

# MODELING DIAPAUSE DEVELOPMENT: PHASE MULTIPLICITY AND SIMULTANEITY

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## ABSTRACT

A simulation model of diapause development is described, based on the hypothesis that diapause is constituted of three distinct processes, or phases. Only the last two phases are explicitly considered. The model incorporates development rate variability in Phases II and III, photoperiod sensitivity during Phase II, and phase simultaneity. Simulation experiments show that partial phase simultaneity is equivalent to having sequential phases with a shorter Phase III. It is also shown that a high degree of phase simultaneity reduces the ability of the diapause process to prevent development completion under adverse conditions and to synchronize development. A model with two sequential phases generated realistic development completion patterns under natural weather conditions using parameters suited for spruce budworm, although accurate estimates of Phase-II parameters were not available. Sensitivity to photoperiod in the latter part of Phase II further reduced the sensitivity of the model to development-rate parameters. Nevertheless, it is concluded that accurate prediction of development completion, particularly in environments where winter temperatures regularly exceed postdiapause development thresholds, requires precise estimates of development rates during the last two phases of diapause. Such estimates may be obtained best from measurements of metabolic rates during diapause.

## INTRODUCTION

Few models have been developed to simulate diapause development in insects. Most phenology models assume that diapause is over in late winter, at a time when temperatures are still too low for postdiapause development to occur. This approach works well for univoltine species with an "obligate" winter diapause, in environments where winter temperatures drop and remain below development thresholds for prolonged periods. In such cases, a date for the initiation of postdiapause development summation can be chosen objectively (e.g. Lyons and Lysyk 1989; Régnière 1990). However, to model postdiapause development in species with facultative diapause or in environments where temperatures regularly exceed postdiapause development thresholds throughout the year, diapause processes must be simulated directly. This is due to the impossibility of choosing an objective, constant point in time where diapause can be considered satisfied, and postdiapause development summation can begin. The modeling approach has been to view the diapause phenomenon as consisting of two processes, a concept proposed and developed by several authors (Lees, Mansingh, Hodek and Zaslavski, as cited in

Zaslavski 1988). The two processes, or phases, were thought to occur sequentially (Logan et al. 1976) or simultaneously (Hilbert et al. 1985).

In this paper, the first phase of diapause, prediapause development, is not considered explicitly. Rather, it is assumed that individuals have reached the diapause state (Phase II). The behavior of a general model of diapause and postdiapause development is investigated, taking into account individual variability in development rates during both phases, partial or complete phase simultaneity, and photoperiod sensitivity in late diapause. The differences are emphasized between sequential and simultaneous phases in terms of the model's ability to synchronize the completion of development and to prevent it from occurring under adverse conditions. The model is also applied to the simulation of spruce budworm diapause development under natural conditions of temperature and photoperiod.

## MATERIALS AND METHODS

### Model Description

In the model, no attempt is made to simulate diapause induction, although this is a very important process in insects with a facultative diapause. Rather it is assumed that diapause is obligate, or that it has been induced. Diapause is viewed in this model as consisting of two distinct processes (phases II and III), each with its own thermal responses (Fig. 1). Phase II has been called diapause development (Andrewartha 1952), reactivation (Danilevski 1961 as cited in Zaslavski 1988) or diapause regulating process (Hilbert et al. 1985). It often is seen as a slow, cool-temperature process. Phase-III development has been called postdiapause (Tauber and Tauber 1976), morphological development (Hilbert et al. 1985) or activation (Zaslavski 1988). It is most often characterized by a faster, warm-temperature response. Strictly speaking, Phase III occurs after Phase II only when the two processes are completely sequential.

