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Reynolds, J. 1974. A Generalized Phenology Submodel for Desert Plants. U.S. International Biological Program, Desert Biome, Utah State University, Logan, Utah. Reports of 1973 Progress, Volume 1: Central Office/Modelling, RM 74-59.

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1973/74 PROGRESS REPORT

# A GENERALIZED PHENOLOGY SUBMODEL FOR DESERT PLANTS

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**US/IBP DESERT BIOME**
**RESEARCH MEMORANDUM 74-59**

**in**

**REPORTS OF 1973 PROGRESS**
**Volume 1: Central Office, Modelling**
Auxiliary Submodels Section, pp. 67-79

**MAY, 1974**

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Citation format: Author(s). 1974. Title.
US/IBP Desert Biome Res. Memo. 74-59.
Utah State Univ., Logan. 13 pp.

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## INTRODUCTION

One of the major objectives of the International Biological Program (IBP) is to develop large-scale systems models to simulate carbon flow through natural ecosystems. Research emphasis toward this end has focused on many important ecosystem processes, e.g., primary productivity, population dynamics, nutrient cycling, etc., all of which must be incorporated into the models. In order to predict the activities of the different trophic levels in an ecosystem, temporal realism for ecosystem phenomena must be achieved. Because of this need, it has been recognized from the outset that phenological information would be an integral part of any large systems model. Consequently, there has been considerable interest in phenology within the representative biomes of the US/IBP in both field studies (US/IBP Phenology Committee, 1972) and mathematical modeling (Lieth, 1974). A Desert Biome approach developed for modeling phenology will be presented in this paper.

The response of plants to environmental stimuli is reflected in a change in their activity. This could involve, for example, the initiation of flowering buds, the germination of seeds, or the onset of senescence. These changes, or phenophases (Lieth, 1970), within the life cycles of plants are important in delimiting many ecosystem events such as the beginning and end of growing seasons and energy transfers between trophic levels (Bliss, 1967; Lieth, 1970, 1971). The use of meteorological data to predict some of these phenological changes has been practiced for many years where, in general, correlations between certain phenophases and specific environmental triggers are sought. Probably the most well-known example is the concept of heat-units or degree-days (Wang, 1960) which characterizes plant development as a function of its thermal environment. Other factors, such as the cumulative sum of air temperature (Jackson, 1966) and the cumulative sum of the product of daily air temperature and insolation (Capiro, 1971), have also been used to predict flowering time in certain species of plants with varying degrees of success.

It is clear that the seasonal and yearly stochastic variations in the physical environment to which plants are coupled make prediction of phenophases based solely on calendar dates unsatisfactory. This is especially true in desert ecosystems where extreme conditions prevail. Consequently, it is necessary to have phenology as a variable which can be determined as a function of current environmental conditions. The role of a phenology submodel in an ecosystems model is to provide current information on the phenological status or developmental stage of each primary producer. This information will, in turn, be used to regulate other activities in the model, e.g., photosynthesis, carbohydrate translocation, etc., thereby obtaining realistic simulations of biomass dynamics.

## MODELING PHENOLOGY IN DESERT ECOSYSTEMS

Deserts are essentially "water-controlled" ecosystems because of the infrequent, discrete and unpredictable inputs of water (Noy-Meir, 1973) and the tight coupling of the organisms to this available moisture. For example, creosotebush (*Larrea divaricata*) in the Colorado Desert in southern California was found to flower any time of the year in response to increased soil moisture (Oechel et al., 1972), and Brum (1973) has documented the importance of spring and summer rainfall in the germination and establishment of saguaro (*Carnegiea gigantea*). Probably few exceptions exist where major plant activities are not a direct response to soil moisture levels. This concept is examined in depth by Noy-Meir (1973). Of course, in spite of the importance of water, other environmental variables can have a modifying effect on the physiological response of a plant. In fact, *Larrea* would not have exhibited a year-around flowering capacity had air temperature been limiting at the time of water influx (Oechel et al., 1972).

Bridges et al. (1972) have proposed modeling phenology in deserts using a "pulse-reserve" paradigm in which various qualitative phenological states of plants are triggered by different combinations of environmental variables -- water being the most important. If the relationships between phenological events and environmental triggers are known, as Beatley (1974) has worked out in great detail for Mojave Desert plants, this approach may prove to be useful, at least where such detailed data are available. As yet, however, it appears that this method would not provide the resolution necessary in a systems model (Reynolds, 1974). However, a phenology model for desert plants should ideally include the flexibility which would allow the inclusion of any threshold trigger that has been defined for certain phenophases in a species as well as quantitatively tracking phenological progression. In this paper a generalized phenology submodel is presented for desert plants. This submodel was developed to provide a framework for utilizing a variety of environmental data (e.g., soil moisture status, air temperatures, heat-sums, etc.) to simulate phenology and, in addition, provide for internal plant thresholds (e.g., carbon fraction ratios) which can further regulate the phenological status of a plant.

# MODEL DESCRIPTION

## SELECTION OF LIFE-FORMS AND PHENOPHASES

A balance must be made in any modeling attempt with regard to the detail needed to accurately represent important biological phenomena and the complexity of the model which can limit its understanding and usefulness. Thus, in addition to obtaining a realistic representation, a minimum level of complexity was sought in formulating the submodel.

The submodel was structured to handle two functional plant groups; perennials (including grasses, forbs, succulents, evergreen shrubs, winter- and drought-deciduous shrubs), and annuals (grasses and forbs). Although the division of all plants into an annual or perennial distinction is broad, it was justified on the basis of the closer functional similarity of, for example, the life cycle of a perennial grass and a perennial shrub than that of a perennial grass and an annual grass. Phenophases were selected to cover the general spectrum of morphological development of plants during their life cycles, from germination to vegetative growth (e.g., swelling leaf buds, emergent leaves, twig elongation, etc.) and reproductive growth (e.g., floral bud development, flowering, fruiting, etc.) to, finally, dormancy and/or senescence. Six phenophases were defined for annuals and five for perennials, as listed below:

| Annuals | Perennials |
|---|---|
| 1. Seed dormancy | 1. Dormancy |
| 2. Seedling | 2. Leafing-out |
| 3. Vegetative growth | 3. Vegetative growth |
| 4. Flowering | 4. Flowering |
| 5. Fruiting | 5. Fruiting |
| 6. Senescence/death | |

In addition, perennial seed germination was simulated, corresponding to the first three phenophases of the annuals listed above.

Dormancy was selected to represent a seed phase in annuals and winter- and/or drought-induced dormancy in perennials. Some evergreen desert shrubs remain metabolically active throughout the year (Chew and Chew, 1965; Oechel et al., 1972); thus the dormant stage actually represented a "quiescent" stage for certain plants in that a relatively fast response to increased levels of soil moisture and favorable soil and air temperatures was possible as reported for *Larrea* and *Ambrosia* (Ackerman and Bamberg, 1972).

The seedling phenophase for annuals was distinguished since the process of establishment must be achieved before vegetative growth was permitted. Leafing-out was an arbitrary term selected to represent the period immediately following the breaking of dormancy in perennials; for evergreens it may simply be an increased level of photosynthetic activity and greening of leaves, whereas for deciduous shrubs it would be the initial production of new leaves from internal reserves before active photosynthetic growth resumes.

