Flight and oviposition behaviour of the African stem borer, *Busseola fusca*, on various host plant species

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Abstract

The African stem borer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae), is an important pest of maize and sorghum in sub-Saharan Africa. As in many other lepidopteran insects, the ability of *B. fusca* to recognize and colonize a variety of plants is based on the interaction between its sensory systems and the physical and chemical characteristics of its immediate environment. In this study, we tried to identify the behavioural steps of *B. fusca* leading to host selection and oviposition. Three Poaceae species commonly cultivated in Kenya for human consumption and animal forage were used in this study: the two most preferred hosts, maize (*Zea mays* L.) and sorghum [*Sorghum bicolor* (L.) Moench], and one non-preferred host, Napier grass (*Pennisetum purpureum* Schumach). Wind tunnel observations revealed that volatiles produced by the different plant species did not appear to strongly influence the general orientation of *B. fusca* towards the plant, as similar behavioural steps were exhibited by the female moth regardless of the plant species involved. This indicated that the females were not able to recognize their preferred hosts from a distance. After landing, the female typically swept her ovipositor on the plant surface, simultaneously touching it with the tips of her antennae, and then oviposited. This behaviour was more frequently observed on maize and sorghum than on Napier grass, and indicated that both antennal and ovipositor receptors are used by the female moths to evaluate the plant surface before deciding to oviposit. As a result, the females laid more eggs on the two crops than on Napier grass. We conclude therefore that females recognized their preferred hosts only after landing. Tactile and contact-chemoreception stimuli from the plants seemed to play a major role in oviposition decisions of *B. fusca*.

Introduction

In contrast to polyphagous insects, oligophagous insects have a narrow range of potential host plants, and therefore are strongly selective in their choice of host plants (Bernays & Chapman, 1994). *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) is oligophagous (Le Rü et al., 2006a,b; Ong'amo et al., 2006; Ndemah et al., 2007) and considered to be the most important insect pest of maize (*Zea mays* L.) and

sorghum [*Sorghum bicolor* (L.) Moench] (both Poaceae) in the cooler ecozones of East and Southern Africa, such as areas at mid-altitude and the highlands (Kfir et al., 2002). Various control strategies based on host plant resistance and cultural control have been attempted, some with partial or local success, but none have provided a comprehensive solution (Kfir et al., 2002). Recently, habitat management strategies have been developed, such as the 'push-pull' method, a stimulo-deterrent diversionary tactic (Khan et al., 2000). Using this method, stem borers are attracted and retained on trap plants (pull) planted as border rows, while repellent intercrops (push) prevent them from

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infesting the crop. The effective use of such strategies requires a good understanding of the host selection and acceptance processes of the insect pest. As pointed out by Hora & Roessingh (1999), oviposition behaviour on plants has been relatively poorly explored in moths, compared to butterflies. However, detailed observations on the oviposition behaviour have been made for some moth species and particularly for noctuids, such as *Sesamia nonagrioides* (Lefebvre) (Robert & Frérot, 1998) and *Mamestra brassicae* (L.) (Rojas et al., 2000). Although a wealth of information is available on the oviposition response of *B. fusca* on various plant species (van Rensburg et al., 1987, 1989; Haile & Hofsvang, 2002), no detailed study of its oviposition preference behaviour has been reported yet.

As in many other lepidopteran insects, the success of *B. fusca* to recognize and colonize a variety of plants is based on the interaction between its sensory systems and the physical and chemical characteristics of its immediate environment. In *B. fusca*, the sensory equipment consists of receptors that receive plant volatiles (multi-porous chemoreceptor sensilla on the antennae) and that probe the plant surface (mechanoreceptors and uniporous gustatory sensilla on the antennae, tarsi, and ovipositor) (Calatayud et al., 2006).

