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THE RELATIONSHIP OF CUMULATIVE SUMS AND MOVING AVERAGES OF TEMPERATURE TO REPRODUCTIVE PHENOLOGICAL CHANGE IN *CLARKIA*

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ABSTRACT

Flowering time (anthesis) differs among populations in the *Clarkia unguiculata* complex, and these differences appear to be adaptive with respect to avoiding the severe summer drought of the native habitats. As habitat elevation decreases, flowering time and soil drying occur earlier.

Six populations of the *C. unguiculata* complex were grown in four temperature environments to assess the effect of temperature on the timing of five developmental stages (phenophases). Regressions were calculated using the days from planting to a given phenophase (age) as the dependent variable, and values of 126 combinations of moving average lengths, cumulative sums, threshold temperatures, and daily air temperature maxima, minima, and means when the various phenophases occurred as the independent variables.

The timing of all phenophases was significantly correlated more often with moving averages than with cumulative sums, and it took longer to reach a given phenophase at lower temperatures. The absence of interpopulation and interphenophase differences suggests that the temperature environments of native habitat during flowering are similar and that observed differences in flowering time in uniform culture are the result of different responses to other environmental factors, such as insolation and soil water potential. Flowering and habitat characteristics are combined into a graphical model that illustrates the importance of flowering in response to temperature to avoid summer drought.

INTRODUCTION

An important part of the ecology of a species is its phenological response to its environment. In plants, flowering (bud initiation through anthesis and fruit set) when resources are inadequate for successful reproduction would have little selective value. Flowering time is a distinguishing characteristic of most species and populations of the *Clarkia unguiculata* Lindl. complex, in both natural and artificial growth (Vasek, 1964, 1968; Vasek and Sauer, 1971). Flowering typically occurs in the field during late spring as air temperatures rise from winter to summer values and soil water reserves become rapidly depleted (Vasek and Sauer, 1971). However, drought stress is not to be a primary control on flowering time because greenhouse samples, grown under severe and light drought stress, showed no differences in flowering time (Sauer, 1971). Thus, flowering time would seem to be related to temperature factors. Age (days elapsed since first watering) also would seem to be a factor since very young plants do not flower. The purpose of this paper is to present an analysis of laboratory data and conclusions related to the question of which estimate of temperature change is best related to reproductive phenological change. Six populations of the *Clarkia unguiculata* complex were used, and an effort was made to associate interpopulation differences with interhabitat differences. Finally, a model incorporating the results of field and laboratory work on *Clarkia* flowering is presented. Field observations and data related to this study have been reported earlier (Vasek and Sauer, 1971).

The *Clarkia unguiculata* complex (Onagraceae) are annual species and occur naturally on the periphery of the Central Valley of California (Vasek, 1964, 1968). *Clarkia unguiculata* is interpreted to be the parental species from which *C. exilis*, *C. temblorlensis*, and *C.* "Caliente,"

an undescribed species, have evolved during periods of exceptionally severe and early drought (Vasek, 1964, 1968). Three sites near Bakersfield, California, were studied, representing three degrees of aridity. These sites have been described in detail elsewhere (Vasek and Sauer, 1971) and thus will be discussed briefly here. The highest site, Parker Creek Canyon (*C. unguiculata* and *C. exilis*), approximately 29 km SE of Bakersfield, California, with an elevation of 2600 ft (790 m), is the most mesic site. High Canyon (*C. unguiculata* and *C. temblorіensis*), approximately 9 km S of Parker Creek Canyon with an elevation of 1100 ft (335 m), is closer to the valley floor and noticeably more xeric than Parker Creek Canyon. Low Canyon (*C. unguiculata* and *C.* "Caliente"), approximately 1 km W of High Canyon with an elevation of 950 ft (290 m), is slightly more xeric than High Canyon. At each site there are adjacent or sympatric populations of parental and derivative species. The derivative populations complete flowering before the parental species; flowering occurs first at Low Canyon, followed by High Canyon, and finally Parker Creek Canyon. These populations thus offer an opportunity to compare closely related, but genetically isolated populations with repsect to an ecological adaptation, flowering time.

Precipitation varies in seasonal periodicity and amount (Twisselman, 1967; Fritts, 1956). The annual average at the nearest U.S. weather station, Bakersfield (elevation 490 ft, 160 m) is 6 inches (18 cm) (U.S. Weather Bureau, 1970), and the higher elevation *Clarkia* sites can be expected to receive slightly more. Average monthly growing season temperatures at Bakersfield vary from a minimum temperature of 36 to 40°F (3 to 5°C) in January to a maximum temperature of 85 to 90°F in June (U.S. Weather Bureau, 1970).

Flowering time in other species has been correlated with several environmental factors, including temperature and seasonal rainfall periodicity. Long-term (30 years) observations at an arboretum and single season observations at contrasting sites in Indiana showed flowering (anthesis) was correlated with an accumulation of degree hours (Lindsey and Newman, 1956; Jackson, 1966). The use of heat sums (cumulative sums of temperature) has been criticized on the basis that plant requirements for temperature and other factors change with developmental state (Wang, 1960). Insolation has been combined with temperature in a cumulative sum to predict the flowering time of lilac (*Syringa vulgaris* L.) (Caprio, 1971). The alpine species *Geum turbinatum* appeared not to flower until the 3 cm soil temperature rose above 10°C (Holway and Ward, 1965). Vegetative and reproductive development of native species of the Upper Snake River plains were advanced by higher temperatures and decreased by cloud cover during the growing season and low rainfall preceding the growing season (Blaisdel, 1958). Rainfall periodicity was correlated with flowering time in races of *Heterotheca subaxillaris* (Burk, 1966). The interaction between rainfall periodicity and photoperiod appeared to have selected flowering time races of *Heteropogon contortus* (Tothill, 1966). It is interesting to note that reproductive maturation in some insects is regulated in part by temperature (Dingle, 1972).

This study did not address the problem of floral bud initiation, but rather the timing of floral and fruiting phenophases.

MATERIALS AND METHODS

Seeds of each population were obtained from approximately 50 individuals transplanted from the field as small seedlings, fall, 1969, and grown to maturity in an experimental garden at the University of

California, Los Angeles. Bird predation and disease reduced the number of transplanted individuals. Ripe seeds of five to twenty individuals in each population were combined and sown, about 10 per pot, in 9 cm^2 plastic pots (700 cm^3) in a 20% peat, 20% sand, 60% loam soil mix. Twenty pots of each population were placed randomly in each of three growth chambers. Plants were thinned to one per pot when large enough to handle, after about 2 weeks. The numbers of fruits, open flowers, and floral buds longer than 1 mm were recorded twice weekly.

Comparisons were made between plants grown in four progressively slower warming treatments, produced by three growth chambers and one greenhouse. Three growth chambers (Percival PGW-108) were programmed for temperature change (Table 1). The actual temperatures are shown in Fig. 1. During a 24-hr cycle, temperatures increased linearly from minimum to maximum values from 0500 to 0700 hrs, and light intensity (maximum approximately 2000 ft-c at bench height) increased in three steps in the same 2 hours. From 1700 to 1900 a similar decrease in temperature and light intensity simulated dusk. Temperature data before age 56 days are the values at which the temperature controls were set. These controls were inaccurate, and after age 56 days maximum and minimum temperatures were recorded daily from a centrally located thermometer until the plants died. The soil was kept moist almost continuously. The growing temperatures were intended to simulate the microclimate of the natural habitats, with the exclusion of freezing and very high temperatures (occasional maxima greater than 40°C, Vasek and Sauer, 1971). The number of surviving individuals in each sample varied from 15 and 20; for data analysis, all samples were reduced to 15.

