Involvement of the Antennal and Maxillary Palp Structures in Detection and Response to Methyl Eugenol by Male *Bactrocera dorsalis* (Diptera: Tephritidae)

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Abstract

The oriental fruit fly, *Bactrocera dorsalis* (Handel) is one of the most destructive pests of fruits. The discovery of methyl eugenol (ME) as a potent male attractant for this species has led to its successful use in area-wide fruit fly control programs such as male annihilation. While the antenna is recognized as primarily responsible for male flies’ detection of attractants such as ME, little is known of the involvement of the maxillary palp. Using behavioral assays involving males with intact and ablated antennae and maxillary palp structures, we seek to ascertain the relative involvement of the maxillary palp in the ability of the male fly to detect ME. In cage bioassays (distance of ≤40 cm from the source), >97% of unmodified males will normally show a response to ME. Here, we showed that 17.6% of males with their antennae ablated were still attracted to ME versus 75.0% of males with their palps ablated. However, none of the antennae-ablated males were able to detect ME over a distance of >100 cm. Furthermore, wind tunnel bioassays showed that maxillary palp-ablated males took a significantly longer time compared to unablated males to successfully detect and eventually feed on ME. These results suggest that although the antennae are necessary for detection of ME over longer distances, at shorter distances, both antennae and maxillary palps are also involved in detecting ME. Hence, those palps may play a larger role than previously recognized in maneuvering males toward lure sources over shorter ranges.

Key words: oriental fruit fly, methyl eugenol, antenna, maxillary palp, ablation
of novel pest management strategies (Brito et al. 2016, Reisenman et al. 2016). Hitherto, much work has been focused on the antennae (Hansson 1999, Hansson and Stensmyr 2011) compared with maxillary palp, although it is known that the antenna and maxillary palp form two bilateral and symmetrical pairs of olfactory organs on an insect's head. As a peripheral and accessory olfactory organ closely located to the proboscis, in some insects the maxillary palp is capable of detecting odors in concentrated form either through direct or at least close contact, in contrast to that of the antenna where detection of diffused odors occurs over longer ranges (Wasserman and Itagaki 2003, Dweck et al. 2016). To date, however, these phenomena have not been adequately investigated in Tephritid pest species although it was recently suggested from bioassays involving the Queensland fruit fly, Bactrocera tryoni (Froggatt) (Diptera: Tephritidae) in a 1-liter jar, that the palp is involved in the detection of another male attractant, cue lure (Verschut et al. 2018).

Extending the seminal work of Metcalf and coworkers done over four decades ago describing how B. dorsalis males respond to ME (Metcalf et al. 1975), more recent reviews of the literature on B. dorsalis olfaction, especially that pertaining to ME, have focused almost entirely on the role of the antennae (Zheng et al. 2013; Wu et al. 2016; Liu et al. 2017, 2018). While it has been established that the ability of these male flies to be attracted to lures such as ME depends on the presence and activation of olfactory receptor neurons in the sensilla of the antenna (Zheng et al. 2012; Liu et al. 2017, 2018), it is also known that olfactory sensilla also exist in the maxillary palp (Zhang et al. 2011). This includes the type of sensilla basiconica earlier described as thin-walled multiporous pitted sensilla (Dickens et al. 1988) that are also present in the antenna (Lee et al. 1994).

We hypothesized that the maxillary palp may also play a role in ME detection since both antenna and palp contain similar types of olfactory sensilla which may house receptors that are responding to ME. In this article, we report our findings on the involvement of maxillary palp in complementing the antenna based detection of ME by male B. dorsalis at shorter versus longer ranges.

Materials and Methods

Insects

A laboratory stock of Bactrocera dorsalis (maintained since 2009 with 9 generations per year with irregular introgression) was bred at 25–29°C with 83–90% relative humidity under a 12:12 (L:D) h photoperiod. The flies were cultured using artificial diet as previously described by Hee and Tan (1998). Within 3 days after emergence (DAE), the flies were sexed and maintained separately in cages (30 × 30 × 30 cm) to prevent mating. Sexually mature virgin males (14–20 DAE) that responded maximally to ME (Tan et al. 1987) were used for bioassays. All experiments were carried out in the morning between 0800 and 1000 hours that coincided with the period of optimum response of the male flies to ME (Tan 1985).

