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MODELLING FLOWER DEVELOPMENT IN CITRUS

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Introduction

Quantitative models for plant growth and development have been used widely, particularly in crop-management research (e.g. Duncan 1971; Hesketh, Baker and Duncan, 1971, 1972; Fick and Loomis, 1975; Capinera, Detling and Parton, 1983; Osawa, Shoemaker and Stedinger, 1983). A general underlying structure of many of these models has included a system of differential equations which describes the 'state' of the crop, usually in terms of carbon allocation to various vegetative and reproductive structures (e.g. De Wit, Browver and Penning de Vries, 1970; Hesketh, Baker and Duncan, 1972). This approach has proved specially effective in herbaceous cropping systems (e.g. cotton, Wang *et al.*, 1977; alfalfa, Shoemaker, 1979) and natural herbaceous systems (e.g. grasslands, Detling, Dyer and Hunt, 1979), partly because experiments can be conducted to obtain precise information on physiological processes.

The application of this approach to modelling phenological changes in arboreal cropping systems has been more limited, largely because of the difficulty in experimentally establishing parameter values for the various growth processes involved. Consequently, quantitative models for arboreal systems often have had a rather more narrow focus than the prediction of overall carbon allocation. Of especial interest has been the phenological modelling of specific portions of the plants such as the vegetative buds (e.g. Osawa, Shoemaker and Stedinger 1983), flowers (e.g. Bellows and Morse, 1986; Lovatt *et al.*, 1987), and fruit (e.g. Newman *et al.*, 1967). The approach among these workers has been to relate stages of phenological development to a quantitative time scale, either calendar or physiological, usually by sampling over a wide range of conditions or years to provide a collection of data from different environmental conditions. The data are employed to search for similarities in either date or physiological time of development to specific phenological stages.

The *raison d'être* for these models has primarily been to examine the impact of various management strategies on growth and yield (e.g. Hesketh, Baker and Duncan, 1971, 1972). In some cases, complimentary models for development of insect pest populations have been constructed (e.g. Gutierrez *et al.*, 1975; Wang *et al.*, 1977; Shoemaker, 1979; Capinera, Detling and Parton, 1983). The joint models have then been employed to examine the impact of different management strategies on the plant-pest interactions, this is especially important in modelling flower and young

fruit development in citrus because several critical decisions concerning pest insect populations face grove managers during the flowering period. The matter is complicated because of the role citrus orchards play in honey production. Although most citrus varieties (except tangelos) do not require pollination by bees, citrus flowers are an excellent source of pollen and nectar. Citrus nectar produces a very light, high-quality honey which can contribute a substantial portion of honey production (citrus honey represents about 25% of annual honey production in California, USA (Bellows *et al.*, 1985)). Citrus orchards are used widely to provide rearing stimuli for the spring brood important in summer crop pollination. In addition, citrus is an important link in the rotation of honey bee colonies between food sources because it blooms after the early *Prunus* (e.g. almonds) and avocados and before seed alfalfa and melons.

At potential conflict with the needs of beekeepers are the concerns of the grove manager regarding pest management before, during and after the flowering period. Various lepidopterous species, such as fruit tree leafroller (*Archips argyrospilus*) and citrus cutworm (*Xylomyges curialis*), may appear in damaging numbers before or during the bloom period, while citrus thrips (*Scirtothrips citri*) are commonly of economic importance at the end of the bloom period. The initiation and termination of the bloom period is defined by two events: the date when 10% of the flowers in the south-west quadrant of the tree have opened (10% anthesis) and the date when 75% of the flowers in the north-east quadrant of the tree have matured and lost petals (75% petal fall). Pesticide use is prohibited in orchards during this period to protect the bees. Thus it is important to know, as far in advance as possible, when the bloom period will begin and end so that plans for integrating pest suppression and honey production will involve minimal conflict.

In an effort to provide a quantitative tool which might aid in predicting the timing of the bloom period, as well as describing the development of the population of inflorescences, we developed two different types of models which describe the phenology of bloom in the 'Washington' variety of naval orange. The first model was developed to quantify when (on a physiological time scale) the two events marking the bloom period occur. The second model describes the development of flowers from the young bud stage through opening to petal fall. Together the two models provide a fairly comprehensive account of developments during the bloom period.

