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A temperature-driven daily process model for onion thrips populations in onions

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Abstract: A temperature-driven process model was developed to describe the seasonal patterns of populations of onion thrips, *Thrips tabaci* Lindeman, in onion crops. The model used daily cohorts (individuals of the same developmental stage and daily age) as the population unit. After each day, individuals in a daily cohort either move to the next daily cohort in the same developmental stage, advance to the first daily cohort of the next developmental stage, or be removed from the population due to mortality and/or emigration. Stage transitions were modelled as a logistic function of accumulated degree-days (DD) to account for variability in development rate among individuals. Daily survival was modelled as a logistic function of daily mean temperature. Parameters for development, survival, and fecundity were estimated with published data.

A single invasion event was used to initiate the population process, starting at 1-100 days after onion emergence (DAE) for 10-100 days at a daily rate of 0.001-0.9 adults/plant/day. The model was validated against five observed seasonal patterns of onion thrips populations from two unsprayed sites in the Riverina, New South Wales, Australia, during 2003-2006. Performance of the model was measured by a fit index based on the proportion of variation in observed data explained by the model (R^2) and the differences in total thrips-days between observed and predicted populations.

Satisfactory agreement between simulated and observed seasonal patterns was obtained within the range of invasion parameters tested. Model best-fit was obtained at invasion starting dates of 6-98 DAE with a daily invasion rate of 0.002-0.2 adults/plant/day and a duration of 30-100 days. Under the best-fit invasion scenarios, the model closely reproduced the observed seasonal patterns, explaining 73-95% of variability in adult and larval densities during population increase periods. The results showed that small invasions of adult thrips over a period of days with a gradual population build-up of thrips within onion crops were sufficient to bring about the observed seasonal patterns of onion thrips populations. Sudden mass invasions may reproduce well the rapid ascending phases of the population build-up but these alone would fail to account for the low population periods. Support for small gradual invasions was found in sticky traps data, which showed that onion thrips were moving into the onion field in small numbers long before the first thrips were detected in onion, and in egg monitoring data, which revealed onion thrips eggs in newly emerged onion leaves.

According to the model, applications of contact insecticides are better timed before the accumulated adult populations have reached 10% of total adult thrips-days during seasons of early to intermediate invasions (1-60 days after onion emergence), and when accumulated adult populations are between 10% and 50% during seasons of late invasions (>60 days after onion emergence). Model simulations also suggest that management practices that delay or reduce onion thrips invasions are critical in controlling peak infestation levels. Such practices include removal of volunteer onions (sprouts from left-over bulbs from previous seasons) and weed control, which reduce the source populations, and the application of a systemic insecticide at sowing, which protect onion plants from onion thrips infestation during the early growth stages. Temperature driven, the model can be directly used to assess the impact of climate change on onion thrips populations. After modifications of species-specific parameters, the model can be easily adapted to describe the population dynamics of other insect species.

Keywords: *Thrips tabaci, onion, colonization process, population model*

1. INTRODUCTION

Onion thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), is a worldwide pest of onion (*Allium cepa* L.). Heavy infestations may reduce yield and the marketability of onion bulbs. In addition to the direct impacts, onion thrips is an efficient vector for iris yellow spot virus, a potentially destructive disease in onion. Thrips feeding also predisposes onion plants to invasion by the fungal pathogen *Alternaria porri*, which causes the disease purple blotch.

Among its wide range of crop and weed hosts, onion thrips appear to favour onions, occurring anywhere onion is grown. The favourable host status coupled with large monocultures and general lack of control by natural enemies in the field, make onion crops ideal breeding grounds for onion thrips, enabling populations to grow steadily from detection to harvest. In a yellow onion crop in Canada, the onion thrips population increased from barely detectable to over 1000/plant in less than three months (Fournier et al. 1995). Sometimes, the population build-up process is temporally disrupted by unfavourable weather events such as heavy rain or extreme high temperatures. However, the general upward trend is still evident before the population collapses towards the end of the crop season (Lu and Lee, 1987, Liu 2004). Large migration events may also disrupt the population build-up process (Bocak 1996).

In Australia, large populations of onion thrips develop in onions wherever the crops are grown and multiple applications of insecticides are used to control the pest each season (Mo 2007). To better understand the population dynamics, a temperature-dependant population model for onion thrips populations in onion crops was developed based on published data. The model was then used to investigate the effects of timing and intensity of invasions on the seasonal patterns of the insect by comparing model outputs to observed seasonal patterns under several different invasion scenarios. Implications of the model in the management of onion thrips are discussed.

