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Role of Genes in Regulating Host Plants Expansion in Tephritid Fruit Flies (Diptera) and Potential for RNAi-Based Control

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Abstract

Host plant expansion is an important survival strategy for tephritids as they expand their range. Successful host expansion requires tephritids to adapt to the chemical and nonchemical properties of a novel host fruit, such as fruit color, phenology, and phytochemicals. These plant properties trigger a series of processes in tephritids, with each process having its own genetic basis, which means that various genes are involved in regulating host plant expansion by tephritids. This review summarizes current knowledge on the categories and roles of genes involved in host plant expansion in several important tephritid species, including genes related to chemoreception (olfactory and gustation), vision, digestion, detoxification, development, ribosomal and energy metabolism. Chemoreception- and detoxification- and digestion-related genes are stimulated by volatile chemicals and secondary chemicals of different hosts, respectively, which are involved in the regulation of nervous signal transduction that triggers behavioral, physical, and chemical responses to the novel host fruit. Vision-, nerve-, and development-related genes and metabolism-associated genes are activated in response to nonchemical stimuli from different hosts, such as color and phenology, to regulate a comprehensive adaptation of the extending host for tephritids. The chemical and nonchemical signals of hosts activate ribosomal and energy-related genes that result in the basic regulation of many processes of host expansion, including detoxification and development. These genes do not regulate novel host use individually, but multiple genes regulate multilevel adaptation to novel host fruits via multiple mechanisms. These genes may also be potential target genes for RNAi-based control of tephritid pests.

Key words: invasive species, novel host, gene regulation, Tephritidae, genetic mechanism

Tephritid fruit flies are well-known agricultural pests, and there are approximately 4500 species worldwide (White and Elson-Harris 1992). As typical herbivores, host plant expansion is an important survival strategy for tephritid flies, especially when introduced into new areas. Host plant expansion is the ability of an herbivore to use novel host plants without losing their ability to use their original hosts (Piñero et al. 2017), which facilitates the establishment of tephritids when entering new geographic areas and expanding their damage (Masselière et al. 2017). Therefore, understanding the mechanism of host plant expansion will be helpful for the control of tephritid pests.

Host expansion is well documented in the most destructive species of the genera *Anastrepha*, *Bactrocera*, *Ceratitis*, *Dacus*, and *Rhagoletis* among tephritid flies because they have expanded their range worldwide (Hendrichs et al. 2015, Motswagole et al. 2019) (Table 1). For example, the ancestral hosts of *Zeugodacus cucurbitae*

(Coquillett) (Diptera: Tephritidae) in India are primarily cucurbits, but it began to infest papaya (*Carica papaya*) in Hawaii (Back and Pemberton 1917), and it expanded its host range to include mango (*Mangifera indica*) in Africa (Vayssières et al. 2007). The peach fruit fly *Bactrocera zonata* (Saunders) (Diptera: Tephritidae) expanded to oranges (*Citrus sinensis*) and tomatoes (*Solanum lycopersicum*) when introduced from southeastern Asia to Egypt (Awad et al. 2015).

Because of the typical frugivorous pest, the tephritids spend some stages of life from eggs and larvae to pupae in the fruit of host plants. Therefore, the microenvironment of host fruits to which flies try to expand will have an important influence on the survival and adaptation of fruit flies. Therefore, when tephritids successfully expand their host range from ancestral host fruits to new hosts, they must adapt well to the chemical and nonchemical properties of the microenvironment from the novel host fruits, including their

Table 1. Summary data for host plant expansion by some important tephritid species after expansion or introduction into new habitats

Genus	Species	Original area	Native host plant	Expansion areas	Novel host plant after expanding	References
<i>Anastrepha</i>	<i>A. parishi</i> Stone	Guyana	Psidium guava (Myrtaceae), Oenocarpus Bacaba (Arecaceae)	Costa Rica, Suriname, Venezuela, Brazil	<i>Myrciaria dubia</i> (Myrtaceae)	Adaime et al. (2012)
	<i>A. fraterculus</i>	Most countries of the Americas from the USA to Argentina	Myrtaceae fruits	Brazilian Amazon basin	Citrus hosts	Uramoto et al. (2008)
<i>Bactrocera</i>	<i>B. dorsalis</i>	Northern south-east Asia, southern China	Mango, papaya, guava, orange (<i>Citrus sinensis</i>) etc. more than 250 hosts	Italy, Bangladesh, Hawaii islands, Africa, central China, South Pacific	Blueberry (<i>Vaccinium corymbosum L.</i>) Ohelo berry	Qin et al. (2018) Hee et al. (2015)
	<i>B. zonata</i>	Southeast Asia from Indonesia to Thailand and Vietnam to India and Pakistan and the islands of Mauritius, Muluccas, Reunion, and Sri Lanka	Peach (<i>Prunus persica</i>)	The Middle East region including Egypt, Yemen, Iran, Saudi Arabia, United Arab Emirates, Oman, Palestine, and Lebanon	Fruits: mango (<i>Mangifera indica</i>), guava (<i>Psidium guajava</i>), orange (<i>Citrus sinensis</i>), apricot (<i>Armeniaca vulgaris Lam.</i>), and apple (<i>Malus pumila</i>). Vegetables: Pepper (<i>Piper nigrum</i>), tomato (<i>Solanum lycopersicum</i>), and eggplant (<i>Solanum melongena</i>).	Awad et al. (2015)
	<i>Z. cucurbitae</i>	Indo-Malayan region	Cucurbit crops	Africa, temperate Asia and a number of Pacific islands	Mango (<i>Mangifera indica</i>), papaya, guava (<i>Psidium guajava</i>), navel oranges (<i>Citrus sinensis</i>), clementine tangerines	Vayssières et al. (2007) Elfekih et al. (2016)
<i>B. tau</i>		Throughout tropical and subtropical Asia and the South Pacific	<i>Cucurbitaceae</i> hosts	North of Asia	Phaseolus vulgaris (<i>Leguminosae</i>), Psidium guava (Myrtaceae), Citrus (<i>Rutaceae</i>), orange (<i>Citrus sinensis</i>), carambola (<i>Averrhoa carambola</i>)	Singh et al. (2010)
					Table grape (<i>Vitis vinifera</i>) Tansvaal red milkwood, (<i>Mimusops zeyheri</i>) cherimoya (<i>Annona cherimola</i>), Solanum mauritianum (<i>Solanaceae</i>)	
<i>Ceratitis</i>	<i>C. capitata</i>	East Africa	Infests over 350 different host fruits including very different fruits, such as citrus (<i>Rutaceae</i>), coffee (<i>Coffea</i>), olive (<i>Canarium album</i>), argan (<i>Argania spinosa</i>), apple (<i>Malus pumila</i>), pear (<i>Pyrus communis</i>), and cherry	Throughout Africa, the Middle East, the Mediterranean region and other adjacent European countries, the Hawaiian Islands, Australia and Central and South America	Table grape (<i>Vitis vinifera</i>) Tansvaal red milkwood, (<i>Mimusops zeyheri</i>) cherimoya (<i>Annona cherimola</i>), Solanum mauritianum (<i>Solanaceae</i>)	Gómez et al. (2019) Nash et al. (2019)
<i>Dacus</i>	<i>D. ciliatus</i>	East Africa	Cucurbitaceae hosts	African continent, Indian Ocean Islands, the Middle East, and Asia	tomato (<i>Solanum lycopersicum</i>), pepper (<i>Piper nigrum</i>), kidney bean (<i>Phaseolus vulgaris Linn.</i>), Abelmoschus esculentus	Alagarmalai et al. (2009) Badii et al. (2015)