The reproductive phase is important for consumer sections in the other portions of the ecosystem model; thus a separation was made into flowering and fruiting states. The eventual senescence and death of annuals were also separated into a distinct phenophase to complete their life cycle, whereas for perennials, a return to dormancy followed the reproductive phase.

# MODEL STRUCTURE

Plant development was viewed as a continuous phenomenon; i.e., the within-population variability in phenological progression rates was taken into account. To achieve this, the percentage of the population of a species in each phenophase at any given time was simulated, a technique used in a grassland phenology model (Sauer, 1973). This was also desirable in that much of the Desert Biome phenology data exists in this form (West and Fareed, 1973).

The phenophases are shown as compartments in Figure 1, where the interconnecting arrows indicate the natural progression of plant development. It was assumed that phenological progression, i.e., the transfer of the percentage of the population between the "compartments," could be predicted by empirical relationships between each phenophase of the certain endogenous and exogenous variables. These relationships took the form of rate coefficients which govern the magnitude of all transfers between compartments, or phenophases. The general form of a flow rate between two phenophases was:

$$F_{ij} = f(X_1, X_2, \ldots, X_n, \text{RATMX})$$

where

$F_{ij}$ = the flow rate from phenophase $i$ to $j$

$X_i$ = the environmental or endogenous parameters involved in this flow

RATMX = the maximum allowable rate of flow under optimum conditions

The flow rates were time-varying and were calculated on the basis of an interacting factor approach common in photosynthesis models (e.g., Brittain, 1974; Cunningham and Balding, 1972; Hari and Luukkanen, 1973; and Schultze et al., 1974). For example, the effect at time $t$ of soil water potential and air temperature on a certain physiological activity (e.g., vegetative growth) would each vary between 0 (no growth) and 1 (optimum growth), depending on the functional relationship involving the current measured values of soil water potential and air temperature and vegetative growth. The resultant overall flow rate ($F_{ij}$) would be the product of the two values and RATMX. A comparison of this technique to the limiting factor approach is given in Cunningham and Balding (1972).

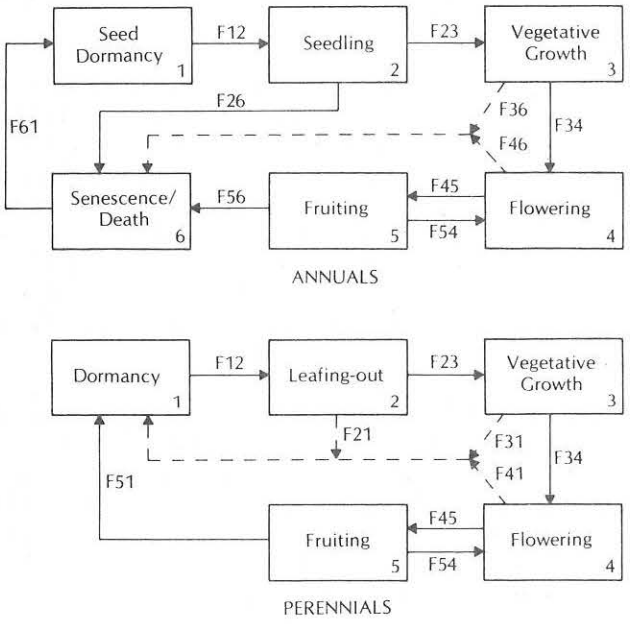


**Figure 1.** Annual and perennial phenophases represented as compartments. Arrows indicate the natural progression of plant development.

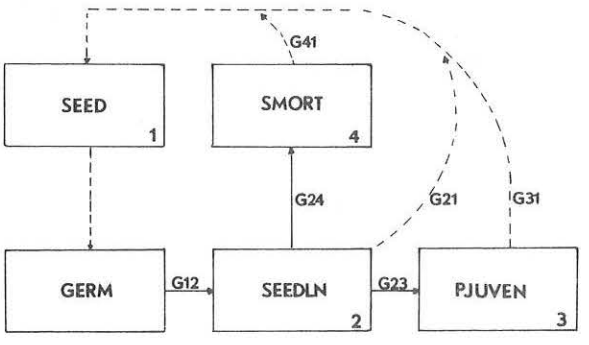


**Figure 2.** Compartmental representation of phenophases in perennial germination.

Computationally, the percentage of biomass in phenophase $i$ ($X_i$) at time $t$ is as follows:

$$X_i(t) = X_i(t\text{-}1) + \Sigma F_{ji}(t\text{-}1)\, X_j(t\text{-}1) - \Sigma F_{ij}(t\text{-}1)\, X_i(t\text{-}1)$$

where $F_{ij}(t\text{-}1)$ represents the flow rate coefficient from phenophase $i$ to $j$ at time $t$-1. This representation was simply a donor-controlled system of first-order difference equations. With this approach, the changing distribution of the percentage of the population between compartments represented phenological progression or plant development (Sauer, 1973).

## FLOW RATES

In this section each flow rate will be described with respect to specific phenological states. All flows are written as $F_{ij}$ (Fig. 1) or, in the case of perennial germination, $G_{ij}$ (Fig. 2). For convenience, associated FORTRAN names are given throughout for easy reference to the computer listing in Appendix 1 (e.g., the FORTRAN equivalent for the percentage of the population of the $i$th species in the $j$th phenophase is PHASE(I,J)).

### Germination and Establishment

*Annuals*

Germination ($F_{12}$) was simulated by predicting the percentage of total carbon in all shed seeds, PHASE(I,1), that became above-ground biomass. This percentage, GERM, was given by PREDGM x PHASE(I,1), where PREDGM was determined from a functional relationship which related soil water potential to germination response (Fig. 3a). Under optimum soil moisture conditions, a large percentage of the total seed reserve in the soil will germinate; under poor conditions, an increasingly smaller percentage germinates. Before germination can occur, however, soil temperature (SOILTE) must be above a certain threshold value (SOILTH) and coldhardening requirements, if any, must be satisfied. Germination can occur more than once during the growing season, which is directly dependent on influxes of soil moisture from rainfall.

For the coldhardening requirement to be satisfied, soil temperature must be less than a certain threshold (COLDT) for a predetermined number of days (COLDTH). In the model, a counter (ICOLDS) is used to register the number of days this threshold has been met within the preceding $n$th days. Elaboration of this is possible, e.g., combinations of high and low soil temperatures, which appear to be important for some desert annuals in New Mexico (Whitson, pers. comm.).

The general form for germination is:

$$F_{12} = f(\text{PREDGM, ICHARD, IGTEMP, RATMX})$$

where

PREDGM = $a + \beta \exp(\xi \cdot$ soil water potential)

ICHARD $= \begin{cases} 0 \text{ if ICOLDS} < \text{COLDTH} \\ 1 \text{ if ICOLDS} \geq \text{COLDTH} \end{cases}$

IGTEMP $= \begin{cases} 0 \text{ if SOILTE} < \text{SOILTH} \\ 1 \text{ if SOILTE} \geq \text{SOILTH} \end{cases}$

RATMX = the maximum rate of germination (percent day$^{-1}$)

Immediately following germination, establishment ($F_{23}$) is considered. It is assumed that soil moisture is the most significant variable affecting establishment success. The functional relationship used is shown in Figure 3b, relating soil moisture (SM23E) to the interphenophase flux. Note that a change in soil moisture near the drier portion of the range of soil water potential values is more significant in terms of the flow rate coefficient (SM23E) than when occurring near the wet end. Under moist conditions a large portion of the percentage ends in the vegetative growth stage ($F_{23}$; Fig. 1), whereas under dry conditions, mortality is high ($F_{26}$; Fig. 1). The flows are:

$F_{23}$ = f(SM23E, RATMX) and

$F_{26}$ = f(SM26E, RATMX)

where

SM23E = $a$ (1. — exp (— $\beta$ ·( $\xi$ — soil water potential)))

SM26E = 1. — SM23E

RATMX = the maximum rate of interphenophase transfer (percent day$^{-1}$)

*Perennials*

For perennials, the simulation of germination ($G_{12}$; Fig. 2) is essentially the same as discussed above for annuals. For each species a seed reserve exists (SEED), of which a certain percentage (GERM) will germinate in response to suitable conditions. Soil moisture determines the percent survival (SEEDLN to PJUVEN) or death (SEEDLN to SMORT), once germination has occurred. Once the growing season has passed, the total percentage that is distributed among the compartments is shunted back to SEED to represent the total seed reserve for the next season (the absolute value of which is determined by other submodels). In general, perennial germination and establishment are as follows:

$G_{12}$ = f(PREDGM, ICHARD, IGTEMP, GERMRX)

$G_{23}$ = f(SM23E, GERMRX)

$G_{24}$ = f(SM24E, GERMRX)

where

PREDGM, ICHARD, IGTEMP, SM23E are as defined for annuals

SM24E = SM26E, where SM26E is as defined for annuals

GERMRX is the maximum rate of each interphenophase flux (percent day$^{-1}$)

Breaking Dormancy

Perennials break winter dormancy ($F_{12}$; Fig. 1) as a response to various environmental variables. The thermal environment is assumed to be important in this respect (Jackson, 1966; Taylor, 1969). The concept of degree-days is used, as in Waggoner (1974), to predict the appearance of the leafing-out phenophase:

$$\text{Heatsum} = \int_{t_o}^{t} (T - T_h)\, dt$$

where

T = current air temperature

$T_h$ = the threshold air temperature

t = current time

$t_o$ = arbitrarily taken as t-60

When the heatsum (SMHEAT) has reached a specified critical level (THHEAT), leafing-out will occur. Other parameters can modify the response of the plant, e.g., soil moisture (SM12; Fig. 3c) and photoperiod (IPHOT1). The general form for leafing-out is:

$F_{12}$ = f(IDTEMP, SM12, IPHOT1, RATMX)

where

IDTEMP $= \begin{cases} 0 \text{ if SMHEAT} < \text{THHEAT} \\ 1 \text{ if SMHEAT} \geq \text{THHEAT} \end{cases}$

SM12 = $a + \beta \exp(\xi \cdot$ soil water potential)

IPHOT1 $= \begin{cases} 0 \text{ if daylength} < \text{specific photoperiod (PHOTOR)} \\ 1 \text{ if daylength} \geq \text{specific photoperiod (PHOTOR)} \end{cases}$

RATMX = the maximum rate of leafing-out (percent day$^{-1}$)

### Vegetative Growth and Flowering

Once perennial dormancy has been broken, transfer from the leafing-out phenophase to vegetative growth ($F_{23}$; Fig. 1) is related to the increase in physiological activities of the plant. It is assumed that this is reflected in the respiration:photosynthesis ratio (CR23) in that, before the breaking of dormancy, respiratory losses and photosynthetic gains probably balance each other (R=P) in evergreen shrubs, whereas in other perennials, respiratory losses are probably higher (R > P). The functional relationship between R:P and CR23 is shown in Figure 4 where, as the ratio decreases, the transfer to vegetative growth increases. In addition, soil water potential is employed as a rate-determining factor (SM23; Fig. 3c). The flux to vegetative growth is given as:

$$F_{23} = f(CR23, SM23, RATMX)$$

where

$$CR23 = a + \beta \exp(\xi \cdot R{:}P))$$

$$SM23 = a + \beta \exp(\xi \cdot \text{soil water potential})$$

RATMX = the maximum rate of transfer (percent $day^{-1}$)

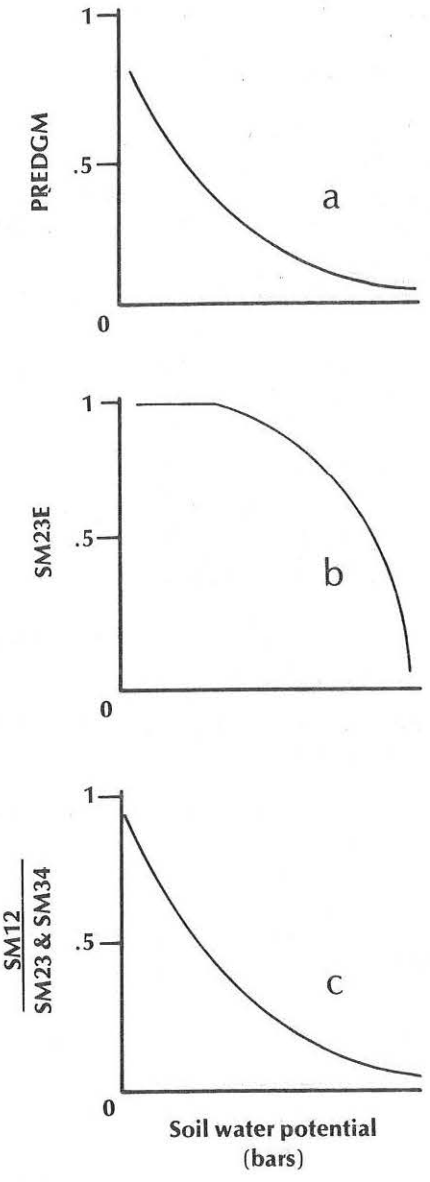


Figure 3. Functional relationship of soil water potential to: (a) percent seed reserve germination; (b) effect of soil moisture on establishment success; and (c) effect of soil moisture on interphenophase flows (1,2), (2,3) and (3,4).

### Flowering and Fruiting

The criteria used in determining the flowering phenophase ($F_{34}$; Fig. 1) are photoperiod (IPHOT2), soil moisture (SM34; Fig. 3c) and flower development (CR34; Fig. 5), in the form of the ratio of reserve carbon in all organs (CVEGO(I,IR)) to the total carbon in the plant (AVEGO(I)). The carbon ratio was chosen on the basis of the results of earlier executions of the photosynthesis and translocation submodels, where this ratio was highly correlated to flowering. The flow rate is given by:

$$F_{34} = f(IPHOT2, SM34, CR34, RATMX)$$

where

$$IPHOT2 = \begin{cases} 0 \text{ if daylength} < \text{specific threshold (PHOTOF)} \\ 1 \text{ if daylength} \geq \text{specific threshold (PHOTOF)} \end{cases}$$

$$CR34 = a\ (1. - \exp(\beta \cdot \text{carbon ratio})$$

$$SM34 = a + \beta \exp(\xi \cdot \text{soil water potential})$$

RATMX = the maximum rate of flux (percent $day^{-1}$)