Cage Bioassay

Males with either their maxillary palps ablated, antennae ablated, and both antennae and maxillary palp-ablated males or no ablations were assessed and compared for their response to ME (1-allyl-3,4-di-methoxybenzene, >98% purity; Merck-Schuchardt, Germany) over a short distance of ≤40 cm. A pair of sterile fine forceps were used to remove both pairs of palps and/or antennae by carefully snipping off their proximal ends e.g., base of antennal scape under a stereomicroscope (Carl Zeiss, Germany). Ablated and untreated intact (non-ablated) male flies (used controls) were then maintained separately in cages with food and water and acclimatized to the bioassay area for at least 12 h prior to experimentation. Each treatment group consisted of 100 sexually mature virgin males housed in a screened cage (40 × 40 × 40 cm).

For the bioassay, flies were offered 0.5 µl of pure ME dispensed on a piece of Whatman No. 1 filter paper placed on a plastic Petri dish (9 cm diameter) in the center of the arena. For each treatment, the total number of responding males were observed and recorded within a duration of 20 min. Only males that responded by a combination of zigzag-oriented flight, landing, and feeding on the ME source were scored as a positive response. The bioassays were conducted between 0800 and 1000 hours and replicated seven times with males from different cohorts. In all experiments, neither the removal of maxillary pulp nor antenna was found to affect the survival of the experimental flies compared to untreated, intact males.

Wind Tunnel Bioassay

A wind tunnel modified from Hee and Tan (1998) was used to assess the ability of male flies with maxillary palps and/or antennae ablation to detect, search and locate the source of ME over a longer distance of >100 cm on a temporal basis. The wind tunnel was constructed of a transparent polyacetate sheet rolled into a cylindrical tube (200 × 30 cm diameter) with ends forming the upwind and downwind areas of the wind tunnel, respectively. Electric fans and honeycomb structures at both ends were used to generate a continuous laminar air flow at a speed of 15 cm/s. In this wind tunnel the total flight distance between the point of release (at the downwind end) and the platform containing ME source (at the upwind end) was over 150 cm.

Four different types of treatments were applied to male flies. These were 1) ablation of maxillary palps only, 2) ablation of antennae only, 3) ablation of both antennae and maxillary palps; and 4) intact untreated males (no ablation) as control. At the upwind end, 0.5 µl of pure ME was dispensed onto a piece of Whatman No. 1 filter paper (9 cm diameter) placed in a plastic Petri dish (9 cm diameter) and supported by a tripod 8 cm in height. Individual males were assayed for response to ME within a 20-min duration. The total time recorded for each individual male to complete the behavioral sequence of taking-off, flying, landing and feeding on ME was also further divided into landing latency, defined as time spent between flight initiation, zigzag-oriented flight and arrival on the platform containing the ME source and feeding latency, defined as the time spent between the first landing, searching and feeding on the filter paper containing the ME source. The experiment was replicated seven times with 5–10 flies from different cohorts for each treatment.

Statistical Analysis

Data obtained from the cage bioassays were subjected to Shapiro-Wilk normality tests followed by one-way analysis of variance (ANOVA). Means were separated by Tukey’s test (P = 0.05). For the wind tunnel bioassays, none of the males with antennae only as well as antennae and maxillary palps’ ablation responded to the ME source presented. Therefore, comparisons of landing and feeding latencies were made only between maxillary palp-ablated and untreated intact males. The Student’s t-test was used to compare landing or feeding latency results between intact and maxillary palp-ablated males unless requirements for normality or homogeneity of data was not met, in which case the Mann-Whitney U-test was used. Statistical analysis was performed using SPSS 25.0 and the α value was set at P = 0.05 for all comparisons.
Results

Cage Bioassay

Our results show that ablation of either or both olfactory organs of male B. dorsalis had a significant effect on the males’ responsiveness to ME over shorter distances of ≤40 cm ($F = 669.99$, df = 3, 24; $P < 0.001$). The intact, untreated males (96.3%) were the most attracted to ME followed by the maxillary palp-ablated males (75.0%) and antenna-ablated (17.6%). None of the males with both antennae and maxillary palps ablated responded to ME (Fig. 1). The ablation of maxillary palps and antennae were both shown to significantly affect male response to ME when compared to intact, untreated males ($P < 0.001$; Tukey’s test).