Lepidopteran insects employ various sensory cues in host plant location and acceptance (Bernays & Chapman, 1994). Before landing, visual and olfactory cues play an essential role (Prokopy & Owens, 1983; Ockenfels & Schmidt, 1992; Rojas & Wyatt, 1999), whereas after landing, olfactory and tactile cues seem to be more crucial (Harris & Rose, 1990; Foster et al., 1997; Robert & Frérot, 1998; Hora & Roessingh, 1999). After landing, the insect acquires information on the quality and suitability of the plant to be colonized (Renwick & Chew, 1994). Hora & Roessingh (1999) pointed out that after alighting on a plant, the final behavioural sequence leading to acceptance or rejection of the site for oviposition depends mainly on contact cues in which both physical factors (e.g., pubescence and surface texture) and chemical cues (volatile and/or surface chemicals) are involved.

In this study, we attempted to identify the behavioural steps taken by *B. fusca* that lead to host selection and acceptance, and finally to oviposition. Through detailed direct observations, we aimed to elucidate the role of the receptors present on the antennae, tarsi, and ovipositor of *B. fusca* and the plant cues involved in host discrimination and acceptance. Three plant species belonging to the Poaceae were used, namely, maize, a crop exotic to Africa, and two native plants, sorghum and Napier grass (*Pennisetum purpureum* Schumach). Maize and sorghum are commonly cultivated in Kenya for human consumption, while Napier grass is used as animal forage. These plant species are frequently found together in cultivated habitats, where *B. fusca* is generally present (Le Rü et al., 2006a,b). However, *B. fusca* was very rarely recovered from Napier grass in the field, contrary to maize and sorghum (Le Rü et al., 2006a,b; Ong'amo et al., 2006; Ndemah et al., 2007), corroborating the results by Wilkinson (1936) that *B. fusca* has no, or a low, oviposition preference for Napier grass.

Materials and methods

Insects

Fourth and fifth instars of *B. fusca,* collected from maize fields in Kenya, were reared on the artificial diet described by Onyango & Ochieng'-Odero (1994) until pupal formation. Pupae were sexed and males and females kept separately in plastic boxes ($21 \times 15 \times 8$ cm) until adult emergence. A cotton pad moistened with water maintained relative humidity at >80%. The insects were kept in a rearing room at $25.9 \pm 0.05\,^{\circ}$C (mean $\pm$ SE), 58.5 ± 0.4% r.h., and an L12:D12 reversed photoperiod with the scotophase lasting from 07:00 to 19:00 hours. This allowed us to carry out all experiments during daytime.

To obtain gravid females, the procedure of Calatayud et al. (2007) was used. One-day-old females were released into a mosquito-net cage ($40 \times 40 \times 63$ cm) at onset of the scotophase. The first females started to call 6 h later. One-day-old males were introduced 1 h thereafter. During the ensuing 1-h period, mating pairs were taken out of the cage and placed individually in plastic cylinders (8 cm high $\times$ 5 cm in diameter). After copulation, the insects were separated and naïve gravid females were used the following night in all experiments. After each experiment, females were dissected to check for the presence of spermatophores in the bursa copulatrix, which in Lepidoptera indicates successful mating (Lum, 1979). Only females bearing spermatophores were considered in the results.

Plants

Maize (cv. 511) and sorghum (cv. serena) seeds were provided by Simlaw (Kenya Seeds Company, Nairobi, Kenya). A variety of Napier grass commonly used by farmers in Kenya was grown from cuttings. Either individual plants (for oviposition response experiments) or five plants potted together (for behavioural observations) were grown in a greenhouse at International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya, in individual plastic pots (13 cm in diameter $\times$ 12 cm high) containing peat. Temperature was approximately 31/17 $^{\circ}$C (day/night) with an L12:D12 photoperiod. The plants were watered three times a week and once with a complete nutrient solution.

As shown by Sétamou & Schulthess (1995), Sémeglo (1997), and Ndemah et al. (2001), noctuid stemborers

such as *Sesamia calamistis* Hampson and *B. fusca* have a high oviposition preference for pretasseling maize plants, and they oviposit egg batches between the leaf sheath and the stem (Kaufmann, 1983). Therefore, plants at the sixth leaf stage with comparable stem diameter and height were used. The plants were exposed to reversed photoperiod conditions 2 days before the start of the experiments.

