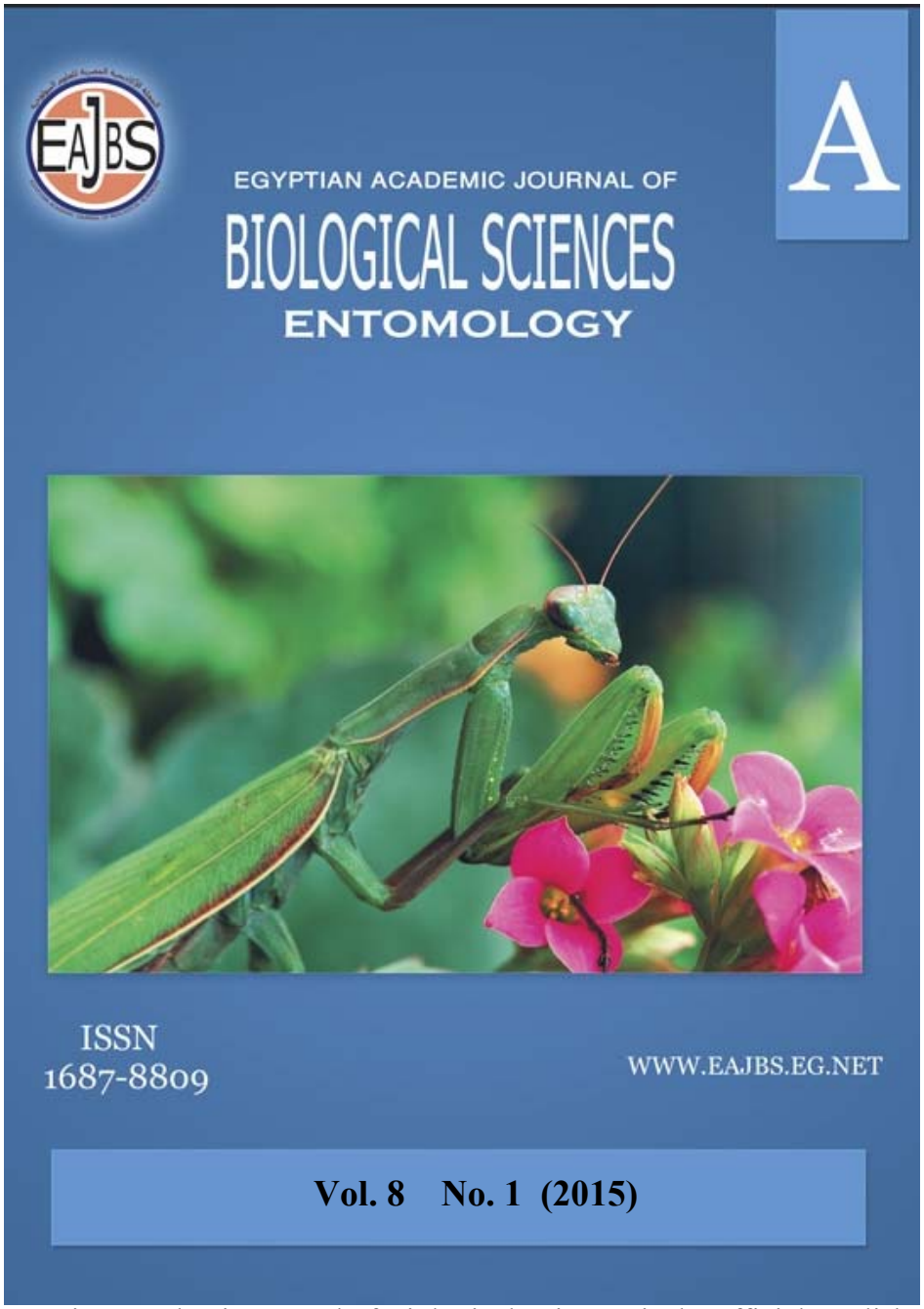

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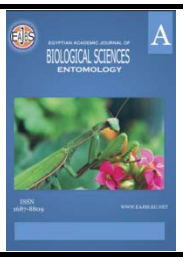

The effect of different host plants on the antennal and mouthparts sensilla of the larvae of *Spodoptera littoralis*; (Lepidoptera; Noctuidae)

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ABSTRACT

The distribution and morphology of various sensory organs (sensilla) on the antenna and mouthparts of *Spodoptera littoralis* larvae were investigated using scanning electron microscopy. In this study we focused on the morphological alterations of the antennal and mouthparts sensilla of *Spodoptera littoralis* last instar larvae reared on different host plants; alfalfa, cotton, and soybean leaves. Based on our results, we found that sensillum chaeticum on the antenna was morphologically affected by shifting the host plant since it became longer in those larvae reared on soybean and alfalfa leaves when compared with those reared on cotton leaves. Furthermore, several morphological variations were observed in sensilla trichodea on the labium, mandibles, and labrum by shifting the host plant. In addition, clear morphological changes were observed in sensillum digitiformium on the maxillary palps due to changing the host plant. On the other hand, no morphological changes in antennal basiconic, trichodium and styloconic galeal sensilla styloconica, maxillary campaniform and placodeum sensilla were observed. Taken together, these results showed that shifting host plants of *Spodoptera littoralis* larvae induced plasticity and morphological changes of the antennal and mouthparts sensilla.

