FLOWERING AND FRUIT–SETTING PATTERNS OF COCOA TREES (*Theobroma cacao* L.) (STERCULIACEAE) AT THREE LOCALITIES IN COSTA RICA[1] /

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Resumen

El patrón mensual de floración y llenado del fruto de un amplio número de árboles de cacao, Theobroma cacao *L. (Sterculiaceae) se estudió en tres sitios del Bosque Tropical Húmedo de Costa Rica. Los sitios diferían en su grado de estacionalidad, con un período seco corto normalmente entre enero y marzo. Los árboles de cacao seleccionados se encontraban bajo diversos tipos de sombra. En los tres sitios, sin importar la sombra, se encontró un descenso en la floración cerca del final de la estación lluviosa, cuando la precipitación fue muy alta. Dependiendo de la respuesta de los árboles de sombra a la sequía, la producción de nuevas flores de cacao varió de mes a mes. La floración y el llenado de frutos varió entre árboles mensualmente en todos los sitios, dificultando la cuantificación del patrón estacional y enfatizando el valor de interpretación cualitativa de los datos relacionados con la floración y el llenado de frutos. Cuando la cantidad de sombra se redujo por caída natural de hojas al final de la estación seca, la fluctuación en la producción de flores se incrementó en la siguiente estación lluviosa. En dos sitios se notó un pico alto de llenado de frutos coincidiendo con la elevada floración de la primera mitad de la estación lluviosa. En todos los sitios se presentaron varios picos de floración y llenado de fruto. La interpretación de los diferentes niveles de llenado de fruto depende del efecto de los factores climáticos sobre las poblaciones de insectos polinizadores en los diferentes sitios. La incidencia de la* Monilia *en los frutos aumentó durante los períodos de buen llenado de frutos y desapareció durante otros períodos del año.*

Introduction

Seasonal cycles of rainfall in the tropics constitute a major force shaping the annual phenological patterns of flowering and fruiting in tropical trees (4, 10, 15, 17, 18, 19, 23). The tree species *Theobroma cacao* L. (Sterculiaceae) "Cacao" or "Cocoa", exhibits marked differences in flowering and fruit-set under widely varying regimes of rainfall, temperature, and humidity both in the field and in the laboratory (21, 22). Changes in photoperiod and temperature interact in complex ways to regulate such phenological patterns in tropical plants (12, 17, 19, 21). The description of flowering and fruit-setting patterns in cocoa under different naturally-occurring regimes of climate is a major prerequisite to understanding the adaptive significance of energy allocation in plants and the role of synchronous flowering on fitness in plant populations (2, 13, 27). This paper report such patterns for cocoa trees at three localities in Costa Rica.

Study sites and methods

Mature cocoa trees, with established histories of flowering and fruit production were studied at the following three localities in Costa Rica: (1) "La Tirimbina", within 10 km of La Virgen (10°23'N, 84°07'W; 220 m elev.), Heredia Province; (2)

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"CATIE" within 3 km of Turrialba (9°54'N, 83°41'W; 602 m elev.), Cartago Province; (3) "La Lola", within 15 km of Siquirres (10°06'N, 83°30'W; 50 m elev.), Limon Province. The "La Tirimbina" locality is within Premontane Tropical Wet Forest, "CATIE" within Lower Montane Tropical Wet Forest, and "La Lola" within Lowland Tropical Wet Forest (11).

At La Tirimbina, two separate cacao farms, "El Uno" and "La Tigra", were studied. One of these (La Tigra) had a broken canopy of advanced secondary growth forest, best described as a sunny habitat with natural canopy. The other plantation (El Uno) had a uniform canopy of *Hevea brasiliensis* rubber trees, and is described as a *Hevea* shaded habitat. At CATIE, the canopy over the cocoa is a mix of planted and naturally-occurring shade trees, and is best described as a "partly shaded habitat". Two cocoa farms at La Lola were studied. One of these, "Area A" consists of a dense uniform shade cover of predominantly *Erythrina* trees, while the other, "Area B", consists of a very broken, disjunct canopy over the cocoa. These areas are considered as "shaded" and "sunny" habitats, respectively. The flowering and fruit-setting patterns of individual cocoa trees were studied in each of these farms as a means of comparing the relative effects of shade cover on these phenologies. Further descriptions of the El Uno and La Tigra farms are given in Young (32, 33) and for La Lola in Trojer (29) and Young (34).

The cocoa trees chosen for study at La Lola were the variety "UF-29", a self-compatible clone that grows well under a variety of conditions. At CATIE, the self-compatible variety "Catongo", with many characteristics similar to UF-29, was chosen. At La Tirimbina, the cocoa trees were of mixed varieties, planted from the same seed stocks in both farms. The trees in all three localities were between 20 and 30 years old.

A series of 20 randomly chosen trees were marked with small yellow plastic tags, each with a code number, in the El Uno farm and a second set of 20 in the La Tigra farm. A total of 52 trees were marked in the same manner in the CATIE farm and 40 trees each in the two areas of the La Lola farm. A monthly census of new flower buds, open flowers, and new fruit (cherelles) was taken for each tagged tree individually in all farms. The census period at El Uno and La Tigra was August 1978 through June 1981; at La Lola it was June 1980 through January 1982. In addition, three sets of 68 tagged trees at La Tigra were sampled in the same manner from July 1980 to June 1981. Two of the three additional sets of tagged trees were located within a few meters of each other and labeled the "A and B series", while the third set was situated further away from these trees. These additional trees provided an expanded sample of trees in different sub-areas of the La Tigra habitat. These census periods provided a representative sampling of phenological patterns during both wet and dry periods at each locality. One trained worker did all of the sampling at El Uno and La Tigra, and a second trained worker did all of the sampling at CATIE and La Lola. For each area at each locality studied, all of the trees were sampled on the same day, and at about the same time each month. All sampling usually took place between 8:00 am and 1:00 pm.

A census of a tagged trees was accomplished by counting all of the buds, open flowers, and young fruit on each tree. When such a count was completed on a given date, the young fruit (cherelles) were removed and discarded. Thus "young fruit" samples consisted of cocoa pods thirty days or less in age in all samples. The census of such pods was considered to be an adequate measure of fruit-set since even diseased pods within this time interval remain on the tree and can be easily counted. Because fruits represent a carbohydrate-rich physiological "sink" for plant species (1), one that removes a major source of nutrients that would otherwise be available for production of leaves and flowers, the removal of fruits in this study represents a source of bias in the data on levels of flower production. At the La Lola cocoa farms studied, the numbers of young fruit bearing signs of the fungal disease *Monilia roreri* were also recorded, providing information on changes in level of infestation at different times of the year. Symptoms of this disease are readily discerned on infected pods in the field (7). Cherelle wilt was not recorded.

Climatic data were obtained either from CATIE (for both CATIE and La Lola) or courtesy of Dr. J. Robert Hunter for La Tirimbina.