Oviposition response experiments

Both no-choice and triple-choice oviposition tests were conducted during the first 3 nights following the mating night, when optimum egg laying (>90%) occurs (Calatayud et al., 2007). In the no-choice tests, one gravid female was allowed to oviposit on a single potted plant (one plant per pot) placed in a mosquito-net cage ($40 \times 40 \times 63$ cm). In the triple-choice tests, one gravid moth was exposed to three plant species (one pot per plant species), placed randomly in a similar cage, but such that the distance between the three pots was about 20 cm. The oviposition response was estimated as the total number of eggs and egg batches laid per female and plant after 3 nights. All experiments were carried out under the same ambient conditions as those used for rearing the insects.

Behavioural observations

Observations were performed 0–4 h after onset of the scotophase, which corresponds to the period of oviposition (Calatayud et al., 2007).

Observations were carried out in a Plexiglass™ wind tunnel ($184 \times 60 \times 40$ cm), equipped with a fan that pushed air through the wind tunnel and an extractor on the opposite site, thereby generating an airflow. Illumination was provided by a 40-W incandescent red light bulb mounted 70 cm above the midsection of the wind tunnel.

Each insect was individually placed in a release cylinder and allowed to acclimate to the wind tunnel conditions (25 °C and 40–50% r.h.). In a no-choice test, two pots of the same species of plant were placed 20 cm from the upwind end of the tunnel, with a distance of about 20 cm between them. After at least 1 h of acclimation, a single female was placed on a 15-cm high carton platform (release platform) located 124 cm downwind from the plants and observed for 10 min. Pre- and post-landing behaviours were recorded. For each plant species, at least 30 naïve gravid females were observed.

The behavioural steps during the pre-landing period included the following: quiescent (Q), the female remained motionless on the release platform; take-off (TO), the female left the release platform; random flight (RF), any flight except oriented flight; oriented flight (OF), zigzagging upwind flight toward plant; and landing (L), the female landed on the plant after oriented flight.

The behavioural steps after landing (L) included the following: stand-still (ST), the female remained still with the antennae facing forward; antennation (A), the female walked on the plant stem, moving the antennae in front of the head and touching the plant surface with the distal segments of the antennae; ovipositor sweep (OS), the ovipositor touched the stem surface with the extremity, making large lateral movements as the female walked up and down the stem, the antennae simultaneously touching the plant surface; and oviposition (O), the female introduced her ovipositor between the leaf sheath and the stem and laid eggs, while holding the antennae alongside the body in a resting position.

Statistical analysis

For the oviposition responses, the data were $\log(x + 1)$ transformed and means were separated by Fisher's protected least significant difference test following one-way analysis of variance (ANOVA) for no-choice tests. For the triple-choice tests, ranks were generated following the Friedman test, using Proc RANK of SAS 9.1 (SAS Institute, 2003), and means were separated using Tukey–Kramer test (Proc GLM) (SAS Institute, 2003).

The pre- and post-landing behaviours were analyzed using Proc CATMOD (SAS Institute, 2002). As in Parr et al. (1996) and Hora & Roessingh (1999), analysis of behaviour was conducted on the total number of transitions between all possible pairs of behavioural steps and the data were pooled for all females. Transitional frequencies were used to form a contingency table.

Log-linear models were constructed, based upon specific combinations, to provide expected values of transitional frequencies for the contingency table (Parr et al., 1996; Hora & Roessingh, 1999). The goodness-of-fit of the log-linear models was assessed by likelihood ratio statistics (G-tests), and where the expected values of a model were not significantly different from the observed table, the assumptions of that model were accepted as necessary and sufficient to explain the observed data. Furthermore, an index was calculated to quantify the dissimilarity between the expected values under the assumptions of each model and the observed values. The probability of each transition given the preceding behaviour was calculated. To identify the transitions that built a significant part of a sequence of behavioural steps, standardized residuals of the observed transitions were calculated and compared to a model that did not include the assumption of dependence of following and preceding behavioural steps. Significant positive transitions – those for which positive standardized residuals were obtained, which were greater than the calculated threshold – were used to construct kinetograms of the pre- and post-landing behaviours. χ^2-tests were used to

compare the percentage occurrence of behavioural steps with respect to plant species. The data on the duration of some behavioural steps were log(x + 1) transformed and means were separated by the Tukey–Kramer test following one-way ANOVA (Proc GLM; SAS Institute, 2003).