Table 1. Temperature programs for three growth chambers.

Temperature (°C)		Age at change (days)		
min	max	Growth chamber 1	Growth chamber 2	Growth chamber 3
4	15	0	0	0
13	21	28	42	56
13	21	42	56	70
13	21	56	70	84
15	38	70	84	98

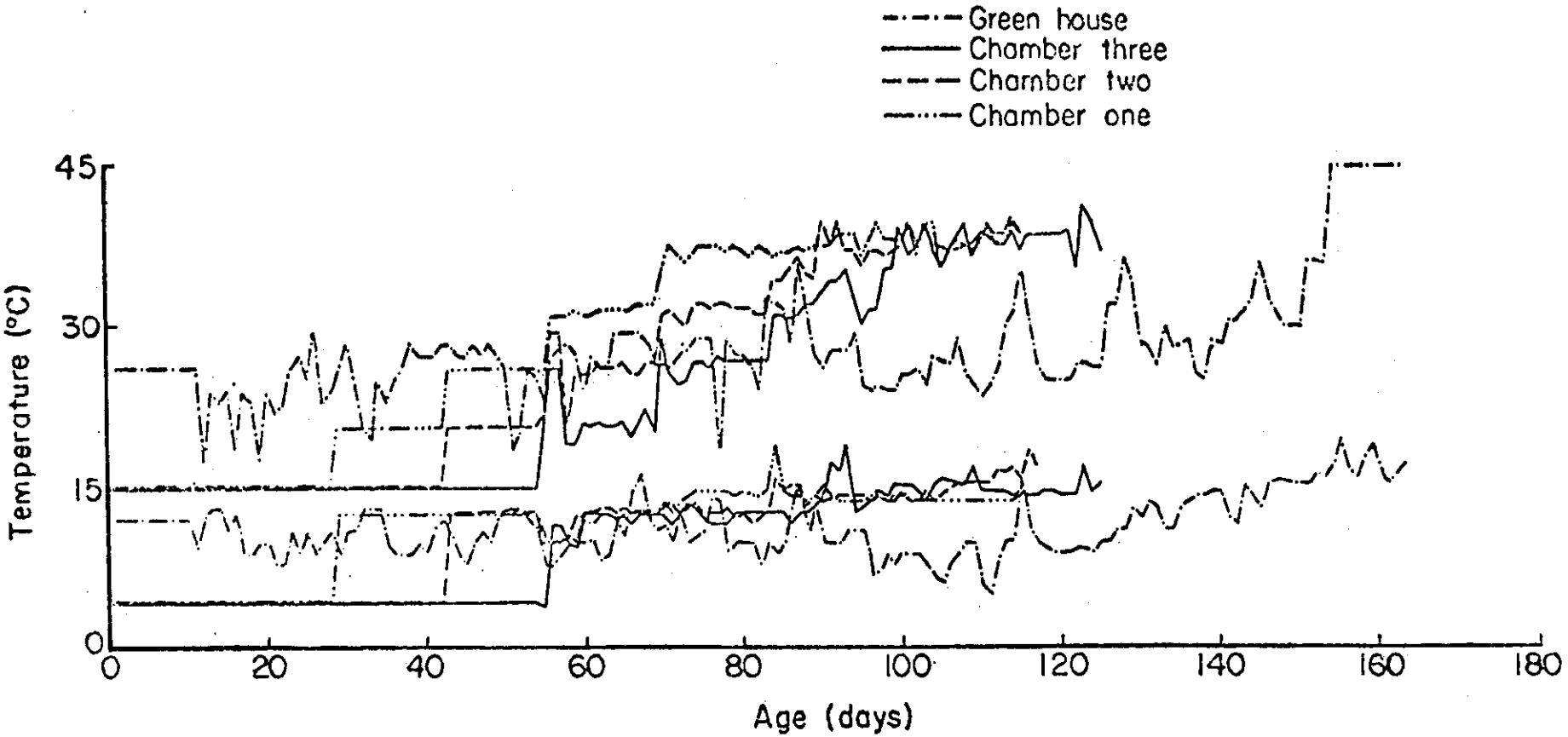


Fig. 1. Maximum and minimum daily temperatures in the three growth chambers and greenhouse. Growth chamber one was the fastest warming environment and the greenhouse was the slowest warming.

A greenhouse was used to simulate a fourth and slowest rate of temperature change in which temperatures were maintained between 5 and 45°C, depending on prevailing weather and equipment inconsistencies (Fig. 1). These plants were grown from the seed source and in the soil described above. Thirty plants of each population were grown in a wood flat 30 cm × 20 cm × 20 cm (12,000 cm^3 or 400 cm^3/plant). Natural day length and insolation were used (Los Angeles, January to June 1970). Before age 11 days, cooler and heater control settings were used in the calculations. The controls were not dependable, and after age 11 days maximum and minimum temperatures were recorded daily from a centrally located thermometer. The numbers of fruits, open flowers, and floral buds were recorded weekly. The soil was kept moist at all times.

Five flowering phenophases were defined: first flower, first fruit, mid-flowering, topping out, and last flower. The age (days elapsed since planting and first watering) of each population in each treatment was determined at the occurrence of each phenophase (Table 2). First flower is the age of the sample when the first open flower is recorded. Mid-flowering is the age of the sample when the numbers of fruit and floral buds are equal and is determined graphically on a plot of total number of fruit and total number of buds versus time. Topping out is the sample age when the buds longer than 1 mm first decrease in number. Last flower is the sample age when the last open flower is observed.

The independent variables that were regressed against the ages at which the various phenophases occurred consisted of 35 moving averages and 7 cumulative sums calculated from temperature maxima, minima, or means in each treatment. The 35 moving averages (Table 3) were calculated

Table 2. Age in days at which each population obtained each phenophase in each treatment. (1 = earliest warming, 4 = latest warming).

Population	Treatment	Phenophase				
		First flower	First fruit	Mid-flowering	Topping out	Last flower
UPC*	1	76	83	92	87	104
	2	83	90	97	94	104
	3	94	101	102	101	111
	4	102	117	128	124	151
EPC	1	65	73	81	87	94
	2	73	76	87	83	101
	3	80	83	94	94	104
	4	90	97	111	102	143
UHC	1	76	80	87	83	97
	2	80	87	92	87	101
	3	90	94	99	94	111
	4	97	109	120	109	159
THC	1	73	76	85	76	101
	2	73	80	87	87	104
	3	83	90	93	87	101
	4	90	102	114	102	151
ULC	1	73	73	82	76	94
	2	73	80	88	83	101
	3	80	87	94	87	104
	4	97	102	112	102	151
CLC	1	73	73	84	80	101
	2	76	80	90	83	104
	3	83	90	100	94	111
	4	84	90	114	102	130

*See text.

Table 3. Identification of independent variables representing the combinations of temperature thresholds and moving average lengths used to calculate the moving averages and cumulative sums.

