Eur. J. Hortic. Sci. 86(5), 520–531 | ISSN 1611-4426 print, 1611-4434 online | https://doi.org/10.17660/eJHS.2021/86.5.8 | © ISHS 2021

Review

What is the level of fruit infestation by pulp-feeding insects? An overview of their meaning and measurement

A. Benavídez[1], M. Ordano[2] and P. Schliserman[1]

[1] Centro de Investigaciones y Transferencia de Catamarca, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Catamarca, San Fernando del Valle de Catamarca, Catamarca, Argentina

[2] Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina, and Instituto de Ecología Regional, Universidad Nacional de Tucumán, Consejo Nacional de Investigaciones Científicas y Técnicas, Residencia Universitaria Horco Molle, Edificio las Cúpulas, Yerba Buena, Tucumán, Argentina

Summary

Despite the economic, ecological, and evolutionary importance of the fruit infestation level by pulp-feeding insects, its meaning and measurement are confusing yet. We show the first overview of the fruit infestation level, which emphasizes the problems to define its biological meaning and estimation ways. Employing a literature search concerning the fruit infestation level, we identify different concepts, estimations, and assumptions. This exercise reveals that commonly the interpretation of the infestation level is confusing. We highlight that the data use of the infestation level may drag interpretation problems that depend on (1) the study objectives, (2) the developmental insect stage, and (3) the sampling management. Also, jargon problems arise concerning the research field and the complexity level of the study. Lastly, we explain how to calculate and report the fruit infestation level taking into account the sampling design and measurement scales. Using fruit flies as a model, we show the main topics and guidelines for better study design of the infestation level, either in agricultural, ecological, and evolutionary contexts.

Keywords
crop protection, frugivorous insects, fruit-pest measurement, insect-plant interactions, pest management, Tephritidae

Significance of this study

What is already known on this subject?

- Fruit infestation results from insect oviposition choice. Natural selective filters act on different insect stages, determining its success.

What are the new findings?

- We show a distinction between the damage and infestation terms. We describe infestation level estimation, caveats, and tips for data management.

What is the expected impact on horticulture?

- The knowledge of the processes of fruit infestation is essential to understand crop-insect interactions and improve pest management.

Introduction

The understanding of the interaction between fruits and pulp feeding insects is a critical point in orchard pest management, ecology and evolutionary biology. Pulp feeding insects may use fruits in several ways. Fruits may be a mating site (Prokopy and Roitberg, 1984), a site for oviposition, a way to defend against parasites and pathogens (Aluja and Liedo, 1993) and clearly, fruits may be a food resource (Fletcher, 1987). Pulp feeding insects may consume fruits at exclusive stages of their life cycle, for example, larvae. They may tunnel through the pulp and feed on the surface. Pulp feeding insects comprise diverse taxa with numerous representatives from orders such as Diptera, Lepidoptera, Coleoptera and Hemiptera (Sallabanks and Courtney, 1992). In this framework, we describe the main topics and guidelines for better use of infestation level in agricultural, ecological and evolutionary contexts.

The infestation by pulp feeding insects plays a moderator role in multiple plant-animal interactions and trophic chains, in ecological and evolutionary terms (Bronstein and Barbosa, 2002). The central interest rests on their role as exploiters of mutualisms (Bronstein, 2001) and how mutualisms keep stability in the long term despite antagonists (Ferriere et al., 2002). In seed dispersal mutualisms, the interest in the study of infestation level focuses on the degree of interference between the fruit-bearing host plant and frugivore seed dispersers (Fedriani et al., 2012; Fedriani and Delibes, 2013). In this sense, the understanding of ecological and evolutionary processes involved in the degree of fruit infestation by pulp-feeding insects has valuable insights in pest management. For example, frugivorous insects are mostly generalist species. They feed and develop in a wide range of specific host plants (Hafsi et al., 2016). In a study evaluating the role of larvae feeding on different host plant species, Wilson et al. (2012) argued that fruit fly larvae infestation has a neutral or beneficial impact on the host plant. Insect activity accelerates fruit decay rate, which may favour the viability of seeds, germination, or elicit frugivorous vertebrate seed dispersal (Wilson et al., 2012). These findings may explain why fruit flies (Diptera: Tephritidae) evolved to host generalization.

The infestation level is an estimation of the intensity of the interaction between the plant host and the insect. Infestation is the cause of damage. Therefore, it represents a pivotal measurement to interpret the process according to either a plant's or insect's point of view, ideally both. However, their estimation is not well understood, and the literature reports about it in very different ways. This lack of regularity or consensus obscures the identification of interaction patterns and the factors which determine its variation. We propose that their clarification will promote the understanding of the ecology and evolution of the variation in fruit infestation, an issue in which orchard owners, pest managers, ecologists and evolutionary biologists are all interested.

A given level of "fruit damage" is sufficient for a farmer to decide on the orchard management in the short-term. However, "fruit damage" includes a series of time- and space-related biological processes at the insect population level and at the agro-ecosystem level which is related to the medium and long-term events of "fruit damage". Moreover, "fruit damage" reflects a "fruit infestation", but there is a significant loss of information to understand, and ultimately, to manage the orchard, if the measurement and, in the worst-case scenario, excludes essential data. Some studies carried out in the past described an uncertain level of association between an insect species and a host plant species since insects are in the plant. This approach assumes that the number of trapped insects represents a surrogate of population abundance, but it does not allow knowing the degree or fruit infestation level effectively. In other studies, the presence or absence of the insect is checked effectively in the host through an identified insect damage, such as a pick on the fruit or a hollow (Cohen and Yuval, 2000; Sarwar et al., 2014). This information, basically reported as a quantification of a nominal or proportional variable maybe not sufficient to understand the processes which operate in time and space. For example, if the goal is to predict the pest dynamics, the quantification of damage precludes the potential forecasts. In turn, the quantification of insects within the fruits was recognized as a better approach to understand the biological processes involved and the factors which determine it (Norrbom and Kim, 1988). Although this fact may appear like a trivial task, nowadays, there are published studies which depict this diversity of approaches to consider the problem of reporting infestation by pulp feeding insects.

Fruit production is a fundamental economic human activity at a global level. A pivotal problem to commercialize fruits is the direct and indirect damage by pulp feeding insects since the wasted fruits cause substantial economic losses (Ekesi et al., 2016). The most emblematic case of the pulp feeding insect is Tephritid fruit flies (Diptera: Tephritidae). They are one of the most critical pests affecting commercial fruit production worldwide (Sarles et al., 2015). At a global level, according to the Food and Agriculture Organization (FAO), Tephritidae caused losses by US$ 1.7 billion every year (Machado da Rosa et al., 2018). Fruit flies cause direct damage to fruits and vegetables by the puncture for oviposition by the female and by larvae feeding, which rot the pulp, by the action of microorganisms present in their digestive system (Aluja, 1994).These pests cause direct damage to important export crops leading to losses of 40% up to 80%, depending on locality, variety and season (Kibira et al., 2010). The presence of these pest species limits access to international markets due to quarantine restrictions imposed by importing countries (Lanzavecchia et al., 2014).

For these reasons, there was an appellant concern to understand the factors which determine the variation in the infestation level.

Therefore, we need a review of the infestation level. We would improve the use and production of data, which generally are available in a variable manner. This fact promotes the loss of essential data and erodes the use of information when looking for general patterns and therefore, looking for a subsequent discovery of excellent pest control practices. Most studies about pulp-feeding insects are related to Tephritid fruit flies which have economic importance. This literature bias limits the possibilities to understand the interaction between host plants and pulp-feeding insects with a broader perspective. Nevertheless, this bias has the advantage to provide tune-fine information about several well-studied plant-insect systems, in agricultural and wild settings. In this context, the use of the infestation level is variable, and as we show, we need to consider this variability.

In the present study, we review the biological meaning of fruit infestation level by pulp-feeding insects, their measurement and jargon. We describe the process of fruit infestation and the types (or classes) of measurement. We identify the related jargon and estimations, taking into account the determining factors (or drivers) of the process. Moreover, we analyze several definitions, limits, and opportunities about the use of estimators of the fruit infestation level. Finally, we discuss and remark several points about the study of their variation regarding the basic and applied implications on the understanding of plant-insect interactions.

Interaction process between pulp feeding insects and host plants

The infestation level is a consequence of the oviposition choice by an individual insect female. The female decision causes different selective filters at the insect's stage, determining the amount of pulp removed and finally, the insect's success. A classic example is the Tephritid fruit flies (Figure 1).

Selection of host plant and oviposition substrate

Pulp-feeding insects do not have parental care, but the female oviposition site choice might be considered indirect parental care (Fox and Czesak, 2000). Host plant selection is critical for development and survival in the next stages of the life cycle (Proffit et al., 2015). Generally, the behavioural scheme of adult females shows the following steps: searching, encounter, landing, fruit surface evaluation and host acceptance (Li et al., 2017). The behaviour determines particular traits which promote a successful egg-laying and larval growth (Janz, 2005).

The selection of the oviposition substrate is a result of an active association between fruit physical properties and remote sensory information, such as olfactory and visual cues (Bruce et al., 2005). Pulp-feeding insects such as fruit flies select the host plant according to kairomone perception (Jang and Light, 1996). The oviposition preference involves physical (colour, firmness, fruit crop, fruit size, texture) and chemical fruit traits (colour, pH, sugar concentration, primary and secondary metabolites) (Aluja and Mangan, 2008; Burrack et al., 2013; Salerno et al., 2020). Moreover, some fruit types protect pulp-feeding insects from predators or facilitate their feeding activity (Wilson et al., 2012; Poyet et al., 2015).