Results

During the census period, the La Tigra cocoa trees sampled produced a total of 126 308 flowers (buds and open flowers combined) and 1 789 new (young) fruit; the El Uno trees during the same period produced 20 473 flowers and 1 247 new fruit. Although flower production was more than six times greater in La Tigra, the levels of fruit production between the two farms were very similar, differing only by about 500 fruit. This production spanned a period of 29 months. The 19-month census period at La Lola yielded a total of 96 933 flowers for both Areas A and B combined, and a total of 26 531 new fruit. The sunny habitat, Area B, produced 55 020 flowers and 13 746 new fruit, while the shaded habitat, Area A, produced 41 913 flowers and 12 785 new fruit during the same period. Even though the sample of trees studied was larger for La Lola than for La Tirimbina (80 and 56 trees, resp.), flower production for all trees studied at La Lola was considerably lower than at the latter locality. The reverse was true for production of new fruit. For the 52 cocoa trees censused at CATIE, a total of 40 684 flowers were counted, and a total of 4 571 new fruit were produced during the 19-month census period. Even though total flower production was slightly less than half that at La Lola for a comparable number of trees, fruit production was proportionately much lower at CATIE than at La Lola for the same time period. As an indication of the effect of shade cover on flowering, a comparison of the March 1982 dry period census of flowers between the shaded and sunny habitats at La Lola reveals considerable difference: 16 735 flowers (418.37 ± 205.13, N = 40) were counted in Area A (shaded habitat) and only 6 246 flowers (156.15 ± 113.43, N = 40) in the sunny habitat (Area B) on the same day (11 March, 1982 at 4:00 pm).

Tables 1 through 5 summarize the monthly abundances of flowers and new fruit on trees at each locality, and for different cocoa habitats within some localities (La Tirimbina and La Lola). There is a tremendous amount of intertree variation in the numbers of flowers and fruit each month for a given habitat (Tables 1 to 5). Furthermore, the distribution of flowers and fruit vary considerably from month at each locality. These data are characterized further by extremely large standard deviations (at times equal to the average), reflecting a great amount of biological variability in these parameters and tree reproductive behavior, and making it very difficult to determine month-to-month patterns associated with changes in local climatic conditions. At best, the data are examined within the context of tropical

Table 1. Monthly mean abundances of flower buds, open flowers, and new fruit on twenty-eight mature cocoa trees (*Theobroma cacao* L.) in the El Uno cocoa farm in northeastern Costa Rica, August 1978 through January 1981.

Date	Flower buds $\bar{X}$ ± S.D.	Open flowers $\bar{X}$ ± S.D.	Total $\bar{X}$ ± S.D.	New fruit $\bar{X}$ ± S.D.
8 Aug. 1978	8.46 ± 18.65	3.32 ± 6.62	11.78 ± 25.33	1.71 ± 2.85
30 Sept.	1.64 ± 3.71	0.50 ± 1.26	2.14 ± 4.97	0.60 ± 1.28
30 Oct.	1.03 ± 3.86	0.21 ± 0.78	1.24 ± 4.64	0.21 ± 0.49
30 Nov.	1.60 ± 5.90	0.75 ± 2.90	2.35 ± 8.80	0.10 ± 0.41
15 Dec.	2.06 ± 4.91	1.06 ± 3.04	3.12 ± 7.95	0.41 ± 0.98
15 Jan. 1979	3.24 ± 7.40	1.34 ± 3.21	4.58 ± 10.61	0.93 ± 4.07
15 Feb.	6.78 ± 13.63	4.14 ± 8.27	10.92 ± 21.90	0.57 ± 1.10
17 March	20.44 ± 20.79	7.13 ± 8.90	27.57 ± 29.69	1.17 ± 4.65
16 April	58.10 ± 63.69	26.96 ± 30.60	85.06 ± 94.29	1.41 ± 1.88
15 May	43.17 ± 62.72	27.72 ± 45.70	70.89 ± 108.42	1.48 ± 2.06
15 June	5.14 ± 10.92	2.25 ± 5.80	7.39 ± 16.72	0.35 ± 0.98
18 July	23.24 ± 35.53	10.10 ± 19.43	33.34 ± 54.96	0.75 ± 1.26
17 Aug.	24.89 ± 32.87	19.14 ± 29.41	44.03 ± 62.28	0.50 ± 1.20
17 Sept.	42.32 ± 63.61	27.07 ± 41.73	69.39 ± 105.34	0.60 ± 1.34
16 Oct.	17.42 ± 37.77	10.29 ± 19.50	27.71 ± 57.27	0.67 ± 0.88
19 Nov.	7.36 ± 15.80	3.79 ± 7.57	11.15 ± 23.57	0.92 ± 1.46
17 Dec.	7.46 ± 13.23	3.89 ± 5.45	11.35 ± 18.68	0.10 ± 0.55
17 Jan. 1980	17.74 ± 11.46	6.68 ± 10.92	24.42 ± 22.38	0.35 ± 0.81
16 Feb.	18.04 ± 33.65	12.39 ± 25.09	30.43 ± 58.74	0.25 ± 0.63
25 March	6.89 ± 25.20	3.46 ± 13.89	10.35 ± 39.09	0.10 ± 0.40
11 April	9.39 ± 16.64	5.68 ± 10.96	15.07 ± 27.60	0.37 ± 0.80
12 May	8.46 ± 18.57	3.46 ± 7.69	11.92 ± 26.26	0.14 ± 0.58
15 June	13.53 ± 29.12	7.00 ± 16.89	20.54 ± 46.01	0.21 ± 0.61
15 Aug.	21.57 ± 37.54	11.46 ± 22.45	33.03 ± 59.99	0.39 ± 1.01
15 Sept.	28.29 ± 46.95	15.50 ± 27.92	43.79 ± 74.87	0.25 ± 0.57
16 Oct.	28.18 ± 43.90	13.89 ± 22.84	42.07 ± 66.74	0.53 ± 0.86
15 Nov.	17.89 ± 32.98	8.57 ± 20.92	24.23 ± 28.01	0.57 ± 1.14
16 Dec.	10.60 ± 18.31	5.71 ± 10.78	16.32 ± 29.02	0.28 ± 0.64
13 Jan. 1981	19.46 ± 37.98	11.00 ± 25.00	30.46 ± 62.98	0.39 ± 0.85

seasonality in terms of those periods of marked increase or decrease in flowering and fruit-set, that is, a qualitative phenological pattern, rather than by quantitative changes. The extreme variability of these data precludes any meaningful interpretation of possible correlations between flowering and climatic factors in a quantitative sense. Since the beginnings and end points of these data sets are different in some cases, the data are not entirely comparable. Yet when the sample size of trees censused is enlarged, as done for La Tigra cocoa, the same patterns are seen in the expanded data (Tables 6 and 7), indicating that the sample sizes used provide an adequate representation of phenological patterns.

The monthly distribution of flowering is markedly different between El Uno and La Tigra cocoa farms (Figure 1) in relation to the rainfall regime of this locality. In La Tigra, the farm with the broken canopy of native tree species, flower production fluctuates regularly over relatively short periods (1-2 months), with the most noticeable declines in flowering occurring in short periods of reduced rainfall of varying intensity (Figure 1). The trees in this partly sunny and shaded habitat appear to be acclimatized to the prevailing climatic conditions. In marked contrast, flower production fluctuates much more markedly over larger intervals at the nearby El Uno farm (Figure 1). Peaks in flower

Table 2. **Monthly mean abundances of flower buds, open flowers, and new fruit on twenty-eight mature cocoa trees (*Theobroma cacao* L.) in the La Tigra cocoa farm in northeastern Costa Rica, August 1978 through January 1981.**