Soil moisture (SM45) is probably the determining factor as far as the allocation of carbon to flowers and/or fruits. Under moist conditions, continuous flowering and fruiting are common for many desert plants (as reported for grassland plants; Sauer, 1973), although the total energy allocated to reproduction may be less than that under drier moisture regimes, at least for some plants (Cunningham et al., 1974). Consequently, as shown in the relationship between soil moisture and flowering-fruiting (Figs. 6-7), as the soil dries there is a rapid transfer to fruiting; under moist conditions flowering will continue, with a certain percentage transferred to fruiting at all times. Plant water potential

might be a better parameter in some plants, e.g., cacti. The rates are given by:

$$F_{45} = f(SM45, RATMX)$$

$$F_{54} = f(SM54, RATMX)$$

where

$$SM45 = a\ (1. - \exp(\beta \cdot \text{soil water potential})$$

$$SM54 = 1. - SM45$$

RATMX = the maximum rate of flowering and fruiting (percent day$^{-1}$)

### Senescence and Dormancy

*Annuals*

Senescence ($F_{56}$; Fig. 1) is generally keyed to an internal depletion of carbon when physiological activity is reduced. Therefore, a carbon ratio (CR56 -- fruit carbon:total plant carbon; Fig. 8) was used to simulate senescence. Freezing air temperatures will result in a rapid transfer from all compartments to senescence ($F_{i6}$; Fig. 1). Once this occurs the percentage is distributed back to seed dormancy as a mechanical process to be used to simulate the start of the life cycle for the next occurrence. The general forms of the rates are:

$$F_{56} = f(CR56, RATMX)$$

$$F_{61} = f(RATMX)$$

where

$$CR56 = a + \beta \exp(\text{carbon ratio})$$

RATMX = the maximum rate of flux (percent day$^{-1}$)

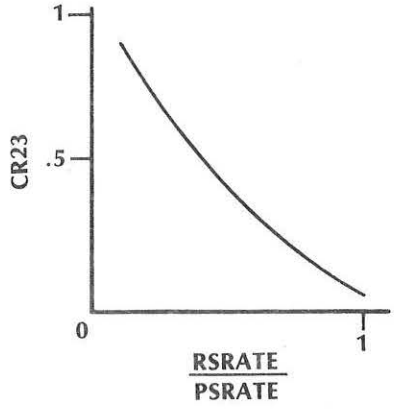


Figure 4. Effect of respiration: photosynthesis ratio on interphenophase flow (2,3).

*Perennials*

For perennials, as the ratio of reserve carbon in the leaf to total plant carbon decreases, the plant rapidly becomes dormant ($F_{51}$; Fig. 1). The form of this relationship is shown in Figure 7. If freezing air temperatures (a species-specific value -- FREEZE) occur, rapid transfer of all percentage of the population is made to the dormant state (Fig. 1). In general:

$$F_{51} = f(CR51, RATMX)$$

$$F_{i1} = f(FREEZE, RATMX)$$

where

$$CR51 = a + \beta \exp(\text{carbon ratio})$$

RATMX = the maximum rate of flux (percent day$^{-1}$)

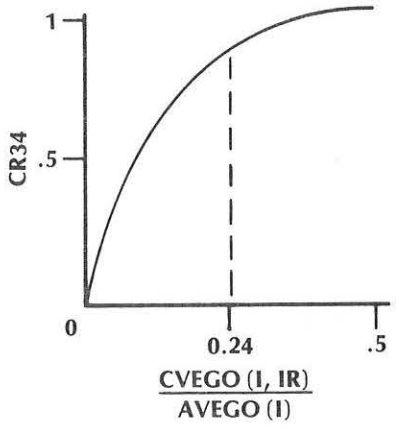


Figure 5. Effect of the ratio of reserve carbon in all organs to the total carbon in the plant on interphenophase flow (3,4).

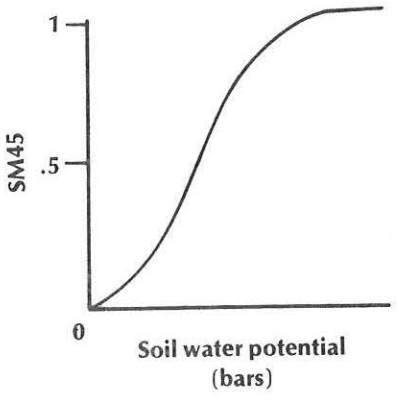


Figure 6. Effect of soil water potential on flowering and fruiting -- interphenophase flows (4,5) and (5,4).

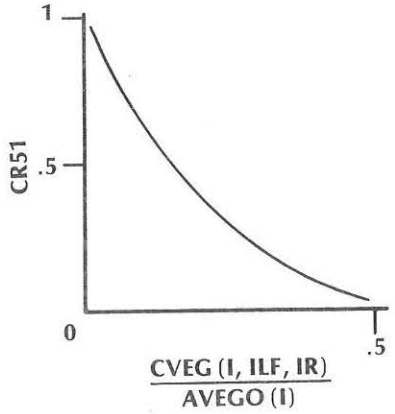


Figure 7. Effect of ratio of reserve carbon in the leaf to total plant carbon in interphenophase flow (5,1).

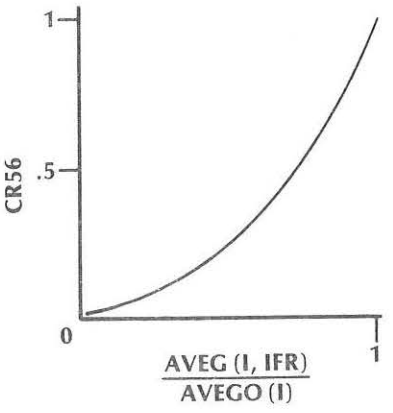


Figure 8. Effect of fruit carbon:total plant carbon on interphenophase flow (5,6).

## MODEL BEHAVIOR

To illustrate the output of this submodel, the general phenological responses of *Hilaria mutica* will be discussed and compared to the simulated model output. *Hilaria* is a large perennial bunchgrass occurring on the west and east edges of the playa bottom at the Jornada Validation Site. It generally begins growth in the early spring as soil and air temperatures increase -- the rate of growth being limited by soil moisture. A rapid flush of growth often occurs in late summer in response to increased soil moisture and higher air temperatures near the optimum for photosynthesis (Cunningham et al., 1974). *Hilaria* has a small amount of green material at the base of the large clumps throughout the winter months, but this is probably insignificant in terms of photosynthetic gains and is not considered in the submodel (i.e., the plant is considered to be completely dormant during certain periods).

In Figure 9 the four-year model simulation of *Hilaria* phenology is shown. The percentage of the population biomass in either a vegetative (VEG) or a dormant stage (DOR) was plotted, where values of VEG less than 100%, when DOR was 0%, represented the percentage of the population biomass which was in the reproductive phenophases of flowering and/or fruiting. The rainfall events which occurred during the years 1971-72 and 1972-73 (March 20 to March 20; Fig. 9) provide excellent contrasts for examining the simulated phenological responses of this species. For reference, specific events referred to in Figure 9 are labeled e1, e2, etc. In the simulation, *Hilaria* broke winter dormancy both years at approximately the same time (March 7-14, e1 and e6) in an apparent response to warmer temperatures. However, the subsequent phenological events were quite different during these two years.

In 1971-72, breaking of dormancy occurred slowly over a period of about 11 weeks (e1 to e2). The first reproductive growth occurred in late July, 18 weeks after breaking dormancy as indicated by the drop in the percentage of the population which was solely in a vegetative state (e3). This corresponded to the first significant rainfall during that summer. Reproductive growth occurred in various magnitudes in response to rainfall up to late November (e4). At this time, the plant species went completely dormant in response to freezing soil and air temperatures (e5).

