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DEVELOPMENTAL RATE AND NUMBER OF GENERATION ESTIMATES FOR CERATITIS CAPITATA (WIEDEMANN) IN FRUIT GROWING REGIONS OF CALIFORNIA

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Abstract - Phenology models for preoviposition, egg, larval, pupal, egg-adult and adult-adult periods of *Ceratitis capitata* (Wiedemann) were elaborated. Results were compared and contrasted to other presented in the literature. The minimum number of times *C. capitata* generations can occur in a given number of days was then estimated for 11 distinct sites in California fruit growing areas for the period 1992-1993 using observed temperatures for this period and 30 year average temperature data. Although not presently detected in California, this analysis shows that *C. capitata* could survive in all of the fruit growing areas if they were introduced and suitable host plants were present.

Key-words - *Ceratitis capitata*, Medfly, developmental thresholds, phenology,

Introduction

California is the largest agricultural state of the United States, with total farm revenue exceeding $18 billion annually. California also leads the United States in fruit production ranking in the top 3 of states nationally in citrus, grapes, apples, pears, stonefruits (apricots, cherries, nectarines, peaches, plums), strawberries and tomatoes among other fruit crops.
The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) is a multivoltine, poliphagous species, widely considered to be the most harmful fruit pest in tropical and subtropical regions where it occurs because of its high level of adaptability and reproductive potential. Both biotic and abiotic factors influence its developmental and reproductive rates. Specific understanding of the actions of biotic and abiotic factors on the life cycle of *C. capitata* in fruit growing regions is an important goal of their effect on population dynamics (Debouzie, 1989). Among the abiotic factors, temperature likely has the greatest impact on *C. capitata* phenology, directly limiting its development and reproduction and the continuity of its generations (Fletcher, 1989).
C. capitata has been introduced into California and elsewhere in the continental United States on several occasions, and there are numerous studies describing these introductions or speculating on the possibility for its successful establishment (e.g. Messenger and Flitters, 1954; Gjullin, 1931; Cunningham, 1989; Cunningham and Couey, 1986; Mangel *et al.*, 1984). Following its detection, each of these infestations was immediately followed by an eradication effort. In every instance, regulatory officials declared the infestations to be eradicated. Detections of *C. capitata* have occurred more frequently in California since 1975.

These introductions may be due to increased immigration and travel into urban areas of California, where all flies have been detected, although it has been suggested that *C. capitata* may be established in the Los Angeles area (Carey, 1991). In any case, there remains a threat to California's fruit production should *C. capitata* become established in primary fruit growing areas. Recently the University of California inaugurated the Center for Exotic Pest Research to systematize information about present and potential exotic pests of California agriculture and to identify research needs at the state and federal level. An important initial effort of the Center will focus on "surveying current scientific information about *C. capitata* from a worldwide viewpoint and developing a cohesive plan for research directed toward improved methodology for dealing with this vexatious exotic pest of California" (Metcalf, 1995). The influence of temperature on fruit fly growth and survival was among the priorities for research from a California Department of Food and Agriculture perspective (Dowell, 1994).

Comprehensive information about *C. capitata* biology and ecology is necessary to predict its potential distribution and abundance in California (Carey, 1992) and to apply effective biological control programs. A measure of infestation potential is the generation index, or the potential number of generations possible per season that can be calculated using phenology and associated temperature data (Meats, 1989). In this study we estimate the minimum number of generations possible for *C. capitata* assuming this pest was introduced into fruit growing regions of California.

Material and methods

Eleven locations (Figure 1) were selected which represent somewhat distinct areas of California fruit production, all of which had complete records of maximum and minimum temperatures for the period 1965 through 1994 available from the meteorology database of the IMPACT computer system (University of California, 1993). Five of the sites were in the Central Valley (Parlier, Merced, Waterford, Lindsay, Marysville), which comprises the majority of California's fruit production. Four of the sites were in southern California (Santa Ana, Riverside, Santa Paula, Oxnard) and two were in the San Francisco Bay area (Livermore, San Jose). Santa Ana and San Jose are largely urban areas at present and sites of multiple *C. capitata* detections over the past 20 years. Citrus is a major crop grown in the vicinity of Lindsay, Riverside, Santa Paula, and Oxnard. Thirty year average temperatures calculated from the IMPACT database, and actual data from 1992 and 1993 at each location were used for the analysis.