Wind Tunnel Bioassay

In the wind tunnel bioassay, all of the flies from the intact, untreated and maxillary palp-ablated treatments flew zigzag and eventually landed at the upwind end of the wind tunnel while none of the antenna- and antenna and maxillary palp-ablated males responded in the same way. There were significant differences between intact, untreated males and maxillary palp-ablated males in terms of landing and feeding latencies when assayed over a longer distance of >100 cm (Table 1). The maxillary palp-ablated males took a significantly longer time (221.3 s) compared to untreated intact males (142.3 s) to detect, initiate a take-off, complete flight orientation with eventual landing (=landing latency) on the ME source (Mann-Whitney U-test, $P = 0.011$). Upon first landing on the ME source, these males (25.0 s) also took a significantly longer time than untreated males (9.6 s) to finally locate the attractant and to feed on it (=feeding latency) ($t = 5.930$, df = 6; $P = 0.00103$).

Discussion

The response of male fruit flies to chemical attractants such as ME is known to involve receptors on both the antenna and maxillary palp organ structures. Although the involvement of the antenna in this response is well established, relatively little has been done heretofore to understand the relative importance of the maxillary palp.

In our study, we evaluated the impact of removing (by ablation) one or both of these structures on ME attractiveness to B. dorsalis males over longer ranges (via wind tunnel bioassays) and shorter ranges (via cage bioassays). We showed that while the antennae are necessary for long-range detection of ME, the maxillary palps are also involved in a complementary manner. In addition, the maxillary palps appear to be important for guiding the males to locating the ME source at closer ranges. The wind tunnel bioassays showed that without the antennae, at a distance of ca. 150 cm, all males failed to detect the presence of ME. In contrast, all of the males with intact antenna but ablated maxillary palps successfully detected ME and flew to the upwind end of the tunnel to feed on it.

This observation supports the general view that antenna is a critical olfactory organ involved in long-range foraging for food and other semiochemicals needed for survival and reproduction of insects (Haverkamp et al. 2018). Even when males with intact antenna but ablated maxillary palps were used, results from both cage and wind tunnel bioassays showed that these males were capable of responding to ME. However, at closer ranges, the ablation of maxillary palps significantly impaired this searching behavior. As evidenced by the significant longer landing and feeding latency periods in the wind tunnel bioassays, those males clearly spent much longer time durations in searching and locating before the eventual feeding on the ME source. This suggests that while both organs are required for successful detection of ME, at least at close ranges, the maxillary palps may play a bigger role than the antennae in orienting the male toward the lure source.

In the cage bioassays, ca. 17% of our antenna-ablated males were observed to still be attracted to ME. This corroborated well with results obtained by Metcalf and colleagues (1975) who found that when B. dorsalis males with both antennae amputated were exposed to ME, ca. 21% of them were still attracted to the lure. Both sets of results clearly show that the total removal of antennae impacts but does not entirely impair the ability of the B. dorsalis males to detect ME. These results also suggest that sensilla involved in response to ME may be present in other olfactory organs such as the maxillary palps. This is supported by our results showing a significant reduction in the maxillary palp-ablated males’ response to ME when compared to males with no structural alterations. Furthermore, when the number of males with either maxillary palp-only and antenna-only ablations still showing response to ME is combined, the sum is very close to the normal rate of males responding to ME as shown by the unaltered males in the control. This further supports our assertion that the maxillary palps are an important part of the circuitry involved in the ME detection by B. dorsalis males.

Table 1. Wind tunnel attraction of male oriental fruit fly to ME as measured by landing and feeding latency after the removal of antennae (ANT) and/or maxillary palps (MP)

| Treatment          | Landing latency$^a$ | Feeding latency$^b$ |
|--------------------|---------------------|---------------------|
| Intact (ANT + MP)  | 142.3 ± 27.0a       | 9.6 ± 1.7a          |
| MP ablation        | 221.3 ± 26.1b       | 25.0 ± 4.2b         |
| ANT ablation       | n/a$^c$             | n/a$^c$             |
| ANT + MP ablation  | n/a$^c$             | n/a$^c$             |

SEM results with different lower case letters (a,b) represent values showing significant differences.

$^a$Time spent between flight initiation and zigzag-oriented search upon detection of ME and eventual arrival on the platform containing the ME source ($P < 0.05$; Mann-Whitney U-test).

$^b$Time spent between first landing, searching and eventual feeding on the filter paper containing the ME source ($P < 0.001$; Student’s t-test).