Date	Flower buds $\bar{X}$ ± S.D.	Open flowers $\bar{X}$ ± S.D.	Total $\bar{X}$ ± S.D.	New Fruit $\bar{X}$ ± S.D.
7 Aug. 1978	138.21 ± 119.01	35.21 ± 48.13	173.42 ± 167.14	0.89 ± 1.95
30 Sept.	148.82 ± 133.11	67.17 ± 56.87	215.19 ± 189.98	0.96 ± 1.45
30 Oct.	55.14 ± 40.85	21.10 ± 17.50	76.24 ± 58.35	0.78 ± 1.34
30 Mar.	103.35 ± 112.11	63.50 ± 69.49	169.85 ± 181.60	0.50 ± 1.03
15 Dec.	79.06 ± 106.07	50.07 ± 71.06	129.13 ± 177.13	1.39 ± 2.57
15 Jan. 1979	78.12 ± 104.20	45.53 ± 64.32	123.74 ± 162.52	0.75 ± 1.60
15 Feb.	66.00 ± 85.53	39.75 ± 55.09	105.75 ± 140.62	1.46 ± 1.91
17 Mar.	100.53 ± 112.36	63.00 ± 87.24	163.53 ± 199.60	1.50 ± 2.16
15 April	93.80 ± 96.78	46.96 ± 56.65	140.76 ± 153.43	2.00 ± 2.25
15 May	74.56 ± 77.63	38.06 ± 51.29	112.62 ± 128.92	1.53 ± 2.23
19 June	110.77 ± 112.00	53.61 ± 67.53	164.38 ± 189.53	0.77 ± 1.35
18 July	90.35 ± 76.39	71.28 ± 57.00	161.63 ± 133.39	0.78 ± 1.13
17 Aug.	133.42 ± 106.43	79.50 ± 69.76	212.92 ± 176.19	1.34 ± 1.81
17 Sept.	74.03 ± 69.41	47.89 ± 48.19	121.92 ± 147.60	1.60 ± 1.89
16 Oct.	171.63 ± 72.18	97.66 ± 50.79	269.29 ± 122.97	2.00 ± 2.04
19 Nov.	41.04 ± 63.70	28.89 ± 48.38	69.93 ± 112.08	1.07 ± 1.64
17 Dec.	128.14 ± 52.01	86.86 ± 41.59	215.00 ± 93.60	2.03 ± 2.11
16 Jan 1980	78.18 ± 93.64	52.61 ± 66.89	130.77 ± 160.53	0.85 ± 1.38
19 Feb.	57.14 ± 86.99	33.68 ± 56.57	90.82 ± 143.56	1.03 ± 1.42
25 March	101.36 ± 143.98	59.75 ± 97.36	161.11 ± 241.25	0.67 ± 1.58
11 April	77.54 ± 87.97	44.18 ± 64.07	121.72 ± 152.04	0.78 ± 1.26
12 May	78.21 ± 64.95	47.21 ± 47.32	125.42 ± 112.27	1.62 ± 1.78
15 June	114.42 ± 123.38	76.14 ± 81.89	190.56 ± 205.27	0.75 ± 1.32
15 Aug.	134.18 ± 77.09	85.86 ± 54.44	220.04 ± 131.53	1.35 ± 1.51
16 Sept	146.61 ± 89.26	90.96 ± 59.80	237.57 ± 149.06	1.28 ± 1.04
16 Oct.	138.89 ± 64.43	83.64 ± 46.05	222.53 ± 110.48	1.42 ± 1.04
15 Nov	53.35 ± 47.94	23.14 ± 21.47	76.49 ± 69.41	1.00 ± 1.16
16 Dec	24.10 ± 58.27	13.28 ± 38.03	37.38 ± 96.30	0.64 ± 1.28
13 Jan. 1981	8.17 ± 34.70	4.82 ± 21.06	12.99 ± 55.76	0.46 ± 0.90
15 Feb.	6.78 ± 21.09	3.46 ± 13.81	10.24 ± 34.90	0.67 ± 1.10
15 March	13.32 ± 27.94	7.42 ± 18.72	20.74 ± 46.66	0.14 ± 0.44
13 April	38.92 ± 66.64	16.53 ± 30.66	55.45 ± 97.30	0.28 ± 0.58
15 May	53.46 ± 62.36	27.21 ± 42.76	80.67 ± 105.12	0.35 ± 0.76
14 June	69.46 ± 80.75	36.75 ± 47.86	106.21 ± 128.61	1.14 ± 1.94

Table 3. Monthly mean abundance of flower buds, open flowers, and new fruit for fifty-two cocoa trees (*Theobroma cacao* L.) in the CATIE cocoa farm at Turrialba, Cartago Province, Costa Rica, June 1980 through January 1982.

Date	Flower buds $\overline{X} \pm$ S.D.	Open flowers $\overline{X} \pm$ S.D.	Total $\overline{X} \pm$ S.D.	New Fruit $\overline{X} \pm$ S.D.
27 June 1980	37.30 ± 40.44	5.75 ± 6.84	43.05 ± 46.49	2.05 ± 3.40
29 July	39.00 ± 33.31	15.34 ± 16.85	54.34 ± 48.14	3.82 ± 3.84
29 Aug.	27.98 ± 25.23	8.11 ± 7.40	36.09 ± 31.86	11.65 ± 11.60
3 Oct.	15.46 ± 13.92	5.73 ± 5.61	21.19 ± 19.06	4.40 ± 5.53
8 Nov.	24.01 ± 30.22	6.67 ± 8.17	30.69 ± 37.97	6.01 ± 7.52
6 Dec.	17.75 ± 22.15	6.71 ± 6.25	24.46 ± 27.55	3.94 ± 4.73
10 Jan 1981	5.42 ± 8.59	3.73 ± 5.89	9.15 ± 14.28	2.32 ± 3.75
6 Feb.	3.25 ± 5.69	3.38 ± 5.97	6.63 ± 11.44	1.29 ± 2.21
5 March	3.38 ± 5.85	1.11 ± 1.95	4.50 ± 7.65	1.82 ± 2.97
6 April	19.54 ± 15.03	7.06 ± 15.67	26.59 ± 30.70	1.21 ± 1.96
9 May	45.09 ± 35.74	9.07 ± 6.83	54.17 ± 41.81	2.61 ± 3.20
8 June	77.96 ± 39.20	20.69 ± 12.30	98.65 ± 50.54	4.80 ± 3.11
10 July	61.65 ± 38.78	17.53 ± 12.23	79.19 ± 49.44	7.17 ± 5.61
10 Aug.	52.23 ± 35.92	26.40 ± 20.43	78.63 ± 54.85	4.19 ± 3.48
5 Sept.	38.57 ± 24.71	19.34 ± 13.48	57.92 ± 37.03	4.63 ± 3.53
19 Nov.	29.46 ± 17.64	7.03 ± 4.10	36.50 ± 20.71	8.34 ± 6.51
16 Dec.	19.32 ± 13.19	3.98 ± 5.63	16.57 ± 24.96	2.25 ± 2.17
14 Jan. 1982	12.21 ± 13.31	3.33 ± 3.50	15.71 ± 16.23	3.23 ± 2.33
16 Feb.	27.54 ± 23.50	8.23 ± 7.46	30.43 ± 35.78	5.92 ± 5.32

Table 4. Monthly mean abundance of flower buds, open flowers, and new fruit on forty mature cocoa trees (*Theobroma cacao* L.) in Area A (shaded habitat) of the La Lola cocoa farm, near Siquirres, Limon Province, Costa Rica, June 1980 through January 1982.