Degree-day accumulations for each developmental stage or period were calculated using the single sine method with a horizontal upper cutoff (Baskerville and Emin 1969) on the IMPACT computer system (University of California, 1993). In Table 1 are presented the lower (T_{min}) and upper (T_{max}) thresholds for each stage or period of *C. capitata* development. Values were obtained using Muñiz & Gil´s method (Muñiz & Gil, 1984).

N	LOCATION	COUNTY
1	Lindsay	Tulare
2	Livermore	Alameda
3	Marysville	Yuba
4	Merced	Merced
5	Oxnard	Ventura
6	Parlier	Fresno
7	Riverside	Riverside
8	San Jose	Santa Clara
9	Santa Ana	Orange
10	Santa Paula	Ventura
11	Waterford	Stanislaus

Fig. 1.- Locations of weather data in California from which *Ceratitis capitata* generation estimates were made

Table 1 Lower and upper development thresholds (°C) for *Ceratitis capitata.*

	Lower	Upper
Preoviposition period	4.544	28.688
Eggs	12.713	36.910
Larvae	12.294	37.605
Pupae	12.564	55.092
Egg-adult	12.486	43.588
Adult-adult	11.975	39.336

If it is satisfied that development can occur, then the number of times (N) that a certain developmental stage or period can occur in a given number of days (d) is

$$N = d/t$$

where t = K/(T-c) is the duration (days) of each developmental stage or period. It follows then, that

$$N = d(T- c)/K = (- dc/K) + dT/K$$

If (dc/K) = a and d/K = b, there is a linear relationship between N and T:

$$N = - a + bT.$$

The accumulated number of times a given developmental period can occur in a given number of days can be calculated by the following expression:

$$N = (1/K) \left(\sum_{i=1}^{i=n} d_i T_i - c \sum_{i=1}^{i=n} d_i \right) \quad (1)$$

We used this formula to estimate the number of *C. capitata* generations that could occur at each of the 11 sites.

Results and discussion

Fletcher (1989) reported other studies of developmental thresholds for *C. capitata* by several authors. Delrio *et al.* (1986) calculated the lower developmental threshold for eggs of *C. capitata* with data in the literature from several authors, applying three different methods to each set of data (thermal summation, linear regression and sigmoid curve). The lower thresholds they calculated varied from 4.5 to 11.6°C. Meats (1989) reported the lower developmental threshold for eggs to be 9.7°C (Fares, 1973; McBride, 1935), for larvae to be

9.7°C (McBride, 1935; Shoukry and Hafez, 1979), and the lower and upper thresholds for pupae to be 13°C and 35°C (Shoukry and Hafez, 1979; El Gazzar, 1979).
Also, the cumulative number of degree-days necessary to complete each immature stage, developmental period and the adult-adult life cycle were calculated from observed and estimated data obtained by MUÑIZ and Gil (1984). These data are presented on Table 2.

Table 2 Degree-day accumulation required for the development of *C. capitata* using observed and estimated data for the duration of each developmental stage or period from Muñiz & Gil (1984).(Figures in parenthesis indicate duration in days of each stage or period).