$^c$None of the males with ANT and ANT+MP ablation elicited any positive response to the ME source presented.
Examination of the ultrastructure of the antenna of *B. dorsalis* shows that the funiculus (third segment of the antennae), is the largest segment of the antenna housing various types of olfactory sensilla including basiconic, coeloconic, and trichoid sensilla (Lee et al., 1994). These sensilla are known to possess pores with different wall thicknesses (Dickens et al., 1988, Hu et al., 2010) allowing passage of volatile chemical molecules into the sensillum lymph for triggering of cascades of biochemical events leading to behavioral changes (Kaupp 2010) in the flies. In contrast to the funiculus, however, only minute number of sensilla are found in the basal segment (first segment), the pedicel segment (second segment) and the fourth segment with a projection of arista which consists mainly of microtrichial and chaetica sensilla that are not known to have pores.

Apart from the antenna, it has also been shown in insects that olfactory sensilla are also located in the maxillary palp (Anton et al. 2003), although much reduced in numbers compared to the antenna (Shanbhag et al., 2000, de Bruyne et al., 1999, Laissue and Vosshall 2008). In the oriental fruit fly, three types of morphologically distinct sensilla have been reported in the maxillary palp known as chaetica, microtrichia, and sensilla basiconica (Zhang et al. 2011). However, only the basiconica type appears to be that associated with olfaction. Thus, in assuming that similar olfactory receptors that respond to ME also exist in the basiconica sensilla, the presence of that sensilla in both maxillary palp and antennal structures is consistent with the notion that the maxillary palps are also involved in the male fly detection of ME. In support of this hypothesis, we showed through various behavioral assays that the antennae and palps are both utilized for successful detection and location of ME.

A plausible explanation of why the wind tunnel results showed that the maxillary palp-ablated males required a longer time (almost three times as long as non-ablated males) to seek the ME source compared to the non-ablated males, to locate, land upon and finally feed on ME remains to be elucidated. Current results show the involvement of the maxillary palps at close range in detection of ME. This, together with the fact that sensilla of the basiconica type are known to occur in both maxillary palp and antenna structures of the oriental fruit fly (Dickens et al., 1988, Hu et al., 2010, Zhang et al. 2011) certainly warrants further investigation into the role that these particular sensilla have in relation to olfactory neurons, receptors, and carriers. We believe that these findings support our suggestion that the maxillary palps be an additional focal point of olfactory research in Tephritid fruit flies. This can hopefully be combined with extensive work conducted recently on the transcriptomes of the oriental fruit fly and other Tephritid species focusing on identifying genes and proteins in these species involved in chemoreception (Zheng et al. 2013, Wu et al. 2015; Elfeikhi et al., 2016; Liu et al. 2016; 2017, 2018; Miyazaki et al. 2018) as part of the search for novel ways to control these highly destructive and invasive pests.

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**References Cited**

Anton, S., J. J. van Loon, J. Meijerink, H. M. Smid, W. Takken, and J. P. Rospars. 2003. Central projections of olfactory receptor neurons from single antennal and palpal sensilla in mosquitoes. Arthropod Struct. Dev. 32: 319–327.

Brito, N. F., M. F. Moreira, and A. C. Melo. 2016. A look inside odorant-bind- ing proteins in insect chemoreception. J. Insect Physiol. 95: 51–65.

de Bruyne, M., P. J. Clyne, and J. R. Carlson. 1999. Odor coding in a model olfactory organ: the Drosophila maxillary palp. J. Neurosci. 19: 4520–4532.

Clarke, A. R., K. F. Armstrong, A. E. Carmichael, J. R. Milne, S. Raghu, G. K. Roderick, and D. K. Yeates. 2005. Invasive phytophagous pests arising through a recent tropical evolutionary radiation: the Bactrocera dorsalis complex of fruit flies. Annu. Rev. Entomol. 50: 293–319.

Dickens, C., W. G. Hart, D. M. Light, and E. B. Jang. 1988. Tephritid olfaction: morphology of the antennae of four tropical species of economic importance (Diptera : Tephritidae). Annu. Entomol. Soc. Am. 81: 325–333.

Dweck, H. K. M., S. A. M. Ebrahim, M. A. Khalaff, C. Koenig, A. Farhan, R. Steicher, J. Weißlog, A. Svatoš, E. Grosse-Wilde, M. Knaden, et al. 2016. Olfactory channels associated with the Drosophila maxillary palp mediate short-and long-range attraction. Elife. 5: e14925.

Elfeikhi, S., C. Y. Chen, J. C. Hsu, M. Belaid, and D. Haymer. 2016. Identification and preliminary characterization of chemosensory perception-associated proteins in the melon fly Bactrocera cucurbitae using RNA-seq. Sci. Rep. 6: 19112.