INTRODUCTION

Insects have a special need to have developed sensory organs to monitor their external environment (Zacharuk, 1985). Larvae are generally restricted in habitat and mobility, and are generally more favored targets for the management and control of pest-insect populations (Zacharuk and Shields, 1991). Knowledge of the sensory organs involved in their food-finding, feeding behavior, and ingestion is paramount in the development and application of those pest control agents, in particular, that require ingestion (i.e. microbial agents) or that will prevent feeding (antifeedants),

olfaction is usually restricted to short-range orientation to optimally nutritious food (Zacharuk and Shields, 1991). Taste and tactile cues for food selection and gustation are of primary importance to the immature stage, along with sensilla that provide temperature, humidity, tactile, and some visual monitoring for orientation and protection (Zacharuk and Shields, 1991)**.** Immature stages develop through several molts, at which times cuticular parts of existing sensilla are replaced and new sensilla may develop (Zacharuk and Shields, 1991).

In the past decades, the structure, morphology and function of the antennal and mouthparts sensory organs (sensilla) of lepidopteran larval insects has been investigated in several larval models (Hallberg, 1981; Faucheux, 1995; Awad, 1999; Lin, 2002; Liu *et al.*, 2011; Song *et al.*, 2014). Sensilla on the antenna and mouthparts of lepidopteran larvae can perform one or more sensory functions (Faucheux, 1995; Liu *et al.*, 2011). In this respect, sensilla on the antennae and mouthparts of lepidopteran larvae can be categorized to several groups according to their functions; mechanoreceptors (chaetica, stylochonica, and campaniform) (Albert, 1980; Devitt and Smith, 1982; Faucheux, 1995), olfactory receptors (Placodea, basiconica, and styloconica) (Faucheux, 1995; Keil, 1996), gustatory receptors (trichodea, styloconica, and campaniformia) (Albert, 1980; Zhang *et al.*, 2011b), contact chemoreceptors (styloconica, and basiconica) (Devitt and Smith, 1982), and cold-sensitive receptors (stylochonica and basiconica) (Zacharuk, 1985; Faucheux, 1995). From other point of view, the function (s) of sensilla in lepidopteran larvae can be categorized depending on their location as following: olfactory sensilla are located on the antenna, maxillary palps and galeae (Morita and Yamashita, 1961; Schoonhoven and Dethier, 1966; Devitt and Smith, 1982). In addition, gustatory sensilla are located on the maxillary palps and galeae and epipharynx (Dethier, 1937; Schoonhoven and Dethier, 1966; Stadler and Hanson, 1975; Schoonhoven and Van Loon, 2002). Mechanosensory sensilla are not restricted to antennae but also distributed on the mouthparts (Faucheux, 1995). The morphological alterations in the antennal and mouthparts sensilla reared on different host plants have poorly investigated. *Spodoptera littoralis* (Boisd.) (Lepidoptera: Noctuidae), the Egyptian Cotton Leafworm is a polyphagous insect attacking a number of plant species including those belonging to several plant families and often acts as a pest on vegetables, fruits, flowers and other crops (Krishnan and Kodrik, 2006). It is reported that, shifting of *Spodoptera littoralis* larvae to different host plants can affect pupal weight, growth index, female longevity and fecundity (Adham *et al.*, 2009; Zhang *et al.*, 2011a). Also, recent study showed that the insect growth regulator, flufenoxuron affected the morphology, length, and dirtribution of the antennal sensilla of adult *Spodoptera littoralis* (Zohry, 2008). However, no data on the changes of antennal and mouthparts sensilla of *Spodoptera littoralis* larvae provided with different food items. Here we tried to answer the question that does feeding of *Spodoptera littoralis* larvae on different host plants can affect structure/morphology of sensilla and consequently function to adapt their feeding style?. In larval stages, sensilla on the antennae and mouthparts are important determinant in food preferential selection (Zacharuk, 1985). Therefore, in this study we investigated the morphological structure, and the changes of the antennal and mouthparts sensilla of *Spodoptera littoralis* larvae reared on different host plants; alfalfa, cotton, and soybean leaves using scanning electron microscope.