Several studies show the association between female fruit flies and volatile compounds or blends emitted by a host plant among many Tephritid genera (Biasazin et al., 2014; Rasgado et al., 2009; Siderhurst and Jang, 2010). Tephritid fruit fly pests prefer to lay their eggs into ripe fruits (Cornelius et al., 2000). In flies of the genus *Drosophila*, females prefer odours associated with sugar (Tempel et al., 1983) or purple over green colour fruits in experimental studies (Takahara and Takahashi, 2017).

Field studies in *Olea europaea* L. cultivars showed that morphometric traits positively correlates with the infestation level by Olive fruit fly (*Bactrocera oleae* L.) (Garantonakis

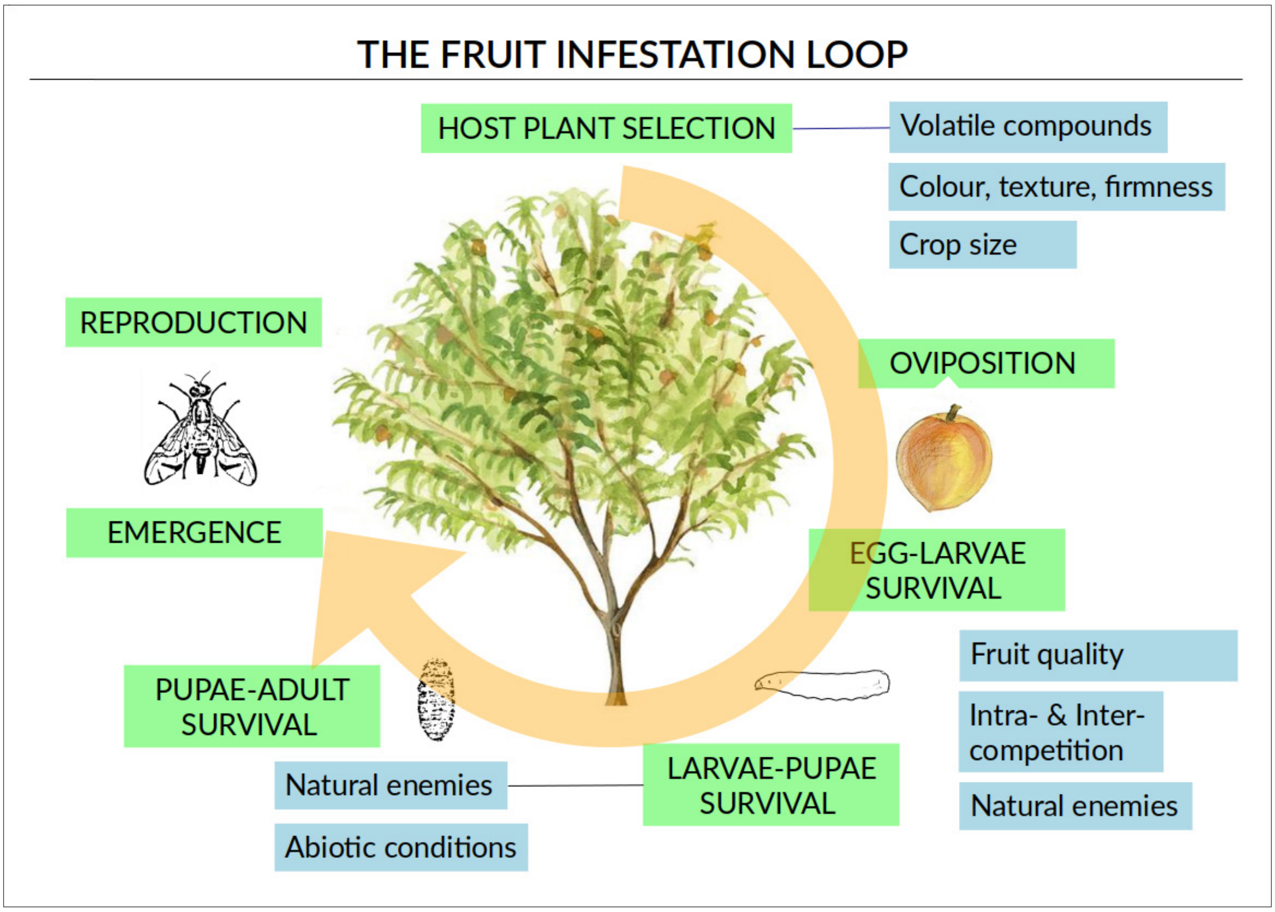

FIGURE 1. Interaction process between pulp-feeding insects and host plants. We show an example of the life cycle of a typical fruit fly. Fruit flies reach a plant host through plant cues or signals constituted by complex fruit traits at the plant and fruit levels (plant level: crop size, volatile compounds; fruit level: colour, texture, firmness, volatile compounds). The location and timing of the individual plant host are also critical interacting factors. Oviposition occurs in at least one fruit among the available fruit display of the individual host plant. An individual female may lay at least one egg per fruit. Fruit may become closed to conspecifics or other species if females mark the fruit with chemical signals. Hatching time is usually short and painful to monitor (first selective filter). The survival rate of the egg-larvae interface depends on fruit quality, intra-specific and inter-specific competition. The interface between the last larval stage and pupation is relatively slow, and it is a crucial stage for management. The survival rate of the larvae-pupae interface depends on abiotic conditions and the incidence rate of natural enemies (second selective filter). The emergence from pupae to adults also depends on abiotic conditions and natural enemies (third selective filter). After emergence, adults soon start looking for a feeding resource needed to reach sexual maturity, copulation and egg-laying. In this stage, survival rate and reproduction success depend on the quality of the nutrients consumed and the mating behaviour. The association between intrinsic traits of insects and biotic-abiotic factors determine the survival rate in a different stage of the life cycle and the intensity or level of the fruit infestation.

et al., 2016; Rizzo et al., 2012). Insects have a set of receptors essential for finding and recognizing a host plant. These characteristics allow them to attack fruits overcoming chemical barriers (Díaz-Fleischer and Aluja, 2003). For example, the variation in the aculeus morphology in Tephritidae may explain the relationship with the host cuticle thickness since species which choose a host plant with a hard cuticle tend to have more pointed aculeus (Díaz-Fleischer et al., 2000).

The females of some Tephritidae species use mechanisms to inhibit the oviposition of conspecifics, reducing the competition with marking pheromones (Arredondo and Díaz-Fleischer, 2006; Nufio and Papaj, 2004). Therefore, there are cases of females who are disturbed by other adult Tephritid flies during the egg-laying, but this competition mechanism is insignificant to others (Duyck et al., 2004).

In summary, the host plant selection by Tephritid fruit flies is a complex phenomenon, and the election of the adequate host involves several factors. The female supposedly chooses the best host to provide the nutritional components and environmental conditions for better survival in the next stages (Birke and Aluja, 2018).

Hatching, larval feeding process and larval survival

Natural enemies affect larval survival and the inter- and intra-specific competition. The intensity of competition in Tephritid fruit flies depends on larval density and abundance of each species within a particular fruit (Liendo et al., 2018). The fruit capacity load (fruit size and pulp availability) determines competition. Furthermore, biological parameters, such as clutch size, the time between clutches and competitive capacity, are essential determinants of competition in plant-eating insects (Denno et al., 1995).

The multiple infestations in the same fruit by one or more females of the same or different insect species can affect larvae, pupae and adult size and performance. In the Apple maggot (*Rhagoletis pomonella* Walshingham), high levels of infestation decreased pupae size (Fedder et al., 1995). Similar patterns show an experimental study of *Bactrocera* *oleae*, where a high density of larvae per fruit reduces the performance of larvae and pupae (Burrack et al*.,* 2009). In the Mediterranean fruit fly (*Ceratitis capitata* Wiedemann), Dukas et al*.* (2001) found that differences in asynchrony in clutches give a competitive advantage to older larvae over younger ones, because older larvae have access to more resources (Duyck et al., 2006). Species have different strategies to minimize competition (Liendo et al., 2018).

Among Tephritidae species, there are different ways of interspecific competition between pairs of species (Duyck et al., 2004). One of them is a hierarchical competition, in which one species dominates and excludes the other, although complete exclusion usually does not occur (Duyck et al., 2004). In Australia and Hawaii, the Queensland fruit fly (*Bactrocera tryoni* Frogatt) and Oriental fruit fly (*B. dorsalis* Hendel) (Duyck et al., 2004), respectively, displaces *C. capitata* by hierarchical competition. Another type of competition is an exploitation competition, which generally occurs at the fruit level. An experimental study carried out in Argentina shows that exploitation competition mediates the interaction between *C. capitata* and the South American fruit fly (*Anastrepha fraterculus* Wiedemann). This study showed that when both species started to consume at the same time, the *A. fraterculus* larvae survival, pupae weight, and duration on larval stage decreased, while pupae weight decreased for *C. capitata* (Liendo et al., 2018).