Model structure

MODEL 1: PREDICTING ANTHESIS AND PETAL FALL

The first model has the form of a discrete event, or event scheduling model. Its objective is to define, on a physiological time scale, the two events of 10% anthesis and 75% petal fall. The first assumption of the model is that these two events occur at some relatively fixed interval following an unknown time at which the tree begins physiologically to accumulate developmental heat units. In this context, the model's simple structure is:

$$\text{Date for 10\% anthesis} = (\text{initiation date}) + (\text{fixed interval 1}),$$

$$\text{Date for 75\% petal fall} = (\text{initiation date}) + (\text{fixed interval 2}),$$

with the constraint that interval 2 is greater than interval 1. Neither the start date nor the fixed interval are known a priori, but must be estimated by seeking dates and intervals which prove suitable for describing the bloom period from a collection of

data sets. In addition, the physiological time scale is unknown and must be specified and descriptive parameters obtained from data. Our approach to resolving these unknowns involved two steps. First, we specified a structure for the physiological scale to be daily accumulations of degree-days. These were estimated as the area under a double sine wave (calculated from minimum to minimum recorded temperatures on successive days) above a threshold accumulation temperature. Secondly, we considered a collection of data sets from several locations over several years, each consisting of temperature records and dates when 10% anthesis and 75% petal fall were recorded. For this collection of data sets, we initially fixed the start date and threshold temperature and then calculated the values for the two fixed intervals which best described the overall data set. This calculation was repeated for initiation dates from 1 January to the bloom period and for values of the threshold accumulation temperature from 5°C to 20°C. Suitability of any set of parameter values was measured by considering the coefficient of variation of the difference between observed and predicted dates for all the data. In this way, the combination of initiation date and threshold temperature which best described the collection of observed results was identified.

Data suitable for use in quantifying the parameters of this model consisted of records from a total of 14 locations and years. For each set of data, daily maximum and minimum temperatures were recorded in or near the orchard using a thermograph housed in a standard weather shelter and situated at approximately 1.5 m above ground. Dates at which 10% anthesis occurred in the south-west quadrant and 75% petal fall occurred in the north-east quadrant of the trees were recorded. Counts of flowers in the appropriate quadrant of the tree were made and scored into developmental categories; the number of trees scored in each orchard varied from three to nine.

MODEL 2: MODELLING FLOWER MATURATION

The maturation of flowers from buds through to young fruit is a continuous process. This process, however, may be conveniently characterized by discrete developmental 'stages' as a flower sequentially achieves identifiable states of development. The maturation of a population of flowers on a tree can be viewed as a population developing through several stages, with a developmental time in each stage characterizing the amount of time a flower spends in that stage before proceeding to the next. We initially recorded the development of a flower population in eight developmental categories, but subsequently summarized them into four developmental stages: (1) young, spherical buds; (2) buds in which petals had expanded (but not opened), giving the bud an elongate, ovoid appearance; (3) flowers which were either partially or fully open; (4) flowers from which one or more petals had fallen (young fruit).

The problem of describing quantitatively the development of a population through several stages is a common one which has received much attention (see McDonald *et al.*, 1989 for a recent review). We adopted the use of the stage-frequency model of Bellows *et al.* (1982). In this model, development from one stage to the next is governed by developmental rates specific to each stage. Losses to the population are governed by mortality rates affecting all stages equally (although the case where different stages have different loss rates is similar, Bellows and Morse, 1986). A special feature of this model is that developmental rates are distributed as a random variable among the population, so that not all individuals change stages at the same

rate. This feature provides a distribution over physiological age of development between stages.