Results

Oviposition response

The number of eggs and egg batches deposited on each of the three plant species in the no-choice or triple-choice tests indicated a strong oviposition preference for maize and sorghum, which received about 3.8 times more eggs than Napier grass (ANOVA: $F_{2,72} = 5.403$, P = 0.0065 for egg batches, and $F_{2,72} = 6.999$, P = 0.0017 for eggs; Table 1; Friedman test: $F_{2,72} = 5.34$, P = 0.0081 for egg batches, and $F_{2,72} = 6.68$, P = 0.0028 for eggs; Table 2).

Table 1 Number of egg batches and eggs laid per *Busseola fusca* female in a no-choice test (mean ± SE; n = 25)

Plant species	Egg batches	Eggs
Maize	2.0 ± 0.2b	147.9 ± 33.6b
Sorghum	2.6 ± 0.4b	145.0 ± 29.1b
Napier grass	1.1 ± 0.3a	37.8 ± 14.3a

Means within a column followed by the same letter are not significantly different (Fisher's PLSD mean separation test following ANOVA: P>0.05).

Pre-landing flight behaviour

The pre-landing behavioural steps shown by the females in response to the different plants were qualitatively similar (Figure 1). However, there were some significant quantitative differences. A higher percentage of insects took off in the wind tunnel when sorghum was presented than maize and Napier grass (2 × 3 contingency table: $\chi^2 = 6.996$, d.f. = 2, P = 0.0303 for TO). After take off and random flight, the

insects more likely displayed orientated flight and landing on a plant in the presence of Napier grass than on maize and sorghum (highest transition probabilities were recorded between TO and OF, RF and OF, and OF and L with Napier grass; Figure 1). There were no significant differences in the latency to take-off, nor in the time taken by insects to reach the plants (ANOVA: $F_{2,34} = 1.275$, P = 0.29 and $F_{2,34} = 2.704$, P = 0.081, respectively; Table 3).

Table 2 Number of egg batches and eggs laid per *Busseola fusca* female on each of the three plant species in a triple-choice test (mean ± SE; n = 25)

Plant species	Egg batches	Eggs
Maize	2.2 ± 0.3b	106.6 ± 25.7b
Sorghum	1.9 ± 0.4b	122.6 ± 23.8b
Napier grass	0.9 ± 0.3a	32.4 ± 12.8a

Means within a column followed by the same letter are not significantly different (Tukey–Kramer test after generating ranks by Friedman test: P>0.05).

Post-landing behaviour

After landing on the plant, the insects were more likely to oviposit on maize and sorghum than on Napier grass (Figure 2). The lowest probability between ovipositor sweep and oviposition was recorded on Napier grass. While a similar percentage of females antennated on all three plant species ($\chi^2 = 4.901$, d.f. = 2, P = 0.086 for A), a significantly lower percentage of insects swept their ovipositor, and even fewer oviposited on Napier grass than on maize and sorghum ($\chi^2 = 24.438$, d.f. = 2, P<0.0001 for OS, and $\chi^2 = 33.975$, d.f. = 2, P<0.0001 for O). Furthermore, after exhibiting ovipositor sweep and antennation, a higher percentage of insects stood still on Napier grass than on maize and sorghum ($\chi^2 = 39.510$, d.f. = 2, P<0.0001 for ST).