In 1972-73, the first reproductive pulse (e7) was seven weeks after the breaking of dormancy (e6), which was followed by three large pulses (e8-e10). This was apparently in response to optimal soil moisture conditions since precipitation occurred throughout the summer starting in mid-June (week 116) and continued into late fall. This unusually wet summer resulted in the simulation of reproductive growth throughout the entire summer as evidenced by the absence of a 100% vegetative population.

Although field data for *Hilaria* phenology do not exist to validate this four-year simulation on a week-to-week basis, field observations and standing crop estimates from 1970 to 1972 (Fig. 10) provide a basis for evaluation. The submodel adequately simulated the periods of *Hilaria* dormancy. This can be seen by comparing the weeks of absolute dormancy simulated in Figure 9 to the absence of live green material in Figure 10. The simulation of reproductive phenology is not as easily evaluated, but the submodel did produce the general observed trends. For example, the greatest reproductive biomass was produced during the wettest summer (Fig. 10; 1972) while the submodel predicted substantial reproductive phenology for this summer (1972-73 simulation year) as discussed earlier.

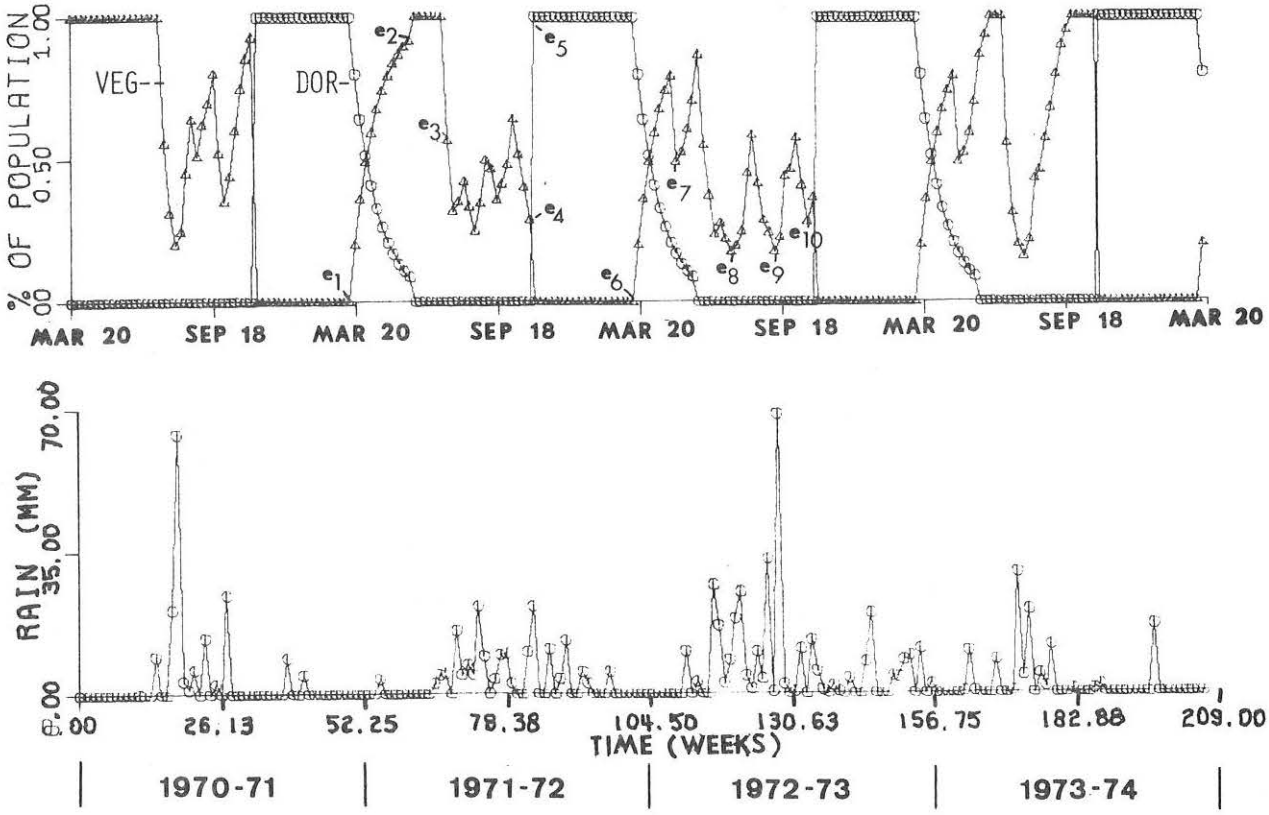


Figure 9. Four-year simulation of phenology for *Hilaria*. See text for explanation.

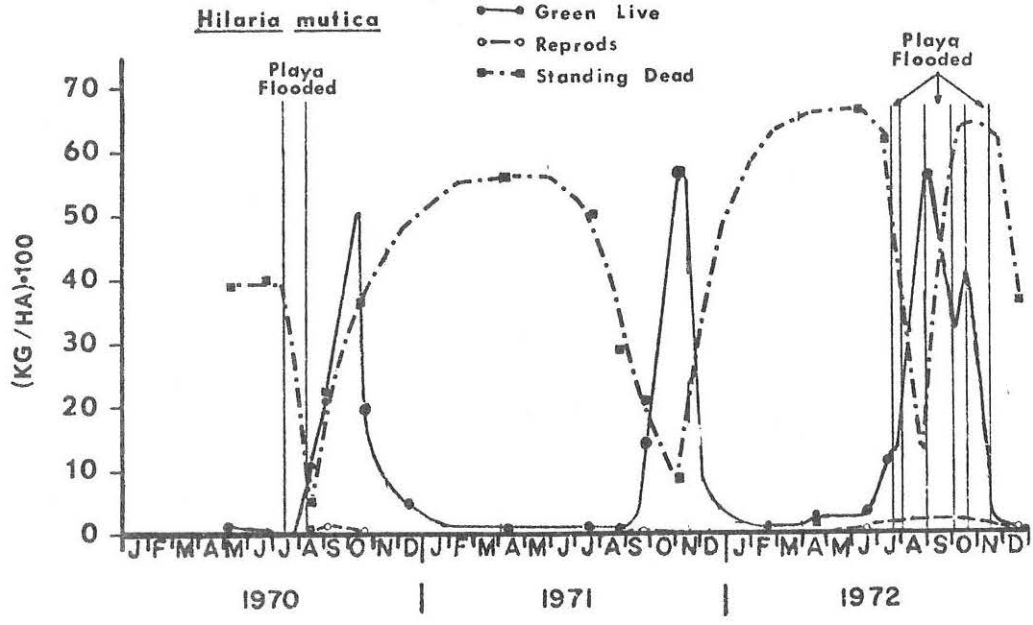


Figure 10. Biomass dynamics for *Hilaria* at the Jornada site from 1970 through 1972.

Illustrated in Figure 11 are the outputs from a 190-day model simulation for two hypothetical plant species, an annual and a perennial. The results of this simulation show the phenological progression of these plants as determined by the specific input coefficients for each plant. As illustrated by this output, a wide range of phenological situations can be simulated by the submodel.

Although actual data may not be available for some species, the user may experiment with different coefficients which govern the rates of phenological progression: these may then be compared to field observations to obtain realistic simulations.

The phenology submodel presented here was developed to accomodate any set of phenological data available; any environmental or endogenous variable can be used to determine a flow rate. New functional relationships can be easily introduced in the submodel to supplement or replace current ones with a minimal amount of effort.

