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The measurement and modelling of losses of cucurbits to Tephritid fruit flies

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ABSTRACT

Losses of cucurbit fruits to Tephritid fruit flies are often assessed as the infestation percentage of mature fruit at harvest, but this way of appraisal may underestimate losses, as attacks on pre-mature fruit that are lost before ripening reduce the mean mass of surviving fruit also. An alternative approach is proposed, which improves accuracy by incorporating the effects of losses of pre-mature fruit. This approach entails computation of an aggregate loss by combining infestation levels in four cohorts of fruit, assuming different rates of compensation by the plant for losses in each cohort. Using data from different sites in India, this "by cohort, compensated" model obtained significantly less variability, among replicates of identically-treated plots, than the mature-fruit-only model, and a pattern of losses comparable to those obtained by incorporating reductions in surviving-fruit mass. The model is more accurate and realistic than the assessment of mature fruit only.

Key Words: *Cucurbits; fruit flies; economic losses; infestation; compensation; India.*

INTRODUCTION

Cucurbit fruits and vegetables (family Cucurbitaceae), including cucumbers, melons, pumpkins and gourds, suffer serious damage from fruit flies (Diptera: Tephritidae), and in particular from the melon fly (*Bactrocera cucurbitae* Coq.), a native of South Asia now found in Africa, Hawaii and elsewhere (Weems and Heppner, 2004). Adult females lay eggs in

ripening fruit, and hatched larvae destroy the fruit as they feed and then burrow out to pupate. Fruit fly damage and controls are generally assessed as percentages of individual infested fruit. Percentages are taken of sample counts of fruit, typically of large or mature fruit, ready for harvest or actually harvested (Latif et al., 2002; Sookar et al., 2004) – here called the “mature only” or “MO” model. Flies also, however, attack immature fruit that are subsequently abscised from the plant, and so do not survive to maturity to be counted at harvestable age. These fruit must therefore be considered lost from the plant, but this is not recorded by MO sampling. This paper proposes a more meaningful and accurate way to sample losses to estimate the reduction in mass of harvested fruit per unit area, the most straightforward indicator of economic loss.

Field observations indicated that fruit abscised from the plant while still developing, following fruit fly attack, are replaced by the development of fruit from other, less-mature fruit nodes, which, without these losses, would be abscised in normal development. These replacement fruit were inferred to be “held back,” and “brought forward from reserve” to fill gaps when these appear, but not, however, to compensate fully for the loss of original fruit. Although not universal, and varying between species and conditions, a similar response pattern has been observed in a variety of crop plants, including strawberry (Cross and Burgess, 1998), raspberry (Charles and Cornwell, 1987), cranberry (Long and Averill, 2003), field beans (Aufhammer et al., 1987) and grain legumes (Sinha and Savithri, 1978). In these cases, compensation is rarely complete, and therefore results in a loss of mature fruit yield, which, on one hand, is less than the initial loss of immature fruit nodes, but, on the other hand, is not completely made good. The abscission of developing fruit that might have compensated for early losses of others is a major contributor to “June drop” whereby initial fruitlets are abscised in many fruiting trees, such as avocado (Davenport, 1983). Generally, the compensating ability declines across the season. In cotton, early bud loss, including by insect attack, is compensated for by adjacent and subsequent fruiting positions (Cook and Kennedy, 2000; Holman and Oosterhuis, 1999), but the compensation ability drops through the season, and the recovery of lost fruit is substantially higher among younger fruit than among older ones (Brook et al., 1992; Lei and Gaff, 2003; Wilson et al., 2003). In Cretan olives, compensation for the attack of the olive fruit fly (the Tephritid *Dacus oleae* (Gmel.)) is 10% in August but only 5% in September (Michelakis and Neuenschwander, 1982).