MATERIALS AND METHODS

Spodoptera littoralis larvae were obtained from the plant protection department at Assiut university farm as egg batches, their larvae were reared on castor leaves (*Ricinus communis*), and then the newly hatched larvae were reared and maintained at entomology laboratory at faculty of Science, Assiut University. For good aeration, the larvae were reared in porous plastic boxes in incubators with humid tightly controlled rearing conditions. To investigate the ultrastructure of antennal and mouthparts sensilla of the last larval instar (6th instar) of *Spodoptera littoralis*, the culture was reared under the laboratory conditions (Temperature = 25 °C, 16L hrs: 8D) and fed on alfalfa (Medicago sativa) for several generations. The newly hatched larvae were subgrouped into three categories; one group was reared on alfalfa, the second group was shifted to be reared on cotton (*Gosspium barbadense*) leaves, and the third group was shifted to be reared on soya bean (Glycine max) leaves. Then the fully grown last 6th instar larvae from the three groups were collected and prepared for investigating the structure and the morphological changes among these three groups using scanning electron microscopy. The processing of samples applied for scanning electron microscope was performed as previously described (Awad, 1999). Briefly, 6th instar larvae were killed in hot water and then heads were separated and fixed in Khal's solution (30% of 95% EtOH, 12% formaldehyde, and 4% glacial acetic acid) in distilled water. Specimens were fixed in Khal's solution for 7–8 days at 4 C° and then washed in the same buffer vehicle three times. Then specimens were post-fixed in a cacodylate buffered solution of 1% osmium tetroxide for 2 hrs at 37 C°. The specimens were washed in the same buffer three times, dehydrated and then infiltrated with amyl acetate for two days. The drying of specimens is accomplished by the critical point drying using liquid Co2, mounted and sputter-coated with gold. The specimens were examined with a Jeol scanning electron microscope (J S M- 5400 L V), at 15 Kv.

RESULTS

General structure of the larval head capsule

Briefly, the head of last instar (6th instar) of *Spodoptera littoralis* larvae is a hypognathous rounded sclerotized capsule. The frontal portion of the head capsule is supplied with the antennae and mouthparts (Fig. 1). There is a pair of antennae, locating on the ventro-lateral surface of the head. They are short and arise from a membranous base between the head capsule and the mandibles. The mouthparts are composed of a labrum, a pair of mandibles, a pair of maxillae, a labium, and a hypopharynx (maxillolabial hypopharengeal complex) (Fig. 1). The changes and alterations of sensory organs (sensilla) on the antennae and mouthparts of *Spodoptera littoralis* last instar larvae fed on different host plants (alfalfa, cotton, and soyabean leaves) were examined and demonstrated as following.

Antennal sensilla

The types of sensilla on the antenna of *Spodoptera littoralis* last instar larvae fed on alfalfa, cotton, and soyabean were examined and photographed using scanning electron microscopy. The antennae of the last instar larvae of *Spodoptera littoralis* consist of three segments; basal segment, medial segment, and distal segment. Except the basal segment, the two other segments bear sensilla (Figs. 2 & 3).

The medial segment of the larval antennae carry three types of sensilla; a single hair like sensillum chaeticum (SCh), two sensilla basiconica (SB1 and SB2), and

sensillum trichodium (ST). SCh is the longest sensillum among the antennal sensilla (Fig. 2). The length of SCh is longer in the larvae reared on soybean and alfalfa leaves, respectively than that fed on cotton leaves (Fig. 2). Sensilla basiconica (SB1and SB2) are stout pegs; have enlarged basal portions (Fig. 3). there is no morphological changes has been noticed in both SB1 and SB2 in the *Spodoptera littoralis* last instar larvae reared on the previously mentioned host plants (Fig. 3). However, there is a short sensillum like projection; a sensillum basiconicum (SB3) appeared close to SB2 in medial segment of the larval antennae reared on only alfalfa leaves (Fig. 3). Sensillum trichodium (ST) is a long cylindrical like process, located at the interior margin of the medial segment (Fig. 3). No clear morphological changes were observed in ST after feeding with the above host plants (Fig. 3).

The distal segment is greatly reduced and borne distally along the dorsal margin of the medial segment; it is much thinner than the medial segment (Fig. 3). It possesses three sensilla basiconica (SB4, SB5, and SB6), in addition to a single sensillum styloconicum (SSt) (Fig. 4). The sensillum basiconisum SB4 is a stout peg, and is longer than SB5 and SB6 (Fig. 4). No changes in the three sensilla basiconica have been observed (Fig. 4). The sensillum styloconicum (SSt) is an elongate cone inserted at the tip of a short thick cylindrical cuticle (Fig. 4). No changes also in SSt have been observed after rearing the last larval instars in alfalfa, cotton, and soybean leaves (Fig. 4).

Labrum sensilla

There are six pairs sensilla trichodae (from T1 to T6) distributed symmetrically on both sides of the dorsal surface (Fig. 5). No regular pattern of morphological changes in the length of sensilla trichodae on the labrum of the last larval instar of *Spodoptera littoralis* reared on the previously mentioned host plants (Fig. 5).

Mandibular sensilla

Each mandible bears two sensilla trichoda (Tr1 and Tr2). They are situated on the basal part of the outer surface of mandibles (Fig. 5). In general pattern, Tr2 is shorter than Tr1 (Fig. 5). On feeding of the larval last instar of *Spodoptera littoralis* on alfalfa, cotton, and soya bean leaves, there is some irregular variations in the sensilla length were observed in the sensilla trichoda on the mandibles (Fig. 5).

Maxillary sensilla

Each Maxilla consists of two appendages; the maxillary palp (MP) and the maxillary galea (MG) (Fig. 6). The maxillary galea (MG) possesses two sensilla styloconica (SSt1, SSt2) on its apex (Fig. 6). Both of the sensilla styloconica have a small slender peg on the top of an elongated thick bulbous base. There are also three flattened elongated sensilla chaetica (SCh1, SCh2, SCh3) arise from the outer margin of MG (Fig. 6). The maxillary galea carries also between SSt1 and SSt2 a single short sharply pointed sensillum basiconicum (SB) (Fig. 6). No changes have been observed by shifting the host plants in all maxillary galea sensilla; sensilla styloconica, chaetica, and sensillum basiconicum (Fig. 6).

