

Passive interplay between resource dynamics and resource consumption may determine the spatio-temporal distribution of a leaf-feeding insect in the canopy of a palm

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In insect–plant systems, it is generally believed that interactions with cause–effect relationships are responsible for spatio-temporal distribution of insects. In contrast, the present study aims at explaining within-plant spatio-temporal patterns in the ‘coconut black-headed caterpillar–coconut palm’ system through passive resource–consumer interactions (without cause–effect relationship). During outbreaks, populations of the caterpillar have been observed to occur at high densities in the lower canopy of the palm before distributing to the upper canopy. This has led to speculations of ‘preference’ to the lower canopy. The present study indicated that infestation began randomly in a palm, which evidences against the speculations. In spite of an initial random distribution, observations showed that population moved from the lower to the upper canopy at later stages of infestation. Further observations and experiments led to the conclusion that caterpillars move in the canopy in search of uninfested fronds; and moths preferably oviposit among the most recently constructed larval feeding galleries. It means that a frond that was initially infested would be substantially consumed before caterpillars dispersed to fresh fronds. On the basis of these evidences and the dynamics of coconut fronds, we present a logical model, which relies on ‘passive’ resource–consumer interactions, to explain the lower to upper canopy spatio-temporal distribution of infestation in this system.

Keywords: Canopy dynamics, insect–plant interaction, *Opisina arenosella*, resource–consumer interaction, within-plant distribution.

In any insect–plant system, factors that are known to influence within-plant distribution of the insect are the preference of the insect to the physical/chemical character of the host plant, or its behaviour like aggregation or cannibalism, or the interactions it is involved with like competition or predation, or its inclination (or otherwise) to

certain abiotic factors. All these can be grouped under ‘active’ interactive factors, as they directly effect distribution. In this article we discount all the active factors, and demonstrate that a ‘passive’ interaction between resource consumption and resource dynamics can determine the within-plant spatio-temporal distribution of an insect herbivore. The coconut palm–coconut black-headed caterpillar (*Opisina arenosella* (Walker) (Lepidoptera: Oecophoridae)) system has been used in the study, wherein fronds (or leaves) of the palm are the resource and caterpillars are the consumers. Caterpillars have been observed to occur at high densities among fronds in the lower canopy before moving to those in the middle and upper canopy of a coconut palm. In this article, we show that this spatio-temporal pattern could arise from a passive interaction between resource dynamics (production and senescence of fronds), and resource consumption by the caterpillar.

The system

The canopy of a mature coconut palm (*Cocos nucifera* L.), a tropical evergreen species, has about 25–30 spirally arranged fronds and each frond has ~200 leaflets arranged on either side of a stout midrib. The canopy of a coconut palm can be conveniently divided into three parts based on the developmental stage of the nut-bearing bunches in their axils. The lower canopy has mature and near-mature nuts, the middle canopy has developing bunches, and the upper canopy has inflorescences in their axils¹. Unlike most trees, the coconut palm has continuous production and senescence of fronds. On an average, for every 30 days one frond is formed at the top while one frond is senesced from the bottom of the canopy^{1–3}, such that every frond moves downwards in the canopy with addition from the top.

O. arenosella is a major leaf-feeding pest of coconut palms in India^{4,5}, Sri Lanka⁶ and Myanmar⁷. Caterpillars are concealed in galleries constructed of larval secretions and faecal pellets, and feed by scraping the lower surface

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of the leaflets (Figure 1 *a*). Damaged portions are left with only the upper epidermis that quickly dries-off. A severely infested frond thus appears scorched when viewed from a distance. During outbreaks, the caterpillars have been observed to occur at high densities in the lower canopy of the palm before their distribution progresses towards the upper canopy⁸⁻¹¹. In support of the above, casual observation of a severely infested coconut grove would reveal completely scorched fronds in the lower canopy and greener ones in the upper canopy. Figure 1 *b-d* shows that the symptoms of damage progress from the lower to the upper canopy.