The model is constructed from two discrete-time equations which together describe the dynamics of the system in terms of the number of individuals entering and leaving each stage. The number of individuals in a stage is considered to be composed of distinct cohorts – individuals which entered the stage together at one time. The development of individuals in each of these cohorts is described by the two equations:

$$y_{i+1}(t) = G_i(j)X_i(t-j), \quad (9.1)$$

$$X_i(t) = s[1 - G_i(j)]X_i(t). \quad (9.2)$$

Development is recorded at discrete time steps. Here $y_{i+1}(t)$ is the number of flowers entering stage $i+1$ at time t . This number of recruits depends on the total number of individuals in a cohort of stage i at time t , X_i , and the proportion of those individuals achieving development to the next stage at time t . This proportion is determined by the distribution of the developmental period for stage i , $G_i(j)$, where j is the physiological age of the cohort X_i at time t . The shape of the distribution G_i is determined by the two parameters μ_i , the mean developmental rate of stage i , and σ_i^2 , the variance of the developmental rate. The discrete distribution G was truncated after 20 elements (after which the proportion of individuals changing stages had fallen below 10^{-4}); values for $G(j)$ for $20 < j < \infty$ were summed into $G(20)$.

The proportion of flowers surviving each time period was governed by the daily survival rate s . A daily application of a constant proportional survival is analogous to an exponential decline in numbers described by

$$N(t) = N(0)\exp(-\delta t). \quad (9.3)$$

Here the numbers present at any time t , $N(t)$, is a product of the numbers initially present ($N(0)$) and the proportion surviving through time t ($\exp(-\delta t)$). The survival rate s of equation (9.2) is given by $s = \exp(-\delta)$.

The model is characterized by one parameter for survival, s , and three developmental distributions, one each for the first three stages of flower development (the fourth stage, young fruit, does not require a developmental distribution because it does not proceed to another distinct stage in this model). The developmental distribution for each stage requires estimates for its two parameters μ and σ^2 . The value for δ (and hence s) was estimated by regressing $\log(\text{numbers of flowers})$ against physiological time. The remaining parameters were estimated by application of non-linear least squares to provide an optimal description of the observed numbers of flowers in each of the four categories over time. Details of the technique are given by Bellows, *et al.* (1982).

The model was applied to data from two study sites in 1983, both in Tulare County, California. At each site, several hundred flowers in both the north-east and south-west quadrants of three trees were marked and individually numbered with tags early in the season, before any had developed past the small, spherical stage. Each of these flowers was then monitored twice weekly, and its developmental stage was recorded. Abscission of flowers was also recorded with reference to the original tag numbers. Data were collected for approximately 30 days, until all but a small fraction of the flowers had matured into small fruit. Temperature records were recorded by a thermograph as previously described. The physiological time scale employed the

threshold temperature identified by the model 1 study above and used 10 degree-days as the discrete time step, but the scale was initiated on the first day of sampling. Model 2 thus describes the changes that took place as the flower population developed during the bloom period. The flower populations in the north-east and south-west quadrants of the tree were considered separately for analysis.

Results

MODEL 1: PREDICTING ANTHESIS AND PETAL FALL

The least coefficient of variation was achieved using a threshold temperature of 9.4°C for the accumulation of degree-days. Using this threshold temperature, two dates from which to begin accumulating degree-days were identified, one each for 10% flower opening in the south-west tree quadrant and 75% petal fall in the north-east tree quadrant. Because these days were only three days apart, the parameters of the model were modified, with only a slight loss in accuracy, to provide a single date, 29 January, from which degree-days could be accumulated for both bloom events. Using this date and the 9.4°C threshold temperature, 10% anthesis was predicted at 298 degree-days, and 75% petal fall at 426 degree-days. The mean deviation in days between the date predicted by the model and the observed dates for the several data sets was 0.0 ± 3.5 (SD) for 10% anthesis and 0.6 ± 2.8 for 75% petal fall (Table 9.1). The mean absolute error (the mean deviation without regard to sign) was 2.6 ± 2.2

Table 9.1 RELATIONSHIPS BETWEEN OBSERVED AND PREDICTED BEGINNING AND END OF THE FLOWERING PERIOD IN THE 'WASHINGTON' NAVEL ORANGE IN CALIFORNIA