Table 1. Continued

Genus	Species	Original area	Native host plant	Expansion areas	Novel host plant after expanding	References
<i>Rhagoletis</i>	<i>R. pomonella</i>	Eastern United States	Hawthorn (<i>Crataegus spp.</i>)	Western United States, British, Columbia, Canada	Domestic apples (<i>Malus domestica</i>), sour cherry (<i>Prunus cerasus var. Montmorency</i>), Rose (<i>Rosa rugosa</i>) and pear (<i>Pyrus communis</i>), black hawthorn (<i>C. douglasii</i>), ornamental hawthorn (<i>C. monogyna</i>)	Sim et al. (2012) Tait et al. (2016)
	<i>R. cingulata</i>	North America	Black cherry (<i>Prunus serotina</i>), bitter cherry (<i>Prunus emarginata</i>)	Europe	Olive (<i>Canarium album Raeusch.</i>) tea olive (<i>Osmanthus fragrans</i>), devilwood (<i>Osmanthus americanus</i>), muttomwood (<i>Turpinia insignis</i>)	Doellman et al. (2019)
	<i>R. cerasi</i>	West Asia	Sweet cherry (<i>Prunus avium</i>), sour cherry (<i>Prunus cerasus</i>)	Europe	Lonicera spp. (<i>Caprifoliaceae</i>)	Bakovic et al. (2018)

phytochemicals, color, and phenology. The color of the host fruit is an important cue to many fruit-infesting insects when selecting a new host (Piñero et al. 2017). The phenology of the novel host, such as the timing of flowering and fruiting, also affects the ability of a tephritid to use a new host (Mattsson et al. 2015). Importantly, host chemicals are key drivers when herbivores encounter a novel host (Hou and Wei 2019) and serve as attractants and barriers to adaptation (Erbilgin et al. 2014).

Phytochemicals include volatile compounds and secondary metabolites (Hafsi et al. 2016) that serve as attractants or defensive compounds to herbivores, such as tephritids. Volatile compounds allow tephritid adults to select among potential hosts while in flight, similar to fruit color. Once tephritid flies overcome the volatile chemicals of a potential new host, they eventually make contact with the host fruit, and then they must adapt to any secondary metabolites present to successfully colonize the host fruit.

These chemical and nonchemical cues of a potential novel host fruit act as selective pressures on tephritids when a novel host is encountered (Hafsi et al. 2016). These selective pressures involve visual identification; behavioral selection; and physical, chemical, and neurophysiological responses by tephritid flies to the novel host fruit (Piñero et al. 2017). There is likely a genetic basis for each of these processes, which suggests that various genes are involved in regulating the host plant expansion of tephritids. Therefore, increasing our knowledge of the categories and roles of these genes in regulating host expansion will deepen our understanding and allow for improved management strategies for tephritid fruit flies.

Gene regulation of host plant expansion has been revealed in several herbivorous insects, including *Subpsaltria yangi* Chen (Hemiptera: Cicadidae) (Hou and Wei 2019), *Drosophila mettleri* Heed (Diptera: Drosophilidae) (Hoang et al. 2015), and *Chilo suppressalis* Walker (Lepidoptera: Crambidae) (Zhong et al. 2017). For example, research on host plant expansion in a cactophilic fly, *Drosophila mojavensis* (Patterson) (Diptera: Drosophilidae),

revealed cytochrome P450, glutathione S-transferases, and UDP-glycosyl transferases as major gene classes involved in new host use (Matzkin 2012).

There has been limited research on the genetic mechanisms of host plant expansion in tephritids. Therefore, the present review summarizes current knowledge on the categories and roles of the genes involved in host plant expansion in tephritids and the related regulatory mechanisms and relates these findings to the development of new control methods (e.g., target gene RNAi control) for tephritid species.

Gene Categories and Roles Involved in Host Expansion in Tephritid Flies

Chemosensory-Related Genes

Volatile chemicals stimulate chemosensory (olfactory and gustatory) receptors in tephritid flies when assessing a potential novel host and trying to expand (Li et al. 2020). Therefore, chemosensory-related genes are involved in the initial process of host plant expansion for tephritids.

Olfactory-related genes of tephritids are one type of chemosensory gene that includes several gene families of odorant-binding proteins (OBPs), chemosensory proteins (CSPs), odorant receptors (ORs), ionotropic receptors (IRs), and sensory neuron membrane proteins (SNMPs), which are primarily involved in the identification of volatile chemicals, including volatiles of host fruits. After receiving odor chemical signals, these olfactory-related genes are triggered to transduce cascades that send information to specific regions of the brain, which ultimately leads to specific behavioral responses (Xu et al. 2019, Ono et al. 2021).

OBP genes play an important role in the first step of chemosensory identification of insects, including tephritids (Song et al. 2018, Tang et al. 2019). OBP genes direct odorant-binding proteins to bind volatile odor molecules specifically by distinct expression

(Campanini et al. 2017) to related olfactory receptors that are bound to olfactory receptor neurons (ORNs) in antennae (Ono et al. 2021). CSP genes are regarded as playing a similar role as OBP genes involved in the initial process of chemosensory signal transmission to corresponding receptors (Li et al. 2020). OBP and CSP genes are major gene types that lead tephritid flies to respond to different chemosensory chemicals, including volatile chemicals of host plants (Xu et al. 2019).