2. MATERIALS AND METHODS

2.1. Model Description

The structure of the model is shown in Figure 1. The life cycle of onion thrips consists of an egg stage, two larval stages, two non-feeding stages (pro-pupa, pupa), and an adult stage. In this model, the two larval stages and the two non-feeding stages of pro-pupa and pupa are combined into single stages. To account for the non-ovipositing period of young adults, the adult stage is split into pre-adult (non-ovipositing) and adult (ovipositing). Hence five stages are considered in the model: egg, larva, pupa, pre-adult and adult. The model splits individuals in a stage into daily cohorts each consisting of individuals that entered the stage on the same date.

At the end of each day, individuals in a daily cohort will either die, move to the next daily cohort of the same stage, or advance to the first daily cohort of the next stage (e.g. hatching of eggs or moulting of larvae, pupation, pupal eclosion, or progressing to reproductive maturity). The number of individuals in a daily cohort moving to the next daily cohort of the same stage at the beginning of each day equals the number of individuals in the previous daily cohort that survived the previous day and have not progressed to the next stage. For the egg, larval, pupal, and pre-adult stages, the number of individuals advancing to the beginning of the first daily cohort of the next stage is the sum of individuals of any daily cohort in the previous stage that has survived that day and accumulated degree-days (DD) equalling or exceeding the required DD for that stage (K).

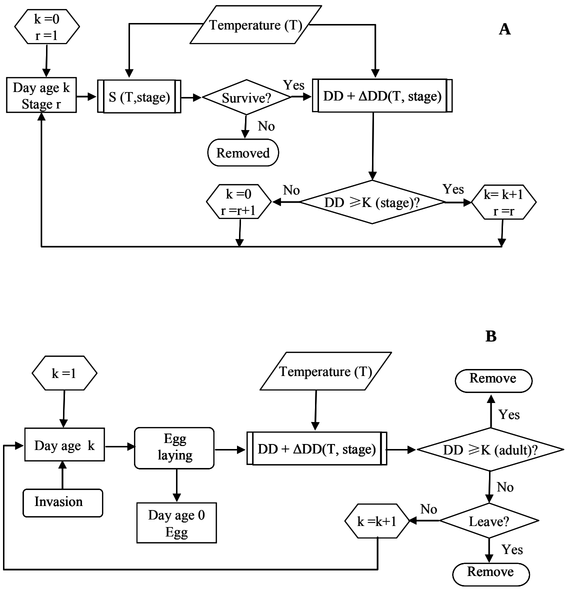

Figure 1. Model flowchart: A. all stages except adult, B. adult (reproductive stage). DD is degree-days, ΔDD (T, stage) is the daily increment in DD at temperature T for the target stage, K(stage) is the degree-day requirement of the target stage.

Daily survival rate of individuals in stage r during day t, S(r, t), was modelled as a logistic function of mean daily air temperature during day t, T(t),

$$S(r,t) = \frac{1}{1 + \exp(A(r) + B(r)T(t))} \tag{1}$$

where A(r) and B(r) are parameters for development stage r.

To account for variability in individual development, proportions of individuals in daily cohort k of stage r advancing to the next stage during day t, P(r, k, t), was estimated from the logistic probability distribution function of Dennis et al. (1986),

$$P(r,k,t) = 1 - \frac{1}{1 + \exp(-\frac{K(r) - DD(r,k,t)}{\sqrt{b^2 DD(r,k,t)}})} \tag{2}$$

where K(r) is the required number of degree-days (DD) for stage r and DD(r, k, t) is the accumulated DD for individuals in cohort k of stage r at the end of day t, and b^2 is a constant indicating the variability of development rates of individuals. Daily DD increment was estimated from daily maximum and minimum temperatures with the single sine-wave method (Roltsch et al. 1999). Temperature data were obtained from Australian Bureau of Meteorology (http://www.bom.gov.au).

Progression of adults to eggs is determined by adult survival rate and fecundity. Adult mortality was modelled as a special development process whereby completion of the adult stage was equivalent to death, with the adult DD requirement estimated as the accumulated DD during the average lifespan of adults. Onion thrips populations in Australia consist of exclusively females, which reproduce asexually. The number of eggs produced each day was the product of the number of surviving adults during that day and a fixed daily fecundity rate.