While there were no significant differences between the times spent standing still on the three plant species

Table 3 Pre- and post-landing behaviours (time in s) of *Busseola fusca* toward three plant species tested separately (means ± SE)

Parameters	Plants		
	Maize	Sorghum	Napier grass
Latency to first take-off (s)	210.6 ± 26.9a	180.4 ± 35.5a	159.1 ± 25.1a
Latency to first landing (s)	304.5 ± 33.9a	272.8 ± 39.6a	208.5 ± 34.2a
Time spent to stand-still (s)	128.1 ± 35.0a	83.8 ± 23.2a	269.6 ± 55.6a
Time spent for antennation (s)	19.2 ± 4.2ab	33.7 ± 6.0b	16.3 ± 3.7a
Time spent for ovipositor sweep (s)	41.3 ± 8.1b	28.2 ± 11.1ab	25.3 ± 4.9a
Total time spent for antennation and ovipositor sweep (s)	60.5 ± 10.2a	59.0 ± 8.6a	44.5 ± 12.2a

Means within a row followed by the same letter are not significantly different (Tukey–Kramer test following ANOVA: P>0.05).
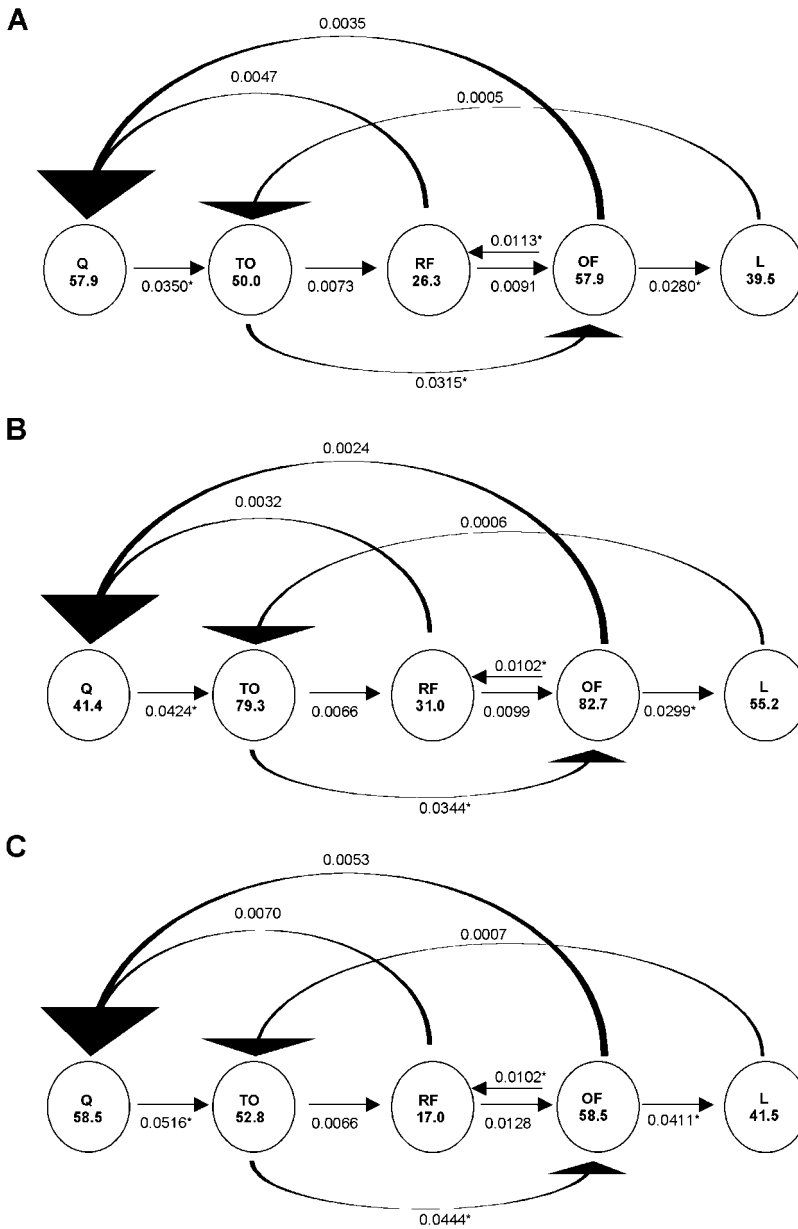
Figure 1 Pre-landing behaviour of naïve mated females of *Busseola fusca* towards three plant species: (A) maize (n = 32), (B) sorghum (n = 28), and (C) Napier grass (n = 49). Decimal numbers with the arrows represent the probability of each significant transition given the preceding behaviour. *Probability of transition >0.01. The percentage of occurrence of each behavioural step over all individuals observed is given below its abbreviation (Q, quiescence; TO, taking-off; RF, random flight; OF, oriented flight towards the plants; and L, landing on the plant).