Development rates in both phases are functions of temperature,  $T$ . In Phase II,

$$d_1 = P_{1,1} \left[ \frac{1}{1 + e^{P_{1,2} - P_{1,3} \tau_1}} - e^{(\tau_1 - 1)/P_{1,4}} \right] \quad [1]$$

where  $P_{1,1}$  to  $P_{1,4}$  are parameters, and

$$\tau_1 = (T_{1,\max} - T) / (T_{1,\max} - T_{1,\min}) \quad [2]$$

In Phase III,

$$d_2 = P_{2,1} \left[ \frac{1}{1 + e^{P_{2,2} - P_{2,3} \tau_2}} - e^{(\tau_2 - 1)/P_{2,4}} \right] \quad [3]$$

where  $P_{2,1}$  to  $P_{2,4}$  are also parameters, and

$$\tau_2 = (T - T_{2, \min}) / (T_{2, \max} - T_{2, \min}) \quad [4]$$

$T_{1, \min}$  and  $T_{2, \min}$  are used as lower development-threshold temperatures, and  $T_{1, \max}$  and  $T_{2, \max}$  as upper thresholds.

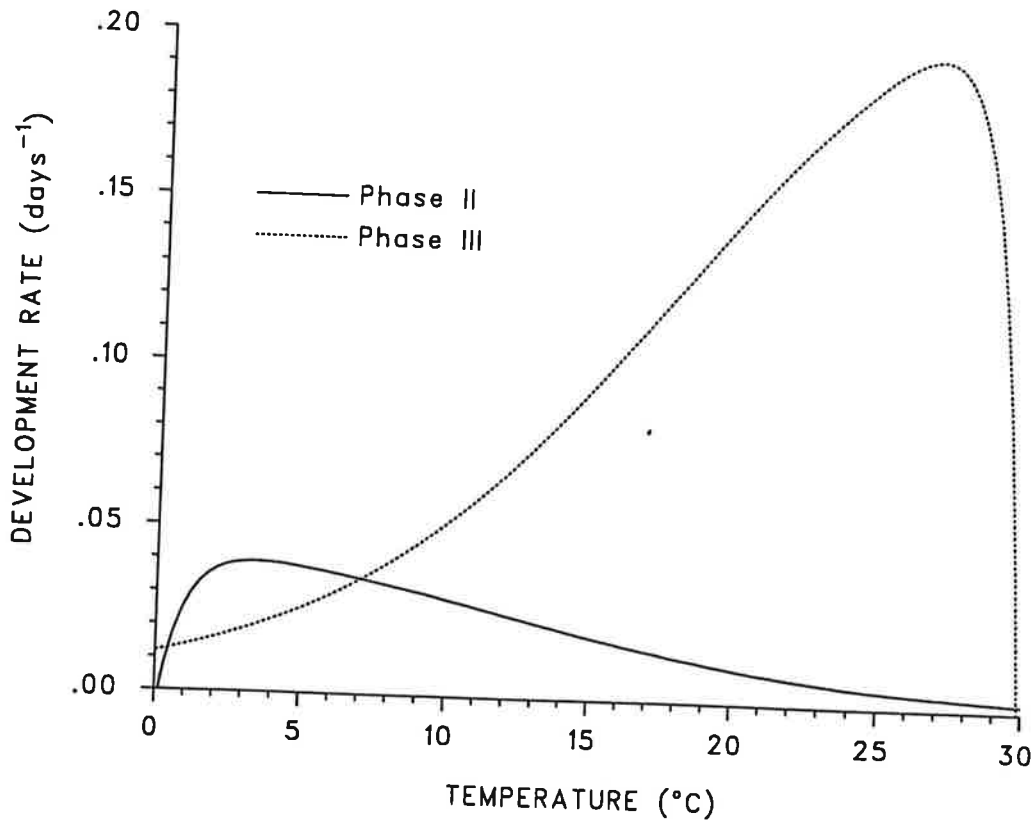


Figure 1. Relationships between temperature and development rate during the last two hypothesized phases of diapause development. Phase II described by equations (1) and (2); Phase III by equations (3) and (4).