This paper proposes and tests a method of measuring cucurbit losses to fruit flies by means of four assumptions, based on observations by farmers and local field scientists. These are that (1) immature fruit attacked by flies are abscised and (2) these are replaced by the development of others, but (3) the compensation this provides is incomplete and (4) compensation ability declines with increasing maturity of the fruit lost. The proposed method samples losses by recording separately the percentage infestation of fruit in different maturity classes, and aggregates these to obtain a single figure.

MATERIALS AND METHODS

MODEL DESCRIPTION

Three alternative models were considered, as ways of addressing this calculation. Let the notation D_1 , D_2 , D_3 , D_4 represent the fractional damage in, respectively, the broad development/size classes or cohorts of “forming,” “small,” “medium” and “mature” fruit. Regarding the capacity of the plant to recover losses of fruit in the various cohorts, as the fraction of losses that may be compensated so that these losses are themselves reduced in transition from one stage to the next, let $C_{1,2}$ be a “compensation factor” representing the fractional recovery of losses in transition from “forming” to “small” fruit, $C_{2,3}$ that for transition from “small” to “medium” and $C_{3,4}$ from “medium” to “mature” fruit. Total loss was modelled in three ways. Models 2 and 3 aggregate losses by assuming that, from one cohort to the next, losses are a fractional reduction in the survivors of the preceding losses;

for example, if one cohort loss were 0.2 (or 20%) and another 0.25 (or 25%) then the total loss exerted by the two (in either sequence) would be $[1-(1-0.2)\times(1-0.25)] = 0.4$ (or 40%).

1. “Mature fruit only” (MO), the model conventionally used, as the infestation of mature fruit ready for harvest, ignoring the levels in previous cohorts:-

$$D_4$$

2. “By cohort, uncompensated” (CU), as the survival to each stage, from the preceding stage, only of that fraction of each cohort that is un-attacked:

$$1-[(1-D_4)\times(1-D_3)\times(1-D_2)\times(1-D_1)]$$

3. “By cohort, compensated” (CC), as the survival to each stage, from the stage preceding, of that fraction of each cohort that is un-attacked, and a part made good from the fraction that was attacked. The compensation for attacked fruit is modelled by a level of compensation, so that the losses of each cohort at each stage are reduced by a compensation factor representing the fractional recovery of losses:

$$1-[(1-D_4)\times(1-D_3\times\{1-C_{3,4}\})\times(1-D_2\times\{1-C_{2,3}\})\times(1-D_1\times\{1-C_{1,2}\})]$$

Compensation among very small fruits is higher than among those ready for harvest, so compensation factors were held to decline across the course of fruit development. Factors were estimated by fieldworkers and farmers, and rounded to obtain simplified estimates as follows:

$$C_{1,2} = 0.875$$

$$C_{2,3} = 0.750$$

$$C_{3,4} = 0.500$$

Note that Models 1 and 2 are both variants of Model 3: Model 1 is Model 3 with all compensation factors as 100%, so that only losses at the final stage have any effect; Model 2 is Model 3 with all compensation factors as zero, so that losses in all cohorts have equal effect.

The implications of the various models may be seen from a set of examples, using a set of typical, actual values of losses (observed in the field in bitter melon) of 9% of forming fruit (Cohort 1), 7% of small fruit (Cohort 2), 3% of medium fruit (Cohort 3) and 10% of mature fruit (Cohort 4). (Losses are expressed as percentages rather than fractions, following local usage among agronomists and farmers). The total loss under the MO model is simply 10%, the losses in Cohort 4. Under the CU model, survival from the various cohorts is as follows:

$$\text{Cohort 1: } 100-9=91\%;$$

$$\text{Cohort 2: } 100-7=93\%$$

$$\text{Cohort 3: } 100-3=97\%$$

$$\text{Cohort 4: } 100-10=90\%$$

The total CU survival is the product of these four, namely $0.91\times 0.93\times 0.97\times 0.90=0.74$, or 74%. The loss this represents to the entire crop is therefore $100-74$ or 26%.