The model starts with invading egg-laying adults of 1-5 d old. Population collapses toward the end of the onion season were modelled by forced exodus of winged adults and pre-adults and reduced survival of other stages, except pupae, following plant fall toward the end of the onion season.

2.2. Model Parameters

Stage-specific development threshold temperature (T_0) and total degree-day requirement (K) of onion thrips were estimated from published data using linear regressions. Data used for the estimation of development parameters were from Lu and Lee (1987), Edelson and Magaro (1988), and Salmasi et al. (2003) for the egg stage, from Lu and Lee (1987), Salas et al. (1993), and Salmasi et al. (2003) for the larval stage, and from Lu and Lee (1987), Salas et al. (1993), and Salmasi et al. (2003) for the pupal stage. Development parameters for the pre-adult stage were directly from Edelson and Magaro (1988). No studies have examined the development variability parameter, b^2, for onion thrips. It was therefore given a fixed value of 2, which corresponds to a standard deviation of ca. 26 DD at a mean value of 100 DD. Parameters of the survival function for the egg stage and the post-hatching period excluding the adult were estimated from Murai (2000) with non-linear regression in S-Plus (Venables and Ripley, 2002). Parameters of adult development were estimated from data of temperature-dependant adult longevity from Lu and Lee (1987) with threshold temperature set the same as in the larval stage. Fecundity of onion thrips was set at one egg per adult per day according to Lu and Lee (1987). The starting date of population collapse was set around the peak dates of thrips densities in observed seasonal patterns. The daily proportion of winged adults and pre-adults leaving onion crops and the daily mortality rate of other stages except pupa during the population declining phase were both set at 0.15.

2.3. Invasion scenarios

Daily invasion rate was tested at 0.001, 0.002, …, 0.009, 0.01, 0.02, …, 0.09, 0.1, 0.2, …, 0.9 adults/plant. At typical onion densities of about 300,000-400,000 plants/ha, the test range corresponds to 0.03-0.04 to 27-36 adults/m^2/day. Invasion starting date was tested at daily intervals between 1 and 100 days after onion emergence (DAE). Invasion duration was tested at10 day intervals between 10 and 100 days. Altogether 27,000 invasion scenarios were tested (27 rates x 100 starting dates x 10 durations). Onion emergence date was estimated based on the threshold temperature of 1.4°C and required heat units of 219 DD (Brewster 1997).

2.4. Model Performance

The goodness-of-fit of the model in describing the observed seasonal patterns of thrips densities under different invasion scenarios were measured by the model fit index, FID:

$$FID = \frac{Min(R^2(A), R^2(L))}{Max(THD(A), THD(L))} \tag{3}$$

where R^2(A) and R^2(L) are the fractions of total variation of thrips densities in the observed data explained by the model for adult and larva, respectively during the population increase period. THD(A) and THD(L) are relative deviations of predicted total thrips-days from observed total thrips-days for adult and larva, respectively. To estimate total thrips-days for observed populations, daily densities of adult and larval thrips were extrapolated linearly from weekly data.

Sensitivity of the model to the three invasion parameters was estimated as the range of the respective parameters for which FID values fall within 10% of the best-fit FID value.

2.5. Model Validation

Five datasets containing seasonal patterns of onion thrips populations were used for model validation. The data were collected in unsprayed brown onion crops during 2003 and 2006 in Coleambally (Cole2003 and Cole2006) and Yanco (Yanco2004, Yanco2005, and Yanco2006) in southwest New South Wales, Australia. Three of the five datasets, Cole2003, Yanco2005, and Yanco 2006, covered the entire onion seasons. The other two datasets, Cole2006 and Yanco2004, covered most of the population increase period.

3. RESULTS

3.1. Model Parameters

Estimates of threshold temperature (T_0) and DD requirement (K) for the development of the egg, larvae and pupa stages are given in Table 1. The linear regressions accounted for 73-85% of the variability of development rate in the egg, larva and pupa stages (r^2). T_0 and K values for the pre-adult stage were taken directly from Edelson and Magaro (1988) and those for the adult stage from adult longevity data in Lu and Lee (1987). The fitted logistic curves satisfactorily described the non-linear relationship between daily survival rate and temperature for the egg stage (R^2 = 0.99) and the combined post-hatch period (R^2 = 0.84). The resulting estimates of the survival parameters were shown in Table 2.

Table **1**. Temperature thresholds (T_0) and DD requirement (K) for the development of eggs, larvae, pupae, pre-adults, and adults of onion thrips, as estimated from published data.