The maxillary palp is two-segmented; basal wide cylindrical shape segment, and apical conical segment (Fig. 7). The basal segment carries a single placoid sensillum (SP). The apical segment carries eight finger-like cuticular projections (sensilla basiconica) on its apex (Fig. 8). They can be divided into three groups: three apical sensilla (A1-A3), three lateral sensilla (L1-L3), and two medial sensilla (M1and M2) (Fig. 8). Investigation of their arrangements and length after feeding the larvae on alfalfa, cotton and soya bean leaves, no clear changes in their arrangements or size were observed (Fig. 8). In addition, carries also a Campaniform sensillum (SC) at the lateral side (Fig. 7). Below the level of SC, there is a sensillum digitiformium (SD) on

the outer surface of the apical segment (Fig. 7) Sensillum digitiformium looks like U shape in the larvae reared on alfalfa leaves (Fig. 9). SD in those larvae reared on cotton looks asymmetrical C shape and shorter than that reared on alfalfa leaves (Fig. 9). However, it was V shape in those larvae reared on soya bean leaves (Fig. 9).

Labium sensilla

The labial region consists of a pair of two-segmented labial palps and a long spinneret (S) from which silk is secreted by larvae (Fig. 10). Each labial palp bears a long sensillum trichodium (STr) on the apex of the second labial segment and a short sensillum basiconicum (SB) merged from the outer margin of the first labial segment (Fig. 10). STr is a spine-like (Fig. 10). The length of STr was almost same in the larvae reared on alfalfa and cotton leaves; however, it was clearly shorter in those larvae reared on soya bean leaves (Fig. 10). The spinneret carries no sensilla (Fig. 10).

DISCUSSION

The types, morphology and distribution of sensilla in immature insect larvae were previously reviewed (Zacharuk and Shields, 1991). The types, numbers, and distribution of sensilla on the larval antennae of *Spodoptera littoralis* resemble those of other lepidopterous larvae (Faucheux, 1995; Awad, 1999; Lin, 2002; Liu *et al.*, 2011; Xue and Hua, 2014). According to our best of knowledge, no available studies investigated the morphological changes of sensilla in relation to host plant shifting in insect larvae. In the current study, we found that, changing the provided food items and rearing of *Spodoptera littoralis* larvae on different host plants induced distinct changes and plasticity in the antennal and mouthparts sensilla. In this respect, it is reported that the treatment of the antijuvenile agent (precocene II) at the egg stage showed changes in the basiconic sensilla on the maxillary palp and galea and on the size of the basiconic sensilla on the second and third antennal segments in lepidopteran *Archips podana Scop* larvae (Triseleva, 2007).

Through the present study we followed the same nomenclatures used by Awad (Awad, 1999). Our results showed that feeding of *Spodoptera littoralis* larvae on different host plants affected size and morphology of some antennal and mouthparts sensilla such as antennal sensillum chaeticum (SCh), labial sensillum trichodium (STr), mandible (Tr) and labrum (T1-T6) sensilla trichodea, and maxillary palps sensillum digitiform (SD). The sensilla on the antennae and mouthparts have important functions during larval stages. The main function of the antennal sensilla is olfactory in lepidopteran larvae (Liu *et al.*, 2011). Behavior experiments showed that the mouthparts sensilla posses olfactory and gustatory functions and possibly have mechanoreceptory functions (Schoonhoven and Dethier, 1966; Ishikawa *et al.*, 1969). In the current study, Sensillum chaeticum (SCh) on the *Spodoptera littoralis* larval antennae became longer in those reared on alfalfa and Soybean leaves when compared with those reared on cotton. These data suggest that this sensilla plasticity and morphological changes may relate to food availability. The antennal sensillum chaeticum on the second segment, mechanosensory sensilla adapted for the reception of tactile stimuli including air currents, vibrations of the substrate, and shocks sensed by the sensilla from exploratory movements of the antennae (Kent and Hildebrand, 1987; Faucheux, 1999).

It is reported that sensilla chaetica are located on the antenna, labrum, labium, mandible and galea in the lepidopteran *Homoeosoma nebulella* larvae (Faucheux, 1995). However, following the terminology of Zacharuk (Zacharuk, 1985), in our research we named the sensilla which are located on the second antennal segment,

labrum, mandibles, and labium of *Spodoptera littoralis* larvae as sensilla trichodea. It is stated that sensilla chaetica on maxillae, mandibles, labrum and labium in lepidopteran larvae are mechanoreceptors (Schoonhoven and Dethier, 1966; Hanson, 1970; Liu *et al.*, 2011). Also, sensilla chaetica are suggested to perform tactile mechanoreceptor functions (Albert, 1980; Devitt and Smith, 1982; Faucheux, 1995).

In addition to coordinating the movement of the mouthparts and the manipulation of food, mechanosensory sensilla give the larva information about the proximity of food and its texture (Faucheux, 1995).