Under the CC model, losses in the first three cohorts, as fruit pass to the succeeding cohort, are partly made good by compensation, and the losses modified by the compensation factors, as follows:

Cohort 1: observed loss (9%) is reduced by its applicable compensation factor (0.875) so the actual loss is $9\times(1-0.875)=1.125\%$, and survival is $100-1.125=98.875\%$

Cohort 2: observed loss (7%) is compensated by its factor (0.75) so the actual loss is $7\times(1-0.25)=1.75\%$, and survival is $100-1.75=98.25\%$

Cohort 3: observed loss (3%) is compensated by its factor (0.5) so the actual loss is $3\times(1-0.5)=1.5\%$, and survival is $100-1.5=98.5\%$

Cohort 4: loss in this cohort is too late to be compensated, so the actual loss is the same as the observed loss (10%) and survival is $100-10=90\%$

The total survival is the product of these four, incorporating compensation, namely $0.98875\times 0.9825\times 0.985\times 0.9=0.8612$, or 86%. The loss this represents to the entire crop is therefore $100-86$ or 14%. Inevitably, the CC loss estimate (14%) is larger than the MO estimate (10%) but smaller than the CU estimate (26%). This corresponds with the literature reports cited above, wherein compensation is present (greater than zero) but imperfect (less

than 100%), and represents the phenomenon that the modelling process is intended to capture.

FIELD STUDIES

This work comprised three field studies in Northern India in 2003 and 2004.

Gourd fruit infestation and survivor mass

Study 1 tested the basic hypothesis that even “surviving” fruit may be underweight when fly attack is intense. It assessed the relationship between the MO infestation in any given plot and the mean mass of its individual surviving, un-attacked fruit. The hypothesis was based on the assumptions that under fly attack some fruit, attacked relatively early on, are shed by the plant, and their replacements, as developing relatively late, are smaller and lighter than the originals would have been. Under more intense infestation, therefore, the mean mass of each individual uninfested fruit may be lower than under less intense infestation, leading to underestimation of actual economic loss, when estimation is by percentage infestation by numbers of MO fruits, as even surviving fruits are relatively underweight.

The experiment was laid out in a 20×45m field of bitter melon (*Momordica charantia* L.) in Varanasi (25°20'N, 83°00'E) in 2003. The area was divided into six plots of 20×7.5 m each, treated with different fruit fly controls. Samples were taken for the analysis of infestation from three separate sub-plots within each treated plot, and on three separate occasions at 10-day intervals, so that each treated plot had nine records, to obtain a total of 54 records altogether. Data were collected within each sub-plot on each occasion as both the numbers and masses of both infested and uninfested mature (MO) fruit per unit area (sampling was of all fruit in each sub-plot, between 46 and 149 fruit in each).

Calculations were made from the totals, in each cell (each sub-plot at each sample occasion), of the number of uninfested fruits (U), the number of infested fruits (N) and the mass of uninfested fruits (M). A comparison was made, cell-by-cell, of the fractional infestation of fruit by number (D) as $D = N/(N+U)$ and the mean mass of one single uninfested fruit (S) as $S=M/U$. This allows the calculation of the additional level of loss, over and above that captured by the MO model, which is due to imperfect compensation of abscised fruit – i.e., the loss component that is not recorded when the MO model is used. This relationship may be used to model full, aggregate losses by adjustment to include the loss of mass per uninfested fruit. This may be done, for each level of infestation (D) indicated in the MO model, by the aggregation of the fraction of fruit numbers lost (D itself) and the corresponding fractional loss in mass of each uninfested fruit (W_D), calculated from the mass of a single uninfested fruit at that infestation level (S_D), relative to that mass when infestation is zero (S_0). (Note that this subscript notation refers to different infestation levels, D , whereas that in the Model Description above refers to cohorts, so the two are not compatible). Mass loss for any infestation level (W_D) was calculated as the mean mass per uninfested fruit at that infestation level (S_D), subtracted from the mean mass per uninfested fruit at zero infestation (S_0) to obtain the fractional loss of mass at that infestation level. The fractional MO loss (D) and the fractional survivor mass loss (W_D) were then aggregated to obtain the total loss of fruit mass per unit area (L_D), the most economically meaningful quantification of loss.