There is a certain amount of individual variability associated with each of these rate functions that can be described by a cumulative distribution of development rates relative to the median ( $\delta$ ) (Fig. 2a). One such distribution can be assigned to each phase (Régnière 1984):

$$Y_1 = g_1(\delta) = \left( \frac{1}{1 + e^{[-K_1(\delta-1)]} (.5^{-Q_1} - 1)} \right)^{1/Q_1} \quad [5]$$

and

$$Y_2 = g_2(\delta) = \left( \frac{1}{1 + e^{[-K_2(\delta-1)]} (.5^{-Q_2} - 1)} \right)^{1/Q_2} \quad [6]$$

The simulation approach used in the model is to partition the population into  $n$  equal classes (or subpopulations), each with its relative Phase-II development rate  $\delta_{1,i}$  (Fig. 2b):

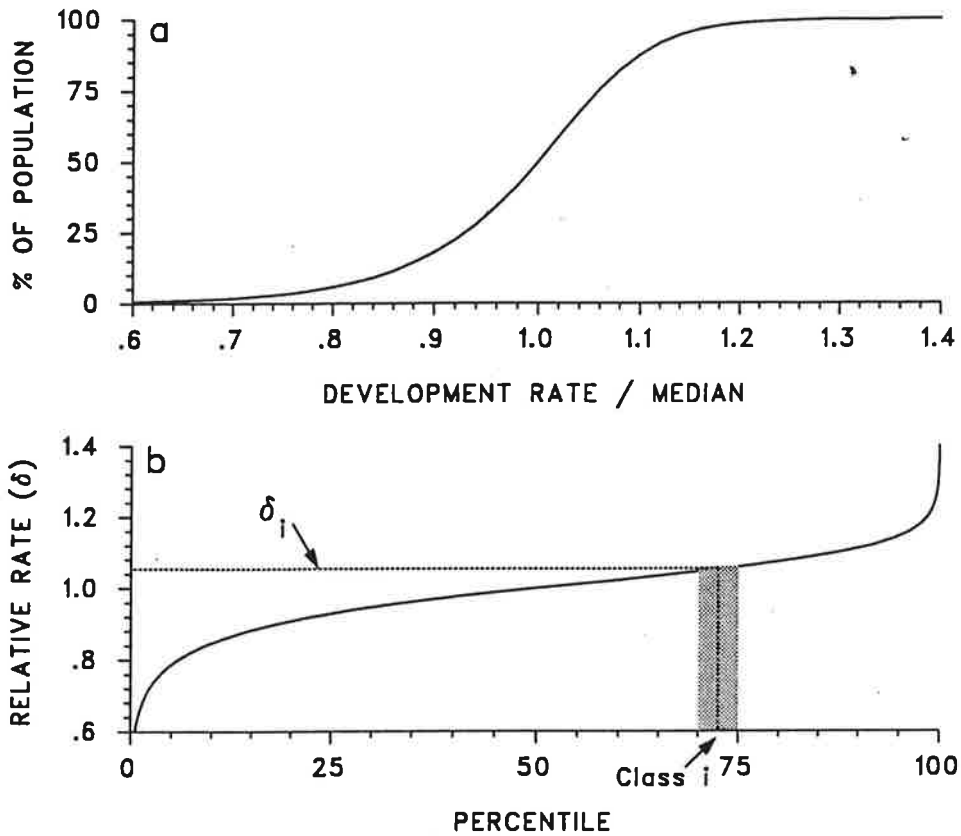


Figure 2. (a) Example of cumulative distribution of development rates, relative to the population median; (b) Inverted distribution used to determine the relative rate for any percentile of the population (a given subpopulation or class is assigned the rate corresponding to the center percentile of the class).

$$\delta_{1,i} = g_1^{-1}(Y_i) \quad [7]$$

where  $Y_i$  is the percentile corresponding to class  $i$ . Each subpopulation is further divided into  $m$  sub-classes (sub-subpopulations) each with its relative Phase-III development rate  $\delta_{2,j}$

$$\delta_{2,j} = g_2^{-1}(Y_j) \quad [8]$$

where  $Y_j$  is the percentile corresponding to subclass  $j$ . Phase-II development is accumulated separately for each class as long as  $D_{1,i} < 1$ :

$$D_{1,i}(t) = D_{1,i}(t-1) + d_1 * \Delta t * \delta_{1,i} \quad [9]$$

where  $\Delta t$  is the time step (days). Within each class  $i$ , Phase-III development also is accumulated for each subclass  $j$  until  $D_{2,i,j} = D_{2,max}$ . Here,  $D_{2,max}$  is a limit that Phase-III development cannot

exceed unless  $D_{1,i}=1$ :

$$D_{2,i,j}(t) = D_{2,i,j}(t-1) + d_2 * \Delta t * \delta_{2,j} \quad [10]$$

Thus, the model can simulate the whole spectrum between strictly sequential ( $D_{2,max}=0$ ) and strictly simultaneous ( $D_{2,max}=1$ ) phases.