The morphological changes in sensilla trichodea on both labial palps, mandibles and labrum are due to shifting of the host plants suggest that *Spodoptera littoralis* larvae altered their feeding behavior via altering mainly their mechanosensory organs. Another sensory organ; sensillum digitiformium suggested to be sensitive to temperature (Devitt and Smith, 1982). it is stated that, in *Helicoverpa armigera* caterpillars the digitiform sensilla on the maxillary palp is the most probable candidate for the CO2-receptor (Keil, 1996). Feeding of *Spodoptera littoralis* larvae on different host plants altered the shape and size of digitiform sensillum.

On the other hand, no clear morphological or distribution changes were observed in the antennal basiconic (SB), trichodium (ST), and styloconic (SSt) sensilla. In addition, no morphological changes in galeal sensilla styloconica (SSt1, SSt2), basiconica (SB) and chaetica (SCh1, SCh2 and SCh3), and maxillary campaniform (SC), and placodeum (SP) sensilla as well as maxillary and labial sensilla basiconica (SB). Sensilla basiconica has been reported to possess contact chemoreceptor, mechanoreceptor, and olfactory functions (Morita and Yamashita, 1961; Schoonhoven and Dethier, 1966; Hanson, 1970; Faucheux, 1995). Also, it is suggested basiconic and styloconic sensilla act as temperature cold-sensitive receptors (Zacharuk, 1985; Faucheux, 1995). Also, it is stated that, sensilla basiconica on the tip of the terminal maxillary palps have a gustatory function in perceiving specific phagostimulants and feeding deterrents (Lin, 2002). They are probably related to olfactory functions (Devitt and Smith, 1982). In addition, galeal styloconic sensilla has important role in food recognition and has olfactory and gustatory functions (Ishikawa *et al.*, 1969; Faucheux, 1995). Sensilla placodea consists of shallow depressions of cuticle functions as olfactory receptors (Lin, 2002). There is a correlation between insect behavioral variations and the phenotypic changes in antennal and mouthparts sensilla (Chapman, 2002; Opstad *et al.*, 2004). In this regard, phenotypic variation in numbers of antennal sensilla among grasshoppers has been observed as a results of differences in crowding, food quality, and the odorous environment experienced by the insects (Chapman, 2002).

It is reported that changes in the sensory organs may due to food variations (Lavoie-Dornik and McNeil, 1987), Consistently, our data showed that considerable morphological changes in the larval antennal and mouthparts sensilla in *Spodoptera littoralis* were observed after shifting the host plants. It could be concluded that feeding of *Spodoptera littoralis* larvae on different host plants affect the morphology, and size of some antennal and mouthparts sensilla in a host plant-specific manner. These morphological changes in the sensilla may due to developmental changes during molting of the larvae from one instar to the next instar and/or due to the variations of the odor of the provided host plant leaves.

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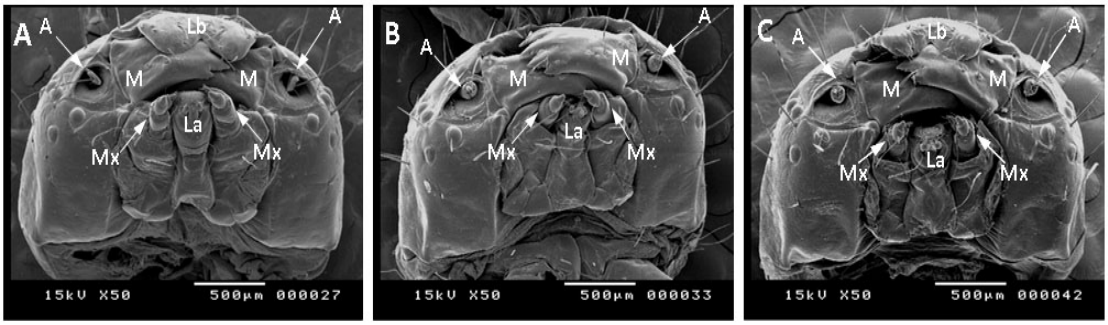

Fig. 1: Scanning electron micrograhs showing ventrofrontal view of the head capsule of *Spodoptera littoralis* 6th instar larvae reared on Alfalfa (A), Cotton (B), and Soybean (C). Antenna, A; Labium, La; Labrum, Lb; Mandible, M; Maxilla, Mx.

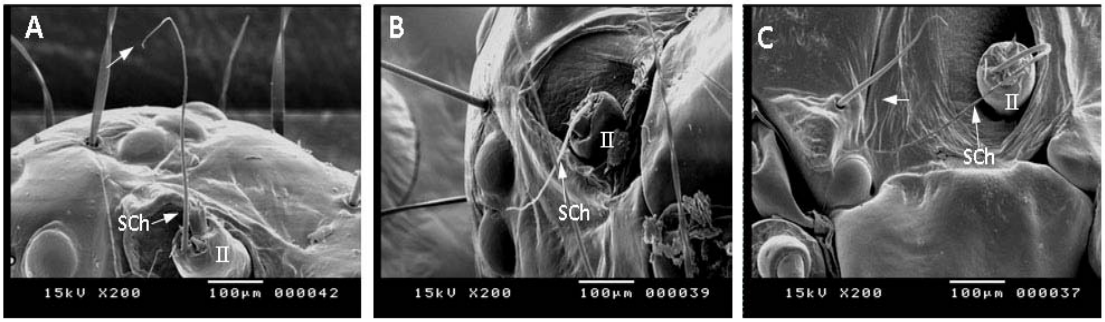

Fig. 2: Scanning electron micrographs of *Spodoptera littoralis* 6th instar larval antennal segment II with different host plants. Alfalfa (A), Cotton (B), and Soybean (C).