Fruit fly larvae feed exclusively in the fruit and are the leading cause of damage. The larval performance depends on several factors, but the host fruit quality is the most relevant (Fernandes-da-Silva and Zucoloto, 1993). In different host fruits, there is a high variation in the survival, growth and development time for larvae of Tephritid species (Drew and Yuval, 2000). Generalist species may have the ability to develop under a wide variety of nutrients, whereas specialist species have specific nutritional requirements (Drew and Yuval, 2000). In an experimental study, Hafsi et al. (2016), found that polyphagous species (Peach fruit fly *Bactrocera zonata* Saunders, *Ceratitis catoirii* Guérin-Mèneville, *C. capitata*, and Natal fruit fly *C. rosa* Karsch), have higher survival rates in fruits with high contents of carbohydrates, fibres, and lipids. On the contrary, oligophagous species (Ocean cucurbit fly *Dacus demmerezi* Bezzi, and Tomato fruit fly *Neoceratitis cyanescens* Bezzi) have higher survival rates in fruits with high water content.

Plant defences, such as secondary metabolites and structural mechanisms in fruits, may play an essential role in larval survival (War et al., 2012). In Cucurbitaceae plants, the larval density per fruit of the Melon fly (*B. cucurbitae* Coquillett) decreases when the concentration of phenols, tannins, and flavonoids increases (Haldhar et al., 2015). The larvae of the African fruit fly (*C. fasciventris* Bezzi) did not survive in fruits with high alkaloids concentration (Erbout et al., 2009). In fruits of *Juglans australis* Griseb., Oroño et al. (2018) found that the infestation level of *C. capitata* and *A. fraterculus* positively correlates with sugar content, and negatively correlates with toxic secondary metabolites.

Another interesting point in the feeding process by larvae is the mutualism with symbiotic microorganisms (Ben-Yosef et al., 2015). Bacterial assemblages in the gut of an insect may promote changes in metabolic pathways to provide more nutrients and reduce secondary metabolites which benefit larval development (Mori et al., 2016; Robert et al., 2019). In Queensland fruit flies (*Bactrocera tryoni*), the larvae development is significantly faster in substrate inoculated with yeasts (Piper et al., 2017).

Pupation

The pupa/pupal stage is the most vulnerable, and pupae mortality may be significant for regulating fruit fly populations (Hodgson et al., 1998). Pupation behaviour has consequences in pupae success and adult emergence. Species of fruit flies can pupate inside fruits or larvae come out of the fruit for pupation in the soil (Fletcher, 1987). In the last case, in general, the larvae fall on the soil surface and are exposed to predators and unfavourable ambient conditions (Aluja et al., 2005), and in Tephritidae, this negatively affects the survival rate (Alyokhin et al., 2001; Eskafi and Fernandez, 1990). The most common predators causing high mortality are ants and beetles (Eskafi and Kolbe, 1990; Urbaneja et al., 2006), entomopathogens and parasitoids (Baeza-Larios et al., 2002). Concerning environmental conditions, temperature, relative humidity and soil traits are considered strong predictors of survival, development time and size of emerging adults (El-Gendy and AbdAllah, 2019).

Adult emergence

The adult emerges once overcomes the previous filters. Larval diet influences body mass development, with impacts on reproductive performance (Shelly and Nishimoto, 2017). In this stage, the quality of the nutrients and its optimal level have a meaningful impact on the longevity, reproductive success and dispersal of fruit flies (Prokopy, 1993). Various studies showed that adult flies need protein sources to attaint sexual maturity, egg production, mating frequency, sexual signalling rate, and pheromones production (Aluja et al., 2001; Yuval et al., 2002; Liedo et al., 2013; Lee, 2015).

Mating behaviour also determines reproductive success. Species of Tephritidae display a wide range of matting systems, *e.g*., many species form aggregations (Lek) where males fight and defend a small territory used to mate with the females (Benelli et al., 2014). In this context, the male has paternal assurance strategies, such as mate guarding, male combat and lengthy copulation duration (Headrick and Goeden, 1994). The female also has aggressive behaviour to maintain single oviposition and to reduce competence among larvae (Benelli et al., 2015). On the other hand, the abiotic and biotic factors (climate, host quality, symbionts, and natural enemies, the intra-specific and inter-specific competition) in association with intrinsic traits of insects have impacts on development, survival and reproduction, and this ultimately determines the infestation level which may be economically damaging.

Measurement types

As previously mentioned, there are different expressions and jargon to refer to either damage or infestation (Table 1.1). The representativeness of the information distinguishes the first significant difference. On the one hand, information representing only a nominal or categorical relationship between the insect and the host plant. On the other hand, information representing the magnitude, degree or intensity.

In this study, we propose a distinction between the damage and infestation terms. Although both terms sound similar, they are used indistinctly in the literature. There are cases where "infestation" is the proportion of fruits with typified signs of damage in a sample. In this sense, the reduction in quantity and quality in crops defines damage (Nutter et al*.,* 1993). The damage is the net result of the infestation process. Infestation occurs when the insects feed or oviposit on the host. The incidence or magnitude of the damage caused

Table 1. Main types of measurement of fruit infestation and damage by pulp-feeding insects. The column of cases represents the different ways reported in the literature to calculate damage and infestation. References are representative cases.

Type of estimator	Perspective	Advantages	Disadvantages	Cases	Example references
Damage	- Plant perspective - Qualitative or quantitative indicator	- Quick and cheap quantification - Monitoring methods rely on visual inspection of external appearance	- Several studies consider fruit damage only when insect ovipuncture is visible, and is challenging to observe - Underestimates the real damage because the female can lay numerous eggs inside the fruit - Visual inspection methods are subjective	Percentage of fruits with damage	Jordano 1987, Cohen and Yuval, 2000, Lee et al., 2015
				Number of fruits with dots or picks	Nath, 1966, Braham et al., 2007, Navarro Llopis et al., 2013
Infestation	- Plant-insect interaction perspective - Quantitative indicator	- Provides information about variation in insect abundance by stage	- Requires significant effort for taking data - Needs laboratory processing	Larvae $fruit^{-1}$	Haramoto and Bess, 1970, Feder et al., 1995, Mazor and Erez, 2004
				Larvae kg^{-1}	Swanson and Baranowski, 1972, Montoya et al., 2000, Ovrusky et al., 2003
				Pupae $fruit^{-1}$	Cunningham and Steiner, 1972; Aluja and Boller, 1992, Papadopoulos et al., 2001
				Pupae kg^{-1}	Rhode et al., 1971, Vargas et al., 1993,Vayssières et al., 2009
				Adult $fruit^{-1}$	Leyva et al.,1991, Wong and Ramadan,1992, Poyet et al., 2015
				Adult kg^{-1}	Liquido et al., 1990, Ekesi et al., 2006, Mwatawala et al., 2009

Table 2. Representation of hypothetical cases of sampling for infestation level calculation, considering the variability in the sample of fruits and insects. See section "Caveats and pitfalls in data analysis" for details.

Variables	Host plant species	A			B		
	Insect species	A	B	Pooled	A	B	Pooled
	Kg variability	Invariable	Invariable	Invariable	Variable	Variable	Variable
	Pupae variability	Invariable	Variable	Variable	Invariable	Variable	Variable
*Period 1**	Fruit (kg)	20	20	20	10	10	10
	Pupae (*n*)	100	50	150	100	50	150
Alfa infestation level	Pupae kg^{-1}	5	2.5	7.5	10	5	15
*Period 2**	Fruit (kg)	20	20	20	5	5	10
	Pupae (*n*)	100	25	125	100	25	125
Alfa infestation level	Pupae kg^{-1}	5	1.25	6.25	20	5	12.5
*Period 3**	Fruit (kg)	20	20	20	2	3	2
	Pupae (*n*)	100	7	37	100	10	110
Alfa infestation level	Pupae kg^{-1}	1.5	0.35	1.85	50	3.33	55
	Mean	3.83	1.37	5.2	26.67	4.44	27.5
	Standard deviation	2.02	1.08	2.97	20.82	0.96	23.85

* Period: months, year or sampling season.

by the infestation may be measured after visual signs arise, but infestation occurs since the beginning. However, there are cases in which no visible external marks or holes are present on the damaged fruits. This measure has essential limitations to evaluate the determining factors and in the last instance, a more comprehensive understanding of the process. It is crucial to make decisions regarding commercialization but not at the cost of information lost. Furthermore, the damage only considers what happens in the plant, and it does not take into account what happens with insects.

In turn, measurement, as the number of pupae per fruit, is a subrogation of the damage made by the larvae and it allows adequate comparisons between systems. For this, despite damage and infestation sound similar in some circumstances, we need a distinction to clarify the quantification and process. This distinction leads us to be careful about the use of jargon. Thus, the inflexion point in which term and estimator can explain and measure plant-insect interaction. This term may be "infestation level", assuming that level is continuous and not hierarchical. We estimate the infestation level as the number of individuals of a given stage (larvae, pupae and adult) per measurement unit (for example, tree, fruit, kilogram, area).

Each stage of the life cycle of an insect has limitations for the infestation level calculation:

a) Egg stage. It involves dissection of fruits to count the number of eggs. This task is not simple. The manipulation of fruits ("environment") affects the development of the eggs.
b) Larval stage. It is the stage causing the fruit damage that we perceive. In the same way as eggs, the manipulation of fruits affects larval development.
c) Pupal and adult stage. Consider separate both stages, because the survival from one stage to another is variable and rarely 100%.

Therefore, we recommend to collect information in two steps: a) to wait an adequate time after the fruit collection to allow the highest percentage of larvae in the fruit move to the pupae stage; b) before removing the fruit sample, dissect the fruit to obtain the remaining larvae. In this way, we can calculate the infestation level by adding the number of pupae plus the number of larvae (see below). Some authors report data on the number of infested samples (Raga et al., 2005; Silva et al., 2007) as a level of damage. In these cases, we suggest as more appropriate the term relative infestation.