Threshold Temperature	Temperature (°C)	Moving Average Length (Days)					Cumulative Sum
		5	10	15	20	25	
Cool	5	1	8	15	22	29	36
	10	2	9	16	23	30	37
	15	3	10	17	24	21	38
Warm	20	4	11	18	25	32	39
	25	5	12	19	26	33	40
	30	6	13	20	27	34	41
	35	7	14	21	28	35	42

using seven threshold temperatures (5, 10, 15, 20, 25, 30, and 35°C) and five moving average lengths (5, 10, 15, 20, and 25 days). Threshold temperatures (degrees C subtracted from observed temperatures) were used to represent the temprature below which no significant phenological change occurred, and the moving average lengths were used to represent the length of time before a given event during which temperature had a significant control on phenological change. Equation 1 shows how a moving average A of length n, threshold l, and temperature (maximum, minimum, or mean) T_t for day t was calculated:

$$A = \frac{\sum_{t=-n}^{l} Q_t}{n}$$

where Q_t equals T_t-l for $T \geq l$ or Q_t equals 0.0 for $T > l$. The seven cumulative sums, based on the seven threshold temperatures, were sums of Q_t from the time the seeds were planted and watered (age = zero days). Thus, there were 42 maximum temperature variables, 42 minimum temperature variables, and 42 mean temperature variables, for a total of 126 independent variables in each treatment. The regression for each population and phenophase included four pairs of points; each pair consisted of the value of the moving averages or cumulative sums at the age at which the phenophase occurred (the independent variable) and the age at which the phenophase occurred (the dependent variable). Correlation coefficient, slope, standard error, and intercept were calculated for each regression line. The FORTRAN program is shown in Appendix I.

Statistical and biological criteria were used to identify significant correlations. The correlation between a particular variable and phenophase was taken to be statistically significant if the absolute value of the computed correlation coefficient r was greater than 0.9500, the 95% confidence

level for a four-point regression. Biological criteria were concerned with the question of how much heat or temperature might be required to significantly affect phenological change. Moving averages less than 2.0°C and cumulative sums less than 5.0°C above the threshold temperature were arbitrarily considered not different from 0.0°C above the threshold temperature and thus unlikely to affect phenological change.

For convenience, the six populations have abbreviated names, based on the species and natural habitat location, as follows:

Parker Creek Canyon:	*Clarkia unguiculata*	(UPC)
	C. exilis	(EPC)
High Canyon:	*C. unguiculata*	(UHC)
	C. temblorіensis	(THC)
Low Canyon:	*C. unguiculata*	(ULC)
	C. "Caliente"	(CLC)

RESULTS

The threshold temperatures used to calculate the moving averages (averages) and cumulative sums are here referred to as cool (5, 10, 15°C) or warm (20, 25, 30, 35°C). Max, min, and mean refer to maximum daily temperatures, minimum daily temperatures, and mean daily temperatures, respectively. The best correlated variables were those which had the highest correlation coefficient of the max, min, and mean temperature variables. "Correlated" implies that the variables referred to were both statistically (5% level or better) and biologically significantly correlated.

Summary of results.--Flowering was delayed by slower temperature rises in all populations and treatments, but to different degrees. In almost all cases, the various threshold temperature values were grouped

by moving average lengths, and often, the r values for all threshold temperatures in a moving average length were equal to the fourth decimal place. The higher threshold temperatures were rarely correlated, probably because they were often equal to or greater than the max, min, or mean temperatures, thus giving a result of zero for the moving averages or cumulative sums.

Cumulative sums were correlated only rarely with the timing of phenological change.

The *C. unguiculata* populations generally had more correlated variables than did the derivative populations.

Moving average lengths, max, min, and mean temperatures, and threshold temperatures were overlapping; thus the temperature variables were not strictly independent. This may explain why so many variables were correlated with some phenophases as in "mid-flowering."

First flower.--Relatively few variables were correlated with the age at which this phenophase occurred (Table 4); there were no correlations in UPC or EPC. Variables calculated from min were relatively more prominent in this phenophase. UHC: There were correlations with cool 10-day averages calculated from max and mean temperatures, and the latter were the best correlated. THC: There was a correlation with only one variable, the 5°C 10-day average calculated from min temperatures. ULC: There were correlations with the 5°C, 5-, 10-, and 15-day averages (min only), and the best correlated variable was the 10-day average. UHC: There were correlations with cool and warm 5-, 10-, 15-, 20-, and 25-day averages (max) and cool 10-, 15-, 20-, and 25-day averages, and the best correlated variables were 5, 10, 15, and 20°C 15-day averages calculated from mean temperatures. THC: There were correlations with cool and warm 10-day averages (max) and cool 10- and 15-day averages

Table 4. The variables significantly correlated with the age at which the phenophase "first flower" occurred. Variables listed in descending order of significance. Underlining indicates most significant variables. Overlining indicates r values equal to fourth decimal place. 99% confidence level indicated by an *, the remaining are at the 95% confidence level. See Table 2 for variable identification.

UPC		
	Max:	none
	Min:	none
	Mean:	none
EPC		
	Max:	none
	Min:	none
	Mean:	none
UHC		
	Max:	10, 8, 9, 11
	Min:	none
	Mean:	8, 9, 10
THC		
	Max:	none
	Min:	8
	Mean:	none

Table 4. Continued.

ULC		
	Max:	none
	Min:	8*, 1*, 15*, 29
	Mean:	none
CLC		
	Max:	none
	Min:	none
	Mean:	1, 3, 2, 9, 10, 8, 17, 16, 15

(mean); the best correlated variables were the cool 10-day averages calculated from mean temperatures. ULC: There were correlations with the 5°C thresholds of the 5-, 10-, 15-, and 20-day averages (min only), and the best correlation was with the 10-day average. CLC: There were correlations with the cool threshold 5-, 10-, and 15-day averages (mean only), and the 5-day averages had the best correlations.

First fruit.--More variables were correlated with the age at which this phenophase occurred than with "first flowers" (Table 5). Minimum temperatures were relatively unimportant in regulating the onset of this phenophase. UPC: There were correlations with cool and warm 10-, 20-, and 25-day averages (max only), and the latter were the best correlated variables. EPC: There were correlations with the 5°C 5-, 10-, and 15-day averages (min only) and the best correlated variable was the 10-day average. UHC: There were correlations with cool and warm 5-, 10-, 15-, 20-, and 25-day averages (max) and cool 10-, 15-, 20-, and 25-day averages calculated from maximum temperatures. THC: There were correlations with cool and warm 10-day averages (max) and cool 10- and 15-day averages (mean); the best correlated variables were the cool 10-day averages calculated from mean temperatures. ULC: There were correlations with cool and warm 5- and 10-day averages (max) and cool 5-, 10-, 15-, and 20-day averages; the best correlated variables were the cool 10-day averages calculated from mean temperatures. CLC: There were correlations with cool and warm 10- and 15-day averages (max) and cool 20- and 25-day averages (mean); the best correlated variables were the cool and warm 10-day averages.

Mid-flowering.--"Mid-flowering" was the phenophase best correlated with temperature in all populations (Table 6). Minimum temperature variables were again relatively unimportant, and there were no

Table 5. The variables significantly correlated with the age at which the phenophase "first fruit" occurred. Variables listed in descending order of significance. Underlining indicates most significant variables. Overlining indicates r values equal to fourth decimal place. 99% confidence level indicated by an *, the remaining are the 95% confidence level. See Table 2 for variable identification.