Except for these two categories of genes, some odor receptor genes also play important roles in host odor recognition of tephritids, such as genes related to odor receptors and ionotropic receptors (ORs and IRs). Odorant receptors of insects are composed of at least two proteins: a conserved coreceptor (ORco) as an ion channel and a specific OR subunit (ORx), which determines the ligand specificity and forms structurally ligand-gated ion channels (Fleischer et al. 2018). The OR genes mediate odorant receptors of insects transmitting the odorant molecules they receive into electric signals that are transmitted to a higher-order neural center (Masson and Mustaparta 1990, Hildebrand 1995). IR genes are related to ionotropic glutamate receptors (iGluRs), which are regarded as ion channels (Fleischer et al. 2018). They also play important roles in odor chemical perception (Wu et al. 2019).

The sensory neuron membrane proteins (SNMPs) gene encodes transmembrane domain-containing proteins that belong to a large gene family of CD36 receptors (Wei et al. 2017). SNMPs regulates the corresponding proteins to identify chemosensory signals, mainly pheromone chemicals (Fleischer et al. 2018).

The GR (gustatory receptor) family is another type of chemosensory protein that is a ligand-gated ion channel broadly expressed in gustatory receptor neurons in taste organs and is mainly involved in taste recognition of CO₂, sugar, and bitterness (Li et al. 2020, Zhang et al. 2022). When receiving taste signals, GR genes are involved in identifying taste and ingestion.

Among tephritid flies, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) and *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) are well-known polyphagous species that have expanded their host plants to more than 250 species (Papanicolaou et al. 2016, Garcia et al. 2020). However, *Bactrocera minax* (Enderlein) (Diptera: Tephritidae) and *Z. cucurbitae* are oligophagous species (Dhillon et al. 2005, Hafsi et al. 2016, Xu et al. 2019) that mainly attack citrus fruits and cucurbit plants, respectively. *Bactrocera oleae* (Gmelin) (Diptera: Tephritidae), *Procecidochares utilis* (Stone) (Diptera: Tephritidae), and *Carpomya vesuviana* (Costa) (Diptera: Tephritidae) are monophagous species infesting olive (*Olea europaea*), crofton weed (*Ageratina adenophora*), and jujube (*Ziziphus jujuba* Mill.), respectively, and all have limited host plant species (Li et al. 2017, 2019; Pavlidi et al. 2017).

Compared to several major olfactory-related gene families, the two polyphagous species have more genes, with 3 CSPs, 35 OBPs, 74 ORs, and 40 IRs in *B. dorsalis* (Wang et al. 2020) and 45 OBPs, 76 ORs, and 70 IRs in *C. capitata* (Papanicolaou et al. 2016), than two host-limited species (1 CSPs, 7 OBPs, 1 ORs, and 2 IRs in *B. oleae* and 1 CSPs, 21 OBPs, 53 ORs, and 29 IRs in *B. minax*) (Xu et al. 2019, Cheng et al. 2020, Tsoumani et al. 2020). A similar situation was observed in the GR family. There are also more GR genes in *C. capitata* (73 GRs) (Papanicolaou et al. 2016) and *B. dorsalis* (52 GRs) (Jiang et al. 2022) than in the host-limited species *P. utilis* (29 GRs) (Li et al. 2019), *C. vesuviana* (22 GRs) (Li et al. 2017), and *Z. cucurbitae* (7 GRs) (Elfekih et al. 2016) (Table 2).

The increased numbers of these genes are associated with chemosensory-related gene family expansion via gene duplication and differentiation (Siciliano et al. 2013, Pearce et al. 2017), which exert

Table 2. Chemosensory-related genes reported for selected tephritids based on documented transcriptome data

Chemosensory-related genes	<i>Anastrepha fraterculus</i>	<i>Anastrepha ludens</i>	<i>Anastrepha obliqua</i>	<i>Zenogodacus cucurbitae</i>	<i>Bactrocera dorsalis</i>	<i>Bactrocera minax</i>	<i>Bactrocera oleae</i>	<i>Ceratitis capitata</i>	<i>Carpomya vesuviana</i>	<i>Procecidochares utilis</i>	<i>Rhagoletis pomonella</i>	<i>Rhagoletis suavis</i>
Chemosensory proteins (CSPs)	/	/	/	/	3	1	1	/	2	6	/	2
Odorant-binding Proteins (OBPs)	23	11	24	13	35	21	7	45	6	40	22	9
Odorant receptor coreceptor (ORcs)	/	/	/	/	74	53	1	76	15	24	7	1
IRs	/	/	/	/	40	29	2	70	/	28	2	/
SNMPs	/	1	/	/	3	4	/	/	2	6	/	/
Ionotropic Glutamate Receptors (iGluRs)	/	/	/	31	/	/	/	/	/	/	/	/
Gustatory receptors (GRs)	/	/	/	/	7	52	/	/	73	22	29	2
Reference	Campagnani Ruiz-Maya et al. (2020)	Campagnani et al. (2017)	Elefekih et al. (2016)	Wang et al. (2019)	Xu et al. (2019)	Tsoumani et al. (2020)	Papanicolaou et al. (2016)	Li et al. (2017)	Li et al. (2020)	Li et al. (2017)	Schwarz et al. (2009)	Rundell et al. (2010)
	and de Britto (2016)			Jiang et al. (2020)	Cheng et al. (2022)							

important roles in tephritid fly adaptation to other hosts and expansion of their host ranges. Obvious chemosensory-related gene expansions were also reported in *Tribolium castaneum* (Herbst) (Coleoptera: Tenibroididae), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), and *Heliconius melpomene* (Linnaeus) (Lepidoptera: Nymphalidae) (Gouin et al. 2017). For example, the pea aphid *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae), with broader host ranges, experienced obvious expansion of the OR, OBP, and GR gene families, with 87 ORs, 18 OBPs, and 78 GRs, compared to the soybean aphid *Aphis glycines* (Matsumura) (Hemiptera: Aphididae), with 47 ORs, 10 OBPs, and 61 GRs (Robertson et al. 2019).

Altering gene expression levels also helps tephritids respond to different host plants and realize host expansion. OR13a and OR82 expression are higher in antennae in *B. dorsalis* in response to 1-octen-3-ol and geranyl acetate, respectively, which are major volatile components of its host fruits, mango (*Mangifera indica*) and almond fruit (*Terminalia catappa*) (Miyazaki et al. 2018). For *B. minax*, increasing the expression levels of several GR genes (BminGR66a, BminGR32aa, BminGR64a and b, and BminGR59f) regulate the taste process in response to different chemosensory stimuli of hosts (Zhang et al. 2022).