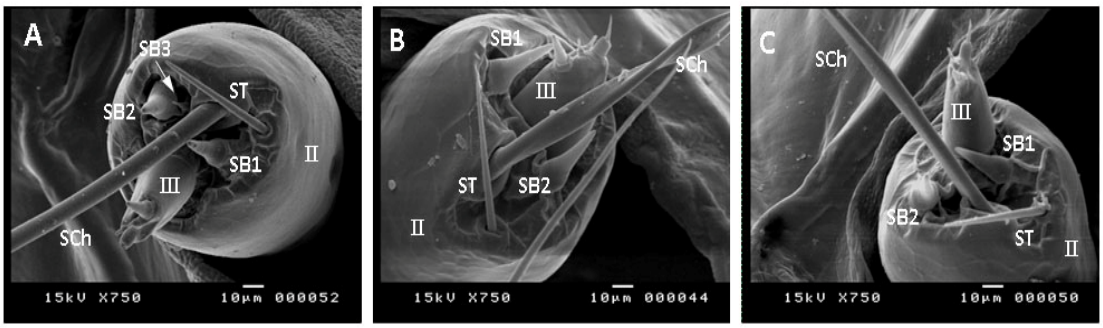

Fig. 3: Scanning electron micrographs of the antennal segments II and III of *Spodoptera littoralis* 6th larval instar reared on Alfalfa (A), Cotton (B), and Soybean (C) showing sensillum chaeticaum (SCh), sensillum trichodium (ST), and sensilla basiconica (SB1, SB2, and SB3).

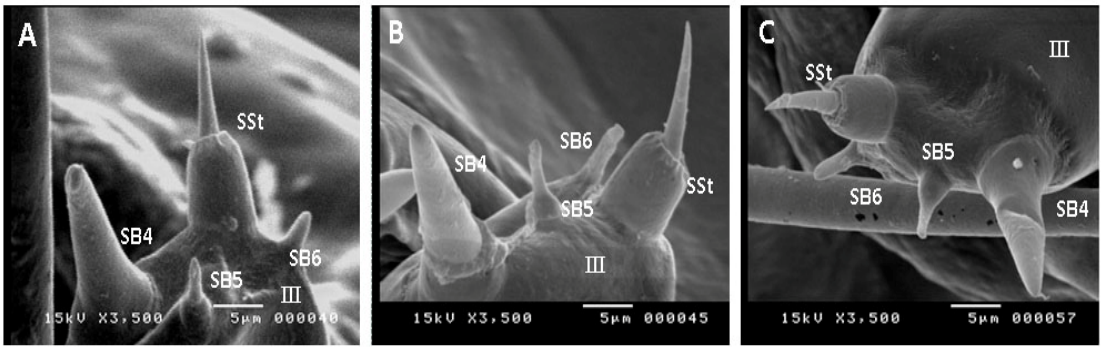

Fig. 4: Scanning electron micrographs of the antennal distal segment (III) of *Spodoptera littoralis* 6th larval instar reared on Alfalfa (A), Cotton (B), and Soybean (C) showing Sensilla basiconica (SB4, SB5, and SB6) and sensillum styloconicum (SSt).

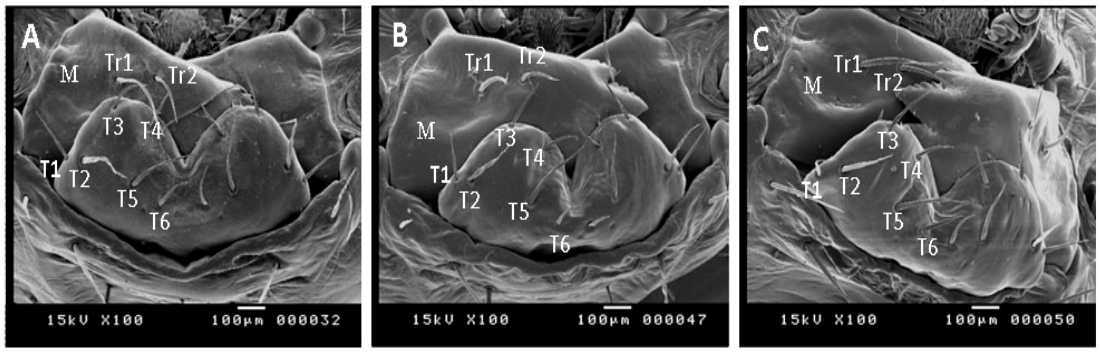

Fig. 5: Scanning electron micrographs of the labrum and mandibles (M) of *Spodoptera littoralis* 6th instar larvae reared on Alfalfa (A), Cotton (B), and Soybean (C) leaves. The labrum carries six pairs of sensilla trichodae (T1–T6) and the left mandible (M) bears two sensilla trichodae (Tr1 and Tr2).