Restrictions within the present format include the annual-perennial distinction, the defined phenophases and the direction of flows (e.g., *Fouquieria*) wherein flowering cannot occur directly from a dormant state. However, these restrictions can be further diminished with a moderate amount of restructuring of the program.

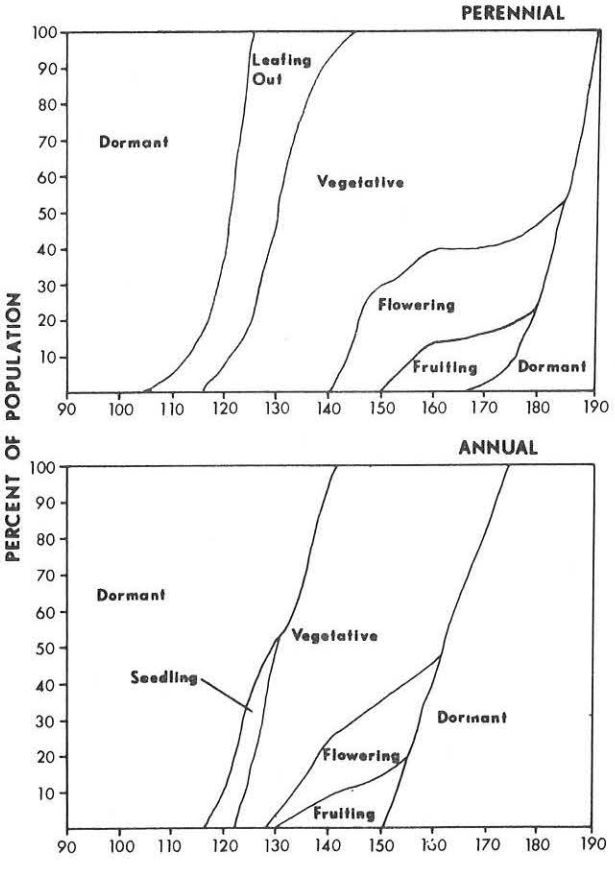


**Figure 11.** Ninety-day simulation for a hypothetical perennial and a hypothetical annual to illustrate model flexibility.

In conclusion, it appears this approach can be used to obtain satisfactory simulations of phenological changes in plants. The use of such coefficients as "RATMX" gives the submodel the flexibility necessary to simulate such situations as a rapid response to an environmental change. Further development must come in the area of incorporating detailed field data into the submodel. A submodel such as this can be a useful tool to synthesize various concepts of phenology into an organized format for use in a large systems model.