Detoxification- and Digestion-Related Genes

Once a tephritid adult identifies a potential novel host fruit for oviposition or feeding, the plant fruit must be suitable for larval development, which includes overcoming any secondary toxic chemicals in the novel host fruit (Hafsi et al. 2016). Therefore, detoxification- and other digestion-related genes also play core roles in mediating the host plant expansion of tephritids.

Common detoxification-related genes of insects include gene families of cytochrome P450s (P450s), glutathione S-transferases (GSTs), UDP-glycosyltransferases (UGTs), carboxyl/cholinesterases (CCEs) and ATP binding cassettes (ABC transporters) (Roohigohar et al. 2021). The cytochrome P450 family belonging to phase I enzymes includes various CYP subfamilies for different tephritid species (Roohigohar et al. 2021). The GST superfamily consists of phase II enzymes divided into at least seven major subclasses: the delta, epsilon, omega, sigma, theta, zeta, and microsomal classes (Li et al. 2018). The PGE phase II enzymes are a large family that can be divided into 13 clades, including the dietary detoxification class (A–C clades), the hormone/semiochemical processing group (D–G clades), and the neurodevelopmental group (I–M clades) (Pavlidi et al. 2013). The ABC transporter superfamily belonging to phase III enzymes can be subdivided into eight subfamilies, from ABC-A to ABC-H.

The cytochrome p450 gene family of phase I mainly contributes to the catalysis of numerous oxidative reactions during endogenous and exogenous metabolism (Li and Liu 2019). The important roles of genes in this family are the metabolism of xenobiotics, plant allelochemicals (Hazzouri et al. 2020), and even insecticides. GSTs are multifunctional genes of phase II enzymes that play a crucial role in the detoxification of endogenous and xenobiotic compounds, including plant secondary metabolites and pesticides. CCE families of phase II have been shown to be involved in the detoxification of plant-derived allelochemicals as well as insecticides (Li et al. 2007). The ABC transporter genes of phase III encoding membrane-bound proteins typically function in the ATP-dependent transport of various substrates across biological membranes (Broehan et al. 2013). The roles of ABC genes are mainly in handling xenobiotics such as plant phytotoxins and insecticides (Pavlidi et al. 2013). These genes can participate in regulating detoxification of host plant secondary metabolites of tephritid flies by coding corresponding enzymes, which help to transform toxins entering the insect system into

hydrophilic compounds that can be eliminated (Celorio-Mancera et al. 2013) and in the adaptability of different hosts (Li et al. 2019, Roohigohar et al. 2021).

The major digestive-related genes include gene families of cysteine proteases, proteases, lipase, glucosidase, and serine proteases (Zhong et al. 2017). The serine proteases (SPs) are members of the supergene family, including chymotrypsin, trypsin, thrombin, subtilisin, plasmin, and elastase, subclasses (Li et al. 2017). Various digestive proteases exert important roles in the nutrition digestion of tephritid flies from novel host plants that they try to expand to. Plant proteins of host plants are an important nutrition source used by tephritid flies. However, protease inhibitors of host plants are a widespread defense against herbivores such as tephritids. Therefore, genes coding various proteases react to protease inhibitors by regulating inhibitor-sensitive proteases or expressing proteases that are not targets of the inhibitors (Celorio-Mancera et al. 2012).

When expanding to other novel hosts, tephritid flies must adapt to different chemical environments from their native hosts. Detoxification-related genes regulate the host expansion of tephritids via gene family expansion similar to chemosensory-related genes. The major gene families of detoxification GSTs, P450s, CCEs and ABC transporters are more numerous in polyphagous *B. dorsalis* (39 GSTs, 90 P450s, 38 CCEs, and 47 ABC transporters) (Pavlidi et al. 2013) and *C. capitata* (28 GSTs, 103 P450s, and 43 CCEs) (Papanicolaou et al. 2016) than monophagous *P. utilis* (21 GSTs, 22 P450s, 17 CCEs, and 22 ABC transporters) (Li et al. 2018, 2019) and *B. oleae* (33 GSTs, 60 P450s, 15 CCEs, and 18 ABC transporters) (Pavlidi et al. 2013) (Table 3). However, reports about digestive gene family expansion in tephritids are still rare.

Overall, detoxification and the digestive-related gene family combined with chemosensory-related gene family amplification exhibit a close association with host range extension. This gene family expansion is helpful for the host plant expansion of fruit flies. Cases in other insects strengthen this idea. For example, *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) (300 hosts) and *Helicoverpa zea* (Lepidoptera: Noctuidae) (123 hosts) are two species of caterpillars (Pearce et al. 2017) that have considerably broader host ranges than any other lepidopterans. Great expansion of detoxification and digestive gene families was found in the two species.

In addition to gene family amplification, detoxification and digestive genes also regulate host expansion of tephritid flies by activating various gene subfamilies, subclasses, or clades. To respond to various toxic environments, including secondary toxic chemicals of different hosts, *B. dorsalis* primarily triggered the delta subfamily of GSTs, CYP3 and CYP4 subclasses of P450s, A–C clades of CCEs, and ABC-A, ABC-B, and ABC-G subclasses of ABC transporters (Pavlidi et al. 2013), *C. ceratitis* activated the epsilon subfamily of GST, CYP6 and CYP12 of P450s, B clade of CCEs (Papanicolaou et al. 2016), and *P. utilis* mainly triggered the delta, epsilon and microsomal subfamilies of GSTs, CYP4, and CYP9 of P450s, C clade of CCEs and ABC-G subclass of ABC transporters (Li et al. 2018), but *R. pomonella* mainly launched CYP4 and CYP6 of P450s (Ragland et al. 2015) (Table 3). For the digestive gene family, *B. dorsalis* (Shen et al. 2013) and *C. capitata* (Silva et al. 2006, Nash et al. 2019) primarily triggered aminopeptidase, trypsin and serine peptidase digestive genes, but *B. oleae*, which is a strictly monophagous species, triggered serine protease and nucleic acid digestive genes to respond to different host secondary chemical environments (Pavlidi et al. 2017) (Fig. 1).