UPC

Max: 33, 29, 31, 30, 32, 26, 25, 22, 24, 23, 12, 11, 8, 10, 9

Min: none

Mean: none

EPC

Max: none

Min: 8, 1, 15

Mean: none

UHC

Max: 15*, 16*, 17*, 18*, 22*, 23*, 24*, 25*, 9, 8, 10, 11, 1, 4, 3, 2, 32, 29, 31, 20

Min: none

Mean: 31*, 30*, 29*, 22*, 23*, 24*, 17, 16, 15, 10, 9, 8

THC

Max: 10, 9, 11, 8

Min: none

Mean: 9, 8, 10, 17, 16, 15

Table 5. Continued.

ULC		
	Max:	1*, 4*, 3*, 2*, 8, 10, 11, 9
	Min:	1
	Mean:	9*, 10*, 8*, 15*, 17*, 16*, 3*, 1*, 2*, 22, 24, 23
CLC		
	Max:	12, 9, 11, 10, 8, 16, 15, 17, 18, 19
	Min:	none
	Mean:	30, 31, 29, 23, 24, 22

Table 6. The variables significantly correlated with the age at which the phenophase "mid-flowering" occurred. Variables listed in descending order of significance. Underlining indicates most significant variables. Overlining indicates r values equal to fourth decimal place. 99% confidence level indicated by an *, the remaining are at the 95% confidence level. See Table 2 for variable identification.

UPC

Max: 19*, 18*, 16*, 17*, 15*, 8*, 11*, 10*, 12*, 9*, 6 , 5, 2, 3, 4, 1, 23, 24, 25, 22, 26, 32, 29, 31, 30, 33

Min: 29, 22, 8, 15

Mean: 17*, 15*, 16*, 24*, 23*, 22*, 9*, 10*, 8*, 31*, 29*, 30*, 3, 2, 1

EPC

Max: 17, 18, 16, 15, 24, 25, 22, 23, 3, 4, 1, 2, 10, 9, 11, 8, 31, 29, 32, 30

Min: none

Mean: 30*, 31*, 29*, 24*, 23*, 22*, 15, 17, 16, 8, 9

UHC

Max: 8*, 9*, 12*, 11*, 10*, 18, 16, 15, 17, 19, 4, 1, 2, 3 25, 22, 24, 23, 26, 29, 32, 31, 30, 33

Min: 29, 21

Mean: 31*, 30*, 29*, 24, 23, 22, 9, 10, 8, 16, 17, 15, 1, 2, 3

THC

Max: 1*, 3*, 4*, 2*, 5*, 11, 9, 10, 8, 12

Min: 22, 29, 15, 8

Mean: 2, 1, 3, 10, 9, 8, 22, 24, 23, 17, 16, 15, 30, 31, 29

Table 6. Continued.

ULC	
Max:	2*, 4*, 3*, 1*, 18, 17, 15, 16, 10, 11, 9, 8, 25, 23, 22, 24 32, 31, 29, 30
Min:	22
Mean:	23*, 24*, 22*, 29*, 31*, 30*, 16*, 17*, 15*, 10, 9, 8, 3, 2, 1
CLC	
Max:	32, 31, 29, 30, 24, 25, 22, 23
Min:	none
Mean:	none

correlations with sums. UPC: There were correlations with cool and warm averages of all lengths (max), 5°C 10-, 15-, 20-, and 25-day averages (min), and cool averages of all lengths (mean); the best correlated variables were the cool 15-day averages calculated from mean temperatures. EPC: There were correlations with cool and warm averages of all lengths (max) and cool 10-, 15-, 20-, and 25-day averages (mean); the best correlated variables were the cool 25-day averages calculated from mean temperatures. UHC: There were correlations with cool (mean) and cool and warm (max) averages of all lengths, and warm 15- and cool 25-day averages (min); the best correlated variables were the cool and warm 10-day averages calculated from maximum temperatures. THC: There were correlations with cool and warm 5- and 10-day averages (max), 5°C, 10-, 15-, 20-, and 25-day averages (min), and cool averages of all lengths (mean); the best correlated variables were the cool and warm 5-day averages calculated from maximum temperatures. ULC: There were correlations with cool and warm averages of all lengths (max), 5°C 20-day averages (min) and cool averages of all lengths (mean); the best correlated variables were the cool 20-day averages calculated from mean temperatures. CLC: There were correlations with cool and warm 20- and 25-day averages (max only), and the latter were the best correlated variables.

Topping out.--The *C. unguiculata* populations only had variables correlated with the age at the onset of "topping out" (Table 7). Few minimum temperature variables were correlated, and there were no correlated cumulative sums. UPC: There were correlations with cool and warm 5-, 10-, 15-, and 20-day averages (max) and cool 10-, 15-, 20-, and 25-day averages (mean), and the best correlated variables were the cool 20-day averages calculated from mean temperatures. ULC: There were

Table 7. The variables significantly correlated with the age at which the phenophase "topping out" occurred. Variables listed in descending order of significance. Underlining indicates most significant variables. Overlining indicates r values equal to fourth decimal place. 99% confidence level indicated by an *, the remaining are at the 95% confidence level. See Table 2 for variable identification.

UPC

Max: 19*, 16*, 18*, 15*, 17*, 23*, 25*, 22*, 24*, 26*, 29*, 31*, 32*, 30*, 33*, 9, 12, 11, 8, 10, 1, 3, 4, 2

Min: none

Mean: 30*, 31*, 29*, 24*, 23*, 22*, 17, 16, 15, 8, 9, 10, 2, 3, 1

EPC

Max: none

Min: none

Mean: none

UHC

Max: 3, 4, 1, 2, 15, 16, 18, 17, 9, 10, 11, 8, 22, 25, 23, 24

Min: none

Mean: 22, 23, 24, 17, 16, 15, 30, 29, 31, 10, 9, 8

THC

Max: none

Min: none

Mean: none

Table 7. Continued.

ULC	
Max:	3, 4, 2, 1
Min:	8, 1, 15
Mean:	9, 10, 8, 1, 2, 3, 16, 15, 17
CLC	
Max:	none
Min:	none
Mean:	none

correlations with cool and warm 5-day averages (max), 5°C 5-, 10-, and 15-day averages (min) and cool 5-, 10-, and 15-day averages; the best correlated variables were the cool 10-day averages calculated from mean temperatures.

Last flower.--Cumulative sums were correlated only in this phenophase and only in three populations (Table 8). There were no correlations associated with the THC populations, but the other populations had a relatively large number of correlated variables. Few minimum temperature variables were correlated. The highest threshold temperatures were correlated with this phenophase. UPC: There were correlations with cool and warm averages of all lengths (max) and cool and warm 15-, 20-, and 25-day averages; the best correlated variables were the cool and warm 15-day averages calculated from maximum temperatures. EPC: There were correlations with cool and warm 5-, 10-, 15-, and 20-day averages (max), cool 20- and 25-day averages (min) and cool averages of all lengths (mean); the best correlated variables were the cool 15-day averages calculated from mean temperatures. UHC: There were correlations with cool and warm 5-, 10-, and 15-day averages and cool cumulative sums (max), cool 5-, 10-, and 15-day averages (min) and cool and warm 5-, 10-, and 15-day averages and the 5°C cumulative sums (mean); the best correlated variables were the cool and warm 10-day averages calculated from mean temperatures. ULC: There were correlations with cool and warm 5-, 10-, 15-, and 20-day averages and the 5°C cumulative sum (max) and the cool and warm 5-, 10-, 15-, and 20-day averages (mean); the best

Table 8. The variables significantly correlated with the age at which the phenophase "last flower" occurred. Variables listed in descending order of significance. Underlining indicates most significant variables. Overlining indicates r values equal to fourth decimal place. 99% confidence level indicated by an *, the remaining are at the 95% confidence level. See Table 2 for variable identification.