To describe the effect of photoperiod on diapause termination, the existence of a critical photoperiod ( $P_{crit}$ , length of photophase in hours) was assumed, above which Phase-II development is considered complete by the insect.  $P_{crit}$  is a function of Phase-II physiological age,  $D_1$  (Fig. 3):

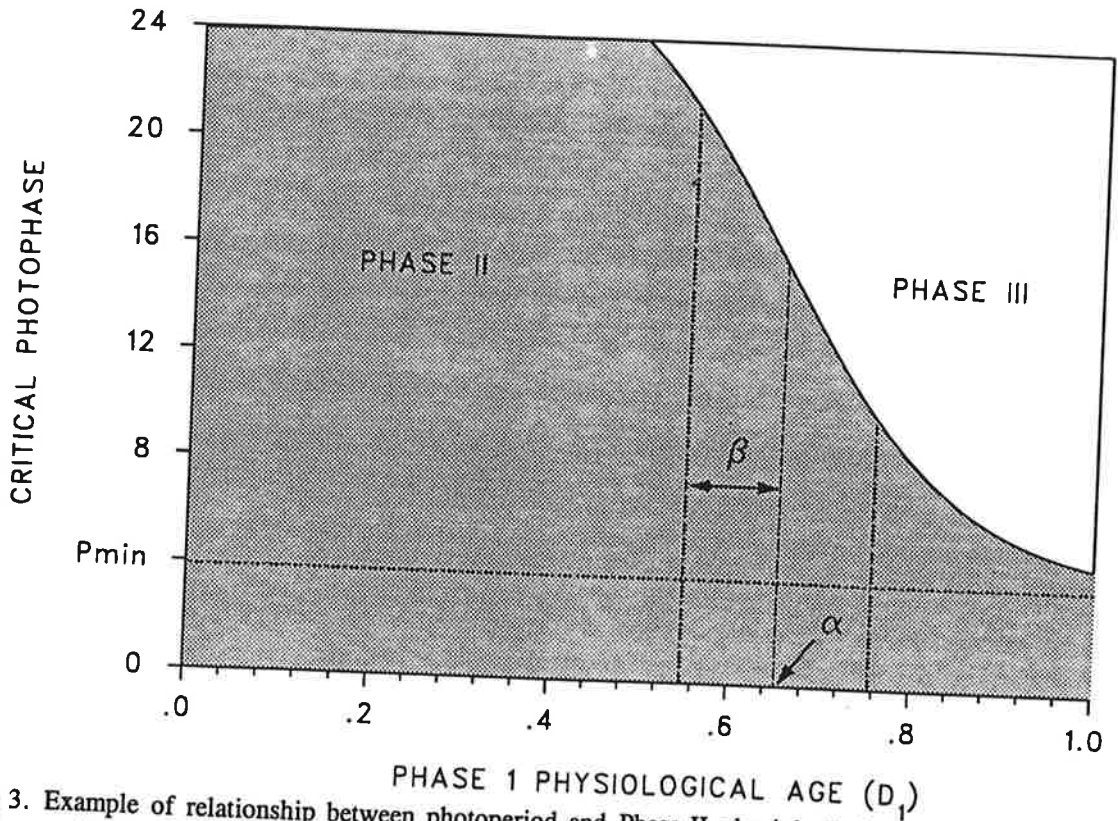


Figure 3. Example of relationship between photoperiod and Phase-II physiological age. As soon as daylength exceeds the critical photophase corresponding to a given subpopulation's physiological age, Phase II is complete and the insects enter Phase III.

$$P_{crit} = P_{min} + \frac{P_{max} - P_{min}}{1 + e^{(D_1 - \alpha) / \beta}} \quad [11]$$

where  $P_{min}$  and  $P_{max}$  are lower and upper critical photoperiods. Parameter  $\alpha$  is the physiological age at which  $P_{crit}$  is half-way between  $P_{min}$  and  $P_{max}$ , while  $\beta$  determines the spread of  $D_1$  over which  $P_{crit}$  changes. This function is sufficiently flexible to describe photoperiod-insensitive cases

( $P_{\min}$  and  $P_{\max} > 24$ ) as well as a whole spectrum of photoperiod responses (Fig. 3). The model sets  $D_{1,i}=1$  as soon as photophase  $\geq P_{\text{crit}}$ .