	Egg	Larva	Pupa	Pre-adult	Adult
T_0	8.6	8.5	7.4	15.7	8.5
K	89.3	84.7	75.8	12.2	123.1
r^2	0.85	0.81	0.73	n.a.	n.a.

Table **2.** Parameters of the daily survival function for the egg stage and the post-hatching period from larva to pre-adult used in the model.

Stage	*A*	*B*	*R*^{2}
Egg	0.5548	-16.3347	0.99
Larva to pre-adult	0.1825	-8.4928	0.84

3.2. Model Validation

Invasion scenarios were found for each of the five datasets tested which allowed the model to adequately describe the observed seasonal patterns (Figure 2). The best-fit invasion scenarios were found at invasion starting dates of 6-98 DAE with a daily invasion rate of 0.002-0.2 adults/plant/day and a duration of 30-100 days (Table 3). Under the best-fit invasion scenarios, the model explained 73-95% of the variation in adult density and 76-95% of the variation in larval density during the population increase periods (Table 3). Predicted total thrips-days during the data periods were within 13% of total observed thrips-days for both adults and larvae in four of the five datasets.

4. DISCUSSION

In unsprayed onion fields, the seasonal patterns of onion thrips appeared uni-modal, characterised by a lengthy non-detection/low density period in the beginning followed by a short and rapid increase and finally a steady-decreasing period shortly before harvest. In this paper, we demonstrated through a population model that small invasions of adults over different periods of time were sufficient to bring about the observed seasonal population patterns.

The model was based on the life process of thrips (egg-larva-pupa-adult-egg) and used actual temperatures to drive the population process, with parameters of development, survival and fecundity estimated from published data. The validity of the model was tested using the observed seasonal patterns of five onion thrips populations in onion crops at two sites during 2003-2006 under a series of single-event invasion scenarios.

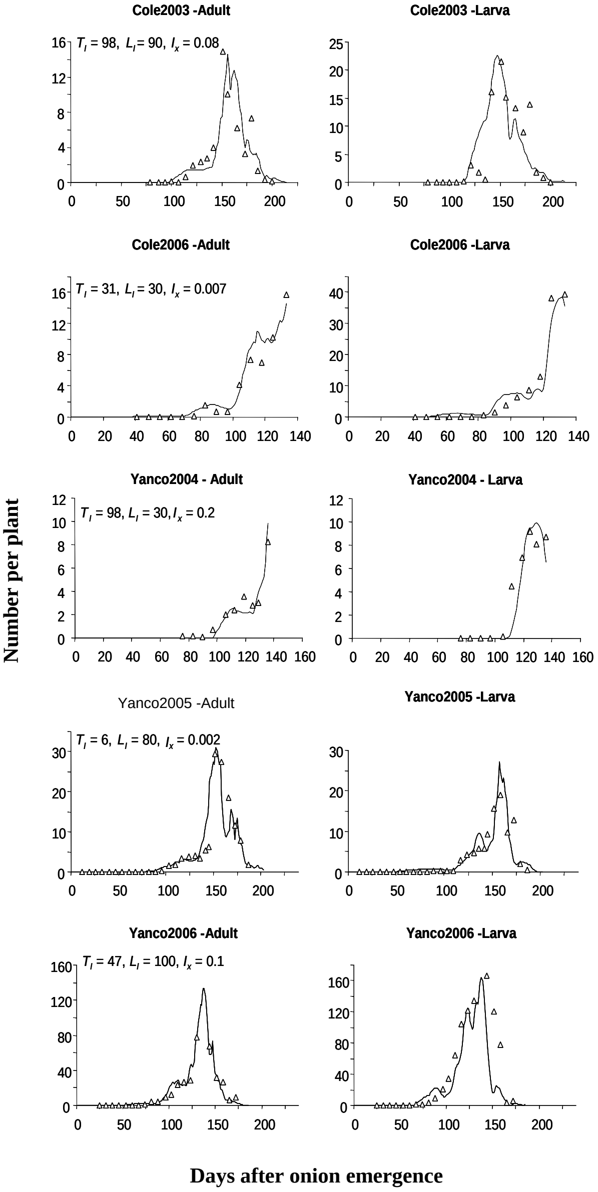

Figure 2. Observed (triangle) and model predicted (line) seasonal patterns of adult and larval densities of onion thrips at two sites in the Riverina, NSW, during 2003-2006 using the best-fit invasion scenarios shown (T_I: invasion starting date, L_I: invasion duration, I_x: invasion rate).