Date	Flower buds $\overline{X} \pm$ S.D.	Open flowers $\overline{X} \pm$ S.D.	Total $\overline{X} \pm$ S.D.	New Fruit $\overline{X} \pm$ S.D.
20 June 1980	146.12 ± 92.48	25.30 ± 16.48	170.42 ± 105.76	26.27 ± 18.09
18 July	3.40 ± 5.08	1.25 ± 1.89	4.65 ± 6.41	7.42 ± 6.60
1 Sept.	11.37 ± 13.91	3.05 ± 3.75	14.42 ± 17.18	1.97 ± 2.48
1 Oct.	12.52 ± 14.83	3.95 ± 3.92	16.47 ± 18.33	6.97 ± 5.24
5 Nov.	6.35 ± 7.19	3.75 ± 4.26	10.10 ± 11.05	10.00 ± 12.53
5 Dec.	9.50 ± 9.64	6.47 ± 6.16	15.97 ± 15.16	17.52 ± 16.23
9 Jan 1981	1.80 ± 2.98	0.60 ± 1.80	2.40 ± 3.60	11.35 ± 17.95
3 Feb.	4.00 ± 7.05	1.80 ± 2.98	5.80 ± 9.83	3.15 ± 4.48
8 March	63.25 ± 49.24	20.70 ± 19.18	83.95 ± 64.99	2.67 ± 4.46
10 April	116.52 ± 92.06	29.37 ± 24.76	72.00 ± 80.06	7.20 ± 10.21
7 May	79.70 ± 43.09	46.42 ± 29.37	126.12 ± 71.29	21.10 ± 15.85
4 June	153.07 ± 96.90	55.57 ± 38.20	208.65 ± 132.91	86.07 ± 90.80
9 July	87.50 ± 51.20	27.25 ± 16.97	114.75 ± 67.06	44.87 ± 42.02
10 August	24.10 ± 17.22	7.12 ± 6.36	31.22 ± 22.94	12.47 ± 9.11
3 Sept.	5.60 ± 8.00	2.40 ± 3.50	8.00 ± 11.01	8.57 ± 6.42
20 Oct.	27.77 ± 18.10	9.75 ± 8.57	37.52 ± 25.87	8.45 ± 5.32
24 Nov.	2.45 ± 3.96	1.10 ± 1.56	3.55 ± 5.16	5.65 ± 4.58
15 Dec.	0.30 ± 0.93	0.02 ± 0.15	0.33 ± 0.95	4.75 ± 3.38
13 Jan. 1982	0.15 ± 0.57	0.15 ± 0.57	0.30 ± 1.13	2.25 ± 1.83
15 Feb.	34.67 ± 22.22	12.35 ± 10.55	47.02 ± 32.01	0.52 ± 1.19

Table 5. Monthly mean abundance of flower buds, open flowers, and new fruits on forty mature cocoa trees (*Theobroma cacao* L.) in Area B (sunny habitat) of the La Lola cocoa farm near Siquirres, Limon Province, Costa Rica, June 1980 through January 1982.

Date	Flower buds $\overline{X}$ ± S.D.	Open flowers $\overline{X}$ ± S.D.	Total $\overline{X}$ ± S.D.	New Fruit $\overline{X}$ ± S.D.
20 June 1980	385.121.85	105.62 ± 55.51	491.00 ± 161.54	3.90 ± 3.36
18 July	21.05 ± 20.64	8.57 ± 8.73	29.62 ± 28.21	9.80 ± 7.74
5 Sept.	15.02 ± 13.79	2.55 ± 2.65	17.57 ± 15.91	21.07 ± 18.19
1 Oct.	12.50 ± 13.55	6.02 ± 4.93	18.52 ± 17.37	19.47 ± 17.60
5 Nov.	10.92 ± 8.64	5.20 ± 3.30	16.12 ± 10.89	32.77 ± 23.41
5 Dec.	4.12 ± 6.00	3.25 ± 4.10	7.37 ± 9.90	26.75 ± 20.56
9 Jan. 1981	0.17 ± 0.63	0.20 ± 0.51	0.37 ± 1.05	10.35 ± 6.67
3 Feb.	0.17 ± 1.10	0.05 ± 0.31	0.22 ± 1.42	1.60 ± 2.99
8 March	17.45 ± 25.65	3.85 ± 7.15	21.30 ± 32.08	0.17 ± 0.67
10 April	137.42 ± 81.89	33.37 ± 21.25	170.80 ± 101.94	5.01 ± 12.53
7 May	48.40 ± 31.64	20.57 ± 14.41	68.97 ± 44.02	11.80 ± 15.05
4 June	135.15 ± 104.01	31.20 ± 24.84	166.35 ± 125.81	22.50 ± 21.78
8 July	84.25 ± 79.87	18.95 ± 13.73	103.20 ± 92.34	30.85 ± 29.25
11 Aug.	81.95 ± 67.86	26.07 ± 17.04	108.02 ± 83.61	15.95 ± 12.81
3 Sept.	34.87 ± 14.95	12.07 ± 6.19	46.95 ± 19.37	8.00 ± 5.30
3 Oct	25.45 ± 15.20	8.55 ± 7.05	34.00 ± 20.26	26.85 ± 20.26
24 Nov	19.30 ± 13.44	6.07 ± 5.76	25.37 ± 18.31	22.00 ± 14.80
15 Dec.	0.22 ± 0.76	0.07 ± 0.34	0.30 ± 0.95	6.90 ± 4.18
13 Jan. 1982	0.35 ± 1.02	0.37 ± 1.64	0.72 ± 2.48	4.30 ± 3.61
15 Feb.	22.77 ± 15.06	9.27 ± 4.71	32.05 ± 18.88	3.24 ± 1.05

Table 6. The monthly abundance of flowers and new fruit on an additional twenty-three tagged cocoa trees in the La Tigra cocoa farm in northeastern Costa Rica, July 1980 through June 1981.

Date	Total	Flower buds $\overline{X}$ ± S.D.	Total	Open flowers $\overline{X}$ ± S.D.	Total	Total flowers $\overline{X}$ ± S.D.	Total	New Fruit $\overline{X}$ ± S.D.
30 July 1980	1 621	70.47 ± 70.64	944	41.04 ± 47.41	2 565	111.51 ± 118.05	22	0.95 ± 1.16
30 Aug.	1 662	72.26 ± 64.84	930	40.43 ± 41.31	2 582	112.69 ± 106.15	18	0.78 ± 1.10
30 Sept.	1 063	46.21 ± 46.03	555	24.13 ± 30.42	1 618	70.34 ± 76.45	18	0.78 ± 0.83
30 Oct	1 582	68.78 ± 54.77	753	32.73 ± 30.21	2 335	101.51 ± 84.98	37	1.60 ± 2.12
30 Nov.	959	41.69 ± 53.83	465	20.21 ± 39.80	1 424	61.90 ± 83.63	20	0.86 ± 0.94
30 Dec.	715	31.08 ± 51.13	301	13.08 ± 27.84	1 016	44.16 ± 78.97	29	1.26 ± 1.32
30 Jan. 1981	378	16.43 ± 49.77	244	10.16 ± 33.96	622	26.59 ± 83.73	3	0.13 ± 0.44
25 Feb.	305	13.26 ± 27.08	153	6.65 ± 16.36	458	19.91 ± 43.44	13	0.56 ± 0.87
30 March	26	1.13 ± 4.06	14	0.60 ± 1.63	40	1.73 ± 5.69	4	0.17 ± 0.81
28 April	1 045	45.43 ± 34.00	418	18.17 ± 19.65	1 463	63.60 ± 53.65	7	0.30 ± 0.74
30 May	1 244	54.08 ± 46.16	635	27.60 ± 26.59	1 879	81.68 ± 72.75	3	0.13 ± 0.33
30 June	1 353	58.82 ± 58.16	688	29.91 ± 30.97	2 141	88.73 ± 89.13	11	0.47 ± 0.87
Totals:	11 953		6 100		18 143		185	
$\overline{X}$ ± S.D.	996.08 ± 520.74		508.33 ± 284.53		1511.91 ± 806.15		15.41 ± 10.25	

production coincide with the early and late phases of the lengthy rainy season at this locality, while marked declines in flowering occur immediately following periods of peak abundance Peak abundance periods are short and associated with the rainy season (Figure 1). During the dry periods the *Hevea* canopy drops its leaves, and such periods generally precede a period of intense flowering. Peak abundances in fruit-set also occur in the rainy months in both farms (Figure 1), and fruit production is generally well-distributed over successive months, with the noticeable exception

Table 7. The abundance of flowers and new fruit on two intermixed sets of tagged Cocoa trees (N = 45) on the La Tigra cocoa farm in northeastern Costa Rica over several months (July 1980 – June 1981).