UPC

Max: 16*, 18*, 17*, 19*, 15*, 5*, 3*, 6*, 1*, 2*, 4*, 22*, 23*, 26*, 24*, 25*, 8, 11, 13, 12, 10, 9 29, 31, 32, 33, 30

Min: none

Mean: 23*, 24*, 22*, 25*, 18, 17, 16, 15, 31, 30, 29, 32

EPC

Max: 10*, 9*, 12*, 11*, 8*, 4, 5, 3, 1, 2, 17, 18, 19, 15, 16, 22, 23, 25, 24, 26

Min: 29*, 30*, 22, 23

Mean: 15*, 17*, 16*, 8*, 9*, 10*, 22, 23, 24, 31, 30, 29, 4, 2, 3, 1

UHC

Max: 5, 6, 3, 4, 7, 1, 2, 14, 13, 10, 11, 12, 9, 8, 21, 36, 16, 17, 19, 20, 18, 15, 37

Min: 2, 1, 8, 9, 16, 15

Mean: 11*, 10*, 9*, 8*, 2, 4, 3, 1, 15, 18, 17, 16, 36

Table 8. Continued.

THC	
Max:	none
Min:	none
Mean:	none
ULC	
Max:	1*, 3*, 5*, 6*, 4*, 2*, 16, 17, 18, 19, 15, 11, 9, 10, 13, 12, 8, 36, 22, 26, 23, 25, 24
Min:	none
Mean:	17, 18, 15, 16, 8, 9, 11, 10, 22, 23, 24, 25, 4, 3, 2, 1
CLC	
Max:	33, 31, 32, 30, 29, 23, 25, 26, 22, 24, 15, 16, 18, 19, 17, 6, 2, 3, 5, 4, 1, 10, 11, 12, 9, 8
Min:	none
Mean:	30, 31, 29, 23, 24, 22, 39

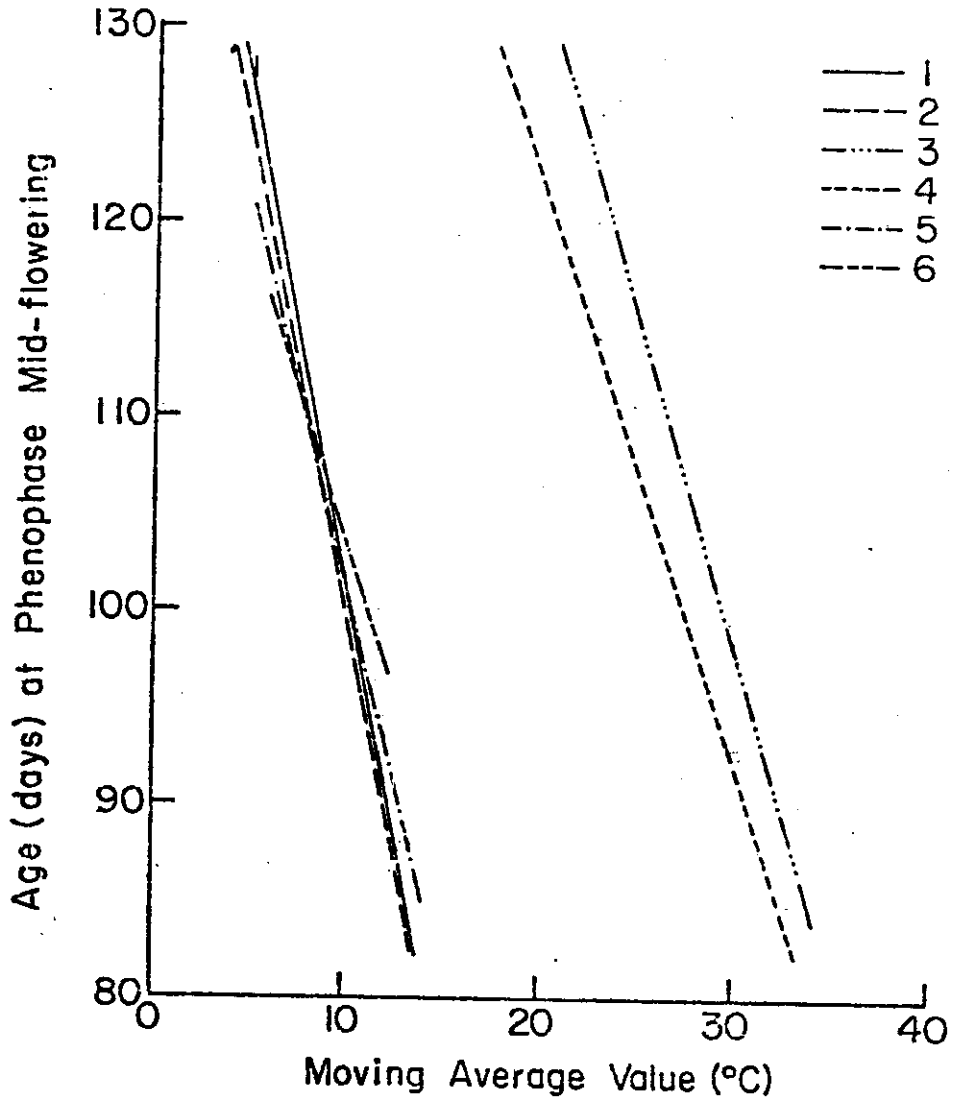
correlations were with the cool and warm 5-day averages calculated from maximum temperatures. CLC: There were correlations with cool and warm averages of all lengths (max), and cool 20- and 25-day averages and the 20°C cumulative sum (mean); the best correlation was with the cool and warm 25-day average calculated from maximum temperatures.

Regression line slopes.--Regression line slopes were positive in the cumulative sum variables and all UHC regressions in the phenophase "last flower," and negative in the remaining regressions. The majority of the regressions were thus negative and indicate that with increasing age, lower temperature values were required to obtain a given phenophase. The regression of the best correlated variable in each population in the phenophase "mid-flowering" is plotted in Fig. 2. Mid-flowering was used because this phenophase had the greatest number of correlated variables. The High Canyon populations UHC and THC are distinct from the other populations (Fig. 2).

DISCUSSION

Reproductive phenological progression is primarily controlled by maximum or mean temperatures in these *Clarkia*. Minimum temperatures did however have some control on the timing of "first flowers." Perhaps freezing night temperatures are detrimental to flowering and sensitivity to night temperatures has evolved in these populations. After frost danger has passed, subsequent reproductive development may be a function of daytime temperatures.