Detoxification- or digestion-related genes also facilitate tephritid fly adaptation to different hosts by altering gene expression levels. *Rhagoletis zephyria* (Snow) (Diptera: Tephritidae) evolved from

Table 3. Detoxification-related genes reported for selected tephritids based on documented transcriptome data

Detoxification-related genes	Subfamily	Species						
		<i>Procecidochares utilis</i>	<i>Bactrocera oleae</i>	<i>Bactrocera minax</i>	<i>Bactrocera dorsalis</i>	<i>Ceratitis capitata</i>	<i>Rhagoletis pomonella</i>	<i>Bactrocera tau</i>
GST	Delta	4	8	6	14	7	/	/
	Epsilon	8	12	11	7	14	/	/
	Omega	1	3	1	6	1	/	/
	Sigma	1	1	1	1	1	/	/
	Theta	2	4	3	3	3	/	/
	Zeta	1	3	/	/	2	/	/
	Delta/Epsilon	/	2	/	6	/	/	/
	Microsomal	4		3	/	/	/	/
P450	Total	21	33	26	39	28	4	4
	Cyp2	/	2	/	6	/	/	/
	Cyp3	/	28	/	50	/	/	/
	Cyp4	5	17	/	30	/	13	/
	Cyp6	4	/	/	/	40	15	/
	Cyp9	5	/	/	/	9	2	/
	Cyp12	2	/	/	/	11	5	/
	Other Cyp	6	/	/	/	43	2	/
CCEs	Mitochondrial	/	13	/	4	/	/	/
	Total	22	60	/	90	103	37	2
	Dietary Class (A–C)	7	7	/	19	16	/	/
	Hormone/semiochemical processing (D–G)	1	3	/	1	11	/	/
	Neurodevelopmental (H–M)	9	2	/	4	15	/	/
	Unclassified	/	3	/	14	1	/	/
	Total	17	15	/	38	43	24	/
	(ABC) transporters	A	/	3	/	4	/	/
Detoxification of xenobiotics	B	5	4	/	4	/	/	/
	C	4	2	/	1	/	/	/
	D	1	1	/	2	/	/	/
	E	/	1	/	1	/	/	/
	F	3	3	/	3	/	/	/
	G	9	4	/	4	/	/	/
	H	/	/	/	/	/	/	/
	Total	22	18	/	47	/	/	/
Glycosyltransferases	Total	/	/	/	/	/	/	1
	UDP-glucosyltransferase	Total	/	3	/	/	/	/
Reference	/	Li et al. (2018, 2019)	Pavlidi et al. (2013)	Wang et al. (2016)	Pavlidi et al. (2013), Li et al. (2019)	Papanicolaou et al. (2016)	Ragland et al. (2015)	Shi et al. (2020)

Rhagoletis pomonella (Walsh) (Diptera: Tephritidae) and experienced host expansion from apple to snowberry plants (Ragland et al. 2015). Increased expression levels were found in some detoxification-related genes, including cytochrome P450, glutathione S-transferases, and glycosyltransferase, in *R. zephyria* facing the apple host environment (Ragland et al. 2015). *Z. cucurbitae* is the species that mainly attacks cucurbit plants, and the fly responds to different secondary chemical environments of *Mucuna pruriens* plants by reducing the expression levels of trypsin and chymotrypsin digestive genes (Samiksha et al. 2020).

Vision-Related Genes

Although the importance of chemical stimuli is highly emphasized in the host expansion of tephritids, other nonchemical stimuli, such

as the color of the novel host fruit, should not be ignored. Many insects locate their host plants primarily by color signals, including beetles, *Altica engstroemi* (J. Sahlberg) (Coleoptera: Chrysomelidae) (Stenberg and Ericson 2007), *Hylastes ater* (Paykull) (Coleoptera: Curculionidae), and *Arhopalus ferus* (Mulsant) (Coleoptera: Cerambycidae) (Kerr et al. 2017). For tephritid flies, *Neoceratitis cyanescens* (Bezzi) (Diptera: Tephritidae) (Brévault and Quilici 2010), *B. minax* (Wang et al. 2019), *B. dorsalis* (Wu et al. 2007), and *Z. cucurbitae* (Piñero et al. 2017) are typical examples of species that appear to select different hosts first by fruit color rather than chemical signals.

Z. cucurbitae realized its host expansion to a novel host, papaya (*Carica papaya*), in Hawaii by strongly relying on the color location of fruits by vision (Piñero et al. 2017). However, the underlying

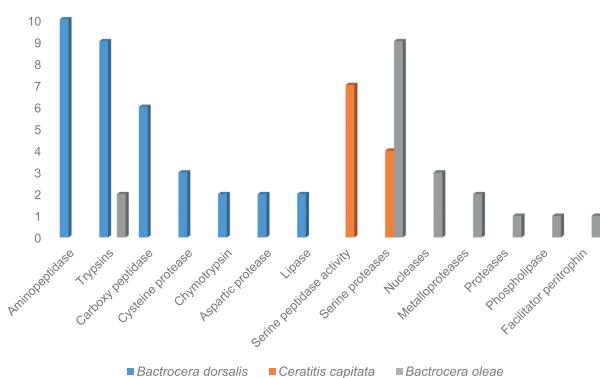


Fig. 1. Major digestion-related genes reported for selected tephritids based on documented transcriptome data. *Bactrocera dorsalis* (Shen et al. 2013) and *Ceratitis capitata* (Nash et al. 2019) are two polyphagous species. *Bactrocera oleae* (Pavlidi et al. 2017) is a host plant-limited species.

genetic mechanism has not been revealed for *Z. cucurbitae*. In fact, nonchemical stimuli, such as color, are associated with vision-related genes that allow the identification of different hosts (Wang et al. 2019).

The genes responsible for color discrimination in Diptera are primarily related to opsin proteins in the photoreceptor cells of the eye (Hardie and Raghu 2001). Six types of Rh opsin-expressed genes (Rh1 to Rh6) have been identified as major genes involved in color recognition and photoreception (Montell 2012) in Diptera insects. The Rh1 and Rh2 opsin genes are associated with motion detection and direction, respectively (Pollock and Benzer 1988, Morante and Desplan 2008). Rh3 and Rh4 are UV-sensitive opsin genes, Rh5 is a blue-sensitive gene and Rh6 is a green opsin gene (Tang and Guo 2001). These opsin genes lead the photoreceptor of eyes to receive various chromophore pigments and then activate a series of visual transduction cascades to launch corresponding color identification behavior.