	OBSERVED DATA					ESTIMATED DATA				
	Temperature (±SEM) (°C)					Temperature (±SEM) (°C)				
	19 ±1	22 ± 1	25 ± 1	28 ± 1	31 ± 1	19 ± 1	22 ± 1	25 ± 1	28 ± 1	31 ± 1
Preov. Period	74.61 (5.16)	60.24 (3.45)	61.38 (3.00)	76.25 (3.25)	72.42 (3.00)	69.55 (4.81)	69.49 (3.98)	69.56 (3.40)	69.68 (2.97)	63.49 (2.63)
Eggs	31.45 (5.00)	27.87 (3.00)	30.73 (2.50)	30.58 (2.00)	36.58 (2.00)	30.76 (4.89)	30.75 (3.31)	30.73 (2.50)	30.73 (2.01)	30.73 (1.68)
Larvae	102.66 (15.30)	92.83 (9.56)	96.72 (7.61)	102.59 (6.53)	117.87 (6.30)	100.58 (14.99)	100.60 (10.36)	100.54 (7.91)	100.54 (6.40)	100.47 (5.37)
Pupae	135.24 (21.00)	132.16 (14.00)	124.40 (10.00)	138.96 (9.00)	247.52 (8.00)	134.21 (20.84)	134.14 (14.21)	134.10 (10.78)	134.17 (8.69)	134.06 (7.27)
Egg-adult	268.93 (41.31)	252.59 (26.56)	251.58 (20.11)	271.90 (17.53)	301.71 (16.30)	265.09 (40.72)	265.14 (27.88)	265.21 (21.20)	265.22 (17.10)	265.25 (14.33)
Adult-adult	326.22 (46.47)	300.70 (30.01)	300.89 (23.11)	332.90 (20.78)	367.09 (19.30)	319.97 (45.58)	320.04 (31.94)	320.03 (24.58)	320.08 (19.98)	320.11 (16.83)

The mean (±SEM) observed and estimated degree-day requirements for development of *C. capitata* calculated from Table 2 (n = 5) are: preoviposition period, 68.98 ± 3.40 and 68.36 ± 1.22; eggs, 31.44 ± 1.42 and 30.74 ± 0.01; larvae, 102.54 ± 4.26 and 100.55 ± 0.02; pupae, 135.66 ± 3.81 and 134.14 ± 0.03; egg-adult period, 269.34 ± 9.09 and 265.18 ± 0.03, and adult-adult period, 325.56 ± 12.27 and 320.05 ± 0.02. These data are very close to those previously reported by Muñiz and Gil (1984).

Differences in *C. capitata* developmental thresholds between authors occasionally leads to different degree-day accumulations for specific life stages or periods. Tassan *et al.*, (1983) obtained a K value of 142.8 degree-days using a lower developmental threshold of 9.7ºC. Messenger and Flitters (1958), using a lower threshold of 11.7 °C and an upper threshold of 35.6°C for eggs in Hawaii, calculated the accumulated degree-days required for eggs to be 29.1, which is very close to our estimation in this study (30.75).

The study of Delrio *et al.* (1986), which resulted in variable lower developmental thresholds, resulted in calculated values for the thermal constant of eggs ranging from 22.4 to 35.9 degree-days.

To be conservative in our estimate of the minimum number of *C. capitata* generations that are possible at the 11 sites, the lowest maximum temperatures for each month were used. The number of generations for each site are calculated using expression (1), with observed temperatures for the period 1992 and 1993 [Tm(1)], and average temperatures [Tm(2)] from 30 years (1965-1994) (Table 3). The minimum number of cumulative generations, through 1992-1993, are shown on Figure 2.

The results show that the decreasing order of sites in terms of minimum number of generations using average temperatures is: Riverside > Lindsay > Santa Paula = Marysville > Merced > Livermore = Oxnard > San Jose > Parlier > Santa Ana = Waterford. These results are based on the assumption that development is not impacted by biotic factors (for example, biological controls are not impacting populations, and suitable fruit hosts are present) and that temperature is the primary abiotic influencing development (assuming lack of winter mortality due to cold conditions or rainfall).

Given our assumptions, it is possible that *C. capitata* could survive and develop in these primary fruit growing areas of California, even where the insect has never been introduced to date. This underscores the significance of this insect should it become introduced into these regions.

More extensive ecological studies would need to be conducted using models which consider other biotic and abiotic factors in order to validate the relative significance of temperature alone as a variable in predicting *C. capitata* development. However, such studies are not possible in California because of the quarantine status of *C. capitata* which requires regulatory agencies to conduct eradication efforts whenever the pest is detected.