The process of diapause simulation at the core of the model is illustrated in Figure 4.

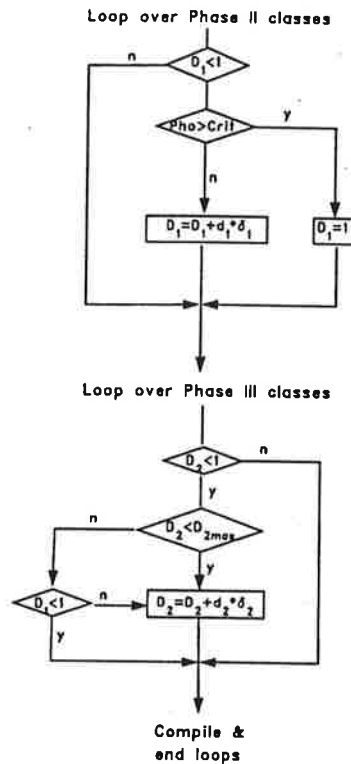


Figure 4. Flow chart of the two-phase simulation process at the core of this model of diapause development.

### Model Behavior

To investigate the behavior of this model, four simulation experiments were conducted. First, the effect of cold-storage duration on the pattern of development completion (e.g., emergence of larvae in spruce budworm, egg hatch in gypsy moth) was tested. Simulated populations were exposed for various periods (from 0 to 100 days) to 5°C, and then transferred to 20°C until completion of development. Five different values of  $D_{2,\max}$ : 0 (strictly sequential phases), .2, .5, .8 and 1 (strictly simultaneous phases) were used. Other parameter values used were:

$$P_{1,1}=0.05, P_{1,2}=3.0, P_{1,3}=5.0, P_{1,4}=0.03, T_{1,\min}=0.0, T_{1,\max}=30.0$$

$$P_{2,1}=0.25, P_{2,2}=3.0, P_{2,3}=5.0, P_{2,4}=0.03, T_{2,\min}=0.0, T_{2,\max}=30.0$$

$$K_1=K_2=23.0, Q_1=Q_2=2.0$$

$$P_{\min}=P_{\max} > 24 \text{ h}$$



The parameters of equations [1] and [3] produce the thermal responses illustrated in Fig. 1, with a Phase-II optimum near 3°C, and a Phase-III optimum near 28°C. Variability-function parameters were the same for both phases. The values of  $P_{min}$  and  $P_{max}$  ensured that photophase would remain below  $P_{crit}$  so that no effect of photoperiod on Phase II termination was introduced in the simulations.

In a second experiment, the development rates (length) of Phase III ( $P_{2,1} = .15, .25, .35, .45$ .) were varied, in a strictly sequential model ( $D_{2,max} = 0$ ), using the same set of experimental conditions (cold-storage durations, temperatures) and parameter values as in experiment 1.

In a third experiment, the diapausing insects were exposed to 20°C for periods of 1 to 30 days before putting them at 5°C for 45 days. Then the insects were returned to 20°C until completion of development. I used values of  $D_{2,max} = 0, .2, .5, .8$  and 1. Other parameter values were the same as in experiment 1.

In the fourth experiment, the insects were kept for 16, 18, 20 or 22 days at 5°C, and then transferred to 20°C at photoperiods of 10L:14D, 13L:11D or 16L:8D. Development-rate function parameters were the same as in experiment 1, with  $D_{2,max} = 0$  (strictly sequential phases) and photoperiod-response parameters set to:

$$P_{min} = 4 \text{ h}, P_{max} = 28 \text{ h}, \alpha = 0.65, \beta = 0.1$$

These values produced the curve in Figure 3.