The female moth lays a total of about 250 eggs in small batches of 5–8 eggs¹². Larvae pass through seven instars in case of males and eight instars in case of females, before pupating among the feeding galleries. At 25°C, larval period for males and females is approximately 33 and 39 days respectively; the total life cycle is completed in 60–70 days¹³. *O. arenosella* is one of the few aseasonal

multivoltine insects known to follow discrete generation cycles¹⁴⁻¹⁶. The species exists as spatially segregated populations that are scattered throughout peninsular India and neighbouring countries. As these populations are asynchronous with respect to generation cycles⁵, there is little probability of immigration/emigration between them.

In insects that have low probability of immigration/emigration between populations, the within-plant spatio-temporal distribution patterns are essentially determined by the initial distribution and the pattern of post-initiation spread in the canopy. In the present case, as the observed spatio-temporal distribution reveals a lower-to-upper canopy pattern, we empirically determined if the initial distribution was actually skewed to the lower canopy of the palm. If skewed, this could explain the observed spatio-temporal distribution as a possible outcome of the preference displayed by moths to oviposit among fronds occupying the lower canopy.

Distribution at the beginning of infestation

The distribution of infested portions across the canopy of a palm was assessed at the time when the population was in its first generation (verified by the absence of pupal case). Fronds were numbered serially from the lowermost to the uppermost, and the number of portions damaged by *O. arenosella* in each frond was noted. Such observations were made for ten randomly selected palms in a garden (location – Mudugere, Channapatna Taluk, Karnataka; the orchard had nearly 150 palms aged 18–20 years). The variance/mean ratio will suggest the spatial distribution of these portions across the canopy of the palm.

The ten palms from which data were obtained had a minimum of 24 and maximum of 28 opened fronds. Therefore, analysis was restricted to 24 fronds starting from the lowermost one. Data pooled across the ten trees showed that fronds occupying various positions had at least one infested patch up to a maximum of eight (Table 1). The average number of infested patches per frond position pooled from ten trees was 3.33 ± 1.78 and the variance/mean ratio was 0.96, suggesting random distribution of patches within the palm. Among the 80 infested patches in the 240 fronds pooled from ten trees, 24 were present in the lower, 30 in the middle and 26 were detected in the upper canopy (chi-square = 0.70; $P > 0.05$). These results clearly suggest that distribution at the beginning of an infestation was not biased to the position of fronds in the canopy of a palm. In other words, it meant that at the beginning of an infestation, moths, lay eggs randomly in the canopy of a palm.

The available literature conjectures initial distribution of the population to be in the lower canopy. Nadarajan¹⁰ found higher carbohydrate, lower potassium and balanced C : N ratio in the lower canopy of the palm, and therefore presumed that moths selectively preferred to lay eggs in the lower canopy, which led to high population densities