Moving averages were better correlated with the age at which a phenophase occurred than were cumulative sums. Correlation coefficients



Population		Temperatures	Variable	r	Slope	Intercept	Standard Error
UPC	1	Mean	17	-0.9986	-5.1	152.	1.0
EPC	2	Mean	30	-0.9925	-5.0	150.	2.0
UHC	3	Max	8	-0.9992	-3.5	203.	0.7
THC	4	Max	1	-0.9958	-3.0	182.	1.5
ULC	5	Mean	23	-0.9989	-4.1	142.	0.8
CLC	6	Max	32	-0.9581	-3.3	136.	4.5

Fig. 2. Plot of temperature variables with highest correlation in each of the six populations in the phenophase "mid-flowering."

for cumulative sums, if significant, were low. This result contrasts with earlier work (Lindsey and Newman, 1956; Jackson, 1966) in which cumulative sums were significantly correlated with flowering phenophases; however, these studies did not consider moving averages. I suggest that neither moving averages nor cumulative sums are analogous to the physiological processes that regulate plant development. The fact that a fluctuating function, the moving average, is better correlated with phenological change than a monotonically increasing function, the cumulative sum, may provide further insight into the processes regulating plant development. Waggoner (in press) has suggested flowers appear when a required level of florigenic substance occurs in the plant, a suggestion that can be extended to include the phenophases in this paper. Perhaps in these *Clarkia* production of florigenic substance increases with a rise in temperature, and destruction follows a decrease in temperature. In the case of a cumulative sum plant (Lindsey and Newman, 1956; Jackson, 1966; Caprio, 1971), florigenic substance may be produced faster with increases in temperature, but is not destroyed by a decrease in temperature. Evidence for destruction of the florigenic substance upon cooling comes from *C. exilis* which aborted floral buds and reinitiated vegetative growth when subjected to an accidental cooling trend in a growth chamber (Sauer, unpublished).

These *Clarkia* appear to be more sensitive to moving average lengths than threshold temperatures, because variables significantly correlated with the onset of a phenophase frequently had r values equal to the fourth decimal place for threshold temperatures within a single length of moving average. Perhaps the production of the florigenic substance mentioned above is more a function of time at any temperature above freezing than temperature. However, such a temperature-independent

process is difficult to imagine in light of the temperature-dependence of flowering found here.

Phenophases differed in the number of significantly correlated variables, suggesting phenological change is controlled by combinations of temperature and other environmental factors specific to each phenophase. For example, the number of significant variables in each phenophase is as follows: "First flower," 21; "topping out," 83; "first fruit," 96; "mid-flowering," 191; "last flower," 193. The contrast between "first flower" (21), and "first fruit" (96) is particularly striking as these two phenophases are separated by only the abscission of the corolla from the inferior ovary to produce the green fruit. Perhaps, fruit set and anthesis differ in relative response to temperature change and other variables such as soil water potential and temperature, and insolation. This hypothesis should be tested experimentally. Significant cumulative sum variables were found only in "last flower," and variables calculated from temperature minima only were more frequent in "first flower" than in the other phenophases. Thus, not only do different combinations of environmental factors regulate each phenophase, but that the apparent effect of each factor depends on how it is estimated or measured.

These six *Clarkia* populations differed in the number of correlations at the 99% level of confidence. UPC (63) and ULC (35) would seem to be the most sensitive to temperature change in all phenophases, and CLC (0) the least sensitive to temperature. The *C. unguiculata* populations, with a total of 124 variables at the 99% level of confidence seem to be much more sensitive to temperature than the derivative populations with a total of 24 variables at the 99% level of confidence. Furthermore, the phenophases contrast in the number of variables at the

99% level of confidence ("first flower" - 3, "first fruit" - 2, "mid-flower" - 54, "topping out" - 21, "last flower" - 45) suggesting "first flower" is the least temperature-sensitive phenophase and "mid-flowering" is the most temperature-sensitive. Relative temperature sensitivity between phenophases and populations and the extent to which other environmental factors regulate phenological progression may be related to the adaptive strategies of these populations, and to long-term microclimatic means of the native habitats. Perhaps high sensitivity to temperature in one phenophase, indicated by highly significant correlations with temperature variables for that phenophase, is altered (with phenological development) to sensitivity to another environmental factor, such as soil water potential.

Differences in significantly correlated moving average lengths between populations did not fit with differences in habitat. The Parker Creek Canyon populations at the highest elevation site could be expected to have the lowest threshold temperature, but did not. There also was no fit between the best correlated moving average lengths and habitat characteristics; populations from the slower warming Parker Creek Canyon site might be expected to have a longer moving average length, but did not. Perhaps these populations differ not in the characteristics of temperature such as threshold and moving average but in the relative sensitivity to temperature for flowering. In other words, differences in flowering time may be the result of each population keying differently on available environmental stimuli such as temperature, soil water potential, soil temperature, and insolation.

The negative slopes of the regression lines (Fig. 2) may be evidence for temperature acclimation (plants grown in low temperatures are

phenologically sensitive to low temperatures) or evidence of an age effect on flowering time or both. The inverse relationship between temperature requirements and age (or lateness of growing season) has also been reported for longleaf pine (*Pinus palustris* Mill) (Boyer, 1973). The positive slopes of the significant variables in the UHC samples in the phenophase "last open flower" contrast with the negative slopes of the other populations and do not appear to be related to temperature or soil water potential characteristics of the UHC habitat. Apparently, UHC requires decreasing temperatures with increasing age until the phenophase "last flower" is obtained, when a shift to increased temperature requirement with increasing age occurs.

The inverse relationship between temperature requirements and age in these *Clarkia* indicated by the negative slopes may have a selective value with respect to the springtime decrease in soil water potential as follows: Soil water potentials are high and near field capacity through most of the winter and spring up to the time of *Clarkia* flowering (Vasek and Sauer, 1971). If young plants were to flower at the same temperature stimulus as plants delayed by normal cool temperatures, an unusually warm spring could cause flowering initiation before optimum use of soil water reserves had been made with respect to carbohydrate accumulation. The photosynthetic capacity of these *Clarkia* is greatly reduced after anthesis by the rapid loss of leaves at anthesis; smaller, foliaceous floral bracts alone remain during the flowering period for additional carbohydrate accumulation. Assuming a relationship between seed productivity and accumulated carbohydrate, it would be adaptive to optimize the relationship between the onset of flowering and carbohydrate accumulation so that flowering would occur before drought prevented seed set, but after soil water reserves had been used to accumulate a maximum

amount of carbohydrate. Temperature rise in these habitats would seem to be closely related to depletion of soil water reserves so that flowering in response to temperature would provide the flexibility necessary to survive yearly variation in the onset of summer drought.

The relationship between phenological change, temperature, and age can be synthesized with native habitat characteristics to construct a model. At the time these populations are flowering, air temperatures are increasing, soil water potentials are decreasing (higher rates of evaporation and transpiration caused by higher air temperatures), and the probability of additional rainfall decreases (U.S. Weather Bureau, 1970). These annual species must flower and mature enough seed before the onset of summer drought to reestablish next year's population. Seed storage in the soil may reduce the need for abundant seed production each year. However, in the event drought was unusually early and severe for several years in succession, seed storage in the soil might not be adequate, and seed production, keyed to temperature before drought occurred, would be essential to maintain the population. The onset of drought varies from year to year; climatic shifts of short and long duration change the seasonal precipitation pattern and quantity, and the associated temperatures and cloud cover and insolation. By flowering in response to temperature, these populations can flower before the onset of drought whether drought comes early or late.