In the genome of polyphagous *C. capitata*, the long wavelength-sensitive genes Rh1, Rh2, and Rh6 and the UV-sensitive genes Rh3 and Rh4 were found, while Rh2-4 and Rh6 were found in the phototransduction pathway of oligophagous *B. minax* (Wang et al. 2019). Moreover, the role of Rh6 in modulating green color discrimination was reported in *C. capitata* (Papanicolaou et al. 2016) and *B. minax* (Wang et al. 2019). In *B. minax*, the function of Rh6, which is responsible for green spectral sensitivity, has been identified by knockdown of the gene *B. minax* in female adults, and *B. minax* flies significantly reduced their preference for green fruit after cutting Rh6 (Wang et al. 2019). Absence of a member of the blue-sensitive opsin subfamily (Rh5) was found in both tephritid species *C. capitata* and *B. minax*, but Rh5 can be specifically expressed in *Drosophila* (Papanicolaou et al. 2016, Sharkey et al. 2020). Reports about vision-related genes directly involved in the host expansion of tephritids are still very few.

Genes Mediating the Phenology Response of Host Plants

Tephritis fruit fly hosts expand to other new host plants, and the phenology of the new host is another nonchemical stimulus that affects fly adaptation. The phenology of the host plant fruits includes the time of flowering, fruiting, or maturation (Mattsson et al. 2015, Rull et al. 2019). Many studies have revealed that dormancy plays a crucial role in assisting insects in responding to various phenological environments, including the phenology of different host fruits (Mattsson et al. 2015, Dowle et al. 2020).

The dormant state of tephritids was determined by the rate of growth and development. Therefore, genes associated with development are crucial factors that regulate the adaptation of phenology of various hosts. For example, genes related to sensing daylength or photoperiodism and the central nervous system (CNS) regulate chronic adaptation (Denlinger 2002, Kozak et al. 2019). Under the regulation of related genes, diapause may involve the deceleration of the developmental progress of tephritids to synchronize the phenological environment (Dowle et al. 2020).

R. pomonella of tephritids is a typical case. The ancestral host of *R. pomonella* is the hawthorn *Crataegus mollis*, but its species host expanded to the domestic apple *Malus domestica* and subsequently formed a new apple race (Bush 1969). Apple fruits ripen earlier than hawthorn. The flies that infest apples and hawthorns must differentially time their life rhythms to match the differences in ripening times of their respective hosts (Mattsson et al. 2015). To realize this process, the flies of the two host races varied their time of overwintering pupal diapause.

Under the pressure of different host fruit phenologies, many development-related genes are involved in regulating the adaptation to the different phenologies of two host plant fruits (regulating overwintering and diapause). Functional genes associated with cell/tissue development (transcripts with epidermal growth factor domains or affecting neurogenesis, cell differentiation, cell cycle, and Wnt signaling pathway), metabolism (OXPHOS), translation (ribosomal), and cell division (core nucleosome) are highly enriched (Dowle et al. 2020). By increasing the expression levels of these genes, the CNS (central nervous system) development of apple flies was elevated during their diapausing period compared to that of hawthorn flies. Adult emergence-associated genes, including key hormone signaling genes, the ecdysone receptor partner *usp*, the ecdysone biosynthesis protein *ecd*, cell cycling genes *Myb* and *rbf*, genes coding Mediator complex proteins, and various genes in the Wnt signaling pathway (*fz*, *fz3*, *nkd*, *fry*, *sgg*, *shf*, *CkIIbeta*, and *CkIalpha*), etc., were enriched to regulate adult fly eclosion to match their host fruit ripeness (Dowle et al. 2020).

Ribosomal Genes

Genes coding for ribosomal proteins are often associated with protein translation by stably expressing 'housekeeping' genes. This type of gene is involved in many basic biological processes, such as digestion, detoxification, growth, and development, in most organisms (Puri et al. 2012). Therefore, ribosomal genes may also be involved in the host plant expansion of tephritids after receiving chemical and nonchemical stimuli. As mentioned above, ribosomal genes increased their expression level to regulate the growth of *R. pomonella* in response to the different phenology of its new host apple (Dowle et al. 2020).

The role of ribosomal genes involved in host expansion and new host adaptation of insects, including tephritis flies, is mainly related to the response of ribosome-inactivating proteins (RIPs) in host plants (Puri et al. 2012). RIPs have been found to have insecticidal functions in many insects, including beetles, mosquitoes, and moths (Celorio-Mancera et al. 2013). Ribosome genes can help insects such as tephritids realize host shifting by regulating their expression levels to counteract the RIPs of various host plants (Zhong et al. 2017). In addition, ribosome genes interact with some epigenetic factors, which leads to chromatin remodeling to change gene expression and regulate different biological processes, including host plant adaptation (Surovtseva et al. 2011, Coléno-Costes et al. 2012).

In response to different secondary chemicals, ribosomal genes were also involved in host detoxification of different species of the *R.*

pomonella complex. *R. zephyria* and *R. pomonella* are sister species in the *R. pomonella* complex that specialize in snowberry and domestic apple plants, respectively (Ragland et al. 2015). In reciprocal transplant tests of these two *Rhagoletis* taxa, microarray data indicated significant enrichment of mitochondrial ribosomal proteins when the two fly species fed on their new hosts, which contain different complements of phenolic and glycosidic (*R. zephyria* fed on apples, and *R. pomonella* fed on snowberries) in laboratory studies (Ragland et al. 2015).

Several studies on lepidopteran species revealed the role of ribosomal genes in response to host expansion (Govind et al. 2010, Celorio-Mancera et al. 2013). For example, ribosomal genes were downregulated in *C. suppressalis* (Quan et al. 2016) when extended to the novel host water oats (*Zizania latifolia*), which may be a more suitable host for *C. suppressalis* than its native host, rice. In contrast, ribosomal genes were upregulated in *H. armigera* when shifting to unsuitable novel hosts (Celorio-Mancera et al. 2012).

Energy Metabolism Genes

The role of genes associated with the oxidative phosphorylation (OXPHOS) pathway is primarily involved in energy metabolism and provides energy in the form of ATP for most organisms and most biological actions (Ghiselli and Milani 2020). The OXPHOS pathway is coupled with the mitochondrial electron transport chain, and mitochondria are major sites of reactive oxygen species (ROS) production in the majority of eukaryotic cells (Orrenius et al. 2007, Kowaltowski et al. 2009). The level of mitochondrial oxygen flow through the OXPHOS pathway influences ROS homeostasis and regulates the energy supply in different biological processes (Mittapalli et al. 2007, Orrenius et al. 2007).