		Flower buds		Open flowers		Total flowers		New Fruit
Date	Total	$\overline{X}$ ± S.D.	Total	$\overline{X}$ ± S.D.	Total	$\overline{X}$ ± S.D.	Total	$\overline{X}$ ± S.D.
				A series-marked trees 1-28				
30 July 1980	1 351	51.96 ± 61 86	760	29.23 ± 36.80	2 111	81.19 ± 98 66	9	0.33 ± 0.72
30 Aug.	1 534	56.81 ± 65.54	805	29.81 ± 34.74	2 339	86.62 ± 100.28	36	1.33 ± 2.44
30 Sept.	826	30.59 ± 36.83	393	14.55 ± 20.52	1 219	45.14 ± 57.35	7	0.25 ± 0.84
30 Oct.	978	36.22 ± 41.03	435	16.11 ± 21.29	1 413	52.33 ± 62.32	18	0.66 ± 1.05
30 Nov.	175	6.48 ± 11.18	87	3.22 ± 8.62	262	9.70 ± 19 80	10	0.37 ± 0.72
30 Dec.	0		0		0		0	
30 Jan. 1981	0		0		0		0	
26 Feb.	49	1 18 ± 4 61	11	0.40 ± 1 89	60	2 21 ± 6.50	9	0 33 ± 0 66
30 March	9	0.33 ± 1.18	2	0.07 ± 0.37	11	0.40 ± 1.55	0	
28 April	97	3.59 ± 6.24	35	1.29 ± 2.96	135	4.88 ± 9.20	5	0.18 ± 0.54
30 May	1 518	56.22 ± 43.65	727	26.92 ± 26 44	2 245	83 14 ± 70.09	8	0.79 ± 0.59
29 June	1 819	67.37 ± 53.73	900	33.33 ± 36.64	2 719	100.70 ± 90.37	5	0.18 ± 0.47
Totals	8 356		4 157		12 513		107	
$\overline{X}$ ± S.D.		696.33 ± 686 42		346.25 ± 350.96		1 042.83 ± 90.37		8 91 ± 0.47
				B series-marked trees 1-17				
30 July 1980	1 460	85.88 ± 81.16	813	47.82 ± 54.94	2 273	133.70 ± 136.10	10	0.58 ± 1.08
30 Aug.	1 243	73.11 ± 77.81	749	46.81 ± 53.90	1 992	119.92 ± 131.71	19	1.11 ± 1.07
30 Sept.	1 560	91.76 ± 93.56	911	53.58 ± 60.15	2 471	145.34 ± 153.67	8	0.47 ± 0.77
30 Oct.	1 732	101.88 ± 85.79	1 083	63.70 ± 71.29	2 815	165.58 ± 158.08	18	1.05 ± 1.16
30 Nov.	78	4.58 ± 8.35	37	2.17 ± 4.99	115	6.75 ± 13.24	6	0.35 ± 0.96
30 Dec.	5	0.29 ± 1.17	3	0.17 ± 0.70	8	0.46 ± 1.87	6	0.35 ± 0.83
30 Jan. 1981	5	0.29 ± 1.17	2	0.11 ± 0 47	7	0.40 ± 1.64	6	0.35 ± 0.83
28 Feb.	35	2.05 ± 4 26	4	0.23 ± 0.94	39	2.28 ± 5.20	5	0.29 ± 1.17
30 March	0		0		0		0	
30 April	24	1.41 ± 3.03	6	0.35 ± 0.82	30	1.76 ± 3.85	0	
30 May	1 430	8.37 ± 69.81	654	40.87 ± 33.52	2 084	130.24 ± 103.33	0	
29 June	1 732	108.25 ± 78.88	930	58.12 ± 46.45	2 662	166.37 ± 125.33	23	1.35 ± 1.84
Totals	9 304		5 192		14 496		101	
$\overline{X}$ ± S.D.		775.33 ± 760.97		432.66 ± 435.16		1 208 ± 1 193.68	8.41 ± 7.42	
overall Totals:	17 660		9 349		27 0009		208	

of November and December. These months are usually very rainy at La Tirimbina, resulting in both a marked decline in flowering and fruit-set (Figures 1 and 2).

Even though climatic conditions behave rather uniformly over the year at Turrialba, with somewhat noticeable peaks in rainfall occurring in the November-December periods, the most intense flowering occurs in the first half of the rainy season (during June-August) (Figure 3). The least productive period coincides or immediately follows the very rainy months of November and December, with such declines very noticeable in relatively dry periods such as January and February at this locality (Figure 3). The phenological pattern of flowering of the "Catongo" cocoa at Turrialba matches more closely the observed pattern of flowering in the shaded cocoa habitat (El Uno) at the La Tirimbina locality (Figures 1 and 3). Both habitats have a well developed shade cover and many of the trees at Turrialba exhibit marked deciduousness in the dry months. Periods of maximum fruit set coincide with those rainy months that have high flowering. In the dry months of January and February are also periods of greatly reduced fruit set at this locality (Figure 4).

Maximal flower production is clearly associated in both areas at La Lola with the period March through September, a uniformly rainy period (Figure 5). Moderate to slight buffering of the dry season (January-February) in terms of sustained flowering

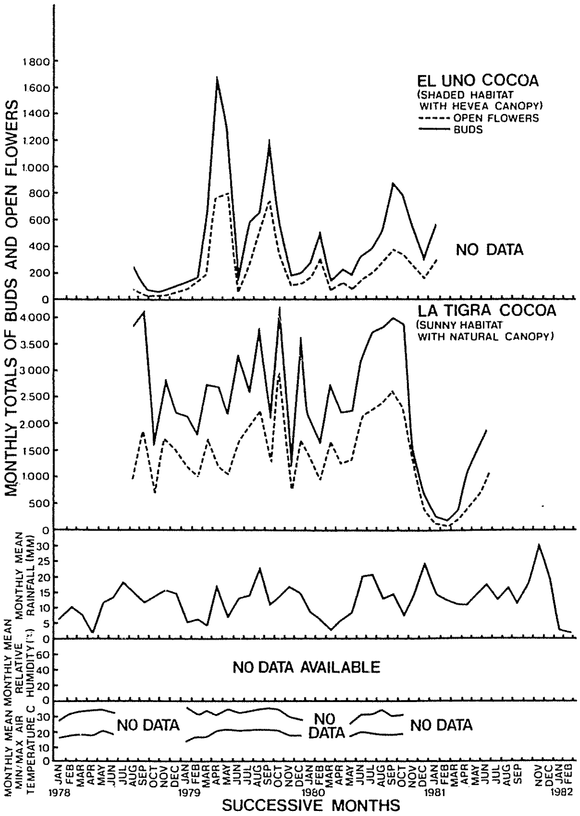

Fig. 1. Phenological patterns in flowering of cocoa trees in relation to local climatic conditions at the El Uno and La Tigra habitats within the La Tirimbina locality in northeastern Costa Rica.