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# APPENDIX 1

## Program Listing

### *Subroutine* PHENOL

```
      SUBROUTINE PHENOL
C
C  AM1,AM2  PARAMETERS USED IN THE MITCHERLICH EQUATION
C  BM1,ETC
C  AE1,AE2  PARAMETERS USED IN THE EXPOTENTAL FUNCTION
C  BE1,ETC
C  AIRTTH   THRESHOLD AIR TEMPERATURE USED TO DETERMINE DEGREE DAYS
C  COLDT    MINIMUM SOIL TEMP NEC FOR COLD HARDENING REQUIREMENT
C  COLDTH   NO. DAYS NEC. THAT SOIL TEMP BE LESS THAT COLDT TO MEET COLD
C           HARDENING REQUIREMENT
C  FREEZE   VALUE OF MIN AIR TEMP THAT TRIGGERS DORMANCY/DEATH
C  GERMRX   MAX RATE OF PERENNIAL GERMINATION PHENOLOGICAL PROGRESSION
C  GERM     PERCENT OF SHED SEED RESERVE THAT WILL GERMINATE
C  ICOLDS   COUNTER FOR NO. DAYS SOIL TEMP BELOW COLDT
C  ICLDMA   VECTOR CONTAINING PREVIOUS 90-DAY RECORD OF RESULTS OF
C  ICHARD   0-WHEN COLDHARD. REQ. NOT MET, 1 WHEN MET
C           TESTS TO MEET COLDHARDENING REQ (0-NO, 1-YES)
C  IGTEMP   0 IF SOIL TEMP NOT ADEQ FOR GERMINATION, 1 IF ADEQUATE
C  IPHENO   1=DORMANCY  2=SEEDLING OR LEAFING OUT  3=VEGETATIVE GROWTH
C           4=FLOWERING 5=FRUITING  6=SENSCENCE/DEATH
C  IPHOT1   0 IF DAYLENGTH NOT ADEQ FOR BREAKING DORMANCY OF PERENNIALS
C  IPHOT2   0 IF DAYLENGTH NOT ADEQ FOR FLOWERING IN ALL PLANTS
C  PJUVEN   PERENNIAL SURVIVING PAST THE SEEDLING STAGE AFTER GERM
C  PHASE    PHENOPHASES (COMPARTMENTS) CONTAINING PERCENT OF BIOMASS
C           IN THAT PARTICULAR PHENOLOGICAL STATE
C  PHOTOF   DAYLENGTH NEC FOR FLOWERING
C  PHOTDR   DAYLENGTH NEC FOR BREAKING DORMANCY
C  PREDGM   VARIABLE (0 TO 1) DETERMING AMOUNT OF SEED RESERVE GERM-
C           INATING AS A FUNCTION OF SOIL WATER POTENTIAL
C  RATMX    MAX RATE OF PHENOLOGICAL PROGRESSION FROM PHENOPHASE
C           I TO J
C  SEED     REPRESENTS TOTAL SEED CARBON IN SOIL FOR PERENNIALS - IS
C           EQUILIVANT TO PHASE 1 OF ANNUALS
C  SEEDLN   PERENNIAL SEEDLINGS - EQUIL. TO PHASE 2 OF ANNUALS
C  SMORT    PERENNIAL SEEDLINGS THAT FAIL TO BECOME ESTABLISHED -
C           A PERCENT (EQUIV. TO PHASE 6 IN ANNUALS WHEN FLOW FROM PHASE
C           2, I.E., ANNUALS FAILING TO ESTABLISH
C  SOILTH   SOIL TEMP NEC FOR GERMINATION
C  SMHEAT   COUNTER FOR ACCUMULATION OF DEGREE DAYS
C  THHEAT   THRESHOLD DEGREE DAYS NEC. FOR BREAKING PERENNIAL DORMANCY
C
C-----------------------------------------------------------------------
      DIMENSION RCHECK(20)
      DIMENSION PHASE(15,6,GERM(15,SEED(15,SEEDLN(15,SMORT(15,
     -          PJUVEN(15
      COMMON /INCOMV/ I,II,IPHENO(15,IPHENN(15,PSRATE(15,RSRATE(15,
     - TROOT,ORGTEM(10,ORGSWP(10,WST,WSWP,TIME(15
      COMMON /IPARAM/ IN,IA,IP,IR,IS,ILF,IST,IFR,IRT,LIFORM(10,IANUAL,
     - IPHER0,ISHAD,LSOIL,NGOV,IGOV(5,LTO(15,10,IDUMP(16,KDUMP,
     - ISTL
      COMMON /PARAM/
     -          SMHEAT(15),THHEAT(15),RATMX(15,6),SOILTH(15),ICOLDS(15)
     -,         COLDT(15),COLDTH(15),ICLDMA(90,15),PHOTOF(15),PHOTDP(15
     -),         AIRTTH(15),HEATMA(60,15),GERMRX(15,3),Y6(9930),FREEZE(1
     -5),         AM1(15),AM2(15),AE1(15),AE2(15),AE3(15
     -,         BM1(15),BM2(15),BE1(15),BE2(15),BE3(15),BE4(15),BE5(15)
     -,         CE1(15,CF2(15,CE3(15,CE4(15,CE5(15
      COMMON /SPEC/ Q1(21,NSPECV,Q2,NORGAN,NFRACT,Q3(2,NOLIT,NCHECK,
     -  IDAY,IYRDAY,Z35(20,NDEBUG,Z36(121,NVECOH,Y7(52
      COMMON/OTHER/ATOT,ATOTO,SNODEP,SOILTE(5,PRECMM, WATER(5
      COMMON/METFOR/EVAP,TDAY,TNIGHT,DAYWVP,DWINAV,DWINMX,DAPHOT,
     -DAYRAD,DUST,DUSCON(6,RAINCC(6,SRODE,DAYSUN,DRUNMI(16,DRUNOR(6,
     - DRUNL(5,6,DASNOW,DARAIN
      COMMON /TOTALS/ Z3(60,CVEGO(15,6,Z4(16,AVEGO(15,Z5(56,
     - AVEG(15,10,Z6(952,ASEEDH(10,Y8(110
      COMMON /STAT/ CVEG(15,10,6,Y10(1040
C
      FUNEXP(AE,BE,CE,XE)=AE+BE*EXP(CE*XE)
      FUNMIT(AM,BM,XM)=AM*(1.0-EXP(BM*XM))
C-----------------------------------------------------------------------
      IF(IDAY.EQ.IDUMP(KDUMP))WRITE(6,7654)
      IF(NDEBUG.NE.0)WRITE(6,7654)
 7654 FORMAT(' EXECUTING SUBROUTINE PHENOL')
C
      IFORM  = LIFORM(I)
C
      IRAIN1=IRAIN2
      IRAIN2=IRAIN3
      IRAIN3=0
      KEY=DARAIN
      IF(KEY.EQ.0) GOTO 804
      IRAIN3=1
C
C-----------------------------------------------------------------------
C     SECTION FOR CALCULATING HEATSUM AND COLDHARDENING REQUIREMENTS
C-----------------------------------------------------------------------
C.....HEAT SUM (SMHEAT) CALCULATION FOR PERENNIALS (60 DAY SUM)
  804 DO 800 INUM=1,59
  800 HEATMA(INUM,I) = HEATMA(INUM+1,I)
      HEATMA(60,I) = TDAY-AIRTTH(I)
      SMHEAT(I) = 0.
      DO 801 INUM=1,60
  801 SMHEAT(I) = SMHEAT(I) + HEATMA(INUM,I)
C
C.....COLDHARDENING CALCULATION BASED ON PREVIOUS 90-DAY EVENTS
C       THAT IS, COLD HARD. REQ. HAS TO BE MET IN LAST 90-DAY PERIOD
      DO 802 INUM=1,89
  802 ICLDMA(INUM,I) = ICLDMA(INUM+1,I)
      ICLDMA(90,I) = 0
      IF (SOILTE(LSOIL).LE.COLDT(I)) ICLDMA(90,I) = 1
      ICOLDS(I) = 0
      DO 803 INUM=1,90
  803 ICOLDS(I) = ICOLDS(I) + ICLDMA(INUM,I)
C
C-----------------------------------------------------------------------
C     SECTION FOR ANNUAL AND PERENNIAL SEED GERMINATION
C-----------------------------------------------------------------------
C
      IGTEMP=0
      ICHARD=0
C
C.....GERMINATION OF ANNUALS AND PERENNIALS
C     CALCULATE INITIAL PERCENT OF SEED CARBON THAT WILL GERMINATE
C     FOR PURPOSES OF INITIALIZING GERM(I) .  THIS CAN OCCUR
C     ANY TIME CONDITIONS ARE SUITABLE FOR GERMINATION
C
      IF(SOILTE(LSOIL).GE.SOILTH(I)) IGTEMP=1
      IF(ICOLDS(I).GE.COLDTH(I)) ICHARD=1
C
      GOTO (66,67,67),IFORM
   66 KEY=PHASE(I,1)
      IF(KEY.EQ.100) GOTO 65
      GOTO 69
   67 KEY=SEED(I)
      IF(KEY.EQ.100) GOTO 65
      GOTO 69
C
   65 IF(IGTEMP.EQ.0.OR.ICHARD.EQ.0) GOTO 73
   69 PREDGM=FUNEXP(AE1(I),BE1(I),CE1(I),WATER(LSOIL))
C
      GOTO (30,31,31),IFORM
   30 KEY=PHASE(I,1)
      GOTO 32
   31 KEY=SEED(I)
   32 IF(KEY.EQ.100) GOTO 72
C
      IF(IRAIN1.EQ.1.OR.IRAIN2.EQ.1) GOTO 72
      GOTO  73
C
   72 GOTO (70,71,71),IFORM
C
   70 GERM(I)=PREDGM*PHASE(I,1)+GERM(I)
      GOTO 73