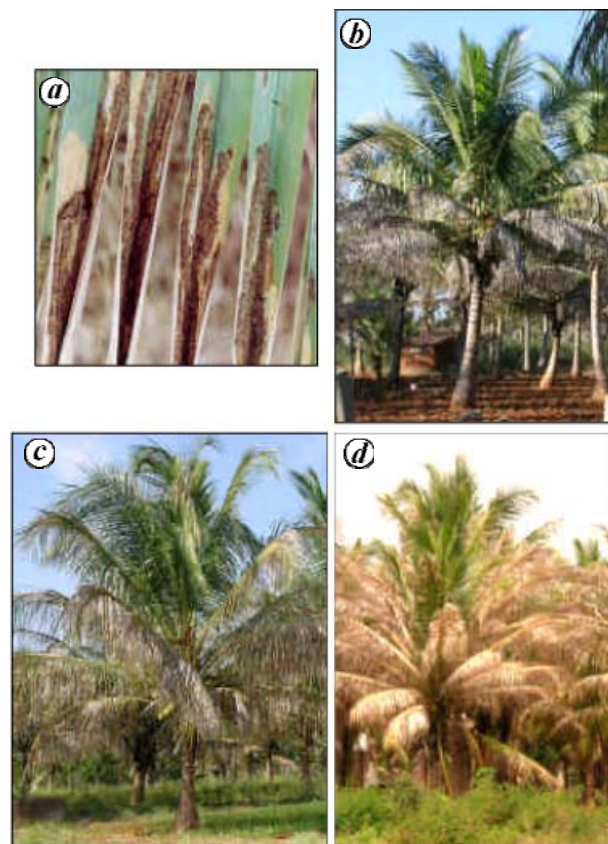


Figure 1. Coconut palms showing symptoms of damage caused by *Opisina arenosella*. *a*, Larval feeding galleries constructed of silk and faecal pellets on the under surface of the leaflets. *b*, Lower canopy appears nearly exhausted, while the middle and upper canopies do not show any symptom. *c*, Lower canopy is exhausted, middle canopy is significantly damaged and upper canopy is free of any symptom. *d*, Lower and middle canopies appear exhausted and symptoms can be seen in the upper canopy.

in that portion. And, as resources exhausted in the lower canopy, the populations moved upwards resulting in the observed lower-to-upper-canopy distribution. However, this is a mere speculation as it is not based on any primary information on either the moths' preference to the position of fronds, or, on the initial distribution of population in the canopy. On the contrary, a laboratory experiment has demonstrated that the developmental biology of *O. arenosella* is not influenced by the position of the frond that is consumed¹¹, which challenges ideas on preference to the chemistry of the lower canopy. The fact also remains that the herbivore consumes fronds in the middle and upper canopy (Figure 1 d), which suggests that it may not exhibit any preference. Finally, the present study demonstrates that the initial distribution of damage across the canopy of a palm is random. This evidence is sufficient to rule out speculations that moths might prefer the lower canopy to lay eggs.

Distribution at an advanced stage of infestation

Subsequently, we empirically verified the movement of the population from the lower towards the upper canopy

Table 1. Distribution of infested patches at the beginning of infestation among fronds occupying different positions of the coconut canopy

Position of frond starting from the bottom	Number of infested patches
1	4
2	3
3	3
4	8
5	1
6	2
7	2
8	1
9	4
10	6
11	3
12	3
13	3
14	4
15	1
16	6
17	1
18	4
19	3
20	4
21	2
22	3
23	6
24	3
Mean	3.33
Variance	3.18
Variance/mean	0.96

Data pooled from ten palms; there were two palms with 26 and two palms with 28 fronds. There was one infested patch occurring in each of the 25th to 28th frond positions.

in another orchard at an advanced stage of infestation. In this orchard, where the symptoms of damage were present in the lower, middle and the upper canopies (location – Kuppala, Kadur Taluk, Karnataka; the orchard had nearly 500 palms aged between 20 and 24 years), ten palms were selected and a damaged frond from each of the three canopy levels was sampled from all the ten palms. The number of leaflets damaged and left undamaged by *O. arenosella* in each frond was noted and data were compared across canopy levels. If damage actually spread from the lower to the upper canopy, the proportion of damaged leaflets was expected to decline with canopy height. Chi-square test was applied to test the hypothesis that distribution of damage was independent of the position of the fronds in the canopy. Simultaneously, the number of individuals of *O. arenosella* in each leaflet was noted, and their distribution and density was compared across canopy levels using a rank–abundance plot. The leaflets were ranked on the basis of the number of individuals of *O. arenosella* present, arranged in descending order and plotted against abundance. The slope of the curve indicated the kind of spatial distribution (slope = 0, when perfectly uniform; slope = -1, when perfectly random and slope < -1 and fits a log model, when aggregated), while the intercept was used as a measure to compare the relative densities, provided the distributions were comparable. The value of the intercept would be useful in comparing the densities when the variance is greater than the average, which, in the present case, would imply that there would be a few leaflets with a large number of individuals and a large number of leaflets with few individuals of *O. arenosella*. The intercept would be highly sensitive to those few leaflets containing the largest number of individuals and least sensitive to the other extreme; unlike the average, which is an insensitive measure of the absolute density. In situations where the variance is lesser than or equal to the average, 'average density' would provide a good comparison. Student's *t*-test was used to test the differences among intercepts for the three curves.

