland SWD captures were recorded for all weeks during the strawberry cultivating period in Jinju (Fig. 6). We also considered the number of days that subzero daily minimum temperatures (23, 29, and 22 days) and monthly mean minimum temperatures (−2.9, −6.0, and −2.6 °C) were recorded during December, January, and February, respectively, in 2018–2019 period, but they were more or less similar to those of the corresponding period in Gokseong and Damyang. Thus, temperature alone did not explain the absence of zero-captures in Jinju. By considering the results of the study by Haro-Barchin et al. (2018) showing the relationship between landscape complexity (forest cover) and the abundance of SWD, a possible explanation for continual SWD captures in Jinju emerges. It is possible that the higher woodland cover in this region resulted in the lack of zero-captures, although a future hypothesis-based test for this explanation is necessary. A rough aerial view measurement of the woodland cover within a 5-km radius of the sampling area revealed that Jinju had the largest woodland cover (57.1 km^2) compared to that of either Gokseong (46.4 km^2) or Damyang (36.8 km^2). Thus, the higher woodland cover, along with higher temperatures during the 2018–2019 period, may explain the observed continual SWD captures in Jinju, which were not present in the other regions. Future studies that evaluate the relationships between woodland cover and capture number will allow for further scrutiny regarding the population dynamics of SWD.

Zero-capture period at the strawberry greenhouses

Our trapping results from all regions collectively suggest the presence of a three-month zero-capture period inside the greenhouses (2018DEC3 to 2019FEB4) (Figs. 3–6). Considering that this zero-capture period lies within the period of time during which minimal capture or zero-captures were observed in the woodland, the observed zero-capture period inside the greenhouses may be the result of the winter drop in the woodland. These results may suggest that woodland areas are sources for SWD populations. In addition, the fewer captures and the longer duration of the zero-capture period registered inside the greenhouses compared to that outside the greenhouses and the higher captures recorded outside the greenhouses in all monitoring regions support that the environments inside the greenhouses are not suitable habitats for SWD compared to woodlands. Additionally, the emergence of no single SWD from any fallen strawberry supports the conclusion that SWD do not live inside greenhouses. In fact, when SWD were not captured in woodland areas, SWD were rarely captured inside or outside the strawberry greenhouses, with the exception of three cases that presented the lowest trap capture level (2019APR3, outside the greenhouse in Gokseong; 2018MAY3, inside the greenhouse in Damyang; and 2019JAN2, outside the greenhouse in Damyang).

In Korea, strawberry greenhouses, which are mostly located in the plain region, are often found to be adjacent to rice paddies or other cultivated crops and fruits that are not actively cultured during winter season, particularly during the currently acknowledged zero-capture period inside the greenhouses. Thus, the captures inside and outside the greenhouses are highly likely to be the result of SWD dispersing from neighboring woodland areas, although the exact dispersal mechanisms are not yet known. Therefore, the zero-capture period observed inside the greenhouses, which lasted for nearly three months, might be the result of temperature-induced declines in SWB populations in the neighboring woodland areas. Consequently, the possibility of SWD entering the strawberry greenhouses, particularly during the zero-capture period inside the greenhouses, and subsequently depositing their eggs in greenhouse strawberries may be very low as long as the woodland SWD populations also remain low.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aspen.2020.01.004.

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