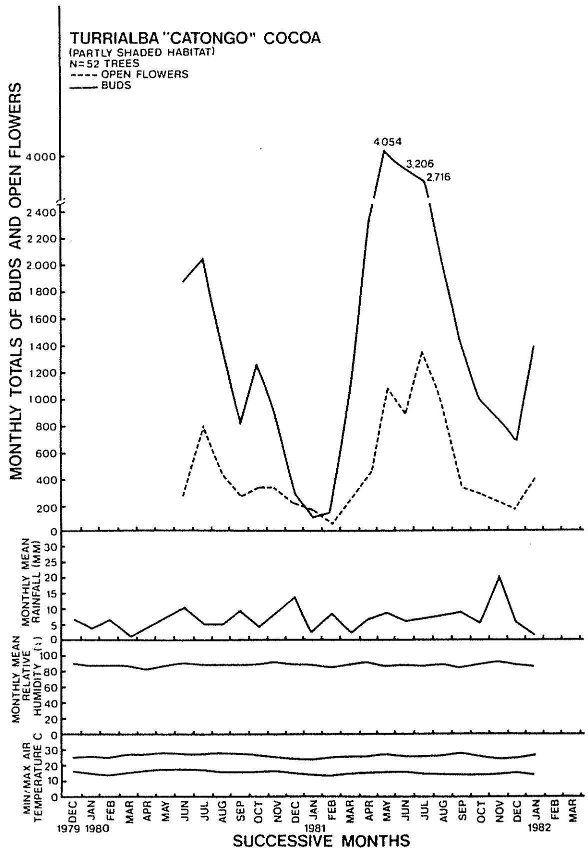

Fig. 3. Phenological patterns in flowering of cocoa trees in relation to local climatic conditions at Turrialba (CATIE), in the central highlands of Costa Rica.

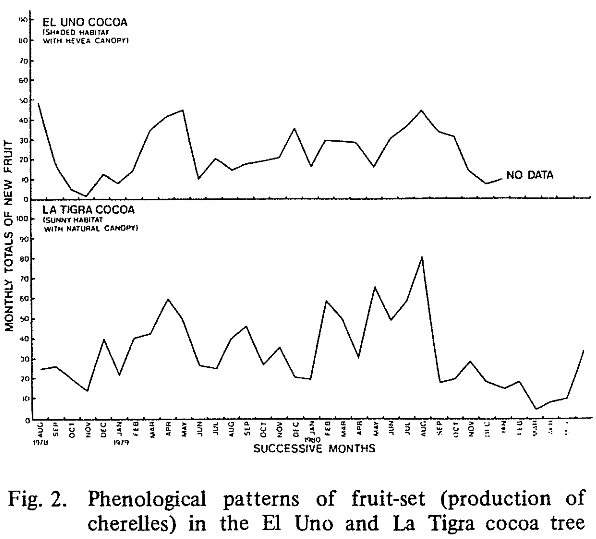

Fig. 2. Phenological patterns of fruit-set (production of cherelles) in the El Uno and La Tigra cocoa tree habitats.

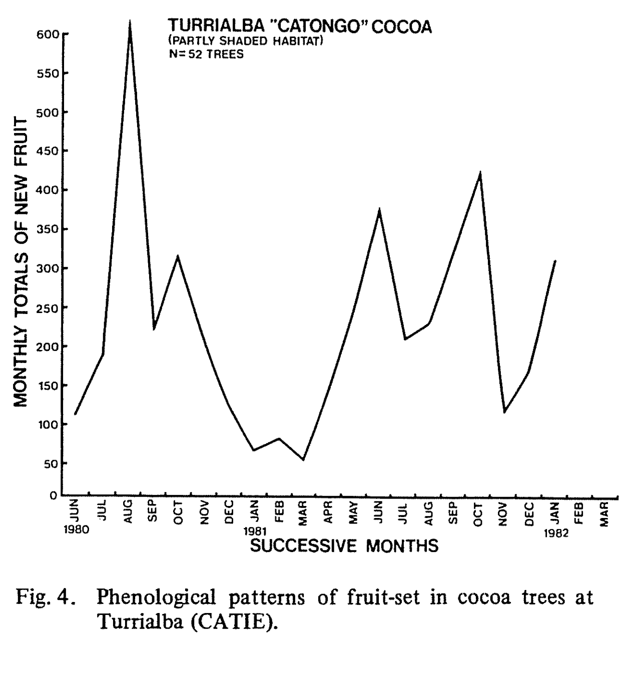

Fig. 4. Phenological patterns of fruit-set in cocoa trees at Turrialba (CATIE).

is most evident in the shaded habitat (Area A) at La Lola, although overall decline in flowering at this time is associated with the rainy months of November and December, as it was at the other localities studied (Figure 5). Peak fruit-set is clearly associated with the early phase of the rainy season, coinciding and immediately following the initial stages of renewed, intense flowering that occurs at this time here (Figures 5 and 6). A second, less pronounced "pulse" of intense fruit-set occurs late in the rainy season, a consequence of the sustained rainy season flowering, and the termination of the first pulse of fruit-set that occurs at the onset of the rainy season here. The marked decline in flowering in the sunny habitat (Area B) at La Lola that occurred between August 1980 and January 1981 coincides with a less marked decline of fruit-set (Figure 6). Overall decline in fruit-set in Area B, however, is much more pronounced than in Area A at the same time, as trees in the more exposed habitat (Area B) may respond more

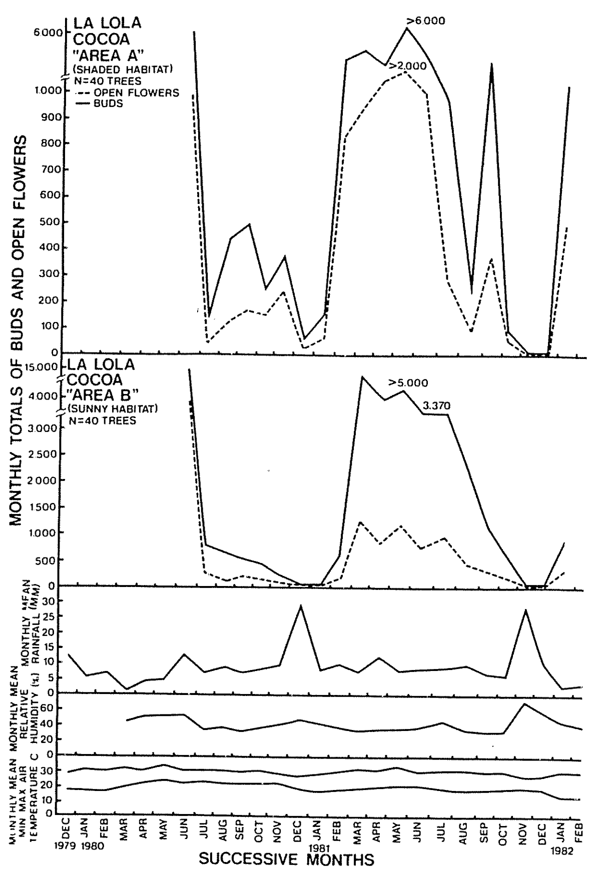

Fig. 5. Phenological patterns in flowering of cocoa trees in relation to local climatic conditions at the La Lola locality, for both shaded (Area A) and sunny (Areas B) habitats, near the Caribbean coast in Costa Rica.