Cell-by-cell, across the 54 records, the mass of an individual fruit (S_D) was regressed against percentage infestation (D) by MO. The loss of mass per individual fruit (W_D) was estimated as the subtraction of the output of the regression equation for that level of infestation (S_D) from the mass of a fruit when infestation was zero (S_0). The aggregate loss of mass of uninfested fruit (L_D) incorporated both the numerical loss of uninfested mature fruit (D) and fractional reduction of individual mass in those uninfested fruit (W_D), by combining the two as $L_D = 1-(1-D) \times (1-W_D)$. For example, if the mass of an individual fruit when infestation at MO is 0 were $S_0 = 20$ g, and the mass of an individual fruit when infestation at

MO is $D = 0.25$ (or 25%) were $S_{0.25} = 16$ g, the added loss attributable to loss of mass would be $W_{0.25} = (20-16)/20 = 0.2$ (or 20%), and the aggregated mass loss of all fruit per unit area ($L_{0.25}$) would be $1-(1-0.25)\times(1-0.20) = 0.4$ (or 40%). The following is the complete set of notations: N is the number of infested fruit; U is the number of uninfested fruit; M is the mass of uninfested fruit; D is the fraction of fruit infested ($N/(N+U)$) (as sampling was of mature fruit only, all D were D_4 in the notation in Model Description above); S_D is mass of one individual uninfested fruit (M/U) at infestation level D (calculated by regression of S against D); S_0 is mass of one individual uninfested fruit at zero infestation; W_D is the fractional loss of mass per individual uninfested fruit at infestation D , relative to zero-infestation ($W_D = (S_0 - S_D)/S_0$); L_D is fractional aggregated loss of mass of uninfested fruit per unit area ($L_D = 1-(1-D)\times(1-W_D)$).

Relative stability of infestation models

Study 2 tested the hypothesis that a more accurate and realistic model should have a role in “damping-out” random variation between replicate plots of infestation assessment that are all treated the same way. The study assessed the relative reliability of the MO and cohort (CU and CC) models, by comparison of the between-replicate variation of plots treated in the same way, when the data in each were processed via each of the candidate models. This was done using data from four fruit fly control field experiments, in bitter melon in Bhubaneswar (20°14'N, 85°50'E) and pumpkin (*Cucurbita pepo* L.) in Sardarkrushinagar (24°10'N, 72°26'E). Two experiments were of farm-level fruit fly controls, one in Bhubaneswar of eight treatments in four completely randomized blocks and one in Sardarkrushinagar of four treatments in five completely randomized blocks (Stonehouse et al., 2005, respectively Experiments 1 and 4). The other two were local replications of six treatments (variations of controls at the level of the farm and village; Stonehouse et al., 2007), each replicated twice in each location (though replication was lost in one location to leave five usable sets). These provided a total of 74 plots in 23 experiments – four replicated five times, eight four times and eleven twice.

The coefficient of variation (CV) was calculated within each individual treatment cell from each experiment, among the identically treated replicates within it, separately with the data manipulated by each of the candidate models. The CV values were then compared to establish whether they differed among the results of the various models.