Results showed that the proportion of damaged leaflets progressively declined with canopy height. All leaflets in the lower ($n = 1643$), 83.35% of leaflets in the middle ($n = 1730$) and 44.64% of leaflets in the upper ($n = 1895$) canopy suffered damage. This difference in damage was significant across canopy levels (chi square = 387.70; $P < 0.00$). Among the total damaged leaflets (Figure 2), the proportion of unoccupied leaflets (i.e. damaged leaflets presently without individuals of *O. arenosella*) decreased with canopy height (40.17, 12.62 and 2.48% in the lower, middle and upper canopy levels respectively; chi square = 451.66; $P < 0.00$). Among the occupied damaged leaflets pooled for the palm, the proportion was highest in the middle canopy (41.07%), followed by the lower and upper canopies (32.04 and 26.89% respectively; chi square = 127.05; $P < 0.00$). Rank–abundance curves (Figure 3), obtained by plotting the rank of the leaflets

arranged in descending order against the abundance of *O. arenosella*, for all the three canopy levels, fit a logarithmic model with negative slope (sample sizes were large and R^2 values were >0.95 for each canopy level), suggesting an aggregated distribution of individuals in the leaflets in all canopy levels. There was significant difference among

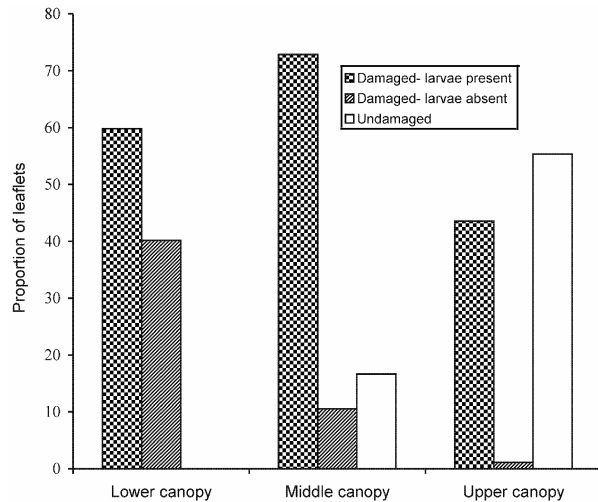


Figure 2. Proportion of damaged and undamaged leaflets (white columns) in the lower, middle and upper canopies of the coconut palm. Damaged leaflets have been further divided into those with larvae (black columns) and those without larvae (grey columns) of *O. arenosella*.

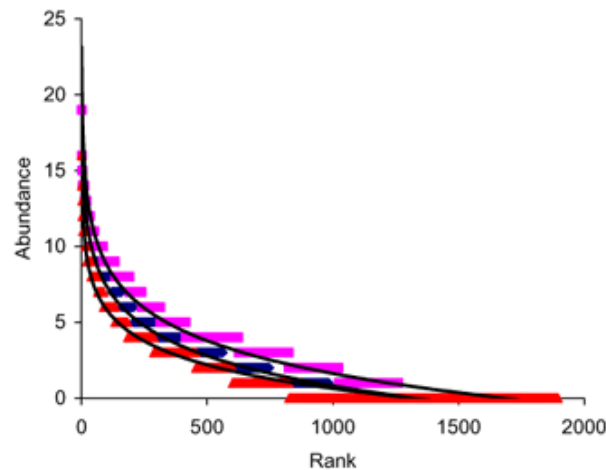


Figure 3. Rank of leaflets (rank) plotted against the number of individuals of *O. arenosella* in each leaflet (abundance), showing the spatial distribution of *O. arenosella* in lower (blue), middle (pink) and upper (red) canopies. Ranks were assigned in decreasing order of the number of individuals of *O. arenosella* contained. Samples were obtained from ten palms. One frond each was sampled from the lower, middle and upper canopies of each palm. There were 150–200 leaflets in each frond. The rank–abundance curves fit a log model for each of the canopy levels [y (lower) = $-2.85\ln(x) + 20.52$, $R^2 = 0.98$, $n = 1643$; y (middle) = $-3.12\ln(x) + 23.15$, $R^2 = 0.97$, $n = 1730$; y (upper) = $-2.26\ln(x) + 16.24$, $R^2 = 0.96$, $n = 1895$].