For each seasonal pattern, an invasion scenario was found under which the model adequately represented the observed seasonal patterns. According to the best-fit invasion scenarios, onion thrips adults started invading onion crops at 6-98 days after onion emergence, or from mid-June to mid-September, depending on site and year. Invasions starting as early as six days after onion emergence are surprising but possible. Trapping data showed that onion thrips adults were flying around in onion fields in small numbers long before the first thrips were detected on onion plants (Mo, 2007) and egg monitoring data showed that eggs were laid in onion plants as early as the hook-leaf stage (Mo et al., 2008). Two of the five seasonal patterns were best described with daily invasion rates of 0.002-0.008 adults/plant, one by a daily invasion rate of 0.08 adults/plant, and two by daily invasion rates of 0.1-0.2 adults/plant. From these low population bases, onion thrips populations were able to grow exponentially to the observed peak density of 14.9-77.6 adults/plant. This is not surprising considering the resource-rich and natural-enemy-poor environment of onion crops (Saxena 1981, Workman and Martin 2002, Liu 2004). Invasion duration did not appear as critical as invasion starting date and intensity in shaping the seasonal patterns. The best-fit invasion scenarios suggested invasion duration of 30-100 days depending on site and year, however, invasion duration of 10-50 days produced similar patterns to the observed seasonal patterns.

Table **3**. Best-fit invasion starting date (D0, DAE), invasion duration (D, days), and daily invasion rate (I, no./plant/day) of the model according to the model fit index, FID, and the resulting proportions of variance in the observed data explained by the model and relative deviations of predicated total thrips-days from observed total thrips-days (THD). Subscripts A and L denote adults and larvae, respectively.

					Increase period		All season/data period			
Data	D0	D	I	FID	R^2_A	R^2_L	R^2_A	R^2_L	THD_A	THD_L
Cole2003	98	90	0.08	0.72	0.73	0.76	0.61	0.68	-0.01	0.02
Cole2006	31	30	0.007	0.90	0.95	0.95	0.95	0.95	0.11	-0.07
Yanco2004	98	30	0.2	0.80	0.88	0.85	0.88	0.85	-0.13	0.11
Yanco2005	6	80	0.002	0.80	0.81	0.81	0.82	0.69	-0.02	0.02
Yanco2006	47	100	0.1	0.79	0.90	0.91	0.90	0.61	0.18	-0.31

Although not needed in bringing out the observed seasonal patterns, mass invasions can not be ruled out in the population process of onion thrips in onion crops and indeed are very likely when neighbouring host crops are harvested. However, sticky trap data collected at the sites of the validation datasets during 2003-2006 did not reveal any such events (Mo 2007). Similarly Hill (1995) noted that mass invasions were not required for high infestations of onion thrips to occur in fennel (*Foeniculum vulgare* Miller) crops.

The eventual collapse of populations was modelled in this study by exodus of adults and reduced survival of the resident individuals following plant maturation. The recent mathematical models of Matis et al. (2008) showed that population fluctuations in aphid populations were adequately described by making death rate dependant on cumulative past population size. While the same mechanism may also apply to thrips populations, it appears insufficient to explain the decline of onion thrips populations following crop maturation in this study. Thrips densities in this study started to decline at a wide range of peak densities from relatively low (<15 adults/plant) to relatively high (>120 adults/plant).

Results of a simulated chemical control event of 85% efficacy under this model suggest chemical applications of contact insecticides are better timed before the accumulated adult populations have reached 10% of total adult thrips-days during seasons of early to intermediate invasions (1-60 days after onion emergence), and when accumulated adult populations are between 10% and 50% during seasons of late invasions (>60 days after onion emergence). According to the observed seasonal patterns in this study, the timing of 10% accumulated adult populations occurred around the time when populations started rapid increase and timing of 50% accumulated adult populations occurred around the time of population peaks. Model simulations also suggest that management practices that can delay or reduce onion thrips invasions are critical in controlling peak infestation levels. Such practices include removal of volunteer onions (sprouts from left-over bulbs from previous seasons) and weed control, which reduce the source populations, and the application of a systemic insecticide at sowing, which protect onion plants from onion thrips infestation during the early growth stages. Temperature driven, the model can be directly used to assess the impact of climate change on onion thrips populations. After modifications of species-specific parameters, the model can be easily adapted to describe the population dynamics of other insect species

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