This model is presented in graphical form in Fig. 3. Line 1 represents the decrease in temperature requirements for flowering as modified by age. Line 2 represents change in the appropriate temperature variable with the progression of the growing season. Flowering occurs at the intersection of these two lines. Line 3 represents the decreasing probability of additional rainfall to replenish decreasing soil water

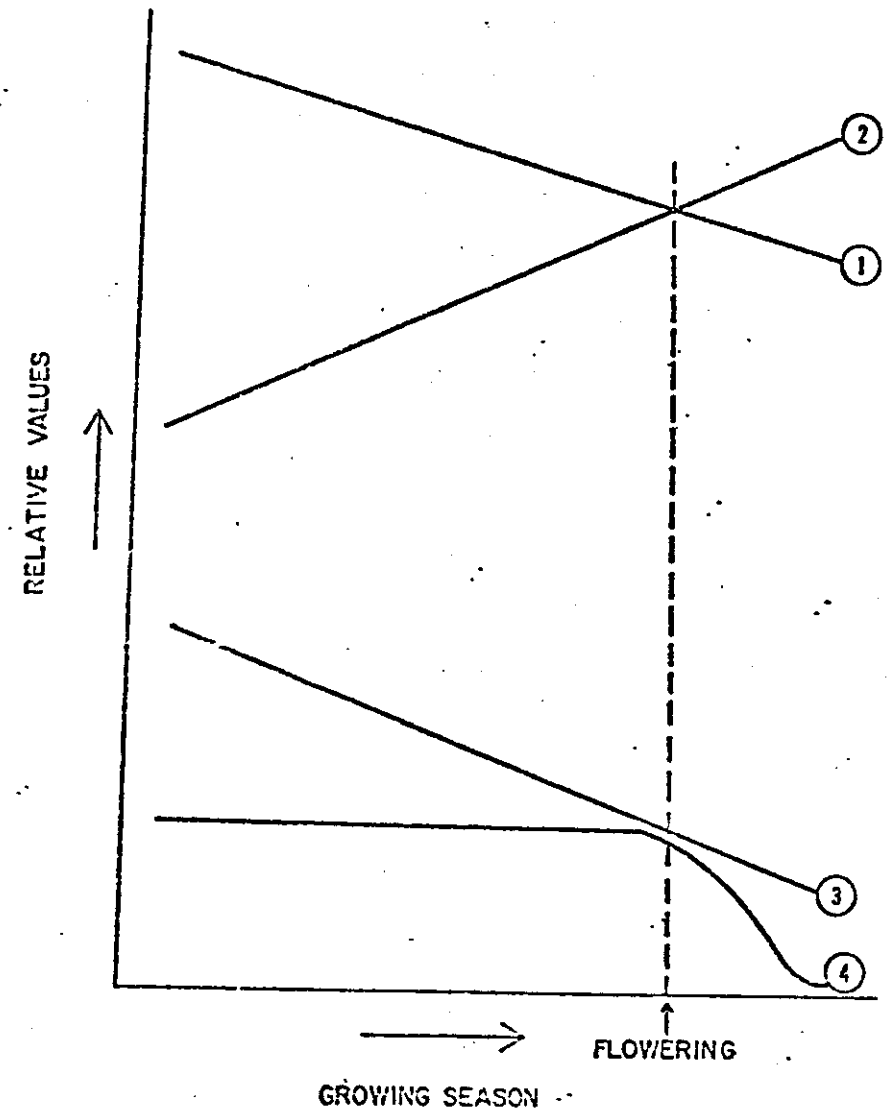


Fig. 3. Graphical representation of relationship changes between flowering time and environment. See text for explanation.

reserves (line 4). Flowering time on the abscissa of Fig. 3 varies from year to year, in response to variations in temperature, precipitation, and soil water loss. The value of this model is its organization of factors that at present appear to regulate, in large part, reproductive success and strategy in these *Clarkia*. To be useful in other phenological studies, it should be developed from a graphic to a simulation model, and the results compared to independent field data to test the validity of the concepts in the model.

CONCLUSIONS

1. Daily maximum or mean air temperatures, and occasionally daily minimum temperatures, are significantly correlated with reproductive phenological change in these *Clarkia*.
2. Moving averages are better correlated with reproductive phenological change than are cumulative sums.
3. Age of the plants, or temperature acclimation, or both, interact with temperature to regulate, in part, reproductive phenological change.
4. Absence of obvious interpopulation differences and trends in threshold values and moving average lengths suggest the temperature environment at time of flowering is the same in each population and the observed difference in flowering time under uniform culture in these populations results from different response levels to other factors such as soil water potential, soil temperature, and insolation.
5. The flexibility necessary to survive climatic fluctuations is derived from flowering in response to temperature. Seeds are thus matured before the onset of lethal summer drought.