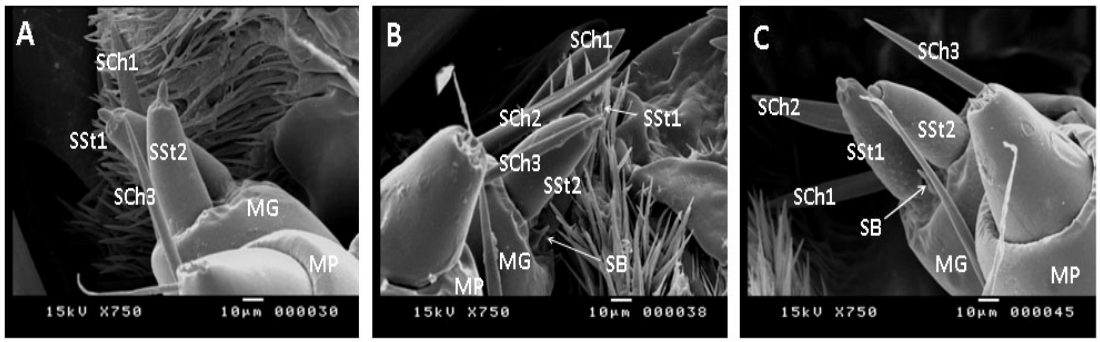

Fig. 6: Scanning electron micrographs of the maxillae of *Spodoptera littoralis* 6th instar larvae reared on Alfalfa (A), Cotton (B), and Soybean (C) showing the maxillary palp (MP) and the maxillary Galea (MG). MG carries two sensilla styloconica (SSt1, SSt2), sensillum basiconicum (SB) and three long sensilla chaetica (SCh1, SCh2, SCh3).

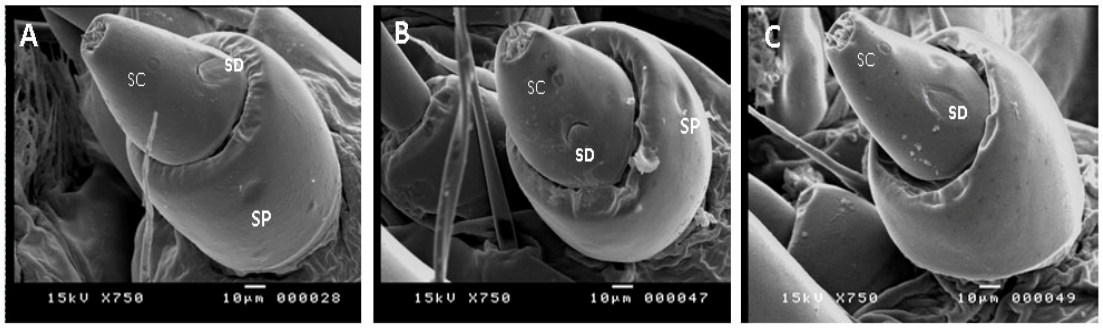

Fig. 7: Scanning electron micrographs of the maxillary palp of *Spodoptera littoralis* 6th instar larvae reared on Alfalfa (A), Cotton (B), and Soybean (C) showing the two-segmented maxillary palp. The distal segment of the maxillary palp bears eight sensilla basiconica ,sensillum digitiformium (SD) and campaniform sensillum (SC). The basal segment has only placoid sensillum (SP).

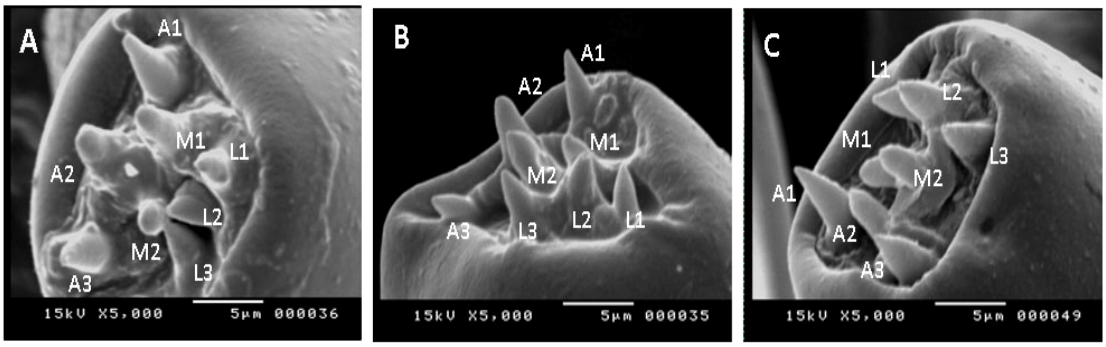

Fig. 8: Scanning electron micrographs of *Spodoptera littoralis* 6th instar larvae reared on Alfalfa (A), Cotton (B), and Soybean (C) showing the distal segment of the maxillary palp which bears eight sensilla basiconica (SB); apical sensilla basiconica (Al-A3), lateral sensilla basiconica (Ll-L3), a medial sensillum basiconicum (M1,M2).