Table 3 Lowest maximum temperatures (Tm; ºC) and estimated minimum number (N) of generations (adult-adult) per month of *C. capitata* in 11 California fruit areas. Results were obtained using a minimum threshold of 11.975 and K = 320.05. (1): Estimated were based upon (1): observed temperatures during 1992-1993 and (2): 30 years average temperatures for the period (1965-1994).

		LIVERMOR.C				PARLIER.A				MERCED.C				STA-ANA.A			
Month		Tm 1992	N	Tm 1993	N	Tm 1992	N	Tm 1993	N	Tm 1992	N	Tm 1993	N	Tm 1992	N	Tm 1993	N
Jan	(1)	2.8	0	4.4	0	3.3	0	4.4	0	2.8	0	3.9	0	11.7	0	11.7	0
	(2)	12.2	0	12.2	0	-	-	-	-	10.0	0	10.0	0	-	-	-	-
Feb	(1)	11.1	0	7.8	0	10.6	0	13.9	0.2	14.4	0.2	12.2	0	12.8	0.1	12.8	0.1
	(2)	15.0	0.3	15.0	0.3	-	-	-	-	13.9	0.2	13.9	0.2	-		-	-
Mar	(1)	14.4	0.2	12.2	0	15.6	0.4	13.9	0.2	16.7	0.5	14.4	0.2	15.6	0.4	15.0	0.3
	(2)	16.1	0.4	16.1	0.4	-	-	-	-	17.2	0.5	17.2	0.5	-	-	-	-
Apr	(1)	19.4	0.7	17.2	0.5	21.1	0.9	18.3	0.6	21.1	0.9	18.3	0.6	18.3	0.6	17.8	0.5
	(2)	18.9	0.6	18.9	0.6	-	-	-	-	20.6	0.8	20.6	0.8	-	-	-	-
May	(1)	23.3	1.1	19.4	0.7	25.6	1.3	21.7	0.9	26.7	1.4	23.3	1.1	19.4	0.7	18.3	0.6
	(2)	22.8	1.0	22.8	1.0	-	-	-	-	24.4	1.2	24.4	1.2	-	-	-	-
Jun	(1)	20.6	0.8	18.3	0.6	23.3	1.1	18.9	0.6	25.0	1.2	23.3	1.1	19.4	0.7	17.2	0.5
	(2)	26.1	1.3	26.1	1.3	-	-	-	-	30.6	1.7	30.6	1.7	-	-	-	-
Jul	(1)	23.3	1.2	25.0	1.3	27.8	1.5	28.9	1.6	30.0	1.7	31.7	1.9	23.3	1.1	22.2	1.0
	(2)	30.0	1.7	30.0	1.7	-	-	-	-	34.4	2.2	33.9	2.1	-	-	-	-
Aug	(1)	23.9	1.2	23.3	1.1	27.8	1.5	28.9	1.6	32.2	1.9	30.0	1.7	23.8	1.1	22.8	1.0
	(2)	30.0	1.7	30.0	1.7	-	-	-	-	33.3	2.0	33.3	2.1	-	-	-	-
Sep	(1)	22.8	1.0	20.6	0.8	26.1	1.3	22.2	1.0	29.4	1.6	26.7	1.4	24.4	1.2	19.4	0.7
	(2)	28.3	1.5	28.3	1.5	-	-	-	-	30.0	1.7	30.0	1.7	-	-	-	-
Oct	(1)	16.1	0.4	17.8	0.6	17.2	0.5	21.1	0.9	18.9	0.7	22.8	1.0	18.9	0.7	20.0	0.8
	(2)	21.7	0.9	21.7	0.9	-	-	-	-	22.2	1.0	22.2	1.0	-	-	-	-
Nov	(1)	11.7	0	11.7	0	13.3	0.1	12.2	0	13.9	0.2	13.9	0.2	18.9	0.6	16.7	0.4
	(2)	15.0	0.3	15.0	0.3	-	-	-	-	15.0	0.3	15.6	0.3	-	-	-	-
Dec	(1)	5.0	0	5.0	0	2.2	0	2.2	0	5.0	0	5.0	0	15.0	0.3	15.0	0.3
	(2)	12.2	0	12.2	0	-	-	-	-	11.1	0	11.1	0	-	-	-	-

Table 3 (Cont.)