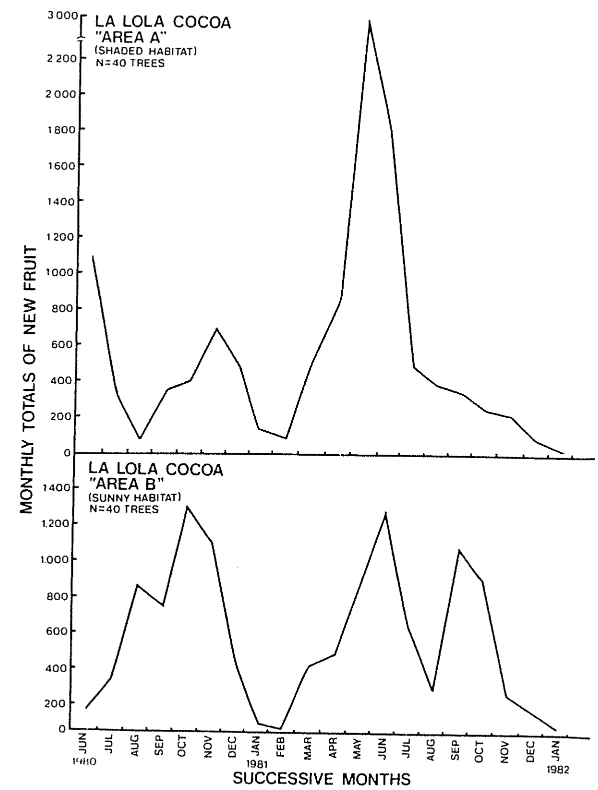

Fig. 6. Phenological patterns of fruit-set at La Lola.

quickly to dry conditions at this time (late December and well into January) (Figure 6). Periods of high fruit-set result in greater infestations of the *Monilia* fungus at these times than in other periods when fruit-set is very low (Table 8).

At all three localities, phenological patterns in rainfall are far more variable than those of other climatic parameters such as minimum-maximum temperatures and relative humidity (Figures 1, 3, and 5).

Discussion

The overall finding of this study is the coinciding of peak periods of flowering in cocoa trees with the rainy season, particularly the first half of this period, at three localities in Costa Rica that vary to some degree in terms of annual cycles of seasonality. A consequence is that fruit-set patterns also fluctuate in direct relation to flowering patterns: periods of high fruit-set coincide with periods of high flower production in cocoa. Oscillations in leaf flushing often complement similar cycles in flowering in cocoa (1). Very rainy conditions at the end of the rainy season results in an enforced decline in flowering, with very low fruit-set occurring in such periods as well as during the early phase of the dry period which usually follows the wettest months in these localities. The type of shade cover, and the degree to which it is altered by seasonal rainfall conditions, is a secondary influence upon the flowering and fruit-set patterns in *T. cacao*. Intense fluctuations in flowering are seen in *T. cacao* trees covered with either natural shade or planted shade (*Hevea, Erythrina*) that become markedly deciduous, with considerable leaf-crop in the dry season, or driest months of the year. Dry conditions in the tropics generally generate marked and regular cycles of leaf-flushing and flowering in a variety of tropical plants (19). When the shade cover over *T. cacao* opens up as the dry season progresses, the cocoa trees receive physiological "shock", sudden, increased insolation, which may trigger flowering by the end of the dry period, or very early into the following rainy season. Trees under a natural shade cover that does not respond as intensely to the dry conditions may exhibit a less pronounced and more irregular response to seasonal changes in rainfall. A shade cover tree such as *Erythrina* may exhibit asynchronous responses to dry conditions (4), which in turn establishes a highly variable canopy over short distances of a cocoa habitat. Slight changes in photoperiod at different times of the year in the tropics may also affect the intensity of flowering and fruiting patterns of some plants (17). Opler *et al.* (19) noted that some tree species in lowland tropical wet forest may have several distinct periods of flowering within a year, and cocoa also exhibits such behavior as shown in the present study for various tropical wet forest sites.

Uniform thick shade cover, such as the *Hevea* canopy at El Uno, dampens overall flower production relative to what occurs in an adjacent cocoa habitat (La Tigra) with a broken, natural canopy. Yet there appears to be very little correlation between levels of flower abundance and overall production of cherelles under these contrasting ecological conditions. Fruit-set in many plants is limited by internal, physiological constraints rather than external factors (27). Thus a confounding factor in this study is the fact that cherelles were removed each month, thus possibly distorting the observed responses of trees to seasonal rainfall patterns. Yet such an effect would presumably be similar for the trees at the three localities studied, thus adding an approximately equal bias to the observed numbers of fruits and flowers in all cases. In spite of this, it is necessary to exercise great caution in interpreting the observed differences in monthly totals of cherelles and flowers within a locality as being solely a response to seasonal changes in the external environment (e.g., rainfall).

Another factor influencing levels of fruit-set is variety of cocoa studied. The mixes of both self-compatible and self-incompatible trees in the El Uno and La Tigra habitats lowers overall pollination frequency when compared with pure stands of self-compatible cocoa (such as the cocoa studied at both La Lola and Turrialba). The relatively much higher fruit production observed at La Lola might be the result of very high pollination frequency within the self-compatible UF-29 variety, very warm temperatures throughout the year, and regular agronomic practices. In contrast, the lower fruit yield at Turrialba might be in part due to the very high elevation of this locality, the associated more uniform cloud cover throughout the year, and intrinsic variety differences between UF-29 and "Catongo" cocoas. Cuatrecasas (5) noted that *T. cacao* requires high air humidity and temperature, adequate shade, and 2 000 – 8 000 mm rainfall annually to thrive optimally, and that elevations above 300 m are generally sub-optimal conditions in most regions. Such differences in locality and the spatial availability of self-compatible and self-imcompatible varieties of *T. cacao* may indirectly influence the effectiveness of pollinating insects in determining levels of fruit-set. While some studies have shown that when populations of pollinating insects are sufficient, there is little or no difference in fruit-set levels between self-compatible and self-incompatible plantings of *T. cacao* (see review in Entwistle, 1972), when pollinator populations are experimentally increased, fruit-set sometimes increases (34) suggesting naturally-occurring low abundance of pollinators. Such a condition may result in considerable difference in levels of fruit-set between self-compatible and self-incompatible trees in the same plantation.

Rainfall is most likely the major environmental factor in both timing and spacing the flowering cycles of tropical plants, even though the precise mechanism of triggering the response remains unknown (18). Yet it is very difficult to separate out the effects of rainfall from that of air temperature changes. Overall, the climatic data suggests that decline in rainfall is associated with decline in temperature, although such patterns warrant further study. The timing and spacing of flowering in a tropical plant is also adaptive in relation to the activity of pollinators (18), and the evolution of synchronous flowering may enhance the attraction of pollinating animals (2, 3).

Theobroma cacao exhibits fluctuations in flowering in those cocoa-growing tropical regions where there are marked seasonal patterns in rainfall (1). The evolutionary history of *T. cacao* as an understory tree species of Amazonian rain forest (1) places adaptive constraints on the species in more seasonal regions

Table 8. The montly levels of infestation of monilia on new fruit of cocoa (*Theobroma cacao* L.) on eighty trees in shaded (Area A) and sunnt (Area B) habitats of the La Lola cocoa farm, near Siquirres, Limon Province, Costa Rica, June 1980 through January 1982.