intercepts (20.52, 23.15 and 16.24 for the lower, middle and upper canopy respectively) of the three curves (Student's t -test; $P < 0.05$ for all paired comparisons). The results show that the number of damaged leaflets and proportion of damaged leaflets that did not contain *O. arenosella* progressively decreased with canopy height. All the leaflets in the lower canopy sustained damage although ~40% did not contain *O. arenosella*, while nearly all the leaflets damaged in the upper canopy contained the herbivore. This suggests that the populations moved from the lower to the upper canopy. As the slopes of the rank–abundance curves for all the three canopy positions suggested an aggregated distribution of the population, the intercept could be used as a measure to compare the relative densities of *O. arenosella*. At the time of sampling, higher intercept for the middle, followed by the lower and upper canopies suggested that the populations were highest in the middle canopy, in spite of damage being greater in the lower canopy. All the evidences indicate that caterpillars exhausted fronds in the lower canopy before moving to the middle and upper canopies.

This put forth an intriguing situation, where, in spite of an initial random distribution, populations at an advanced stage of infestation moved from the lower towards the upper canopy.

Post-initiation mode of spread of population

To solve the above problem, we investigated the mode of spread of the population in the canopy after the initial distribution. Here, it is interesting to note that moths have been experimentally shown to preferably lay eggs among larval frass^{11,12}, and, in the field eggs have always been discovered among portions of leaflets that have been damaged by caterpillars of the previous generations^{5,11,17}. Therefore, we hypothesized that exhaustion of food might trigger caterpillars to spread over uninfested portions, and moths would further the infestation by laying eggs among the recently damaged portions of the leaflets.

The first part of the hypothesis was tested using data on size of the smallest faecal pellets among the portions infested during the current generation. Size of faecal pellets reflects the larval instar quite accurately (refer Weiss¹⁸ for a review on the varied ecological applications of insect defecation). Three facts were considered for the use of faecal pellets: (i) all larval instars construct feeding galleries using their faecal pellets, and the galleries would be adhering to the portions fed by the larvae; (ii) the populations have discrete generation cycles, which means that there is discontinuous oviposition, and (iii) there is a systematic lower-to-upper-canopy consumption pattern (at advanced stages of infestation), which facilitates distinction between recent and old damage. The logic followed is as follows: if moths laid eggs in un-infested portions of the canopy, hatchlings should initiate feeding at the site

of oviposition and the smallest faecal pellets present in the feeding galleries should belong to that of the first instar larvae. Therefore, if the smallest faecal pellets among recently infested portions were larger than those of the first instar larvae, there was enough reason to consider egg-laying to initiate within-plant spread of infestation.

In a closely observed orchard infested since approximately two years (location – K. B. Doddi, Channapatna Taluk, Karnataka; the orchard had nearly 500 palms aged ~20 years), a frond damaged during the current generation was taken down and all the infested portions that did not contain any pupal case were sampled. Ten such fronds were sampled from randomly selected palms before the onset of pupation during the current generation. Presence of pupal case indicated that the portion was damaged during the previous generation. The galleries ($n = 120$) were observed under a microscope and the smallest faecal pellets were separated from each infested patch and lengths of the ten smallest pellets were recorded. Average length of the smallest pellets was compared with the 'standard' pellet length for each instar. 'Standard' pellet size for each larval instar was determined in the laboratory by measuring the faecal pellets of 50 caterpillars every day, from the day they hatched till pupation. The lengths of ten defecated pellets of each caterpillar were measured every day under a microscope. At the end of each larval instar, which is marked by the presence of moulted skin and head capsule, average and range for the instar was determined and a 'standard' was prepared (Table 2). From the field-collected samples, the average size of the smallest faecal pellets was compared with the standard range. It may be noted that there was an overlap in the standard range of pellet size for any two successive instars. Therefore, if the average size of the smallest pellet (field-collected) occurred in the non-overlapping zone of, say, the x th instar, the value assigned to the x th instar was 'one'. However, if the same occurred in the overlapping zone of the ' x th and $x + 1$ th' or ' x th and $x - 1$ th' instar, a value of 0.5 was assigned to both instars. The null hypothesis states that there are no faecal pellets of first instar larvae among the portions observed. Thus a deci-