Site	Year	10% anthesis south-west tree quadrant			75% petal fall north-east tree quadrant		
		Observed (calendar date)	Predicted (calendar date)	Error (days)	Observed (calendar date)	Predicted (calendar date)	Error (days)
Riverside	1981			-	20 April	19 April	- 1
Riverside	1982	12 April	18 April	+ 6	20 April	4 May	+ 4
Riverside	1983	11 April	9 April	- 2	28 April	3 May	+ 5
Riverside	1984	15 March	16 March	+ 1	4 April	2 April	- 2
Riverside	1985	2 April	2 April	0	16 April	14 April	- 2
Lindsay	1983	22 April	22 April	0	13 May	12 May	- 1
Lindcove	1983	20 April	15 April	- 5	9 May	6 May	- 3
Lindcove	1984	31 March	3 April	+ 3	25 April	21 April	- 4
Lindcove	1985	15 April	12 April	- 3	29 April	30 April	0
Fresno	1983	24 April	24 April	0	13 May	15 May	+ 2
Fresno	1984	12 April	19 April	+ 7			
Bailey	1985	15 April	13 April	- 2	29 April	30 April	+ 1
Kern	1985	12 April	10 April	- 2	30 April	27 April	- 3
Proag	1985	15 April	16 April	+ 1	5 May	5 May	0
Sunnyside	1985	16 April	12 April	- 4	3 May	29 April	- 4
Mean error (\pm SD)				0.0 \pm 3.5		- 0.6 \pm 2.8	
Mean absolute error (\pm SD)				2.6 \pm 2.2		2.3 \pm 1.6	
Coefficient of variation (absolute error)				0.5		0.9	

days for anthesis and 2.3 ± 1.6 days for petal fall. The correlation between dates predicted by the model and the dates observed was highly significant for both anthesis and petal fall ($P < 0.0001$). For 10% flower opening in the south-west tree quadrant, the correlation coefficient was $r = 0.94$; for 75% petal fall in the north-east tree quadrant, $r = 0.97$.

MODEL 2: MODELLING FLOWER MATURATION

Survival of inflorescences through the bloom period was high in the two 1983 study sites (Table 9.2). Survival rates varied from 0.980 to 0.991 flowers surviving/flower/10 degree-days. These rates resulted in percentage survival over the bloom period of 63.5 to 86.7%. These rates are much higher than reported for 1982 for a similar location, where survival during the bloom period was 51% (Bellows and Morse, 1986). Survival through the bloom period was generally greater in the north-east quadrant of the trees, although these differences were significant only at the Lindsay site (Table 9.2).

The model described the observed densities of flowers in the four stages well, explaining more than 98% of the variance for each of the four populations (Figure 9.1). In general, the populations were almost entirely in the small, spherical bud stage when the study began. These flowers developed at varying rates into the elongate stage. This distribution of development was perpetuated through the bloom period, contributing to the overlap in occurrence of flowers in each of the four stages as the season progressed. Open blossoms were present for approximately 150 degree-days, equivalent to approximately 17 calendar days. For the model description, 10% anthesis occurred on 25 April (observed date was 22 April), while 75% petal fall occurred on 13 May (observed date was also 13 May).

The model reconstructs for each population the developmental distribution (the proportion of the individuals changing stages distributed over age) for each stage. The distributions for the Lindsay site are shown in Figure 9.2. The south-west quadrant showed slightly quicker development of small, spherical buds into elongate buds as well as slightly quicker development of open flowers into young fruit. Development of elongate buds into open flowers was similar in both quadrants. The slight advancement in development in the south-west quadrant probably reflects the impact of incident radiation on temperature in the tree canopy, possibly accelerating development via slight increases in microclimatic temperature. The developmental distribution of buds (both small and elongate) was somewhat protracted, while the development of open flowers was brief with a very kurtotic distribution. This indicates that there was little variance among flowers in the length of time between opening and

Table 9.2 SURVIVAL RATES AND OVERALL SURVIVAL OF FLOWER POPULATIONS IN THE NORTH-EAST AND SOUTH-WEST QUADRANT OF 'WASHINGTON' NAVEL ORANGE TREES, TULARE CO., CALIFORNIA, 1983