Association of mature-only and cohort-compensated model outcomes

Study 3 assessed the association between the infestation attributed by the MO model, and the additional infestation added by the inclusion in the four-cohort CC model of data from cohorts 1, 2 and 3. Using data from Study 2, an estimate was made of the additional loss at each infestation level, over and above the loss estimated by the MO model, by the inclusion of the losses incorporated by the CC model as consequences of fruit fly attacks on the earlier cohorts. The total CC loss calculation was separated into its MO and modelled other-than-MO components, allowing them to be compared to the additional losses, in survivor fruit mass, calculated in Study 1. Using the notation from Model Description calculation 3 above, this was the association between

MO loss D_4

and

Other-than-MO loss ($D_{1,2,3}$)
 $1-[(1-D_3\times\{1-C_{3,4}\})\times(1-D_2\times\{1-C_{2,3}\})\times(1-D_1\times\{1-C_{1,2}\})]$

RESULTS

1. GOURD FRUIT INFESTATION AND SURVIVOR MASS

The mean mass of an individual uninfested fruit (S , in g) was regressed against the percentage fruit infestation estimated by the MO model (D), in each of the 54 cells evaluated, with data treated in various ways. In comparison of the regression relationships with the

data untransformed and transformed by conversion to logarithms, the closest fit, as the highest r^2 value (0.1402), was obtained with mass per fruit converted to logarithms and infestation data untransformed, and this association was statistically significant (regression $F=8.4812[1,52]^{***}$) and obtained a regression equation of $S = \text{EXP}(3.8954-0.0103 \times D)$. This finding that, for elevated losses of fruit by number, there was an additional loss of mass of the individual survivor fruit, confirmed the central hypothesis that MO represented an underestimate of the loss of mass of uninfested fruit per unit area, and thus of economic loss.

Table 1. Modelled effects of the reduction of mass per uninfested fruit, in enhancing the aggregate damage by fruit flies, at different levels of the infestation of fruit by number.

Infestation of mature fruit only (MO) (%) (D)	Mass of individual uninfested fruit (g) (S_D)	Loss of mass per individual uninfested fruit (%) (W_D)	Aggregate loss (mass of uninfested fruit) (%) (L_D)
0	49	0	0
10	44	10	19
20	40	19	35
30	36	27	49
40	33	34	60
50	29	40	70
60	27	46	78
70	24	51	85
80	22	56	91
90	19	60	96
100	18	64	100

Table 1 contains the values of fruit infestation, the mass of individual fruit and aggregate losses, calculated from the regression relationship, arrayed for convenience along a scale of 0..10..20% etc. The inclusion of the fruit-mass-loss calculation considerably augmented the loss estimates in comparison with those for percentage infestation alone, in a relationship characteristically increasing and then decreasing with increasing D , with a maximum departure between 40 and 50% MO loss. According to the regression relationship, when percentage infestation of harvested fruit is the only measure of infestation, when losses are "10% infestation" (a typical field value), this may underestimate true losses by nearly a half (i.e., as 10% instead of 19%).

2. RELATIVE STABILITY OF INFESTATION MODELS

Across the 23 replicated experiments, the CVs across replicates were calculated when the plot losses were modelled in three different ways, and the means of these CV values are given in Table 2, along with the outcome of planned comparisons of the MO model with each of the other two, by Wilcoxon sign-rank test (Sokal and Rohlf, 1995). The use of the MO model obtained significantly greater variation among replicates of identically treated cells than the cohort models, and highly significantly greater than the cohort-compensated model.

3. ASSOCIATION OF MATURE-ONLY AND COHORT-COMPENSATED MODEL OUTCOMES

The association of the modelled losses in cohorts 1, 2 and 3 ($D_{1,2,3}$) with MO loss was statistically significant (a linear plot obtained the best fit, as $r^2=0.3023$, regression $F=31.1959[2,72]^{***}$; the regression was carried out with bitter melon and pumpkin data

pooled, as the use of separate regressions did not improve the fit) and obtained the regression model: $D_{1,2,3} = 2.6014 + 0.9961 \times D_4$.

Table 2. Mean coefficients of variation (CV, as SD/mean) among the data from the various replicates in 23 experimental cells in four experiments, with “infestation” calculated according to three different models, with the outputs of Wilcoxon test comparisons (all $n=23$) of mature fruit only (MO) model with the other two.