Estimation of the fruit infestation level or degree

For the estimation of fruit infestation level, we recommend several steps (Figure 2). They include field survey, laboratory processing, and data analysis.

Field survey

Before taking the sample units, we need to take into account the study objectives and design. It is important to consider (1) how many host plant species constitute the sample; (2) the size of the sampling area; (3) the scale (species, population, individual plant, fruit). These points may aid to determine the sampling design and sample size. Furthermore, the number of fruits per sample and the number of samples collected depends mainly on fruit availability and abundance during the season. We recommend collecting ripe and semi-ripe fruits (the main period of attack) randomly and directly from trees or ground, depending on the objectives of the study.

Laboratory survey

The collected fruits are packed in bags and sent to the laboratory. In the laboratory, we recommend (if possible) to measure fruit traits (for example, weight [mass], diameter, sugar concentration, seed load, and number of seeds in multi-seeded fruits). Then, place fruits in plastic containers with a suitable medium for pupation (insect-free sand or vermiculite) and cover the crate with an organdie lid. It is necessary to sift the sand weekly to collect fly pupae until the sample removal. Dissect the fruit to look for the larvae or pupae hidden in the pulp. With these data, we can calculate an infestation level. In some genera, it is challenging to identify the species of the pupae. Therefore, we recommend transferring the pupae to a container with sand with an organdie lid until adult emergence.

Caveats and pitfalls in data analysis

The simplest case of measuring the infestation level is to collect a sample of fruits from a host plant and to check if there are insects for a specific period or date at a given location or spatial unit. However, it is well known that both plant and insect reproductive phenology vary over time. Unfortunately, numerous studies report data in several ways, and it is essential to clear up how to report and interpret the temporal data. We describe the problem with hypothetical cases.

Taking into account whether the sample is variable or invariable, there are four possibilities for reporting temporal data (Table 2). Since the estimation of the infestation level requires fruits and insect sampling, the calculation of the infestation level will depend on whether the fruit sample is invariable or not and whether the insect sample is invariable or not. Indeed, general and realistic situations are variable. However, for didactic purposes, three possibilities are shown in this work, either realistic or not.

Suppose that all cases have a sampling with three periods (months 1 to 3) and we count the number of pupae for two insect species (a and b) for a host plant species (A) (Table 2, left). Case A is a systematic sampling design with an invariable fruit sample per period and a variable number of pupae per period. In this case, note that the infestation level calculated as the mean of the three periods equals the infestation level calculated from the sum of the three periods due to the denominator has a constant value. It is the same for the case of an invariable number of pupae, which is realistic for insects with invariable egg-laying (*i.e.*, one larva per fruit as it happens with codling moth, *Cydia pomonella* L.). Thus, it is not crucial if the infestation level is reported as the mean of the three periods, even if it is from the sum of the three periods.

In case B (Table 2, right), the fruit sample is variable, and the denominator value also varies. Therefore, it is not the same to report the infestation level calculated as the mean of the three periods than the infestation level calculated from the sum of the three periods. Since temporal variation in fruit availability is a realistic and common field situation, authors should report all periods with partial (per period) estimates and global (sum) estimates of infestation level in order to avoid further estimates or interpretations become wrong.

Another case is when, regardless of the fruit sample variation, the number of pupae is zero. Since the numerator is zero, the infestation level is zero. Sometimes, authors overwhelm reporting the zero values. However, we suggest reporting zero values because they are informative of the absence or no detection of insects.

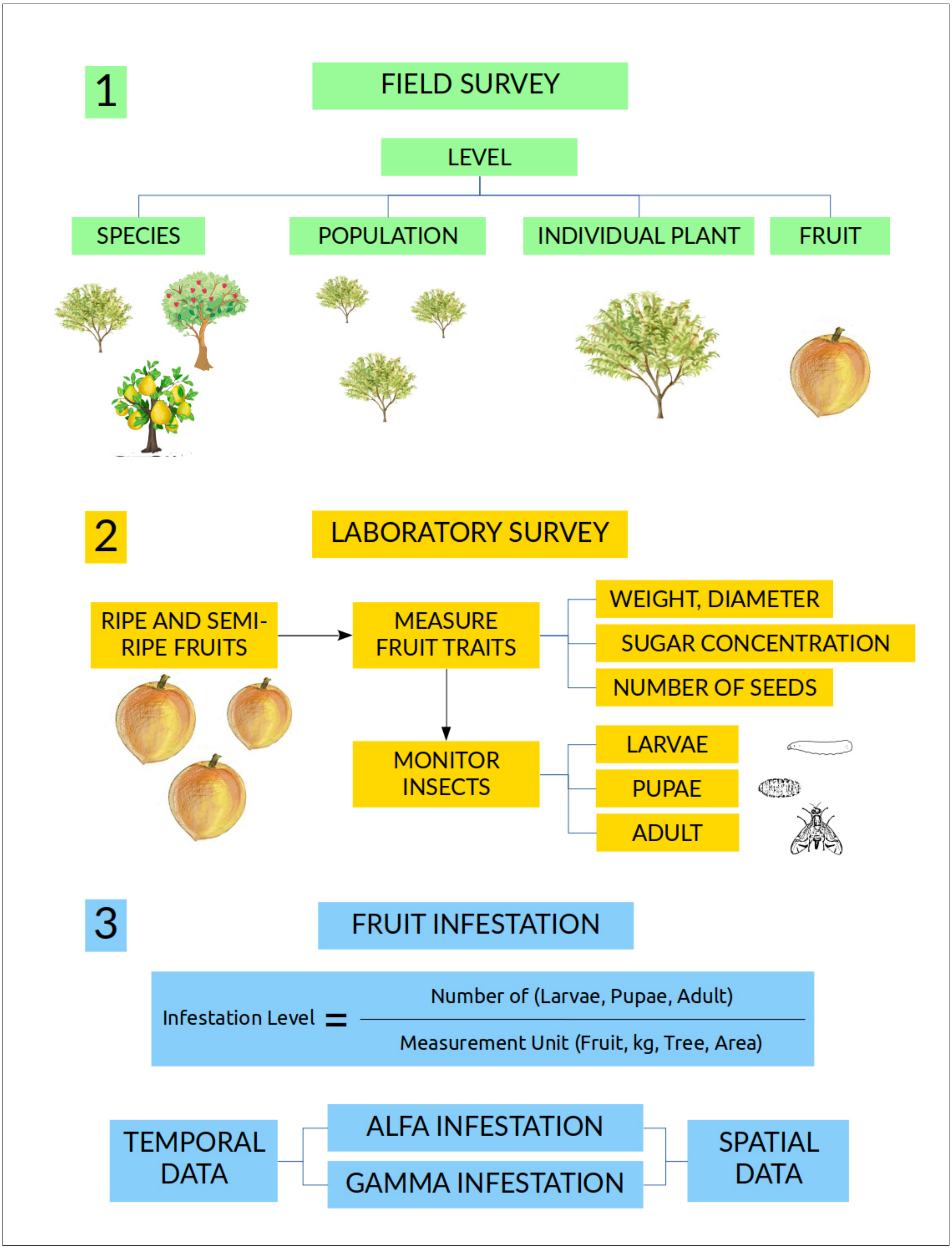

FIGURE 2. Flow chart indicating the steps for the estimation of the fruit infestation level. The first step is the study design and to decide the scale of the work (community, population, individual plant or fruit). In a study area, we collect a sample of ripe and semi-ripe fruits from trees or ground. During the second step, in the laboratory, we measure fruit traits and place them in a suitable medium for optimal development of larvae and pupae. In the last step, we calculate the infestation level on the base of the number of individuals over a measurement unit. At this point, it is necessary to take into account if there are temporary data. How to report them depends on the variability in the fruit sample and on the number of insects. We can report temporal data of two types: a) "alfa" infestation for specific data (for each period), and b) "gamma" infestation as the mean sum of several periods.

Finally, the other concern in data reporting refers to the relationship between the sampling technique and the results. Ideally, it sounds better to know the variation of the infestation level at several scales, fruit, plant, population and species. In general, a fruit sample from a host results in several insect species from one plant host species; and larvae and pupae are often difficult to identify beyond family or genera. Different insect species emerging from the same vessel conform a "pooled sample" (Table 2), and we recommend their report. Thus, a rule is to report the obtained data per plant host and insect at the finest-grained scale and the biological organization level measured. For market purposes, we may report both the number and mass of the sampled fruits together with the market fruit unit (*e.g.*, harvest, tree, bin), beyond biological considerations.

In order to distinguish the jargon, we suggest classifying the different scales as (1) "alfa" ("punctual") infestation level for the data of a given locality, period and plant host, either at the fruit, plant, or population level; (2) "gamma" ("global") infestation level for the infestation level calculated as the mean of several periods or from the sum of the sampling periods. For practical and logistic reasons, the most commonly available data is a gamma infestation level, and the ideal reporting should also include the alfa infestation level.