Site	Quadrant	Survival rate (95% confidence limits) (proportion surviving/flower/ 10 degree-days)	Overall survival (%)
Lindsay	NE	0.99381 (0.99138, 0.99625)	86.7
Lindsay	SW	0.98045 (0.97797, 0.98293)	63.5
Lindcove	NE	0.99247 (0.99055, 0.99439)	84.7
Lindcove	SW	0.98934 (0.99147, 0.98722)	79.0

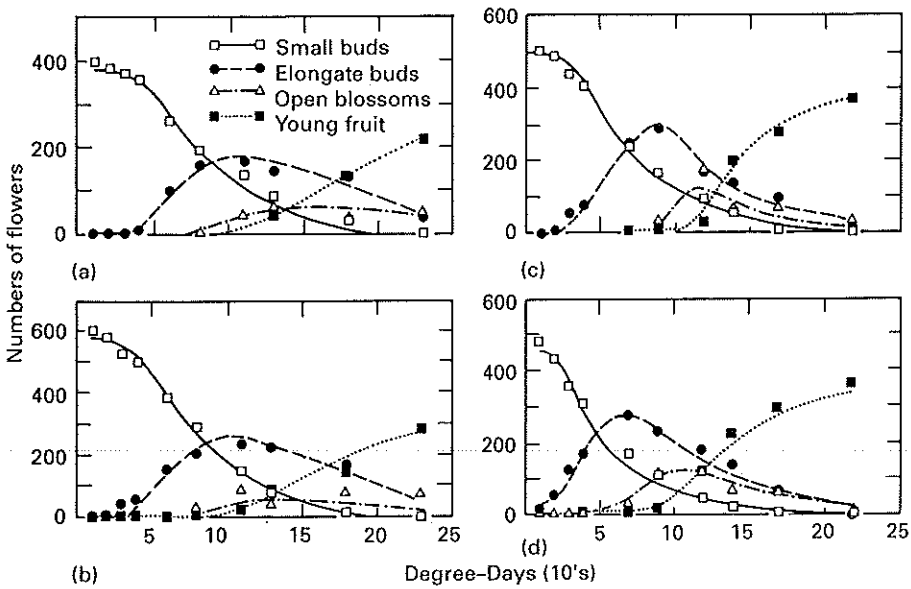


Figure 9.1 Observed (points) and predicted (lines) densities of flowers in four developmental stages: small buds (\square —), elongate buds (\bullet —), open blossoms (\triangle —), and young fruit (\blacksquare —); (a) Lindsay, NE tree quadrant, $R^2 = 0.99$; (b) Lindsay, SW tree quadrant, $R^2 = 0.98$; (c) Lincove, NE tree quadrant, $R^2 = 0.98$; (d) Lincove, SW tree quadrant, $R^2 = 0.98$

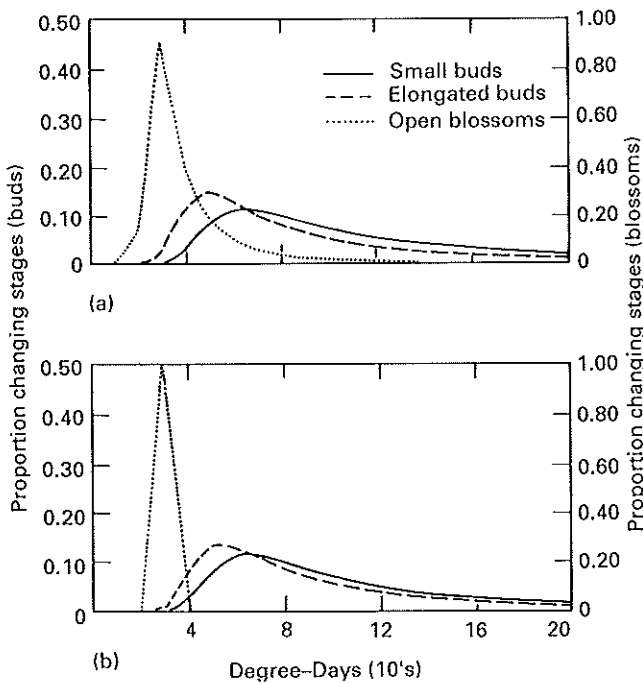


Figure 9.2 Developmental distributions for flowers at Lindsay in the (a) NE and (b) SW tree quadrants. Small buds (—), elongate buds (---), open blossoms (···)