Model	1 Mature only (MO)	2 Cohort uncompensated (CU)	3 Cohort compensated (CC)
Mean CV	0.3363	0.1966	0.1816
Ts (difference from MO)	-	55*	18**

* significant at 0.05, ** significant at 0.01 probability level.

Table 3. Comparison of percentage losses estimated by the “mature only” (MO) model in comparison with those by the “cohort-compensated” (CC) model, and by the incorporation of survivor mass (from Table 1).

Infestation of mature fruit only (MO) (D_4)	Modelled infestation in three “pre-mature” cohorts ($D_{1,2,3}$)	Aggregate loss (cohort compensated) (A_D)	Aggregate loss (survivor mass compensated) L_D (Table 1)
0	3	3	0
10	13	21	19
20	23	38	35
30	32	53	49
40	42	65	60
50	52	76	70
60	62	85	78
70	72	92	85
80	82	96	91
90	92	99	96
100	100	100	100

Table 3 contains the implications of this relationship, as the MO loss (D_4), the modelled additional losses in cohorts 1, 2 and 3, and the inferred overall, aggregated loss level (A_D). The relationship between D and A_D may be compared with that between D and L_D , taken from Table 1, arriving at a similar relationship by a different route, as A_D uses the cohort aggregate values to model the total loss of fruit mass per unit area, and therefore should approximate L_D . The aggregate estimates of the two are broadly similar, particularly in the lower reaches (below 50% infestation), where the majority of actual field losses occur (the higher values represent extrapolations, which are rarely encountered in the field).

DISCUSSION AND CONCLUSIONS

The MO model underestimated cucurbit losses to fruit flies, as the mass of “uninfested” fruit was reduced when attack was intense, taken to be a consequence of imperfect compensation for fruit attacked and shed before maturity.

The CC model indicated its suitability in two ways. First, the incorporation of information from forming small and medium-sized fruit, as well as mature fruit, obtained

significantly less variability, among replicates of plots with the same fruit fly controls used, than the MO model using data from mature fruit only. Second, the calculation of added losses, over and above those to mature fruit only, by the aggregation of losses to the three cohorts prior to mature fruit, using the cohort-compensated model, obtained estimates of total loss, as a function of MO loss, comparable to those obtained by the incorporation of reductions in uninfested fruit mass.

Overall, as the model with the lowest variation and approximating the loss reductions observed in uninfested fruit mass, the cohort-compensated model, amalgamating losses over fruit size cohorts, with partial compensation of losses in the earlier cohorts, suggests itself as suitable for general use in the field. In comparison with a more direct alternative of sampling fruit and weighing survivors, as was done in Study 1, it allows data to be gathered non-destructively, as fruit do not need to be removed, an important advantage when sampling in remote areas or the fields of marginal farmers. The sampling process and synthesis of data to obtain an aggregate loss figure may be used by researchers and others seeking to quantify fruit fly losses to cucurbits, to estimate the scale of fly problems and the agricultural and economic returns to fly controls.

The characteristics of cucurbits that allow the calculations described, as long-season annuals producing a sequence of fruit, and therefore with several stages present together, are not shared by most other crops or fruit fly hosts. It remains to be seen whether the calculations described may be of use in assessing losses of other crops.

The calculation does not explicitly model plant physiological processes, and the compensation factors selected from subjective estimates are open to refinement and improvement and may differ between species and varieties. Additionally, this process may not capture all economic returns, as not all economic compensation processes take the form of increases in mass of "held-back" fruit. For example, compensation losses of olive yield to the olive fly is not all by fruit replacement but also by increases in the size and oil content of individual fruit (Ait Radi et al., 1990; Neuenschwander et al., 1980). In some table fruit, such as apples, loss compensation may increase the size of individual survivor fruit and thus their price and total economic returns (Krzewińska et al., 2002). The measurement and quantification of compensation capacities are a field for future research.

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