Others considerations

Many factors and interactions affect the development of pest insect populations. For instance, temperature, rain, host availability, season and altitude, crop arrangement, or quality of habitat patches strongly affect fruit fly activity and abundance (Ekesi et al., 2006; Vayssieres et al., 2015; Wang et al., 2016). These factors vary in space and time, and adult populations show periodic fluctuations throughout the year, and this affects the infestation level. For example, the susceptibility of a potential host species will depend on whether the seasonal occurrence of the fly population is synchronous with the period of fruit maturation (Messina et al., 1991). Like many crop pests, the infestation level of fruit flies varies over the years (Burrack et al., 2013). Therefore, to known and forecast pest effects on crops, it is necessary to record the temporal series of infestation levels.

Another regard that intervenes in the evaluation of the level of infestation is the factors related to climate change. As we have known, the increase in temperature has implications in the greater susceptibility of plants to attack by insects. Additionally, temperature variation affects insect physiology and behaviour, reducing their development time (increases the number of generations/year), accelerate its metabolic rate and increasing food consumption, causing the level of infestation to increase (Hellmann et al., 2008).

Climate change also affects the distribution and abundance of pest insects, favouring invasions to places where these insects were in low proportions or absent. Many pest species within the genera Anastrepha, Bactrocera and Ceratitis have a tropical origin and the ubiquity of its host plants facilitated the invasion of many of them (Hill et al., 2016).

Any poleward range expansion associated with climate change opens up new habitats for these species, in many cases in regions with high fruit production (Stephens et al., 2007; Ni et al., 2012; Fu et al., 2014). Specifically, the warming of the climate in temperate regions improves the conditions for flies to establish themselves, through fewer frosty days, a longer growing season and a higher frequency of warm nights (Papadopoulos et al., 2013). Because Tephritids often have a high dispersal capacity and rapid growth and reproduction rates (Tscharntke et al., 2005), climate change could promote that fruit flies becomes a more significant severe problem due to an increase in the levels of fruit infestation.

Furthermore, a potential research path to improve management strategies rests on the extent and ways by selective factors affect the dynamics of plant-insect interactions. For instance, selected plant varieties (linked to artificial selection from plant breeding) and management practices might function as selective forces acting on insect populations (Varshney et al., 2005).

Importance of standard measurements for pest management

The knowledge of the infestation level is essential to understand the process of crop-insect interaction and may have essential implications in pest management. This measure provides quantitative information about the population dynamics of insects. To control fruit fly population, the farmers might involve the use of control methods that may include the use of beneficial natural enemies, cultural control, chemical, and physical control (Sarwar, 2015; Ekesi et al., 2016). For example, knowledge of the temporal and spatial variation in infestation level may help to reduce the doses of chemical applications or help to know which control methods or combinations are adequate for a given cultivar or variety, period or specific areas. The infestation level helps to produce management criteria and establish the fruit fly host status and pest labelling by government agents for quarantine restrictions. This knowledge about Tephritid fruit fly species and their relative utilization in a given area is crucial for developing control strategies of low environmental impact.

Conclusions

This overview provides a conceptual basis of the infestation level useful for field estimation and further analysis. Our perception is that we must preclude the use of different fruit infestation levels because it is inefficient. We need more in-depth work on standardization procedures because we can get a more significant benefit in terms of published biological information and terms of understanding of the processes associated with the interaction between the host plant and the pulp feeding insects.

Data are more substantial than they are usually perceived. The reporting of the infestation level should be more careful than before. The availability of data which results from damage information is crucial, but so is the information on the biological processes of both sides of the plant-insect interaction.

Measuring the infestation levels of pupae and adults would be relevant for applied and basic studies, and it would be an effort necessary to increase the understanding of the plant-insect interactions with a broader perspective. Through this overview, we claim for a proper process to take advantage of the information and to be more efficient in the development of crop pest management strategies.

Acknowledgments

Thanks to Karina Aguilar-Tejada, Sergio Ovruski, Alejandro Amado, Guido van Nieuwenhove, Javier Altamirano, and Marcela Correa for literature search, data recording and reviewing. To Claudia F. Marinho for insect images.

Funding

This research was funded by PIP-CONICET 1353 to PS; Z-0113-1 from Fundación Miguel Lillo to MO; CIT-CONICET-fellowship to AB.

References

Aluja, M. (1994). Bionomics and management of *Anastrepha*. Annu. Rev. Entomol. *39*, 155–178. https://doi.org/10.1146/annurev.en.39.010194.001103.

Aluja, M., and Boller, E. (1992). Host marking pheromone of *Rhagoletis cerasi*: foraging behavior in response to synthetic pheromonal isomers. J. Chem. Ecol. *18*, 1299–1311. https://doi.org/10.1007/BF00994357.

Aluja, M., and Liedo, P. (1993). Fruit Flies Biology and Management (New York: Springer-Verlag). https://doi.org/10.1007/978-1-4757-2278-9.

Aluja, M., and Mangan, R.L. (2008). Fruit fly (Diptera: Tephritidae) host status determination: Critical conceptual, methodological, and regulatory considerations. Ann. Rev. Entomol. *53*, 473–502. https://doi.org/10.1146/annurev.ento.53.103106.093350.

Aluja, M., Jácome, I., and Macías-Ordoñez, R. (2001). Effect of adult nutrition on male sexual performance in four neotropical fruit fly species of the genus *Anastrepha* (Diptera: Tephritidae). J. Insect Behav. *14*, 759–775. https://doi.org/10.1023/A:1013037400676.

Aluja, M., Sivinski, J., Rull, J., and Hodgson, P.J. (2005). Behavior and predation of fruit fly larvae (*Anastrepha* spp.) (Diptera: Tephritidae) after exiting fruit in four types of habitats in tropical Veracruz, Mexico. Environm. Entomol. *34*, 1507–1516. https://doi.org/10.1603/0046-225X-34.6.1507.

Alyokhin, A.V., Mille, C., Messing, R.H., and Duan, J.J. (2001). Selection of pupation habitats by oriental fruit fly larvae in the laboratory. J. Insect Behav. *14*, 57–67. https://doi.org/10.1023/A:1007849629409.

Arredondo, J., and Díaz-Fleischer, F. (2006). Oviposition deterrents for the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae) from fly faeces extracts. Bull. Entomol. Res. *96*, 35–42. https://doi.org/10.1079/BER2005399.

Baeza-Larios, G., Sivinski, J., Holler, T., and Aluja, M. (2002). The ability of *Coptera haywardi* (Ogloblin) (Hymenoptera: Diapriidae) to locate and attack pupae of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), under seminatural conditions. Biol. Control *23*, 213–218. https://doi.org/10.1006/bcon.2001.1010.

Benelli, G., Daane, K.M., Canale, A., Niu, C.Y., Messing, R.H., and Vargas, R.I. (2014). Sexual communication and related behaviours in Tephritidae: Current knowledge and potential applications for integrated pest management. J. Pest Sci. *87*, 385–405. https://doi.org/10.1007/s10340-014-0577-3.

Benelli, G., Romano, D., Messing, R.H., and Canale, A. (2015). Population-level lateralized aggressive and courtship displays make better fighters not lovers: Evidence from a fly. Behav. Process. *115*, 163–168. https://doi.org/10.1016/j.beproc.2015.04.005.

Ben-Yosef, M., Pasternak, Z., Jurkevitch, E., and Yuval, B. (2015). Symbiotic bacteria enable olive fly larvae to overcome host defenses. R. Soc. Open Sci. *2*, 150–170. https://doi.org/10.1098/rsos.150170.

Biasazin, T.D., Karlsson, M.F., Hillbur, Y., Seyoum, E., and Dekker, T. (2014). Identification of host blends that attract the African invasive fruit fly, *Bactrocera invadens*. J. Chem. Ecol. *40*, 966–976. https://doi.org/10.1007/s10886-014-0501-6.

Birke, A., and Aluja, M. (2018). Do mothers really know best? Complexities in testing the preference-performance hypothesis in polyphagous frugivorous fruit flies. Bull. Entomol. Res. *108*, 674–684. https://doi.org/10.1017/S0007485317001213.

Braham, M., Pasqualini, E., and Ncira, N. (2007). Efficacy of kaolin, spinosad and malathion against *Ceratitis capitata* in Citrus orchards. B. Insectol. *60*, 39.

Bronstein, J.L. (2001). The exploitation of mutualisms. Ecol. Lett. *4*, 277–287. https://doi.org/10.1046/j.1461-0248.2001.00218.x.

Bronstein, J.L., and Barbosa, P. (2002). Multitrophic/multispecies mutualistic interactions: The role of non-mutualists in shaping and mediating mutualisms. In Multitrophic Level Interactions, T. Tscharntke, and B.A. Hawkins, eds. (Cambridge, U.K.: Cambridge University Press), p. 44–65. https://doi.org/10.1017/CBO9780511542190.003.

Bruce, M.J., Heiling, A.M., and Herberstein, M.E. (2005). Spider signals: are web decorations visible to birds and bees? Biol. Lett. *1*, 299–302. https://doi.org/10.1098/rsbl.2005.0307.

Burrack, H.J., Fornell, A.M., Connell, J.H., O'Connell, N.V., Phillips, P.A., Vossen, P.M., and Zalom, F.G. (2009). Intraspecific larval competition in the olive fruit fly (Diptera: Tephritidae). Environm. Entomol. *38*, 1400–1410. https://doi.org/10.1603/022.038.0508.

Burrack, H.J., Fernández, G.E., Spivey, T., and Kraus, D.A. (2013). Variation in selection and utilization of host crops in the field and laboratory by *Drosophila suzukii* Matsumara (Diptera: Drosophilidae), an invasive frugivore. Pest Mgt. Sci. *69*, 1173–1180. https://doi.org/10.1002/ps.3489.