petal fall. The parameters describing these distributions reflect these differences (Table 9.3). The larger values for σ in the south-west quadrant imply an earlier development for distributions with the same mean (Bellows, 1986). The estimated value for σ of zero for the open flower stage in the south-west quadrant effectively groups development into a single time step, reflecting the rapid and relatively invariant development of open blossoms into small fruit.

The model further predicts the numbers entering the various stages each day (Figure 9.3). This figure again indicates earlier development in the south-west

Table 9.3 ESTIMATED VALUES (\pm SE WHERE CALCULABLE) FOR THE PARAMETERS μ AND σ FOR THE DEVELOPMENTAL DISTRIBUTIONS FOR THE LINDSAY SITE (FIGURE 9.2)

Stage	North-east quadrant		South-west quadrant	
	μ	σ	μ	σ
Small bud	0.0	0.1459 \pm 0.0048	0.0	0.1506 \pm 0.006
Elongate bud	0.0	0.2134 \pm 0.0151	0.0	0.1926 \pm 0.0180
Open flower	0.4622 \pm 0.1291	0.3392 \pm 0.4007	0.5	0.0

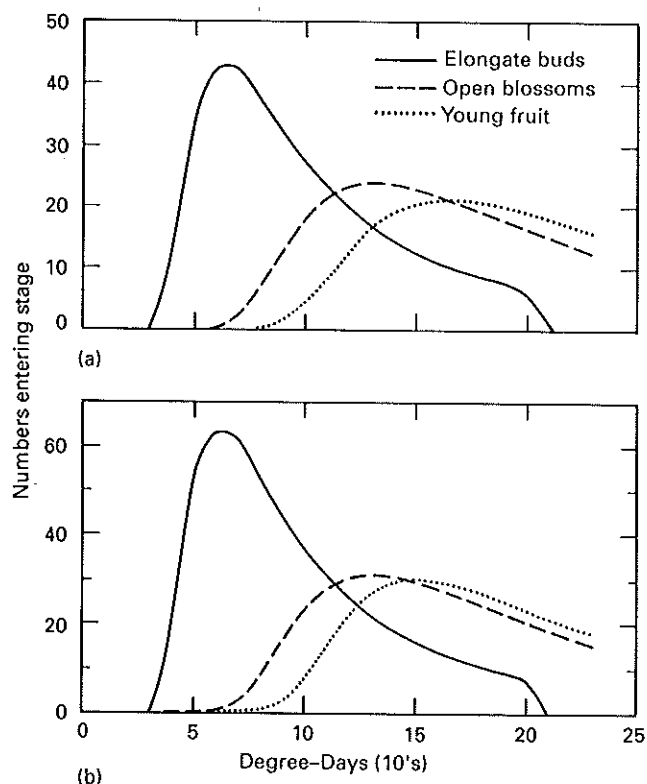


Figure 9.3 Numbers recruited to the elongate bud stage (—), open flowers (---) and young fruit (····) vs. time: (a) Lindsay, NE tree quadrant; (b) Lindsay, SW tree quadrant

Table 9.4 PREDICTED NUMBERS OF FLOWERS ABSCISSING DURING EACH OF FOUR DEVELOPMENTAL STAGES, TULARE COUNTY, CALIFORNIA, 1983

Stage	Numbers abscissing	Proportion of initial population abscissing	Numbers abscissing	Proportion of initial population abscissing
		<i>Lindsay, NE quadrant</i>		<i>Lindsay, SW quadrant</i>
Small buds	20.4	5.4	91.8	15.6
Elongate buds	66.0	17.3	128.1	21.6
Open blossoms	55.0	14.5	45.0	7.6
Young fruit	10.0	2.6	44.3	7.5
		<i>Lindcove, NE quadrant</i>		<i>Lindcove, SW quadrant</i>
Small buds	27.3	5.5	27.6	6.1
Elongate buds	40.4	8.1	55.1	11.3
Open blossoms	23.8	4.8	38.1	7.8
Young fruit	25.3	5.1	32.2	6.6

quadrant, reflected here in each of the later three flower stages (round buds were all present together at the beginning of the study, and hence their recruitment is not distributed over time). The distribution in developmental times of Figure 9.2 results in a considerable spread in the appearance of elongate buds, open flowers, and young fruit.