Hansson, B. S. 1999. Insect olfaction. Springer, Berlin, Germany.

Hansson, B. S., and M. C. Stensmyr. 2011. Evolution of insect olfaction. Neuron. 72: 698–711.

Haverkamp, A., B. S. Hansson, and M. Knaden. 2018. Combinatorial codes and labeled lines: how insects use olfactory cues to find and judge food, mates, and oviposition sites in complex environments. Front. Physiol. 9: 49.

Hee, A. K. W., and K. H. Tan. 1998. Attraction of female and male Bactrocera papayae to conspecific males fed with methyl eugenol and attraction of females to male sex pheromone components. J. Chem. Ecol. 24: 753–764.

Hu, F., G.-N. Zhang, F.-X. Jia, W. Dou, and J.-J. Wang. 2010. Morphological characterization and distribution of antennal sensilla of six fruit flies (Diptera: Tephritidae). Ann. Entomol. Soc. Am. 103: 661–670.

Kaupp, U. B. 2010. Olfactory signalling in vertebrates and insects: differences and commonalities. Nat. Rev. Neurosci. 11: 188–200.

Khamis, F. M., N. Karam, S. Ekesi, M. DE Meyer, A. Bonomi, L. M. Gomulski, F. Scolari, P. Gabrieli, P. Siciliano, D. Masiga et al. 2009. Uncovering the tracks of a recent and rapid invasion: the case of the fruit fly pest Bactrocera invasiva (Diptera: Tephritidae) in Africa. Mol. Ecol. 18: 4798–4810.

Lee, W., J. Chang, Y. Hwang, and T. Lin. 1994. Morphology of the antennal sensilla of the oriental fruit fly, Dacus dorsalis Hendel (Diptera: Tephritidae). Zool. Stud. 33: 65–71.

Liu, Z., G. Smagghe, Z. Lei, and J. J. Wang. 2016. Identification of male- and female-specific olfactory genes in antennae of the oriental fruit fly (Bactrocera dorsalis). PLoS One 11: e0147783.

Liu, H., X. F. Zhao, L. Fu, Y. Y. Han, J. Chen, and Y. Y. Lu. 2017. BdorOBP2 plays an indispensable role in the perception of methyl eugenol by mature males of Bactrocera dorsalis (Hendel). Sci. Rep. 7: 13894.

Liu, H., Z. S. Chen, D. J. Zhang, and Y. Y. Lu. 2018. BdorOR88A modulates the responsiveness to methyl eugenol in mature males of Bactrocera dorsalis (Hendel). Front. Physiol. 9: 987.

Metcalfe, R. L., W. C. Mitchell, T. R. Fukuto, and E. R. Metcalf. 1975. Attraction of the oriental fruit fly, Dacus dorsalis, to methyl eugenol and related olfactory stimulants. Proc. Natl. Acad. Sci. U. S. A. 72: 2501–2505.

Miyazaki, H., J. Otake, H. Mitsuno, K. Ozaki, R. Kanazaki, A. Chui-Ting Chiang, A. Kah-Wei Hee, R. Nishida, and H. Ono. 2018. Functional characterization of olfactory receptors in the oriental fruit fly Bactrocera dorsalis that respond to plant volatiles. Insect Biochem. Mol. Biol. 101: 32–46.

Nishida, R., K. H. Tan, M. Serit, N. H. Lajis, A. M. Sukari, S. Takahashi, and H. Fukami. 1988. Accumulation of phenylpropanoids in the rectal glands of male Oriental fruit fly, Dacus dorsalis. Experientia 44: 534–536.

Pereira, R., B. Yuval, P. Liedo, P. E. A. Teal, T. E. Shelly, D. O. Mcinnis, and J. Hendrichs. 2013. Improving sterile male performance in support of programmes integrating the sterile insect technique against fruit flies. J. Appl. Entomol. 137: 176–190.

Reisenman, C. E., H. Lei, and P. G. Guerenstein. 2016. Neuroethology of olfactory-guided behavior and its potential application in the control of harmful insects. Front. Physiol. 7: 271.
Schutze, M. K., N. Aketarawong, W. Amornsak, K. F. Armstrong, A. A. Augustinos, N. Barr, W. Bo, K. Bourtzis, L. M. Boykin, C. Cáceres, et al. 2015. Synonymization of key pest species within the Bactrocera dorsalis species complex (Diptera: Tephritidae): taxonomic changes based on a review of 20 years of integrative morphological, molecular, cytogenetic, behavioural and chemoecological data. Syst. Entomol. 40: 456–471.