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APPENDIX I

Listing of the FORTRAN Program

```
TA005,T100,CM130000                    .RHS PHENOLOGY MODEL
FTN.
LGO.
&
      PROGRAM PHEN(INPUT,OUTPUT,TAPE1=INPUT,TAPE2=OUTPUT)
      DIMENSION RA(35,25),YY(5,4,6),TEMPD(4,163),TEMPN(4,163)
      DIMENSION DOA(5),THRSL(7),VARS(4,163,42),XX(4,6,42)
      DIMENSION RSLT(6,42,4),IPT(42)
      M=0
3     M=M+1
C... READ DAY AND NIGHT TEMPERATURES FOR FOUR TREATMENTS.
      READ(1,200)N,TEMPD(1,N),TEMPN(1,N),TEMPD(2,N),TEMPN(2,N),TEMPD(
     13,N),TEMPN(3,N),TEMPD(4,N),TEMPN(4,N)
      IF(M.LT.163)GO TO 3
200   FORMAT(I3,2X,8F5.0)
C... READ THRESHOLD TEMPERATURES AND MOVING AVERAGE LENGTHS TO BE USED.
      READ(1,100)(THRSL(I),I=1,7)
      READ(1,100)(DOA(I),I=1,5)
100   FORMAT(20F4.0)
C... READ PHENOLOGY DATA.
      DO 101 IR=1,5
      DO 102 IS=1,4
      READ(1,150)(YY(IR,IS,IT),IT=1,6)
102   CONTINUE
101   CONTINUE
150   FORMAT(10X,6F10.1)
      WRITE(2,300)(DOA(I),I=1,5)
      WRITE(2,320)(THRSL(I),I=1,7)
300   FORMAT(1H ,"PERIODS OF DAYS USED IN MOVING AVERAGES",5F6.1)
320   FORMAT(1H ,"LOW TEMPERATURE THRESHOLDS FOR GROWTH",11F6.1)
C... CALCULATE MOVING AVERAGE VARIABLES.
      JKS=0
55    JKS=JKS+1
      DO 5 ICH=1,4
      DO 6 IDAY=1,163
      TMAX=(TEMPD(ICH,IDAY)-32.)/1.8
      TMIN=(TEMPN(ICH,IDAY)-32.)/1.8
      IF(JKS.EQ.1)TEMP=TMAX
      IF(JKS.EQ.2)TEMP=TMIN
      IF(JKS.EQ.3)TEMP=(TMAX+TMIN)/2.
      IV=0
      DO 7 IA=1,5
      DO 8 IB=1,7
      IV=IV+1
      NDAY=DOA(IA)-1
      DO 9 IE=1,NDAY
C     RA(IV,IE)=RA(IV,IE+1)
      NDAY=NDAY+1
      RA(IV,NDAY)=AMAX1(TEMP-THRSL(IB),0.0)
      Q=0.0
      DO 10 J=1,NDAY
```

```
10      Q=Q+RA(IV,J)
        VARS(ICH,IDAY,IV)=Q/DOA(IA)
8       CONTINUE
7       CONTINUE
C... CALCULATE CUMULATIVE SUM VARIABLES.
        DO 11 ISUM=1,7
        IV=IV+1
        IDAYY=IDAY-1
        IF(IDAYY.LT.1)IDAYY=1
        VARS(ICH,IDAY,IV)=VARS(ICH,IDAYY,IV)+AMAX1(TEMP-THRSL(ISUM),0.0)
11      CONTINUE
6       CONTINUE
5       CONTINUE
C... FIND INDEPENDENT FOR PHENOLOGY STAGE AND LOAD IT INTO MATRIX XX.
        DO 50 IPHEN=1,5
        DO 12 ICH=1,4
        DO 13 ISPS=1,6
        MID=YY(IPHEN,ICH,ISPS)+.5
        DO 14 IV=1,42
        XX(ICH,ISPS,IV)=VARS(ICH,MID,IV)
14      CONTINUE
13      CONTINUE
12      CONTINUE
        SN=4.0
        DO 15 ISPS=1,6
        DO 16 IV=1,42
        SUMX=0.0
        SUMY=0.0
        SUMXX=0.0
        SUMYY=0.0
        SUMXY=0.0
        DO 17 ICH=1,4
        X=XX(ICH,ISPS,IV)
        Y=YY(IPHEN,ICH,ISPS)
        SUMX=SUMX+X
        SUMY=SUMY+Y
        SUMXX=SUMXX+X*X
        SUMYY=SUMYY+Y*Y
        SUMXY=SUMXY+X*Y
        IF(ICH.EQ.4) GO TO 18
        GO TO 17
18      A=SUMXY-SUMX*SUMY/SN
        B=SUMXX-SUMX*SUMX/SN
        C=SUMYY-SUMY*SUMY/SN
        IF(B.EQ.0..OR.C.EQ.0.) GO TO 21
C... CALCULATE REGRESSION COEFFICIENT OR SLOPE OF LINE.
        BB=A/B
        RSLT(ISPS,IV,2)=BB
C...CALCULATE COEFFICIENT OF CORRELATION
        RR=A*A/(B*C)
        RRR=SQRT(RR)
        RSLT(ISPS,IV,1)=RRR
C... CALCULATE INTERCEPT OF LINEAR REGRESSION.
        RSLT(ISPS,IV,3)=SUMY/SN-BB*SUMX/SN
```

```
C... CALCULATE STANDARD ERROR OF ESTIMATE.
      SD=SQRT((C-A*A/B)/(SN-2.))
      RSLT(ISPS,IV,4)=SD
      GO TO 17
21    RSLT(ISPS,IV,1)=RSLT(ISPS,IV,2)=RSLT(ISPS,IV,3)=RSLT(ISPS,IV,4)=
     & 0.0
17    CONTINUE
16    CONTINUE
15    CONTINUE
C... SORT RESULTS WITH CORRELATION IN DECREASING ORDER.
      DO 19 ISPS=1,6
      ICOUNT=0
      DO 25 J=1,42
25    IPT(J)=J
20      DO 30 I=1,41
      IQ=IPT(I)
      IQ2=IPT(I+1)
      IF(RSLT(ISPS,IQ,1).GE.RSLT(ISPS,IQ2 ,1)) GO TO 30
      IPT(I+1)=IQ
      IPT(I)=IQ2
      ICOUNT=ICOUNT+1
30    CONTINUE
      IF(ICOUNT.EQ.0) GO TO 40
      ICOUNT=0
      GO TO 20
40    CONTINUE
      IF(IPHEN.EQ.1)WRITE(2,501)
      IF(IPHEN.EQ.2)WRITE(2,502)
      IF(IPHEN.EQ.3)WRITE(2,503)
      IF(IPHEN.EQ.4)WRITE(2,504)
      IF(IPHEN.EQ.5)WRITE(2,505)
      IF(JKS.EQ.1)WRITE(2,601)
      IF(JKS.EQ.2)WRITE(2,602)
      IF(JKS.EQ.3)WRITE(2,603)
      IF(ISPS.EQ.1)WRITE(2,401)
      IF(ISPS.EQ.2)WRITE(2,402)
      IF(ISPS.EQ.3)WRITE(2,403)
      IF(ISPS.EQ.4)WRITE(2,404)
      IF(ISPS.EQ.5)WRITE(2,405)
      IF(ISPS.EQ.6)WRITE(2,406)
      WRITE(2,407)
      DO 45 I=1,42
      JA=IPT(I)
C... CHECK FOR STATISTICAL SIGNIFICANCE.
      IF(ABS(RSLT(ISPS,JA,1)).LT..95) GO TO 195
C... CHECK FOR BIOLOGICAL SIGNIFICANCE.
      DO 42 ICHS=1,4
      IF(JA.LE.35.AND.XX(ICHS,ISPS,JA).LT.2.0) GO TO 190
      IF(JA.GT.35.AND.XX(ICHS,ISPS,JA).LT.5.) GO TO 190
42    CONTINUE
      WRITE(2,400)JA,(RSLT(ISPS,JA,L),L=1,4),(XX(M,ISPS,JA),
     1YY(IPHEN,M,ISPS),M=1,4)
190   CONTINUE
45    CONTINUE
195   CONTINUE
```

```
19     CONTINUE
50     CONTINUE
       IF(JKS.LT.3)GO TO 55
400    FORMAT(1H ,I5,4F10.4,8F10.1)
401    FORMAT(1H ,"CLARKIA UNGUICULATA FROM PARKER CREEK CANYON")
402    FORMAT(1H ,"CLARKIA EXILIS FROM PARKER CREEK CANYON")
403    FORMAT(1H ,"CLARKIA UNGUICULATA FROM HIGH CANYON")
404    FORMAT(1H ,"CLARKIA TEMBLORIENSIS FROM HIGH CANYON")
405    FORMAT(1H ,"CLARKIA UNGUICULATA FROM LOW CANYON")
406    FORMAT(1H ,"CLARKIA CALIENTE FROM LOW CANYON")
407    FORMAT(/," VARIABLE    R         SLOPE    INTERCEPT    ERROR          X 1
      1        Y 1         X 2         Y 2         X 3         Y 3         X 4
      - Y 4")
501    FORMAT(1H1," SAMPLE AGE WHEN FIRST FLOWERS APPEAR.")
502    FORMAT(1H1," SAMPLE AGE WHEN FIRST FRUIT APPEAR.")
503    FORMAT(1H1," SAMPLE AGE WHEN PROPORTIONS OF BUDS AND FRUIT EQUAL")
504    FORMAT(1H1," SAMPLE AGE AT FIRST DECLINE IN NUMBER OF BUDS.")
505    FORMAT(1H1," SAMPLE AGE WHEN LAST FLOWERS PRESENT.")
601    FORMAT(1H ,"MAXIMUM TEMPERATURES ONLY USED.")
602    FORMAT(1H ,"MINIMUM TEMPERATURES ONLY USED")
603    FORMAT(1H ,*MEAN OF MAX AND MIN TEMPERATURES USED.*)
       END
       OBSERVED TEMPERATURES
       THRESHOLD TEMPERATURES.
       MOVING AVERAGE LENGTHS.
       PHENOLOGY DATA.
*
```