The total number entering each stage can be used to apportion total losses to the different stages (Table 9.4). Although the population as a whole was subject to a constant survival rate, flowers spent different amounts of time in different stages. Hence, greater proportionate losses generally occurred during the elongate bud stage, a stage with relatively protracted development.

Application to pest–fruit relationships

Citrus thrips, *Scirtothrips citri* (Moulton), is an economic pest on citrus in California mainly in relation to cosmetic scarring of the fruit. In the absence of chemical treatments, severe fruit scarring by citrus thrips averaged 24.4% (range 6.7–67.1) over the period 1972–1985. Because the majority of citrus production in California is directed toward the fresh fruit market with its high cosmetic standards, fruit scarred by citrus thrips are usually downgraded resulting in lower or negative returns.

Citrus thrips overwinter in the egg stage inside citrus leaves, and immatures hatch in mid-March. On navel oranges, the first spring generation feeds on young citrus leaves of the spring foliage flush and the second and third generations feed primarily on the young fruit. The majority of fruit damage by citrus thrips occurs during a six-week 'critical period' after petal fall (Elmer, Brawner and Ewart, 1973). Just after petal fall until approximately three days later, the fruit is unattractive to the thrips. Beginning three days after petal fall, the fruit is especially susceptible to scarring, with declining susceptibility until the fruit is approximately 2.5–5 cm in diameter (Elmer, Brawner and Ewart, 1973; Rhodes, Bartitelle and Morse, 1986). The majority of citrus thrips fruit damage is believed to be caused by the two immature feeding stages, especially the larger second instars (Wiesenborn and Morse, 1986). These two immature stages are usually found under the sepal of the developing fruit and their concentrated feeding in this region causes the typical citrus thrips ring scar at the top

of the fruit (Elmer, Brawner and Ewart, 1973). Adult citrus thrips also feed on the fruit but are believed to cause less economic scarring because their feeding is not concentrated in one area (Wiesenborn and Morse, 1986). Hence the amount of damage caused by citrus thrips populations is related to not only the abundance of thrips in a particular orchard but also to the relative synchrony between development of the young, susceptible fruit and the immature citrus thrips population.

Pesticide treatments to prevent fruit scarring are often applied at petal fall to provide prophylactic protection of the fruit, however, citrus thrips resistance to available chemicals is a major concern, (Morse and Brawner, 1986). In order to improve sampling a citrus thrips model which describes development in terms of degree-days was developed to assist in sampling second and third generation citrus thrips (Morse, Rhodes and Strawn, 1988). Treatments are especially effective when applied just after hatch of the first instar larvae which are difficult to monitor because of their very small size (Grout *et al.*, 1986).

The citrus thrips model (which uses a 14.6°C developmental threshold) may be combined with the model of citrus flower and fruit development (model 2 above, which uses a 9.5°C threshold) to provide a valuable tool to assist in understanding the phenology of thrips-fruit interactions. Growers have long been puzzled by the variability in citrus thrips scarring which can occur from year to year (Morse, Elmer and Brawner, 1986). Better understanding of this interaction and prediction of the