OXPHOS genes can take part in many biological activities, and therefore they may also be important in the regulation of the response to host plant expansion of tephritid flies. Research on *Bactrocera tau* (Walker) (Diptera: Tephritidae) reared on two native cucurbit hosts and a novel host (banana) showed a large number of upregulated NADH (nicotinamide adenine dinucleotide) genes (59 on average) in the OXPHOS pathway in transcript data of *B. tau* when feeding on banana. These results suggest that OXPHOS genes play an important role in the process of novel host fruit use in *B. tau* (Shi et al. 2020) (Table 4). OXPHOS was also involved in the host expansion of *R. pomonella* in response to the different phenologies of various hosts, as mentioned above.

Certain genes in the fat bodies of tephritids are also involved in the energy supply for many biological processes, including digestion, detoxification, development, and immunity (Yang et al. 2014).

Differentially expressed genes, such as the lipase gene, ATP synthase gene, and alpha-amylase genes (Table 4), were documented in the tephritids *B. dorsalis* and *P. utilis* in response to different secondary chemical environments (Yang et al. 2014, Li et al. 2019).

Genes Regulating Multilevel Adaptation in Response to Host Plant Expansion

The various types of genes summarized above led to multilevel responses in tephritids, including nervous-, behavioral-, chemical-, and physical-level responses, when the flies faced different host environments. These multilevel responses to host expansion result in multilevel adaptations in flies, which lead to successful expansion to a novel host (Fig. 2).

Adaptation to a novel host is a complex process. Multilevel adaptation in fruit flies results from multigene regulation rather than a single gene or several genes performing various regulatory roles. The transcriptome data revealed that olfactory-, digestion- and detoxification-related genes and ribosomal genes were all involved in novel host adaptation in *R. pomonella* (Ragland et al. 2015, Tait et al. 2016). Laboratory strains of *B. tau* also had activated OXPHOS genes and digestive and detoxification genes when the fly responded to a novel host environment (Shi et al. 2020).

The multiple-gene regulation mechanism during host expansion to a novel host was also documented in other insects. For example, *C. suppressalis* launched three types of genes (digestive-related, detoxification-related, and ribosomal genes) simultaneously to regulate adaptation to the new novel host water oat (Zhong et al. 2017). *S. yangi* differentially expressed genes related to digestion, detoxification, oxidation-reduction, stress response, water deprivation, and osmoregulation during adaptation to the new host *Ephedra lepidosperma* (Hou and Wei 2019).

Various genes also regulate the adaptation of tephritids to new hosts via multiple mechanisms. As summarized above, the alteration of gene expression levels, gene family expansion, and the use of various gene types or subfamilies are the major mechanisms involved in novel host adaptation.

The Potential of RNAi Control for Tephritis Based on Target Genes

Many tephritid species attack economically important crops, including vegetables and fruits. The economic losses caused by tephritids reach over US\$2 billion annually (Shelly et al. 2014). Control strategies for tephritids primarily involve chemical use in

Table 4. Energy-related genes of selected tephritids based on documented transcriptome data

Energy-related genes	Species				
	<i>Ceratitis capitata</i>	<i>Rhagoletis pomonella</i>	<i>Bactrocera dorsalis</i>	<i>Bactrocera tau</i>	<i>Procecidochares utilis</i>
Oxidative phosphorylation	3	/	/	59	/
Fatty acid desaturase	/	/	2	/	5
Lipase	/	4	4	/	18
Alpha amylase,	/	/	2	/	/
ATP synthase	/	/	8	/	/
Ribosomal protein S7	/	/	2	/	/
Long-chain fatty acids	/	/	/	/	6
Aldose 1-epimerase	/	/	1	/	/
Beta-glucosidase	/	/	1	/	/
Reference	Nash et al. (2019)	Ragland et al. (2015)	Yang et al. (2014)	Shi et al. (2020)	Li et al. (2019)

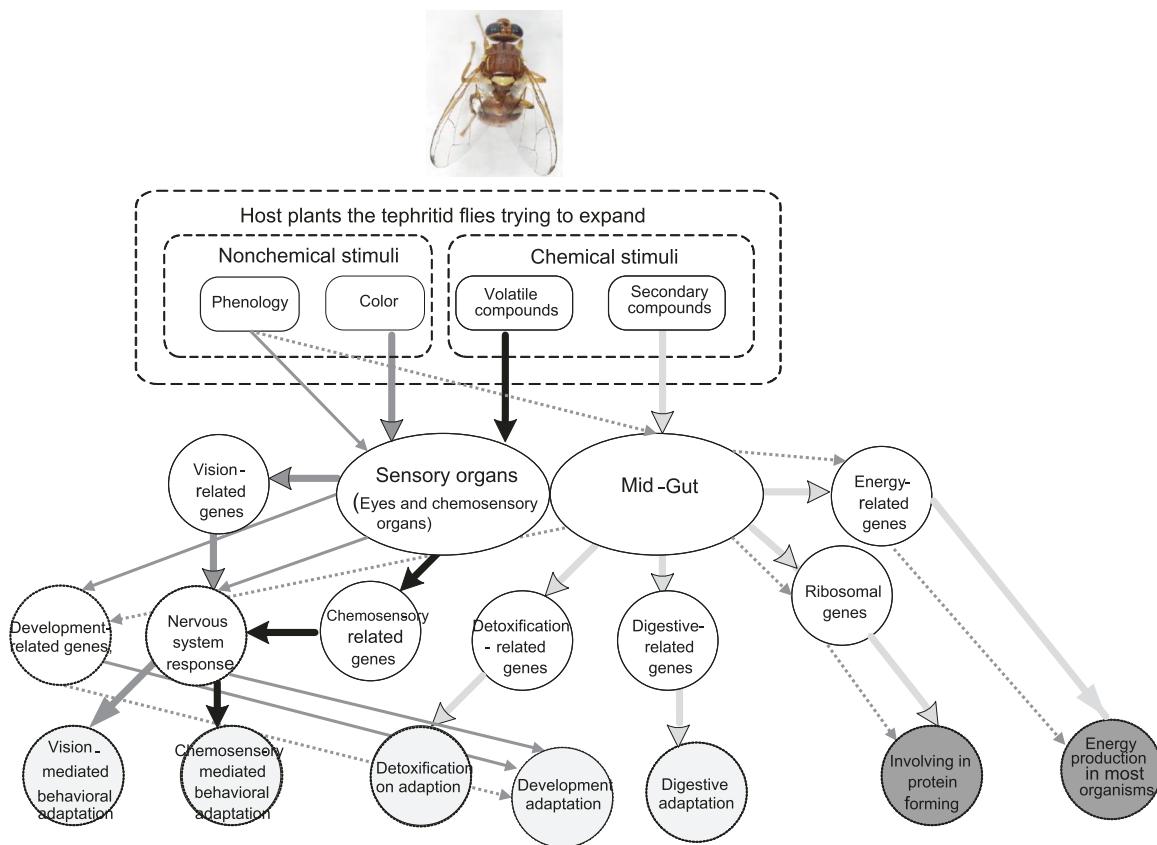


Fig. 2. Molecular mechanisms involved in novel host plant responses of tephritid fruit flies based on documented studies. Boxes represent characteristics of novel host plants that cause adaptation in tephritids. Large ovals represent major fly organs where responses to host stimuli occur. Clear circles represent gene types that mediate novel host adaptation in tephritids. Shaded circles (light) represent the corresponding adaptation response in the fly caused by the different gene types. Two dark circles represent the adaptation mediated by ribosomal genes and energy-related genes. The two types of genes are involved in many basic biological adaptations and include regulation of development and detoxification.