Cohen, H., and Yuval, B. (2000). Perimeter trapping strategy to reduce Mediterranean fruit fly (Diptera: Tephritidae) damage on different host species in Israel. J. Econ. Entomol. *93*, 721–725. https://doi.org/10.1603/0022-0493-93.3.721.

Cornelius, M.L., Nergel, L., Duan, J.J., and Messing, R.H. (2000). Responses of female oriental fruit flies (Diptera: Tephritidae) to protein and host fruit odors in field cage and open field tests. Environm. Entomol. *29*, 14–19. https://doi.org/10.1603/0046-225X-29.1.14.

Cunningham, R.T., and Steiner, L.F. (1972). Field trial of Cue-lure+ Naled on saturated fiberboard blocks for control of the melon fly by the male-annihilation technique. J. Econ. Entomol. *65*, 505–507. https://doi.org/10.1093/jee/65.2.505.

Denno, R.F., McClure, S., and Ott, J.R. (1995). Interspecific interactions in phytophagous insects competition reexamined and resurrected. Annu. Rev. Entomol. *40*, 297–331. https://doi.org/10.1146/annurev.en.40.010195.001501.

Díaz-Fleischer, F., and Aluja, M. (2003). Clutch size in frugivorous insects as a function of host firmness: The case of the tephritid fly *Anastrepha ludens*. Ecol. Entomol. *28*, 268–277. https://doi.org/10.1046/j.1365-2311.2003.00517.x.

Díaz-Fleischer, F., Papaj, D.R., Prokopy, R.J., Norrbom, A.L., and Aluja, M. (2000). Evolution of fruit fly oviposition behavior. In Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior, M. Aluja, and N. Norrbom, eds. (Boca Raton, Florida, U.S.A.: CRC Press), p. 811–841. https://doi.org/10.1201/9781420074468.ch30.

Drew, R.A., and Yuval, B. (2000). The evolution of fruit fly feeding behavior. In Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior, M. Aluja, and N. Norrbom, eds. (Boca Raton, Florida, U.S.A.: CRC Press), p. 749–768. https://doi.org/10.1201/9781420074468-38.

Dukas, R., Prokopy, R.J., and Duan, J.J. (2001). Effects of larval competition on survival and growth in Mediterranean fruit flies. Ecol. Entomol. *26*, 587–593. https://doi.org/10.1046/j.1365-2311.2001.00359.x.

Duyck, P.F., David, P., and Quilici, S. (2004). A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). Ecol. Entomol. *29*, 511–520. https://doi.org/10.1111/j.0307-6946.2004.00638.x.

Duyck, P.F., David, P., Junod, G., Brunel, C., Dupont, R., and Quilici, S. (2006). Importance of competition mechanisms in successive invasions by polyphagous tephritids in La Réunion. Ecology *87*, 1770–1780. https://doi.org/10.1890/0012-9658(2006)87[1770:IOCMIS]2.0.CO;2.

Eskafi, F.M., and Fernández, A. (1990) Larval-pupal mortality of Mediterranean fruit fly (Diptera: Tephritidae) from interaction of soil, moisture, and temperature. Environm. Entomol. *19*, 1666–1670. https://doi.org/10.1093/ee/19.6.1666.

Eskafi, F.M., and Kolbe, M.M. (1990). Predation on larval and pupal *Ceratitis capitata* (Diptera: Tephritidae) by the ant *Solenopsis geminata* (Hymenoptera: Formicidae) and other predators in Guatemala. Environm. Entomol. *19*, 148–153. https://doi.org/10.1093/ee/19.1.148.

Ekesi, S., Nderitu, P.W., and Rwomushana, I. (2006). Field infestation, life history and demographic parameters of the fruit fly *Bactrocera invadens* (Diptera: Tephritidae) in Africa. Bull. Entomol. Res. *96*, 379–386.

Ekesi, S., De Meyer, M., Mohamed, S.A., Virgilio, M., and Borgemeister, C. (2016). Taxonomy, ecology and management of native and exotic fruit fly species in Africa. Annu. Rev. Entomol. *61*, 219–238. https://doi.org/10.1146/annurev-ento-010715-023603.

El-Gendy, I.R., and AbdAllah, A.M. (2019). Effect of soil type and soil water content levels on pupal mortality of the peach fruit fly [*Bactrocera zonata* (Saunders)] (Diptera: Tephritidae). Int. J. Pest Mgt. *65*, 154–160. https://doi.org/10.1080/09670874.2018.1485988.

Erbout, N., De Meyer, M., Vangestel, C., and Lens, L. (2009). Host plant toxicity affects developmental rates in a polyphagous fruit fly: Experimental evidence. Biol. J. Linnean Soc. *97*, 728–737. https://doi.org/10.1111/j.1095-8312.2009.01219.x.

Feder, J.L., Reynolds, K., Go, W., and Wang, E.C. (1995). Intra- and interspecific competition and host race formation in the apple maggot fly, *Rhagoletis pomonella* (Diptera: Tephritidae). Oecologia *101*, 416–425. https://doi.org/10.1007/BF00329420.

Fedriani, J.M., and Delibes, M. (2013). Pulp feeders alter plant interactions with subsequent animal associates. J. Ecol. *101*, 1581–1588. https://doi.org/10.1111/1365-2745.12146.

Fedriani, J.M., Zywiec, M., and Delibes, M. (2012). Thieves or mutualists? Pulp feeders enhance endozoochore local recruitment. Ecology *93*, 575–587. https://doi.org/10.1890/11-0429.1.

Fernandes-da-Silva, P.G., and Zucoloto, F.S. (1993). The influence of host nutritive value on the performance and food selection in *Ceratitis capitata* (Diptera, Tephritidae). J. Insect Physiol. *39*, 883–887. https://doi.org/10.1016/0022-1910(93)90121-7.

Ferriere, R., Bronstein, J.L., Rinaldi, S., Law, R., and Gauduchon, M. (2002). Cheating and the evolutionary stability of mutualisms. Proc. R. Soc. Lond. B. *269*, 773–780. https://doi.org/10.1098/rspb.2001.1900.

Fletcher, B.S. (1987). The biology of dacine fruit flies. Annu. Rev. Entomol. *32*, 115–144. https://doi.org/10.1146/annurev.en.32.010187.000555.

Fox, C.W., and Czesak, M.E. (2000). Evolutionary ecology of progeny size in arthropods. Annu. Rev. Entomol. *45*, 341–369. https://doi.org/10.1146/annurev.ento.45.1.341.

Fu, L.N., Li, Z.H., Huang, G.S., Wu, X.X., Ni, W.L., and Qu, W.W. (2014). The current and future potential geographic range of West Indian fruit fly, *Anastrepha obliqua* (Diptera: Tephritidae). Insect Sci. *21*, 234–244. https://doi.org/10.1111/1744-7917.12018.

Garantonakis, N., Varikou, K., Markakis, E., Birouraki, A., Sergentani, C., Psarras, G., and Koubouris, G.C. (2016). Interaction between *Bactrocera oleae* (Diptera: Tephritidae) infestation and fruit mineral element content in *Olea europaea* (Lamiales: Oleaceae) cultivars of global interest. Appl. Entomol. Zool. *51*, 257–265. https://doi.org/10.1007/s13355-016-0397-4.

Hafsi, A., Facon, B., Ravigné, V., Chiroleu, F., Quilici, S., Chermiti, B., and Duyck, P.F. (2016). Host plant range of a fruit fly community (Diptera: Tephritidae): Does fruit composition influence larval performance? BMC Ecol. *16*, 40. https://doi.org/10.1186/s12898-016-0094-8.

Haldhar, S.M., Choudhary, B.R., Bhargava, R., and Gurjar, K. (2015). Host plant resistance (HPR) traits of ridge gourd (*Luffa acutangula* (Roxb.) L. against melon fruit fly, (*Bactrocera cucurbitae* (Coquillett)) in hot arid region of India. Sci. Hortic. *194*, 168–174. https://doi.org/10.1016/j.scienta.2015.08.001.

Haramoto, F.H., and Bess, H.A. (1970). Recent studies on the abundance of the oriental and Mediterranean fruit flies and the status of their parasites. Proc. Hawaii Entomol. Soc. *20*, 551–566.

Headrick, D.H., and Goeden, R.D. (1994). Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera) mating systems. Stud. Dipterol. *1*, 194–252.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G., and Dukes, J.S. (2008). Five potential consequences of climate change for invasive species. Conserv. Biol. *22*, 534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x.

Hill, M.P., Bertelsmeier, C., Clusella-Trullas, S., Garnas, J., Robertson, M.P., and Terblanche, J.S. (2016). Predicted decrease in global climate suitability masks regional complexity of invasive fruit fly species response to climate change. Biol. Invasions *18*(4), 1105–1119. https://doi.org/10.1007/s10530-016-1078-5.

Jang, E., and Light, D. (1996). Olfactory semiochemicals of Tephritids. In Fruit Fly Pests, B.A. Mc. Pheron, and G.J. Steck, eds. (U.S.A.: Lucie Press), p. 73–90. https://doi.org/10.1201/9780367812430-15.

Janz, N. (2005). The relationship between habitat selection and preference for adult and larval food resources in the polyphagous butterfly *Vanessa cardui* (Lepidoptera: Nymphalidae). J. Insect Behav. *18*, 767–780. https://doi.org/10.1007/s10905-005-8739-z.