Date	Area A				Area B				Area A & B Combined			
	Healthy pods	Infected pods	Total	% Destroyed	Healthy pods	Infected pods	Total	% Destroyed	Healthy pods	Infected pods	Total	% Destroyed
20 June 1980	1 051	48	1 099	4.5	106	50	156	32.1	1 157	98	1 255	7.8
18 July	77	174	251	69.3	385	7	392	1.8	462	181	643	28.1
1 Sept.	79	0	79	0.0	843	0	843	0.0	922	0	922	0.0
1 Oct.	279	0	279	0.0	779	0	779	0.0	1 058	0	1 058	0.0
5 Nov.	298	102	400	25.5	1 103	208	1 311	15.1	1 401	310	1 711	12.3
5 Dec.	441	260	701	37.1	789	281	1 070	26.3	1 230	541	1 771	30.5
9 Jan. 1981	292	162	454	35.6	214	200	414	48.8	506	362	868	41.7
3 Feb.	63	63	126	50.0	36	28	64	43.7	99	91	190	47.3
8 March	38	69	107	64.5	6	1	7	14.3	44	44	114	61.4
10 April	571	5	576	0.8	401	3	404	7.4	972	8	980	0.8
7 May	830	14	844	1.6	472	0	472	0.0	1 302	14	1 316	1.1
4 June	3 409	34	3 443	0.9	895	5	900	0.6	4 304	39	4 314	0.8
9 July	1 666	129	1 795	7.2	1 204	30	1 234	2.4	2 870	159	3 029	5.2
10 Aug.	351	148	499	29.7	622	16	638	2.5	973	164	1 137	14.4
3 Sept.	256	87	343	25.3	260	60	320	18.7	516	147	663	22.2
2 Oct.	212	126	338	37.2	742	332	1 074	30.9	954	458	1 412	32.5
24 Nov.	163	63	226	27.8	621	259	880	29.3	784	322	1 106	29.2
15 Dec.	214	97	311	31.1	276	143	419	34.1	490	240	730	32.9
13 Jan. 1982	90	43	133	32.4	172	70	242	28.9	262	113	375	30.1
15 Feb.	21	5	26	19.2	42	17	59	28.8	63	22	85	25.9

and when the canopy or shade cover is not well developed. Different varieties of cultivated cocoa exhibit differences in the response of flowering to seasonal conditions (1), and some of the observed differences in the present study for cocoa trees at different localities may be related to such an effect. Alvim (1) noted a compensatory effect in cocoa trees: intense fruit-set acts as an energy sink on the tree thereby reducing subsequent flowering. Internal competition for limited nutrients between flowers and young fruits dampens the intensity of flowering at certain times of the year, and superimposes a pattern upon exogenous control by tropical seasonality (1). The observed patterns of decline in flowering at the end of the rainy season at all three localities were in part due to severe flower "knock-down" by heavy rain as well as reduced nutrients at a time when fruit-set had been high. Periods of high fruit production provide the opportunity for increased predation upon fruit by various organisms. Intensely shaded conditions at the end of the rainy season, resulting from both the luxuriance of canopy growth in *T. cacao* and shade trees as well from frequently cloudy conditions, may curtail photosynthetic activity and subsequently flowering in *T. cacao* (20). The observed increase in the frequency of the *Monilia* fungus on cherelles may represent a density-related response by this parasitoid to an increased food supply.

Alvim (1) concluded from work in Bahia, Brazil that flowering in *T. cacao* is inhibited by moisture stress, and that dry periods are times of reduced flowering. The data obtained in the present study provide additional support for this result. The studies of Leston and Gibbs (14) and Gibbs and Leston (8) in Ghana with leaf-flushing in *T. cacao* indicate that trees grown in highly exposed conditions exhibit analomous responses to seasonal conditions. The observed, sudden shifts in flowering observed in the present study in *T. cacao* when shade cover trees exhibit leaf-drop in the dry season. Janzen (13) predicted that the heavy rains that terminate the tropical dry season provide an effective trigger for the synchronized flowering of trees. Such an effect is most pronounced in highly seasonal tropical regions, even though many tree species exhibit varying degrees of synchronous flowering in less seasonal regions (18). Hilty (10) noted that in relatively non-seasonal tropical localities, flowering and fruiting within a tree species may have multiple peaks of intensity. Hutcheon (12) proposed two different flowering patterns operative in *T. cacao*. A pattern of "normal flowering" is regulated principally by internal physiological conditions, while "crazy flowering" is an immediate response to the removal of some inhibitory factor such as moisture stress (12). Depending upon the locality, both control mechanisms operate to determine the phenological patterns of flowering in *T. cacao*. Hutcheon also found that the major burst of flowering at the end of the dry season in Ghana results in the greatest amount of fruit-set. A similar pattern was seen with the present study, particularly at both CATIE in Turrialba and both habitats at La Lola. Both of these localities exhibit a greater amount of seasonality in availability of rainfall than the La Tirimbina locality. As the rainy season progresses, there are increasingly less favourable conditions for flowering in *T. cacao* as well as increased energy allocation to fruit development, and both factors contribute to a marked decline in flowering by the end of the rainy season (12). The deliberate removal of new fruit (cherelles) in the present study may also stimulate sustained flowering, thereby postponing or dampening the effects of fruit development on flowering intensity (12).

Temporal changes in the abundance of new fruit *T. cacao* must take into consideration the changes in distribution and abundance of pollinators. When flowering is both intense and synchronous within a population, a greater number of pollinators may be attracted to inflorescences (2, 27). High fruit-set observed during and immediately following periods of intense flowering, as seen in the present study, may result in part from increased activity of pollinating insects. Cocoa-pollinating insects are more abundant during the rainy season than in the dry season (6, 31, 33, 34), allowing for some synchrony between flowers and pollinators. Yet in some regions there exists considerable asynchrony between abundance cycles of cocoa flowers and pollinators and flowers may increase fruit-set to some degree, many trees possess an internal, physiological limit on fruit-set which is independent of pollination levels (27). By inspection the data suggest a difference in the ratio of fruit-set to flowering for some of the trees studied, such as seen in a comparison of these parameters for La Lola and Turrialba. This difference might be due to a direct or indirect effect of locality upon the abundance of pollinating insects and their annual cycles of population dynamics (24, 25, 26). Peak flowering periods in *T. cacao* provide an abundant resource of adult pollinating midges such as *Forcipomyia* species (Diptera: Ceratopogonidae). Pollinator populations are reduced during the dry season, a time when flowering declines as well. The dry season-related abiotic constraints on the survival of *T. cacao* flowers may further limit the opportunities for pollination and fruit-set, since the dirunal cycle of flower opening and receptivity is highly synchronized to times of the day when relative humidity is high (30).

Summary

Monthly patterns of flowering and fruit-set were studied for large samples of cocoa trees, *Theobroma cacao* L. (Sterculiaceae) at three localities within the Tropical Wet Forest zones of Costa Rica All three localities exhibit varying degrees of seasonality, with a short dry season usually occurring between January and March. Cocoa trees at each locality chosen for study included ones with various kinds of shade cover. At all three localities, and regardless of shade cover, there was a marked decline in flowering near the end of the rainy season when rainfall was very high. Depending upon the response of the shade cover to dry conditions, the month-to-month production of new cocoa flowers varied. Inter-tree monthly levels of flowering and fruit-set varied greatly at all localities, making it difficult to determine quantitative seasonal patterns, and emphasizing the interpretative value of qualitative comparisons involving clearly large differences in flowering and fruit-set data When shade cover was thinned through leaf-drop by the late dry season, fluctuations in flower production varied greatly in the following rainy season At two localities in particular, there was a large peak in fruit-set coinciding with the burst of flowering in the first half of the rainy season. Multiple peaks of flowering and fruit-set occurred at all localities Understanding differences in levels of fruit-set depend upon the effects of climatic factors upon populations of pollinating insects at different localities. The incidence of the fruit disease *Monilia* increased during periods of high fruit-set and disappeared at other times of the year

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