   71 GERM(I)=PREDGM*SEED(I)+GERM(I)
C
C.....ESTABLISHMENT AS A FUNCTION OF SOIL WATER POTENTIAL
   73 SM23E=FUNEXP(AE2(I),BE2(I),CE2(I),WATER(LSOIL))
      SM26E=1.-SM23E
      SM24E*SM26E
C
C-----------------------------------------------------------------------
C     CHECK FOR FREEZING AIR TEMPERATURES :IF POSITIVE TEST EMPTY
C       CONTENTS OF ALL COMPARTMENTS TO DORMANT (PERENNIALS) OR
C       SENSCENSE (ANNUALS)
C-----------------------------------------------------------------------
   75  IF(TDAY.GT.FREEZE(I)) GOTO 76
       KEY=PHASE(I,1)
       IF(KEY.EQ.100) GOTO 99
C
      F12=0.0
      F23=0.0
      F34=0.0
      F45=0.0
      F54=0.0
C
      GOTO (50,51,51),IFORM
C
C.....PERENNIALS
   51 F21=PHASE(I,2)
      F31=PHASE(I,3)
      F41=PHASE(I,4)
      F51=PHASE(I,5)
      G12=0.
      G23=0.
      G24=0.
      G21=SEEDLN(I)
      G31=PJUVEN(I)
      G41=SMORT(I)
      GERM(I)=0.
      GOTO 79
C
C.....ANNUALS
   50 F26=PHASE(I,2)
      F36=PHASE(I,3)
      F46=PHASE(I,4)
      F56=PHASE(I,5)
      F61=PHASE(I,6)*RATMX(I,6)
      GERM(I) = 0.
      IF(PHASE(I,6).LT.1.0) F61=PHASE(I,6)
      GOTO 79
C
C-----------------------------------------------------------------------
C     CALCULATE RATE   COEFFICIENTS
C-----------------------------------------------------------------------
C
   76 IDTEMP=0
      IPHOT1=0
      IPHOT2=0
C
C.....COEFF FOR BREAKING DORMANCY IN PERENNIALS
      IF(LIFORM(I).EQ.IANUAL) GOTO 755
      IF(SMHEAT(I).GE.THHEAT(I)) IDTEMP=1
      IF(DAPHOT.GE.PHOTDR(I))  IPHOT1=1
      SM12=FUNEXP(AE2(I),BE2(I),CE2(I),WATER(LSOIL))
C
C.....COEFF FOR LEAFING-OUT TO VEGETATIVE GROWTH
      SM23=FUNEXP(AE2(I),BE2(I),CE2(I),WATER(LSOIL))
      IF(PSRATE(I).LE.0.0) PSRATE(I)=0.0001
      CR23=FUNEXP(AE3(I),BE3(I),CE3(I),RSRATE(I)/PSRATE(I))
C
C.....COEFF FOR VEGETATIVE TO FLOWERING
  755 IF(DAPHOT.GE.PHOTOF(I)) IPHOT2=1
      SM34=FUNEXP(AE2(I),BE2(I),CE2(I),WATER(LSOIL))
      IF(AVEGO(I).LE.0.000) AVEGO(I)=0.0001
      CR34=FUNMIT(AM1(I),BM1(I),CVEGO(I,IR)/AVEGO(I))
C
C... .COEFF FOR FLOWER TO FRUIT
      SM45=FUNMIT(AM2(I),BM2(I),WATER(LSOIL))
C
C.....COEFF FOR FRUIT TO FLOWER
      SM54=1.-SM45
C
C.....SENSCENCE   ANNUALS:F56  PERENNIALS:F51
      CR56=FUNEXP(AE4(I),BE4(I),CE4(I),AVEG(I,IFR)/AVEGO(I))
```

```
      CR51=FUNLXP(AE5(I),BE5(I),CE5(I),CVEG(I,ILF,IR)/AVEGO(I))
C
C-----------------------------------------------------------------------
C     COMPUTATION OF FLOWS
C-----------------------------------------------------------------------
C
      GOTO (81,82,82), IFORM
C
C.....ANNUAL
   81 F12=GERM(I)*RATMX(I,1)
      F23=PHASE(I,2)*SM23E*RATMX(I,2)
      F26=PHASE(I,2)*SM26E*RATMX(I,6)
      F56=PHASE(I,5)*CR56*RATMX(I,5)
      F61=PHASE(I,6)*RATMX(I,6)
      GOTO 83
C
C.....PERENNIAL GERMINATION
   82 G12=GERM(I)*GERMRX(I,1)
      G23=SEEDLN(I)*SM23E*GERMRX(I,2)
      G24=SEEDLN(I)*SM24E*GERMRX(I,3)
C.....PERENNIAL
      F12=PHASE(I,1)*IDTEMP*IPHOT1*SM12*RATMX(I,1)
      F23=PHASE(I,2)*CR23*SM23*RATMX(I,2)
      F51=PHASE(I,5)*CR51*RATMX(I,5)
C.....ALL PLANTS
   83 F34=PHASE(I,3)*IPHOT2*CR34*SM34*RATMX(I,3)
      F45=PHASE(I,4)*SM45*RATMX(I,4)
      F54=PHASE(I,5)*SM54*RATMX(I,4)
      F21=0.0
      F31=0.0
      F41=0.0
      F51=0.0
      F61=0.0
      F36=0.0
      F46=0.0
C-----------------------------------------------------------------------
C     UPDATE ALL COMPARTMENTS
C-----------------------------------------------------------------------
C
   79 CONTINUE
C
      GOTO (87,88,88), IFORM
C
   87 PHASE(I,1)=PHASE(I,1)+F61-F12
      GERM(I)=GERM(I)-F12
      PHASE(I,2)=PHASE(I,2)+F12-F26-F23
      PHASE(I,3)=PHASE(I,3)+F23-F34-F36
      PHASE(I,4)=PHASE(I,4)+F34+F54-F45-F46
      PHASE(I,5)=PHASE(I,5)+F45-F54-F56
      PHASE(I,6)=PHASE(I,6)+F26+F36+F46+F56-F61
      GOTO 99
   88 SEED(I)=SEED(I)+G21+G31+G41-G12
      GERM(I)=GERM(I)-G12
      SEEDLN(I)=SEEDLN(I)+G12-G24-G23-G21
      PJUVEN(I)=PJUVEN(I)+G23-G31
      SMORT(I)=SMORT(I)+G24-G41
C
      PHASE(I,1)=PHASE(I,1)+F21+F31+F41+F51-F12
      PHASE(I,2)=PHASE(I,2)+F12-F23-F21
      PHASE(I,3)=PHASE(I,3)+F23-F34-F31
      PHASE(I,4)=PHASE(I,4)+F34+F54-F45-F41
      PHASE(I,5)=PHASE(I,5)+F45-F54-F51
C
C**************************** TEMPORARY SECTION ************************
C
   99 CONTINUE
C
      SUM=0.
C
      GOTO (97,98,98), IFORM
C
   97 DUMMY= 100.1-PHASE(I,1)
      DO 90 J=2,6
   90 SUM=SUM + J * (PHASE(I,J)/DUMMY)
      IF(SUM.LT.0.05) SUM=1.
      GOTO 93
C
C.....PERENNIALS
   98 DO 91 J=1,5
   91 SUM=SUM + J*PHASE(I,J)
C
   93 IPHENO(I) = SUM
      PHENXX   = SUM
C
C
C
  100 CONTINUE
C
C*****************************************************************
      IF(IDAY.EQ.IDUMP(KDUMP))WRITE(6,2000)I,IPHENO(I)
      IF(NDEBUG.NE.0)WRITE(6,2000)I,IPHENO(I)
 2000 FORMAT(' I=',I2,5X,'IPHENO(I) =',I2)
      WRITE(6,2006) IYRDAY,
     -              PHASE(I,1),PHASE(I,2),PHASE(I,3),PHASE(I,4),
     -              PHASE(I,5),PHASE(I,6),
     -GERM(I),PREDGM,IGTEMP,ICHARD,IDTEMP,IPHOT1,IPHOT2,IPHENO(I),
     -              PHENXX,SM23E,                SM34,SM45,SM54,
     -      CR34,CR56
 2006 FORMAT(2X,I3,3X,6(F5.1,1X),3X,2(F5.1,1X),3X,6(1X,I1),
             2X,F4.2,2X, 6(1X,F4.2))
      RETURN
C
C-----------------------------------------------------------------------
      ENTRY INPHEN
      READ(5,5) RCHECK
      WRITE(6,4) RCHECK
    4 FORMAT(' ',20A4)
    5 FORMAT(20A4)
      DO 1000 I=1,NVECOH
      READ(5,6)
     -ICOLDS(I),AM1(I),AM2(I),AE1(I),AE2(I),AE3(I),AE4(I),AE5(I),BM1(I),
     1BM2(I),BE1(I),BE2(I),BE3(I),BE4(I),BE5(I),CE1(I),CE2(I),CE3(I),
     2CE4(I),CE5(I),THHEAT(I),SOILTH(I),COLDT(I),COLDTH(I),FREEZE(I),
     3PHOTOR(I),PHOTOF(I),AIRTTH(I),SEED(I),SEEDLN(I),PJUVEN(I),SMORT(I)
     4,GERM(I)
    6 FORMAT(I5,13F5.0/14F5.0/14F5.0)
      READ(5,8) (PHASE(I,J), J=1,6)
      READ(5,8) (RATMX(I,J), J=1,6)
      READ(5,10)(GERMRX(I,J),J=1,3)
    8 FORMAT(6F10.0)
   10 FORMAT(3F10.0)
      DO 9 J=1,60
    9 HEATMA(J,I) = 0.
      DO 11 J=1,90
   11 ICLOMA(J,I) = 0
C
 1000 CONTINUE
      RETURN
      END
```