sion was made to reject the null hypothesis if the faecal pellets of the first instar larvae were found in more than 5% of the observed samples. In addition, the results were expected to reveal the larval instar/s involved in the within-palm distribution of infestation.

The standard sizes of larval faecal pellets determined in the laboratory are presented in Table 2. The pellet size significantly differed across each of the eight instars (Duncan's Multiple Range Test; $P < 0.00$).

A total of 120 field-collected damaged portions from ten infested fronds were observed for the smallest faecal pellets. Their average size ranged from 0.32 to 1.98 mm, which was within the standard range (0.025–2.45 mm). While comparing the mean size of the smallest pellets with the standard, a value of 'one' was assigned to a particular instar in 82 cases and a value of 0.5 was assigned to two adjacent instars in the remaining. The values were pooled for each instar and a frequency distribution was plotted (Figure 4). It is clear from Figure 4 that there was no faecal pellet that could match the size of the first (and second) larval instar, which means that the null hypothesis was accepted. This suggests that first and second instar larvae might not initiate infestation in the portions damaged during the current generation. The results also showed that ~57% of the infestation during the current generation was initiated by larvae in the IV and V instars and <15% of infestation was due to larvae in the III and VIII instars. Larvae in the VI and VII instars also contributed to the within-palm spread of infestation (Figure 4). Lack of faecal pellets of the I and II instar larvae among recently infested portions suggested that oviposition is not directly responsible for the within-palm spread of infestation. Instead, it appears that larvae of IV and V instars are predominantly involved in distribution of infestation within the palm (Figure 4). This suggests that larval movement,

Table 2. Size of faecal pellets of different larval instars of *Opisina arenosella* as standardized in the laboratory

Larval instar	Frass size (mm)
I	0.09 ± 0.03^h (0.025–0.15)
II	0.20 ± 0.04^g (0.125–0.3)
III	0.36 ± 0.07^f (0.25–0.55)
IV	0.63 ± 0.11^e (0.40–0.875)
V	0.96 ± 0.12^d (0.6–1.2)
VI	1.30 ± 0.13^c (1.05–1.6)
VII	1.74 ± 0.13^b (1.42–2.1)
VIII	2.18 ± 0.14^a (1.9–2.45)

Range given in parenthesis; means followed by the same alphabet are not significantly different (Duncan's Multiple Range Test; $\alpha = 0.05$; $n = 50$).

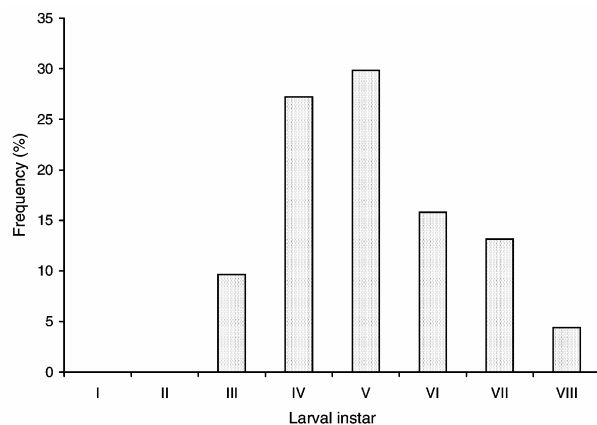


Figure 4. Frequency distribution (in percentage) of larval instars involved in within-palm distribution of infestation. This was estimated by measuring the size of the smallest faecal pellets in the portions infested during the current generation ($n = 120$), and comparing it with that of the 'standard' faecal pellet size for each instar (Table 2).

not ovipositing females, initiate within-plant spread of *O. arenosella* to un-infested portions of the canopy.