		SANJOSE.C				RIVRSIDE.C				STAPAULA.C				WATRFORD.T			
		Tm		Tm		Tm		Tm		Tm		Tm		Tm		Tm	
Month		1992	N	1993	N	1992	N	1993	N	1992	N	1993	N	1992	N	1993	N
Jan	(1)	8.9	0	6.7	0	10.6	0	11.1	0	15.0	0.3	12.2	0	2.2	0	2.2	0
	(2)	12.8	0.1	12.8	0.1	17.2	0.5	17.2	0.5	18.3	0.6	18.3	0.6	-	-	-	-
Feb	(1)	12.8	0.1	10.6	0	11.1	0	11.7	0	14.4	0.2	14.4	0.2	10.0	0	7.8	0
	(2)	15.6	0.3	15.6	0.3	18.3	0.6	18.3	0.6	18.9	0.6	18.9	0.6	-	-	-	-
Mar	(1)	13.9	0.2	13.9	0.2	15.0	0.3	13.9	0.2	15.6	0.4	16.7	0.5	14.4	0.2	13.9	0.2
	(2)	16.1	0.4	16.1	0.4	18.3	0.6	18.3	0.6	19.4	0.7	19.4	0.7	-	-	-	-
Apr	(1)	18.9	0.6	17.8	0.5	18.9	0.6	18.9	0.6	20.0	0.8	20.0	0.8	17.8	0.5	16.7	0.4
	(2)	18.9	0.6	18.9	0.6	21.1	0.9	21.1	0.9	21.7	0.9	21.7	0.9	-	-	-	-
May	(1)	21.7	0.9	20.0	0.8	21.7	0.9	21.7	0.9	21.7	0.9	20.6	0.8	25.0	1.3	21.1	0.9
	(2)	21.7	0.9	21.7	0.9	22.8	1.0	22.8	1.0	21.7	0.9	21.7	0.9	-	-	-	-
Jun	(1)	20.6	0.8	17.8	0.5	21.1	0.9	16.7	0.4	21.1	0.9	19.4	0.7	20.0	0.8	15.6	0.3
	(2)	23.9	1.1	23.9	1.1	27.2	1.4	26.7	1.4	23.3	1.1	22.8	1.0	-	-	-	-
Jul	(1)	24.4	1.2	24.4	1.2	25.6	1.3	26.7	1.4	24.4	1.2	23.9	1.2	26.7	1.4	28.3	1.6
	(2)	26.7	1.4	26.7	1.4	33.3	2.1	32.8	2.0	26.1	1.4	26.1	1.4	-	-	-	-
Aug	(1)	26.7	1.4	22.8	1.0	26.7	1.4	27.8	1.5	25.6	1.3	23.9	1.2	26.7	1.4	26.7	1.4
	(2)	26.7	1.4	26.7	1.4	32.2	2.0	32.2	2.0	26.7	1.4	26.7	1.4	-	-	-	-
Sep	(1)	23.9	1.1	19.4	1.1	27.8	1.5	22.8	1.0	24.4	1.2	22.8	1.0	25.0	1.2	25.0	1.2
	(2)	25.6	1.3	25.6	1.3	28.3	1.5	28.3	1.5	25.6	1.3	25.6	1.3	-	-	-	-
Oct	(1)	17.2	0.5	19.4	0.7	17.2	0.5	21.7	0.9	22.2	1.0	22.8	1.0	15.0	0.3	20.0	0.8
	(2)	20.6	0.8	20.6	0.8	25.0	1.3	25.0	1.3	23.9	1.2	23.9	1.2	-	-	-	-
Nov	(1)	13.9	0.2	15.6	0.3	17.8	0.5	19.4	0.7	20.6	0.8	20.0	0.8	12.2	0	12.2	0
	(2)	15.6	0.3	15.6	0.3	19.4	0.7	19.4	0.7	20.0	0.8	20.0	0.8	-	-	-	-
Dec	(1)	10.0	0	12.8	0.1	11.1	0	17.2	0.5	15.0	0.3	17.8	0.6	2.0	0	2.0	0
	(2)	12.8	0.1	12.8	0.1	17.2	0.5	17.2	0.5	17.8	0.6	17.8	0.6	-	-	-	-

Table 3 (Cont.)