($F_{2,57}$ = 2.161, P = 0.12), antennation time on Napier grass was significantly different only from sorghum ($F_{2,57}$ = 3.565, P = 0.035) and ovipositor sweep time only from maize ($F_{2,57}$ = 4.480, P = 0.016). However, the total time spent by *B. fusca* on both antennation and ovipositor sweep was not significantly different among the three plants ($F_{2,57}$ = 3.256, P = 0.046) (Table 3).

Discussion

The behavioural steps leading to oviposition by a gravid moth generally follow a sequential pattern involving searching,

orientation, encounter, landing, surface evaluation, and acceptance (Renwick & Chew, 1994). Thereby, orientation and encounter are sometimes indistinguishable and are often considered together as the first behavioural step. Landing on the plant is the final step in the orientation process of a gravid moth (Renwick & Chew, 1994).

As in other moth species, general orientation of *B. fusca* toward the plant may be triggered by either visual or chemical cues, and most probably by a combination of both. The role of vision is well-documented (Prokopy & Owens, 1983) and probably occurred also in *B. fusca*, because the insects could distinguish an upright-held object like a plant stem
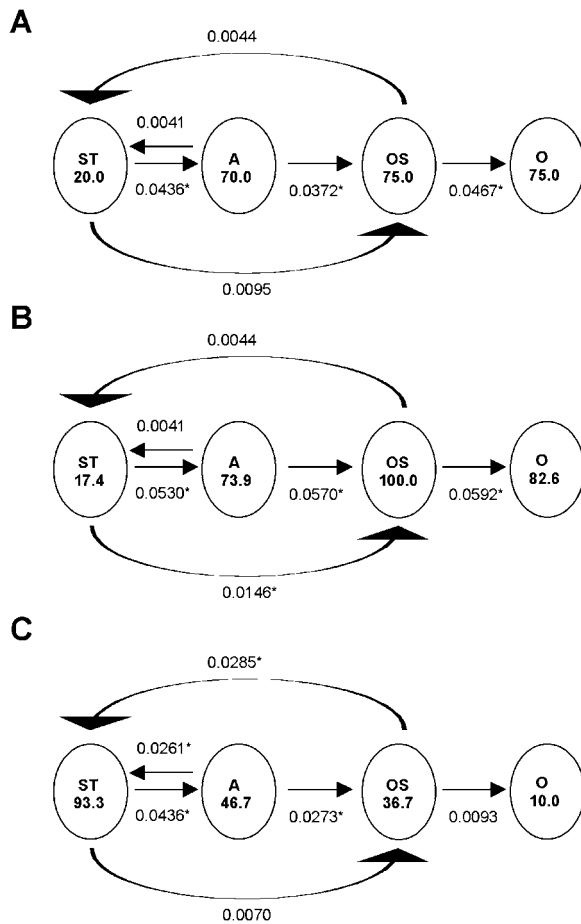
A

B

C

Figure 2 Post-landing behaviour of naïve mated females of *Busseola fusca* on three plant species: (A) maize (n = 30), (B) sorghum (n = 29), and (C) Napier grass (n = 31). Decimal numbers with the arrows represent the probability of each significant transition given the preceding behaviour. *Probability of transition >0.01. The percentage of occurrence of each behavioural step over all individuals observed is given below its abbreviation (ST, stand-still; A, walking and antennating on the plant; OS, ovipositor sweep; and O, oviposition).

by flying directly towards it and then landing (P-A Calatayud, personal observation). The role of vision for landing has also been demonstrated in *Ostrinia nubilalis* (Hübner), where upright-held objects stimulated landing (Foster & Frérot, 1994). Although the colour is generally less important in nocturnally active lepidopterans, such as *B. fusca*, another visual cue such as shape may play an important role in the general orientation towards the plant. For example, the shape of plants has been reported to be particularly important for *Trichoplusia ni* (Hübner) (Shorey, 1964).