Jordano, P. (1987). Avian fruit removal: Effects of fruit variation, crop size, and insect damage. Ecology *68*, 1711–1723. https://doi.org/10.2307/1939863.

Kibira, M.H., Njehia, B., Muriithi, B., Mohamed, S., and Ekesi, S. (2010). Economic evaluation of integrated management of fruit fly in mango production in Embu County, Kenya. Afr. J. Agric. Res. Econ. *10*, 343–353.

Lanzavecchia, S.B., Juri, M., Bonomi, A., Gomulski, L., Scannapieco, A.C., Segura, D.F., Malacrida, A., Cladera, J.L., and Gasperi, G. (2014). Microsatellite markers from the "South American fruit fly" *Anastrepha fraterculus*: A valuable tool for population genetic analysis and SIT applications. BMC Genet. *15* (Suppl. 2), S13. https://doi.org/10.1186/1471-2156-15-S2-S13.

Lee, K.P. (2015). Dietary protein: Carbohydrate balance is a critical modulator of lifespan and reproduction in *Drosophila melanogaster*: A test using a chemically defined diet. J. Insect Physiol. *75*, 12–19. https://doi.org/10.1016/j.jinsphys.2015.02.007.

Lee, J. C., Dreves, A.J., Cave, A.M., Kawai, S., Isaacs, R., Miller, J.C., Van Timmeren, S., and Bruck, D.J. (2015). Infestation of wild and ornamental noncrop fruits by *Drosophila suzukii* (Diptera: Drosophilidae). Ann. Entomol. Soc. Am. *108*, 117–129. https://doi.org/10.1093/aesa/sau014.

Leyva, J.L., Browning, H.W., and Gilstrap, F.E. (1991). Development of *Anastrepha ludens* (Diptera: Tephritidae) in several host fruit. Environm. Entomol. *20*, 1160–1165. https://doi.org/10.1093/ee/20.4.1160.

Li, W.-Z., Teng, X.-H., Zhang, H.-F., Liu, T., Wang, Q., Yuan, G., and Guo, X.-R. (2017). Comparative host selection responses of specialist (*Helicoverpa assulta*) and generalist (*Helicoverpa armigera*) moths in complex plant environments. PLoS ONE *12*, e0171948. https://doi.org/10.1371/journal.pone.0171948.

Liedo, P., Orozco, D., Cruz-López, L., Quintero, J.L., Becerra-Pérez, C., del Refugio Hernández, M., Oropeza, A., and Toledo, J. (2013). Effect of post-teneral diets on the performance of sterile *Anastrepha ludens* and *Anastrepha obliqua* fruit flies. J. Appl. Entomol. *137*, 49–60. https://doi.org/10.1111/j.1439-0418.2010.01568.x.

Liendo, M.C., Parreno, M.A., Cladera, J.L., Vera, M.T., and Segura, D.F. (2018). Coexistence between two fruit fly species is supported by the different strength of intra- and interspecific competition. Ecol. Entomol. *43*, 294–303. https://doi.org/10.1111/een.12501.

Liquido, N.J., Cunningham, R.T., and Nakagawa, S. (1990). Host plants of Mediterranean fruit fly (Diptera: Tephritidae) on the Island of Hawaii (1949–1985 survey). J. Econ. Entomol. *83*, 1863–1878. https://doi.org/10.1093/jee/83.5.1863.

Machado da Rosa, J., Zanelato Nunes, M., Carissimi Boff, M., Mello Garcia, F.R., Boff, P., and Franco, C.R. (2018). Fruit fly (Diptera: Tephritidae) assemblage in a feijoa orchard in Santa Catarina State, Brazil. Rev. Colomb. Entomol. *44*, 110–115. https://doi.org/10.25100/socolen.v44i1.6547.

Mazor, M., and Erez, A. (2004). Processed kaolin protects fruits from Mediterranean fruit fly infestations. Crop Prot. *23*(1), 47–51. https://doi.org/10.1016/S0261-2194(03)00169-8.

Messina, F.J., Alston, D.G., and Jones, V.P. (1991). Oviposition by the Western Cherry Fruit-Fly (Diptera, Tephritidae) in relation to host development. J. Kansas Entomol. Soc. *64*, 197–208.

Montoya, P., Liedo, P., Benrey, B., Cancino, J., Barrera, J.F., Sivinski, J., and Aluja, M. (2000). Biological control of *Anastrepha* spp. (Diptera: Tephritidae) in mango orchards through augmentative releases of *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). Biol. Control *18*, 216–224. https://doi.org/10.1006/bcon.2000.0819.

Mori, B.A., Whitener, A.B., Leinweber, Y., Revadi, S., Beers, E.H., Witzgall, P., and Becher, P.G. (2016). Enhanced yeast feeding following mating facilitates control of the invasive fruit pest *Drosophila suzukii*. J. Appl. Ecol. *54*, 170–177. https://doi.org/10.1111/1365-2664.12688.

Mwatawala, M.W., De Meyer, M., Makundi, R.H., and Maerere, A.P. (2009). Host range and distribution of fruit-infesting pestiferous fruit flies (Diptera, Tephritidae) in selected areas of Central Tanzania. Bull. Entomol. Res. *99*, 629–641. https://doi.org/10.1017/S0007485309006695.

Nath, P. (1966). Varietal resistance of gourds to the fruit fly. Indian Hortic. *23*, 69–78.

Navarro-Llopis, V., Primo, J., and Vacas, S. (2013). Efficacy of attract-and-kill devices for the control of *Ceratitis capitata*. Pest Mgt. Sci. *69*, 478–482. https://doi.org/10.1002/ps.3393.

Ni, W.L., Li, Z.H., Chen, H.J., Wan, F.H., Qu, W.W., Zhang, Z., and Kriticos, D.J. (2012). Including climate change in pest risk assessment: The peach fruit fly, *Bactorcera zonata* (Diptera: Tephritidae). Bull. Entomol. Res. *102*, 173–183. https://doi.org/10.1017/S0007485311000538.

Norrbom, A.L., and Kim, K.C. (1988). A list of the reported host plants of the species of *Anastrepha* (Diptera: Tephritidae). Aphis *81* (U.S.A.).

Nufio, C.R., and Papaj, D.R. (2004). Host-marking behaviour as a quantitative signal of competition in the walnut fly *Rhagoletis juglandis*. Ecol. Entomol. *29*, 336–344. https://doi.org/10.1111/j.1365-2311.2004.00607.x.

Nutter, F.W., Teng, P.S., and Royer, M.H. (1993). Terms and concepts for yield, crop loss, and disease thresholds. Plant Dis. *77*, 211–215.

Oroño, L., Aluja, M., Ovruski, S., Rull, J., Interdonato, R., Prado, F.E., and Hilal, M. (2018). Dynamics of soluble sugars and secondary metabolites in fruit of *Juglans australis* attacked by *Anastrepha fraterculus* and *Ceratitis capitata* (Diptera: Tephritidae). Arthropod-Plant Interact. *13*, 1–11. https://doi.org/10.1007/s11829-018-9639-4.

Ovruski, S., Schliserman, P., and Aluja, M. (2003). Native and introduced host plants of *Anastrepha fraterculus* and *Ceratitis capitata* (Diptera: Tephritidae) in Northwestern Argentina. J. Econ. Entomol. *96*, 1108–1118. https://doi.org/10.1603/0022-0493-96.4.1108.

Papadopoulos, N.T., Katsoyannos, B.I., Carey, J.R., and Kouloussis, N.A. (2001). Seasonal and annual occurrence of the Mediterranean fruit fly (Diptera: Tephritidae) in northern Greece. Ann. Entomol. Soc. Am. *94*, 41–50. https://doi.org/10.1603/0013-8746(2001)094[0041:SAAOOT]2.0.CO;2.

Papadoupoulos, N.T., Plant, R.E., and Carey, J.R. (2013). From trickle to flood: The large-scale, cryptic invasion of California by tropical fruit flies. Proc. R. Soc. B. *280*, 2013.1466. https://doi.org/10.1098/rspb.2013.1466.

Piper, A.M., Farnier, K., Linder, T., Speight, R., and Cunningham, J.P. (2017). Two gut-associated yeasts in a Tephritid fruit fly have contrasting effects on adult attraction and larval survival. J. Chem. Ecol. *43*, 891–901. https://doi.org/10.1007/s10886-017-0877-1.

Poyet, M., Le Roux, V., Gibert, P., Meirland, A., Prévost, G., Eslin, P., and Chabrerie, O. (2015). The wide potential trophic niche of the Asiatic fruit fly *Drosophila suzukii*: The key of its invasion success in temperate Europe? PLoS ONE *10*, e0142785. https://doi.org/10.1371/journal.pone.0142785.

Proffit, M., Khallaf, M.A., Carrasco, D., Larsson, M.C., and Anderson, P. (2015). 'Do you remember the first time?' Host plant preference in a moth is modulated by experiences during larval feeding and adult mating. Ecol. Lett. *18*, 365–374. https://doi.org/10.1111/ele.12419.

Prokopy, R.J. (1993). Levels of quantitative investigation of tephritid fly foraging behavior. In Fruit Flies Biology and Management, M. Aluja, and P. Liedo, eds. (New York: Springer-Verlag), p. 165–171. https://doi.org/10.1007/978-1-4757-2278-9_30.