		LINDSAY.C				OXNARD.C				MARYSVLE.C			
Month		Tm 1992	N	Tm 1993	N	Tm 1992	N	Tm 1993	N	Tm 1992	N	Tm 1993	N
Jan	(1)	5.0	0	6.7	0	11.1	0	11.1	0	2.8	0	6.1	0
	(2)	11.1	0	11.1	0	17.8	0.6	17.8	0.6	10.0	0	10.0	0
Feb	(1)	13.9	0.2	12.8	0.1	14.4	0.2	14.4	0.2	12.8	0	11.7	0
	(2)	14.4	0.2	14.4	0.2	18.3	0.6	18.3	0.6	13.9	0.2	13.9	0.2
Mar	(1)	14.4	0.2	14.4	0.2	14.4	0.2	14.4	0.2	13.9	0.2	13.9	0.2
	(2)	17.8	0.6	17.8	0.6	17.8	0.6	17.8	0.6	16.7	0.5	16.7	0.5
Apr	(1)	23.3	1.1	18.3	0.6	18.3	0.6	17.2	0.5	16.1	0.4	16.7	0.4
	(2)	21.7	0.9	21.7	0.9	18.9	0.6	18.9	0.6	21.1	0.9	25.0	1.2
May	(1)	26.7	1.4	24.4	1.2	18.9	0.7	17.8	0.6	27.2	1.5	21.7	0.9
	(2)	26.1	1.4	26.1	1.4	20.0	0.8	20.0	0.8	25.0	1.3	25.0	1.3
Jun	(1)	23.9	1.1	21.7	0.9	18.3	0.6	18.3	0.6	22.2	1.0	16.7	0.4
	(2)	31.1	1.8	31.1	1.8	20.6	0.8	20.6	0.8	30.0	1.7	29.4	1.6
Jul	(1)	28.9	1.6	30.6	1.8	20.6	0.8	21.7	0.9	33.9	2.1	30.6	1.8
	(2)	35.0	2.2	35.0	2.2	22.8	1.0	22.8	1.0	33.9	2.1	33.3	2.1
Aug	(1)	30.6	1.8	30.0	1.7	22.2	1.0	21.1	0.9	26.7	1.4	27.8	1.5
	(2)	33.9	2.1	34.4	2.2	23.9	1.2	23.9	1.2	32.2	2.0	32.2	2.0
Sep	(1)	29.4	1.6	26.7	1.4	21.1	0.9	21.1	0.9	28.3	1.5	24.4	1.2
	(2)	30.0	1.7	30.0	1.7	23.3	1.1	23.3	1.1	29.4	1.6	29.4	1.6
Oct	(1)	18.9	0.7	21.1	0.9	18.9	0.7	20,0	0.8	18.3	0.6	19.4	0.7
	(2)	22.8	1.0	22.8	1.0	22.2	1.0	22.2	1.0	21.1	0.9	21.1	0.9
Nov	(1)	12.2	0	15.6	0.3	18.3	0.6	19.4	0.7	11.7	0	13.9	0.2
	(2)	15.6	0.3	15.6	0.3	19.4	0.7	19.4	0.7	13.9	0.2	13.9	0.2
Dec	(1)	11.7	0	11.7	0	13.9	0.2	17.8	0.6	11.7	0	10.6	0
	(2)	11.7	0	11.7	0	17.8	0.6	17.8	0.6	10.6	0	10.6	0