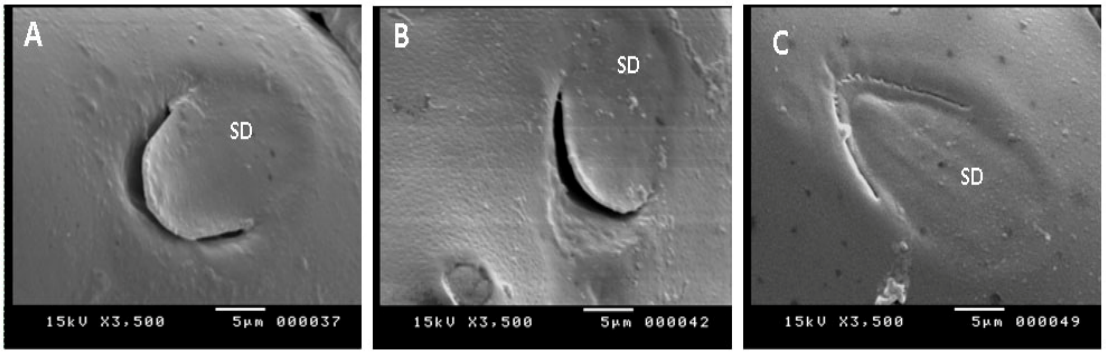

Fig. 9: Scanning electron micrographs showing the sensillum digitiformium (SD) of the maxillary palp of *Spodoptera littoralis* 6th instar larvae reared on Alfalfa (A), Cotton (B), and Soybean (C).

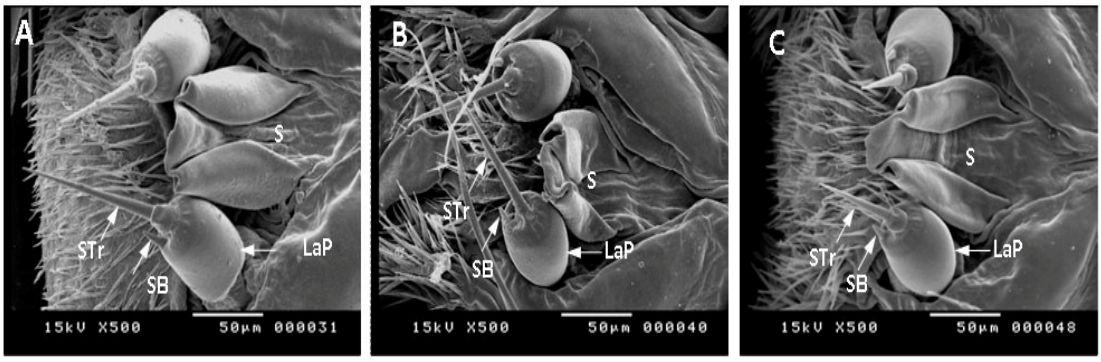

Fig. 10: Scanning electron micrographs of *Spodoptera littoralis* 6th instar larvae reared on Alfalfa (A), Cotton (B), and Soybean (C) showing Labium of the larvae carries the spinneret (Sp) and the labial palps (LaP) distally carries a long sensillum trichodium (STr) and a short sensillum basiconicum(SB).

ARABIC SUMMERY

تأثير تغيير العوائل النباتيه على الشعيرات الحسيه لقرون الاستشعار وأجزاء الفم ليرقات دوده ورق القطن

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لقد تناول هذا البحث دراسه توزيع ومورفولوجيه الشعيرات الحسيه لقرون الاستشعار وأجزاء الفم ليرقات دوده ورق القطن باستخدام الميكروسكوب الالكترونى الماسح. وقد ركز هذا البحث على دراسه التغيرات المورفولوجيه للشعيرات الحسيه الموجوده على قرون استشعار وأجزاء فم يرقات دوده ورق القطن نتيجه تربيتها على عوائل نباتيه مختلفه كالبرسيم اوالقطن أو الصويا. وقد أوضحت هذه الدراسه ان تغيير العائل النباتى له تأثير على الكثير من الشعيرات الحسيه. فالشعيرات الحسيه (Sensillum Chaeticum) الموجوده على قرون استشعار اليرقات التى تربت على ورق البرسيم أو الصويا كانت اطول من تلك التى تربت على ورق القطن. كذلك تم ملاحظه العديد من التغيرات المورفولوجيه للشعيرات الحسيه من النوع (Sensilla Trichodea) الموجوده على الشفه العليا والسفلى وكذلك الفك السفلى ليرقات دوده ورق القطن. بالاضافه للتغيرات المورفولوجيه الواضحه للشعيره الحسيه من النوع (Sensillum Digitiformium) الموجوده على الملامس الفكيه. من ناحيه أخرى فتغيير العائل النباتى لم يؤثر على العديد من الشعيرات الحسيه الاخرى مثل (Sensilla Basiconica) و(Sensilla Trichodium) و (Sensilla Stylochonica) المجوده على قرون الاستشعار بالأضافه للشعيرات الحسيه (Sensillum Campaniform) و (Sensillum Placodium) . من هذه الدراسه يمكن استخلاص ان تغيير العائل النباتى يؤثر على الشعيرات الحسيه ليرقات دوده ورق القطن.