many countries, which may be harmful to the environment and human health. Therefore, more environmentally friendly control methods should be sought and recommended when possible.

RNA interference (RNAi) is an effective method to safely control tephritid flies. RNAi control methods suppress the expression of certain target genes by importing dsRNA (Machado et al. 2018). Therefore, selecting the target genes to be 'silenced' is a key step in the RNAi control method (Zhu and Palli 2020). Some target genes are associated with functions such as temperature sensitivity and sex determination (Meccariello et al. 2017).

For tephritid species, including *Anastrepha suspense* (Loew) (Diptera: Tephritidae) (Sim et al. 2019), *Anastrepha fraterculus* (Wiedemann) (Diptera: Tephritidae) (Dias et al. 2019), *B. dorsalis* (Xie et al. 2017), *B. minax* (Wang et al. 2019), *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) (Cruz et al. 2018), and *C. capitata* (Gabrieli et al. 2016), effective RNAi controls have been developed based on the suppression of functional genes associated with eye pigmentation, embryonic segmentation regulation, postembryonic growth/development, reproduction, embryonic temperature-sensitive lethality and sex determination (Tayler et al. 2019, Choo et al. 2020). Based on these target genes, RNAi can be applied in pest control not only for tephritid species but also for some Coleopterans and Lepidoptera insects by foliar sprays, ingested dsRNA or sterile insect technique (SIT) application (Baum and Roberts 2014, Spit et al. 2017).

However, functional genes related to host plant adaptation are also target genes in RNAi control methods for tephritids. For

example, the vision-related gene R6 or gustation gene GR59f of *B. minax* (Wang et al. 2019, Zhang et al. 2022), digestion-related genes try1, try2, try4, and try5 of *B. dorsalis* (Li et al. 2017), olfactory Orco gene of *B. oleae* (Tsoumani et al. 2020), CSP2 gene of *B. dorsalis* (Yi et al. 2014), and detoxification genes CYP6A41 and CYP6EK1 of *B. dorsalis* (Huang et al. 2012) are associated with host adaptation functional genes, and all of these genes possess an exploitable potential as target genes to control fruit flies.

More target genes related to host plant expansion for tephritids need to be identified for their major functions and implemented in pest management. Although RNAi is an effective and tractable genetic tool, other novel gene tools, such as clustered regularly interspaced short palindromic repeats and the CRISPR-associated protein 9 (commonly known as CRISPR–Cas9) gene editing system, can also provide scalable pest control strategies (Meccariello et al. 2017). Compared with traditional RNAi, CRISPR–Cas9 can knock down or modify the target gene precisely instead of just suppressing the expression of target gene (Jinek et al. 2012). The target genes edited by the CRISPR–Cas9 system can create stable and heritable strains, which can be applied in actual tephritid control.

Applying the CRISPR–Cas9-mediated editing system, some target genes in tephritid flies have been evaluated for their potential for functional application, such as the eye pigmentation gene *we* (Sim et al. 2019), embryonic segmentation gene *prd* (Meccariello et al. 2017), sex-determination gene *Astra-2* (Li and Handler 2019), *tra2* (Aumann et al. 2020), and pupae color gene *wp* (Ward et al. 2021). CRISPR/Cas9-mediated precise editing is a process in which

Cas9 endonuclease recognizes a specific genomic region under the leading of chimeric single guide RNA (sgRNA) (Jinek *et al.* 2012). The CRISPR/Cas9 system editing the functional target gene *shibire*, *tsl* in *B. tryoni* (Choo *et al.* 2020) and the white pupae gene *wt* in *B. dorsalis*, *C. capitata*, and *Z. cucurbitae* (Ward *et al.* 2021) have been applied in the development of genetic sexing strain (GSS) application in SIT control. This gene tool also has broad application prospects in tephritid management based on host plant adaptation-related genes in the future.

Regulation of host adaptation would be an important mechanism to target because this adaptation allows tephritids to expand in new habitats and change to new biotypes. Therefore, developing suitable novel host adaptation functional genes as target genes in genetic disruption control strategies could help prevent tephritids in an environmentally friendly manner.

Conclusion

In this review, we summarized the categories and roles of genes involved in regulating host plant expansion in tephritid fruit flies. These genes include olfaction-, gustation-, vision-, digestion-, and detoxification-, nerve- development-related and include ribosomal genes and energy-related genes regulating host expansion of tephritids by multiple levels and multiple mechanisms. Among these, 6 categories of chemosensory genes, 6 categories of vision-related genes, 7 categories of detoxification genes, 14 categories of digestive genes, and 10 categories of energy-related genes were summarized. These host plant expansion-related genes have exploitable potential as target genes for RNAi control of tephritid flies. After review, the reports about gene regulation in host plant expansion of tephritids are few, and many aspects are valuable to explore continuously. The functions of many host expansion-related genes, such as digestive-, visual-, nerve- and energy-related genes, etc., need to be identified. Some new categories and functions of genes involved in regulating the host expansion of tephritids also need to be identified. The mechanisms by which genes regulate the process of host plant expansion include methylation and neofunctionalization and also need to be revealed. In addition, the effect and efficiency of host plant expansion-related genes as target genes applied in RNAi control of tephritid species are valuable to verify and estimate. We can look forward to more successful examples of environmentally friendly control in tephritid fruit flies in the future.

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Author Contributions

W.S. and G.R. proposed the idea of writing this review. W.S. and H.Y. conceptualized the idea for the review. W.S. performed the literature search and wrote the manuscript draft. H.Y., C.K. and H.P. critically commented and revised the manuscript. J.C. provided some suggestions for the article. All authors read and approved the final manuscript.

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