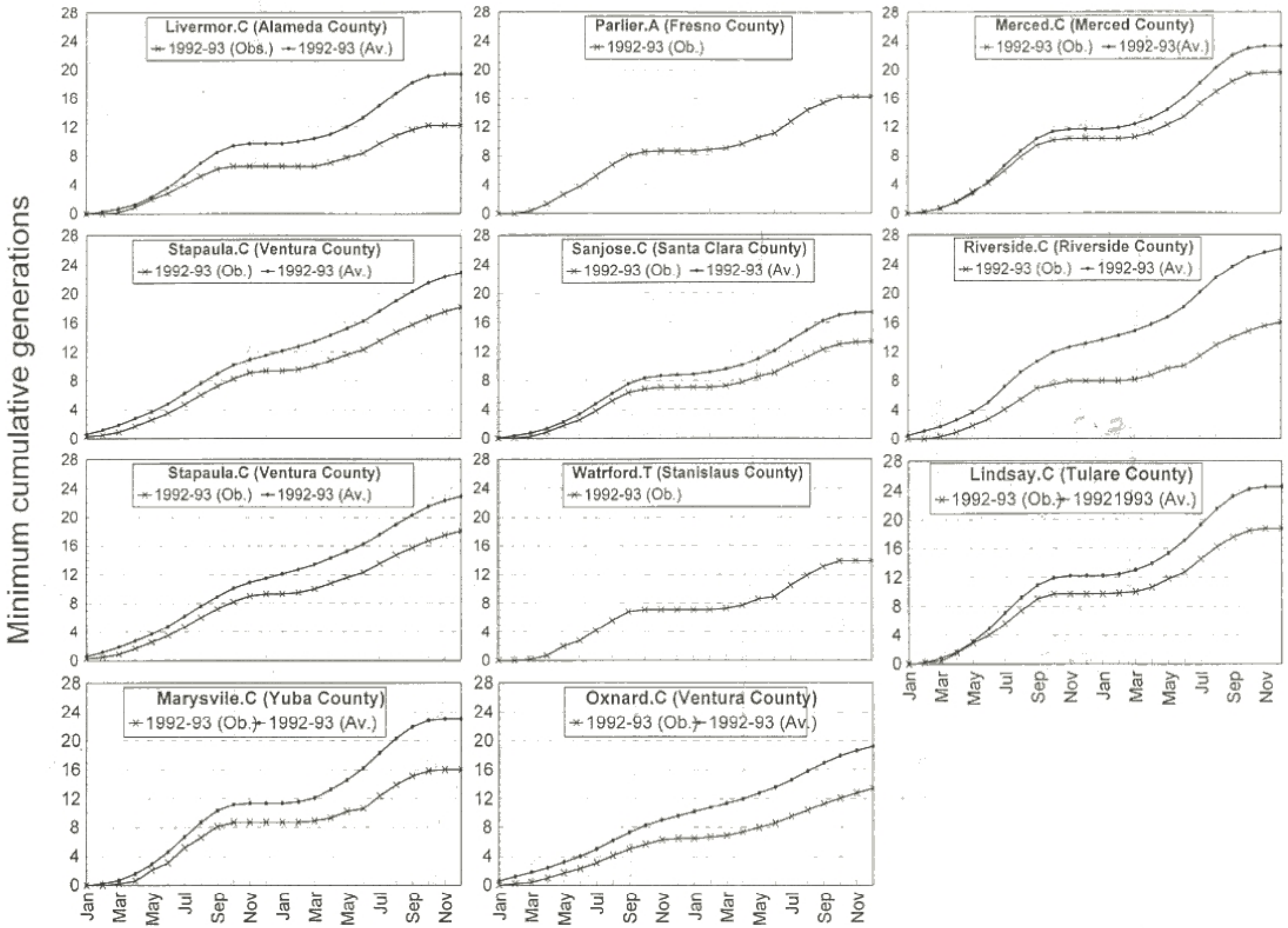

Fig. 2.- Minimum number of cumulative generations of *Ceratitis capitata* in different fruit production regions of California through 1992-1993, based on observed and average temperature data.

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