Although it is known that moths lay eggs among the larval feeding galleries, it is not known if they discriminate the recently constructed galleries from old ones for oviposition. This is a critical part of our hypothesis because, if larval movement initiated distribution to un-infested portions of the palm, then moths should prefer recently constructed galleries to lay eggs and thereby promote the distribution. This was investigated through a two-choice test, where coconut leaflets damaged during the current generation and those damaged one or two generations ago were simultaneously provided to a pair of freshly emerged moths held in a cage. The number of eggs laid on either larval gallery was separately recorded after three days and the mean number of eggs laid/female was calculated. The experiment was replicated 25 times; paired *t*-test, with the number of eggs laid on each of the two substrates in each replication forming the pair, was applied to test the ovipositional preference of moths.

Results revealed that moths, on an average, laid 93.8 ± 41.82 eggs/female on the feeding galleries of the current generation, whereas 48.99 ± 21.11 eggs/female were laid on the larval galleries that were one or two generations old. Paired *t*-test indicated a significant difference between the numbers of eggs laid on the two test substrates ($t = 7.34$; $P < 0.01$). This suggests that moths preferably lay eggs among recently constructed galleries, i.e. among portions of the leaflets damaged most recently.

These results corroborate the hypothesis that larvae initiate spread of infestation to the undamaged portions of the canopy, and oviposition extends infestation among these portions. Therefore, it appears that dispersing moths that colonize fresh palms laid eggs randomly among the fronds of the palm, while moths of the later generations oviposited among the larval feeding galleries. Based on the results obtained so far, we assume that populations of *O. arenosella* may be of two types – dispersing and non-dispersing – which differ in their oviposition behaviour. The dispersing population may oviposit among infestation-free palms, whereas the non-dispersing populations lay eggs among the larval feeding galleries leading to continuous build-up of populations among the palms.

The behaviour of laying eggs in larval feeding galleries would result in the expansion of damaged portions within a frond until the frond gets exhausted and this would trigger larvae to seek other fronds in the canopy. In other words, until a resource (frond) is consumed, consumption does not begin on a fresh resource.

Logical explanation of the observed spatio-temporal distribution

Based on the results detailed earlier, the observed spatio-temporal pattern can be logically explained with the help

of a ‘passive’ resource–consumer model. The resource–consumer system should not be ephemeral, i.e. the consumer should be able to complete a considerable number of generations on a given resource. To start with, we make the following assumptions:

- (a) Consumption is a factor of population size alone, and is increasing with time.
- (b) Resource addition and resource senescence rates are the same and constant, and unaffected by consumption.
- (c) Changes occurring in a resource, since its addition till senescence, do not influence the resource–consumer interaction.
- (d) New resources are consumed only after exhausting the old resource.

Here, consumption may remain restricted to the older resource as long as the consumption rate remains lower than the resource addition/senescence rate. Consumption expands to new resources only when the consumption rate breaks even with the addition/senescence rate and goes beyond.

An extension of the above-mentioned logic to the coconut–*O. arenosella* system implies the following: when consumption rate (number of fronds consumed per generation of *O. arenosella*) is lower than frond addition/senescence rate (number of fronds added/senesced per generation of *O. arenosella*), infestation would move downwards in the lower canopy (which might occur when populations are small). When population sizes increase to the point where consumption rate first equals and then surpasses frond addition/senescence rate, infestation would start expanding to the entire canopy. This would produce a lower-to-upper canopy distribution of infestation.