Shanbhag, S. R., B. Müller, and R. A. Steinbrecht. 2000. Atlas of olfactory organs of Drosophila melanogaster 2. Internal organization and cellular architecture of olfactory sensilla. Arthropod Struct. Dev. 29: 211–229.

Shelly, T. E., and A. M. Dewire. 1994. Chemically mediated mating success in male oriental fruit flies (Diptera: Tephritidae). Ann. Entomol. Soc. Am. 87: 375–382.

Shelly, T., N. Epsky, E. B. Jang, J. Reyes-Flores, and R. Vargas. 2014. Trapping and the detection, control, and regulation of tephritid fruit flies: lures, area-wide programs, and trade implications. Springer, Dordrecht, the Netherlands.

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

Suh, E., J. Bohbot, and L. J. Zwiebel. 2014. Peripheral olfactory signaling in insects. Curr. Opin. Insect Sci. 6: 86–92.

Tan, K. H. 1985. Estimation of native populations of male Dacus spp. by using Jolly’s stochastic method using a new designed attractant trap in a village ecosystem. J. Plant Prot. Trop. 2: 87–95.

Tan, K. H., and R. Nishida. 1996. Sex pheromone and mating competition after methyl eugenol consumption in the Bactrocera dorsalis complex, pp. 147–153. In B. A. McPherson; G. J. Steck (eds.), Fruit fly pests: a world assessment of their biology and management. St. Lucie Press, Delray Beach, FL.

Tan, K. H., L. G. Kirton, and M. Scrit. 1987. Age response of Dacus dorsalis (Hendel) to methyl eugenol in (a) a wind tunnel and (b) traps set in a village, and its implication in population estimation, pp. 425–432. In Economopoulos, A. P. (ed.), Fruit Flies Proc. Second Int. Symp, 16–21 September 1986, Colymbari, Crete, Greece/ Ed. by AP Econ. G. Tsiveriotis Ltd., Athens, Greece.

Vargas, R. I., J. C. Piñero, and L. Leblanc. 2015. An overview of pest species of bactrocera fruit flies (Diptera: Tephritidae) and the integration of biopesticides with other biological approaches for their management with a focus on the Pacific region. Insects. 6: 297–318.

Verschut, T. A., K. Farnier, J. P. Cunningham, and M. A. Carlsson. 2018. Behavioral and physiological evidence for palp detection of the male-specific attractant cue in the Queensland fruit fly (Bactrocera tryoni). Front. Physiol. 9: 990.

Vosshall, L. B., and P. P. Laissue. 2008. The olfactory sensory map in Drosophila. Adv. Exp. Med. Biol. 628: 102–114.

Wasserman, S. L., and H. Itagaki. 2003. The olfactory responses of the antenna and maxillary palp of the fleshfly, Neobellieria bullata (Diptera: Sarcophagidae), and their sensitivity to blockage of nitric oxide synthase. J. Insect Physiol. 49: 271–280.

Wu, Z., H. Zhang, Z. Wang, S. Bin, H. He, and J. Lin. 2015. Discovery of chemosensory genes in the oriental fruit fly, Bactrocera dorsalis. PLoS One 10: e0129794.

Wu, Z., J. Lin, H. Zhang, and X. Zeng. 2016. BdorOBP83a-2 Mediates Responses of the oriental fruit fly to Semiochemicals. Front. Physiol. 7: 452.

Zhang, G.-N., H. Hull-Sanders, F. Hu, W. Dou, J-Z. Niu, and J-J. Wang. 2011. Morphological characterization and distribution of sensilla on maxillary palpi of Six Bactrocera fruit flies (Diptera: Tephritidae). Florida Entomol. 94: 379–388.

Zheng, W., C. Zhu, T. Peng, and H. Zhang. 2012. Odorant receptor co-receptor Orco is upregulated by methyl eugenol in male Bactrocera dorsalis (Diptera: Tephritidae). J. Insect Physiol. 58: 1122–1127.

Zheng, W., W. Peng, C. Zhu, Q. Zhang, G. Saccone, and H. Zhang. 2013. Identification and expression profile analysis of odorant binding proteins in the oriental fruit fly Bactrocera dorsalis. Int. J. Mol. Sci. 14: 14936–14949.