Plant volatiles have often been reported to play a role in directing flight orientation and landing via the antennae (Renwick & Chew, 1994). For *B. fusca*, plant volatiles did not appear to strongly influence the general orientation behaviour toward the plant, because similar behavioural steps were exhibited by the female moth regardless of the plant species involved. However, once in flight, the moths showed the highest change from random to orientated flight when flying toward Napier grass and most likely landed on Napier grass. This may be because Napier grass produced more volatiles than maize and sorghum (Juma, 2005; Chamberlain et al., 2006).

After landing on the plant, the moths showed a strong oviposition preference for the two crop species and rarely oviposited on Napier grass (Figure 2). The probability of oviposition in these experiments matched the oviposition response results of *B. fusca* in the no-choice and triple-choice experiments (Tables 1 and 2; that is, maize = sorghum > Napier grass). This behaviour fits well with the 'mother knows best' principle (Singer et al., 1988; Schoonhoven et al., 1998), whereby a female will choose a plant species for oviposition that guarantees a high survival of her offspring. Indeed, larval survival of *B. fusca* is considerably higher on maize and sorghum than on Napier grass (Khan et al., 1997, P-A Calatayud, personal observation).

Moreover, ovipositor sweep behaviour with simultaneous antennation occurred more frequently on the preferred hosts, maize and sorghum, indicating that such behaviour corresponds most probably with plant surface examination to find a suitable site for oviposition. This behaviour appears to be typical in noctuids. It has also been observed in *S. nonagrioides* (Robert & Frérot, 1998) and *M. brassicae* (Rojas et al., 2000), which have ovipositors similar in morphology to *B. fusca*. It has been clearly demonstrated for *B. fusca* that this behaviour is significantly affected by plant pubescence (Calatayud et al., 2008). Napier grass was the only pubescent host used in this study, explaining in part why this plant was less preferred for oviposition than maize and sorghum. Not only do physical cues play an important role in plant acceptance for oviposition, but chemical cues can also be involved. Although the volatiles were available to the moth after landing, they seemed to be less important than the plant contact chemicals in host acceptance, because contact examination occurred via the tip of both the antennae and the ovipositor, which harbour gustatory sensilla that are able to detect only non-volatile compounds on the plant surface (Calatayud et al., 2006).

Tarsi seem not to be involved in contact evaluation, as we did not observe drumming movement, which is known to provide chemical information about the plant through the tarsal sensilla in certain Lepidoptera (Renwick & Chew, 1994). Nevertheless, during antennation, females walked

over the stem. Taste sensilla have been found on the fifth tarsomere of the prothoracic legs of *B. fusca* females (Calatayud et al., 2006). Thus, when walking on the plant they clearly move their tarsi and thus could also take up cues with the tarsi. Additional work is needed to test this hypothesis.

In conclusion, although visual and volatile chemical cues may play an important role in orientation of *B. fusca* towards the plant, the females were not able to recognize their preferred hosts at a distance. It was only after landing that recognition occurred. Before the oviposition decision, the moth examined the plant surface with her antennal tips (by touching the plant surface) and with her ovipositor tip (by sweeping the plant surface) to identify a suitable site for oviposition. At this stage, the plant contact cues (both physical and chemical) seemed to play a major role in plant acceptance for oviposition by the female moth.

These findings are important for future applications. In a 'push-pull' strategy, it would be preferable to choose as a trap plant a species that produces more volatiles than maize to facilitate the orientation flight behaviour toward the trap plant, but this is not enough. It is even more important to select as a trap plant a species with physical (e.g., non-pubescence) and chemical (e.g., wax composition) characteristics close to those of maize and sorghum, in order to pull as many *B. fusca* as possible.

Acknowledgements

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