It should be noted that, on an average, two new fronds are added and two are senesced in the canopy of a palm in every *O. arenosella* generation. As populations grow exponentially, the absolute number of individuals of *O. arenosella* during the first few generations can be expected to be low. By the time population size increases substantially such that an entire frond ($\sim 10 M^2$ of leaf area) is consumed and larvae move to other fronds, the infestation might be restricted only to the lower canopy. Beyond this point the populations can increase rapidly (as their sizes would already be large and further exponential rise can build very large numbers in a few generations time), and start occupying the entire canopy. This would result in the observed lower-to-upper canopy spatio-temporal distribution pattern, in spite of an initial random distribution in the canopy. This has been diagrammatically explained in Figure 5.

As the rate of resource addition/senescence is constant and resource consumption rate is increasing, it appears that the herbivore has a race against time to distribute its population throughout the canopy (in case the consumption rate is too slow, the palm will be able to senesce all

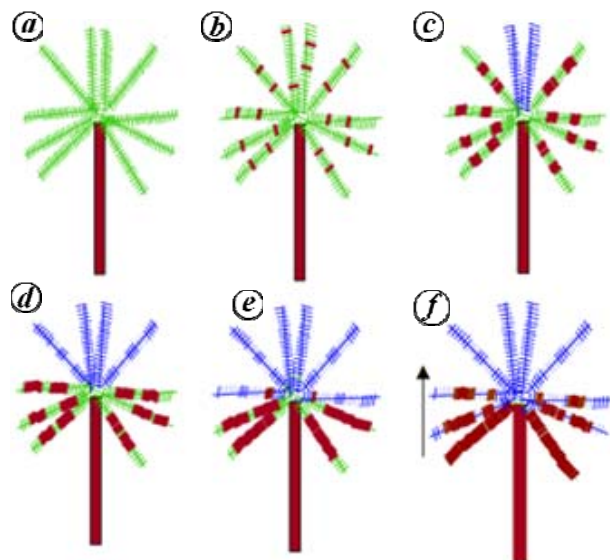


Figure 5. Hypothetical presentation of within-plant spatio-temporal distribution of *O. arenosella*: *a*, An uninfested palm on which moths land to begin infestation. *b*, Beginning of infestation (brown-coloured markings) without any bias to the position of the frond in the canopy. *c*, Infestation increases around the previously infested portions. New fronds added after the beginning of infestation (*b*) are shown in blue colour, while the old fronds (present in stage *b*) continue to be shown in green. The number of fronds added and that senesced are the same. Therefore, the total number of fronds on the palm remains constant. Two fronds are added and two senesced in one *O. arenosella* generation. Infestation does not progress to new fronds until the previously infested fronds are almost exhausted. *d*, Progress in infestation with time, while new fronds continue to be free of infestation. *e* and *f*, Infestation starts spreading to new fronds as the previously infested fronds are almost exhausted. Infestation now shows lower-to-upper-canopy pattern of distribution (indicated by arrow).

the initially infested fronds before the population spreads throughout the canopy). In case there is an increase in the post-infestation rate of frond addition/senescence (which would make the interaction 'active'), it would be an interesting race between the two, and the winner may be decided by 'chance'.

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ACKNOWLEDGEMENTS. We are grateful to Mr Thimme Gowda, Mr Chandrashekar and Mr Acharya, farmers at Channapatna and Kadur, for allowing us to take observations and samples from their coconut gardens. Raghu and Gangadhara lent support in laboratory and fieldwork. We thank Prof. N. V. Joshi, IISc, Bangalore, Drs Shakti Chauhan, IWST, Bangalore and K. Chandrashekar, UAS, Bangalore for joining us in useful discussions. Dr K. N. Ganeshiah, UAS, Bangalore and Dr A. Prabhuraj, UAS, Dharwad gave helpful comments on the manuscript. We acknowledge Drs V. T. Sannaveerappanavar and Puttaswamy, UAS, Bangalore, and Director, IWST, Bangalore for support. K.M. acknowledges Coconut Development Board for providing Senior Research Fellowship.

Received 22 May 2007; revised accepted 5 February 2008