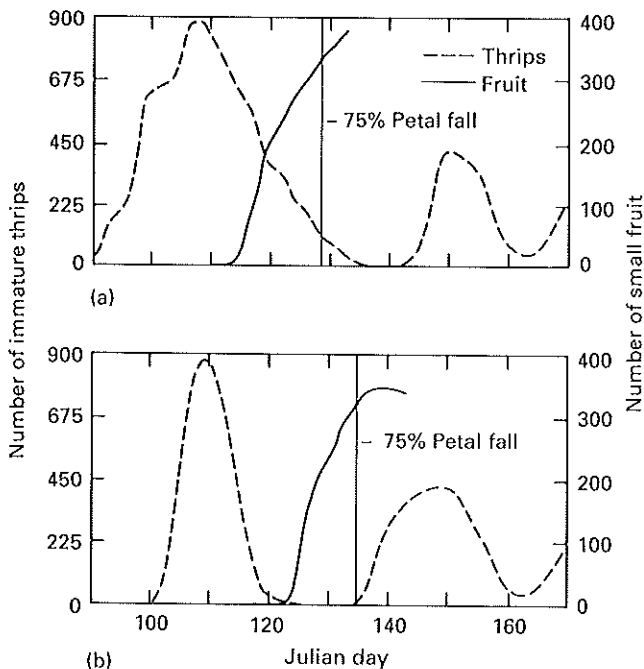


Figure 9.4 Relationship between thrips populations (---) predicted by a model of citrus thrips development and presence of young fruit (—) predicted by model 2: (a) Lindcove, 1983, NW tree quadrant - 75% petal fall occurred on Julian day 128; (b) hypothetical situation for Porterville, California, 1982 - 75% petal fall occurred on Julian day 134

potential amount of fruit scarring in a particular year would greatly assist in better timing field monitoring and treatment programmes.

Figure 9.4a shows the phenology of immature citrus thrips (first and second instars combined) predicted by the citrus thrips model using daily maximum and minimum temperatures (measured on a thermograph placed in a citrus grove in Exeter, California, in 1983). Number of young fruit (e.g., petal fallen flowers) predicted in the north-east quadrant of the tree (from Figure 9.1 above) is presented in the same figure. In this grove, 75% petal fall was predicted on Julian day 128. In the thrips simulation, second generation immatures did not appear until day 142 and not in appreciable numbers until about day 151. Thus, susceptible fruit were present for approximately 20 days (Julian days 131–151) before appreciable numbers of immature thrips were present. The percentage of fruit which suffered severe scarring in an adjacent navel orange grove was 7.8%, a very light amount well below the historical average (Morse, Elmer and Brawner, 1984; Morse and Brawner, 1986).

In contrast, Figure 9.4b shows a hypothetical relationship between citrus thrips phenology and petal fall (the flower population is that reported by Bellows and Morse (1986) for Porterville) which would lead to severe fruit scarring. In this situation, 75% petal fall occurs just prior to hatch of the second generation. Very susceptible 3-day-old fruit would be present just as the number of damaging second immature thrips started to increase.

Interaction of these two models, one for citrus thrips development and one for flower development, is useful primarily in understanding how thrips and fruit phenology may be related. Comparison of actual citrus thrips phenology with degree-day model predictions shows that the model is not entirely accurate and will often predict second generation hatch in advance of the observed event (Rhodes and Morse, unpublished). We hypothesize that foliage quality and abundance during the first citrus thrips generations can slow the rate of development of the first and second generations below that predicted by the degree-day model. Further data are presently being gathered to refine and improve the model.

Discussion

Modelling flower development in citrus plays a relatively specific role in our understanding of this important phase of crop development. The work to date has concentrated on quantifying the timing of events useful primarily in orchard management, but less so in orchard manipulation. The manipulation of fruit set and crop load in citrus is of concern, but so far has remained an unsolved problem.

The approach we have taken in quantifying development to 10% anthesis and 75% petal fall (model 1) is a descriptive one, an approach taken by other workers modelling tree crop development (e.g. Newman *et al.*, 1967; Osawa, Shoemaker and Stedinger, 1983). Such an approach provides a description of events which, in the present case, showed sufficient similarity in different years and locations that description with a fairly simple model provided adequate resolution and precision. It does not, however, incorporate explicitly underlying physiological mechanisms which may affect the timing of flower and young fruit development and retention. Specifically, it has been reported in lemons that vegetative flush follows root flush in a semiannual cycle. If root growth plays a role in the timing of above-ground growth and development, soil temperatures may be implicated as an important environmen-

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