Prokopy, R.J., and Roitberg, B.D. (1984). Foraging behavior of true fruit flies: Concepts of foraging can be used to determine how tephritids search for food, mates, and egg-laying sites and to help control these pests. Am. Sci. *72*, 41–49.

Raga, A., Machado, R.A., de Souza Filho, M.F., Sato, M.E., and Siloto, R.C. (2005). Tephritoidea (Diptera) species from Myrtaceae fruits in the state of São Paulo, Brazil. Entomotropica *20*, 11–14.

Rasgado, M.A., Malo, E.A., Cruz-López, L., Rojas, J.C., and Toledo, J. (2009). Olfactory response of the Mexican fruit fly (Diptera: Tephritidae) to *Citrus aurantium* volatiles. J. Econ. Entomol. *102*, 585–594. https://doi.org/10.1603/029.102.0216.

Rizzo, R., Caleca, V., and Lombardo, A. (2012). Relation of fruit color, elongation, hardness, and volume to the infestation of olive cultivars by the olive fruit fly, *Bactrocera oleae*. Entomol. Exp. Appl. *145*, 15–22. https://doi.org/10.1111/j.1570-7458.2012.01311.x.

Rhode, R.H., Simon, J., Perdomo, A., Gutiérrez, J., Dowling, Jr., C.F., and Lindquist, D.A. (1971). Application of the sterile-insect-release technique in Mediterranean fruit fly suppression. J. Econ. Entomol. *64*, 708–713. https://doi.org/10.1093/jee/64.3.708.

Robert, A., Qadri, M., Blair, J., and Wong, A.C.N. (2019). The microbiome of fruit flies as novel targets for pest management. In Safe and Sustainable Crop Protection. (U.S.A.: American Chemical Society), p. 1–37. https://doi.org/10.1021/bk-2019-1334.ch001.

Salerno, G., Rebora, M., Piersanti, S., Gorb, E., and Gorb, S. (2020). Mechanical ecology of fruit-insect interaction in the adult Mediterranean fruit fly *Ceratitis capitata* (Diptera: Tephritidae). Zoology *139*, 125748. https://doi.org/10.1016/j.zool.2020.125748.

Sallabanks, R., and Courtney, S.P. (1992). Frugivory, seed predation, and insect-vertebrate interactions. Annu. Rev. Entomol. *37*, 377–400. https://doi.org/10.1146/annurev.en.37.010192.002113.

Sarles, L., Verhaeghe, A., Francis, F., and Verheggen, F.J. (2015). Semiochemicals of *Rhagoletis* fruit flies: Potential for integrated pest management. Crop Prot. *78*, 114–118. https://doi.org/10.1016/j.cropro.2015.09.001.

Sarwar, M. (2015). Mechanical control prospectus to aid in management of fruit flies and correlated Tephritid (Diptera: Tephritidae) pests. Int. J. Animal Biol. *1*, 190–195.

Sarwar, M., Hamed, M., Yousaf, M., and Hussain, M. (2014). Surveillance on population dynamics and fruits infestation of Tephritid fruit flies (Diptera: Tephritidae) in mango (*Mangifera indica* L.) orchards of Faisalabad, Pakistan. Int. J. Sci. Res. Environm. Sci. *2*, 113. https://doi.org/10.12983/ijsres-2014-p0113-0119.

Shelly, T.E., and Nishimoto, J. (2017). Does female mate choice confer direct fitness benefits? Results from a tephritid fruit fly. Ann. Entomol. Soc. Am. *110*, 204–211. https://doi.org/10.1093/aesa/saw073.

Siderhurst, M.S., and Jang, E.B. (2010). Cucumber volatile blend attractive to female melon fly, *Bactrocera cucurbitae* (Coquillett). J. Chem. Ecol. *36*, 699–708. https://doi.org/10.1007/s10886-010-9804-4.

Silva, R.A.D., Nascimento, D.B.D., Deus, E.D.G.D., Souza, G.D.D., and Oliveira, L.P.S.D. (2007). Host and parasitoids of *Anastrepha* spp. (Diptera: Tephritidae) in Itaubal do Piririm, Amapá State, Brazil. Ciência Rural *37*, 557–560. https://doi.org/10.1590/S0103-84782007000200041.

Stephens, A.E.A., Kriticos, D.J., and Leriche, A. (2007). The current and future potential geographical distribution of the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). Bull. Entomol. Res. *97*, 369–378. https://doi.org/10.1017/S0007485307005044.

Swanson, R.W., and Baranowski, R.M. (1972). Host range and infestation by the Caribbean fruit fly, *Anastrepha suspensa* (Diptera: Tephritidae). South Florida. Proc. Fla. State Hortic. Soc. *85*, 271–274.

Takahara, B., and Takahashi, K.H. (2017). Associative learning of color and firmness of oviposition substrates in *Drosophila suzukii*. Entomol. Exp. Appl. *162*, 13–18. https://doi.org/10.1111/eea.12521.

Tempel, B.L., Bonini, N., Dawson, D.R., and Quinn, W.G. (1983). Reward learning in normal and mutant *Drosophila*. Proc. Natl. Acad. Sci. U.S.A. *80*, 1482–1486. https://doi.org/10.1073/pnas.80.5.1482.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., and Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecol. Lett. *8*, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x.

Urbaneja, A., Marí, F.G., Tortosa, D., Navarro, C., Vanaclocha, P., Bargues, L., and Castañera, P. (2006). Influence of ground predators on the survival of the Mediterranean fruit fly pupae, *Ceratitis capitata*, in Spanish Citrus orchards. BioControl *51*, 611. https://doi.org/10.1007/s10526-005-2938-6.

Vargas, R.I., Stark, J.D., Uchida, K., and Purcell, M. (1993). Opiine parasitoids (Hymenoptera: Braconidae) of oriental fruit fly (Diptera: Tephritidae) on Kauai island, Hawaii: Islandwide relative abundance and parasitism rates in wild and orchard guava habitats. Environm. Entomol. *22*, 246–253. https://doi.org/10.1093/ee/22.1.246.

Varshney, R.K., Graner, A., and Sorrells, M.E. (2005). Genomics-assisted breeding for crop improvement. Trends Plant Sci. *10*, 621–630. https://doi.org/10.1016/j.tplants.2005.10.004.

Vayssieres, J.F., Sinzogan, A., Korie, S., Ouagoussounon, I., and Thomas-Odjo, A. (2009). Effectiveness of spinosad bait sprays (GF-120) in controlling mango-infesting fruit flies (Diptera: Tephritidae) in Benin. J. Econ. Entomol. *102*, 515–521. https://doi.org/10.1603/029.102.0208.

Vayssières, J.F., De Meyer, M., Ouagoussounon, I., Sinzogan, A., Adandonon, A., Korie, S., Wargui, R., Anato, F., Houngbo, H., Didier, C., De Bon, H., and Goergen, G. (2015). Seasonal abundance of mango fruit flies (Diptera: Tephritidae) and ecological implications for their management in mango and cashew orchards in Benin (Centre and North). J. Econ. Entomol. *108*, 2213–2230. https://doi.org/10.1093/jee/tov143.

War, A.R., Paulraj, M.G., Ahmad, T., Buhroo, A.A., Hussain, B., Ignacimuthu, S., and Sharma, H.C. (2012). Mechanisms of plant defense against insect herbivores. Plant Signal. Behav. *7*, 1306–1320. https://doi.org/10.4161/psb.21663.

Wilson, A.J., Schutze, M., Elmouttie, D., and Clarke, A.R. (2012). Are insect frugivores always plant pests? The impact of fruit fly (Diptera: Tephritidae) larvae on host plant fitness. Arthropod-Plant Int. *6*, 635–647. https://doi.org/10.1007/s11829-012-9205-4.

Wong, T.T., and Ramadan, M.M. (1992). Mass Rearing Biology of Larval Parasitoids (Hymenoptera: Braconidae: Opiinae) of Tephritid Flies (Diptera: Tephritidae) in Hawaii. Advances in Insect Rearing for Research and Pest Management. (San Francisco, U.S.A.: Westview Press), p. 405–426. https://doi.org/10.4324/9780429043246-27.

Yuval, B., Kaspi, R., Field, S.A., Blay, S., and Taylor, P. (2002). Effects of post-teneral nutrition on reproductive success of male Mediterranean fruit flies (Diptera: Tephritidae). Fla. Entomol. *85*, 165–170. https://doi.org/10.1653/0015-4040(2002)085[0165:EOPTNO]2.0.CO;2.

Received: May 28, 2020
Accepted: Jan. 15, 2021

Addresses of authors:
Analía Benavídez[1], Mariano Ordano[2] and Pablo Schliserman[1,*]

[1] Centro de Investigaciones y Transferencia de Catamarca, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Catamarca (CITCA-CONICET/UNCA), Prado 366, K4700AAP, San Fernando del Valle de Catamarca, Catamarca, Argentina

[2] Fundación Miguel Lillo, Miguel Lillo 251, T4000JFE, San Miguel de Tucumán, Tucumán (Argentina); and Instituto de Ecología Regional, Universidad Nacional de Tucumán, Consejo Nacional de Investigaciones Científicas y Técnicas (IER-UNT-CONICET), Residencia Universitaria Horco Molle, Edificio las Cúpulas, Casilla de Correo 34, 4107, Yerba Buena, Tucumán, Argentina

* Corresponding author;
E-mail: schliserman73@yahoo.com.ar
Tel.: +54-383-4428648