### Model Performance Under Natural Weather Conditions

The behavior of the sequential model ( $D_{2,max} = 0$ ) under natural weather conditions was tested using daily minimum and maximum air-temperature records from Montreal, Quebec, Canada (45°30'N, 73°35'W, 57 m altitude), as input. Daylength was calculated from information provided by Withrow (1959), in relationship with latitude (L) and day of the year (D):

$$Phot = 12 + 0.0018 L^2 \sin [ 2\pi(D-80) / 365 ] \quad [12]$$

A half-cosine function (Régnière 1982) was used to interpolate between minima and maxima, with a 4-hour time step ( $\Delta t = 0.167$ ). The entire population was assumed to enter diapause Phase II on August 1, and simulations were run until 100 percent of individuals had completed Phase III. To provide a basis for comparison, development-rate and variability function parameter values reflected those observed in the spruce budworm. For postdiapause (Phase III), these values were taken from Régnière (1987):

$$P_{2,1} = 0.194; P_{2,2} = 3.0, P_{2,3} = 5.84, P_{2,4} = 0.03, T_{2,min} = 2.5, T_{2,max} = 35$$

and

$$K_2 = 18.72, Q_2 = 2.22$$

No parameter estimates were available for Phase II. However, there is good reason to believe that some development occurs below 0°C (unpublished), so  $T_{1,\min} = -2.0$  was used. It is also probable that Phase-II development rates do not exceed approximately 0.02 days<sup>-1</sup> at the optimum temperature of 3-6°C (unpublished). With this in mind, results from simulations with values of  $P_{1,1} = 0.015, 0.020, 0.025$  and  $0.035$  were compared, keeping other parameter values constant at:

$$P_{1,2} = 3.0, P_{1,3} = 5.0, P_{1,4} = 0.03, T_{1,\max} = 30$$

and  $K_1 = 23.0, Q_1 = 2.0$

A series of simulations was done without consideration of photoperiod sensitivity ( $P_{\min} = P_{\max} = 24$ ). In another series, photoperiod sensitivity in late Phase II was included by setting  $\alpha = 0.65, \beta = 0.1, P_{\min} = 8$  and  $P_{\max} = 28$ .

## RESULTS AND DISCUSSION

### Model Behavior

The results of experiment 1 are illustrated in Figure 5. The median time to development completion, including the cold-storage period and time at 20°C, decreased linearly with cold-storage duration between 0 and 28 days, for all values of  $D_{2,\max}$  (Fig. 5a). This decrease was proportional to the amount of Phase-II development that occurred during cold storage. Beyond 28 days, which was the median duration of Phase-II at 5°C (Fig. 1), development time increased with further increases in cold storage duration, up to a maximum due to completion of development at 5°C. This increase in development time resulted from slow Phase-III development at 5°C, and was inversely proportional to  $D_{2,\max}$  (Fig. 5a). Therefore, in this experiment, increasing phase-simultaneity resulted in a reduction in the ability of the diapause process to prevent development completion in cold storage.

Variability in development time, expressed here as the range (days) between 10 and 90 percent development completion, was high in all cases of storage duration under 28 days (Fig. 5b), because in these cases Phase-II development was forced to proceed at 20°C. Variability dropped sharply in insects kept 28 days or longer at 5°C. This is a phenomenon often observed, and has been called "synchronization". The model shows that synchronization results from the accumulation (queuing), at cold temperature, of insects in early Phase-III, which proceeds more slowly than Phase II at low temperature (Fig. 1). Once temperature increases, the insects develop rapidly and complete development synchronously. This synchronization was maintained with increasing periods at 5°C, until insects started to complete Phase III in cold-storage. However, the ability of the model to produce consistent synchronization was greatly reduced at higher values of  $D_{2,\max}$  (Fig. 5b). These patterns are more easily understood by examining in more detail the results of a number of simulations (Fig. 6). In a strictly sequential model ( $D_{2,\max} = 0$ ), increasing the cold storage period results first in accelerating Phase-II development, and



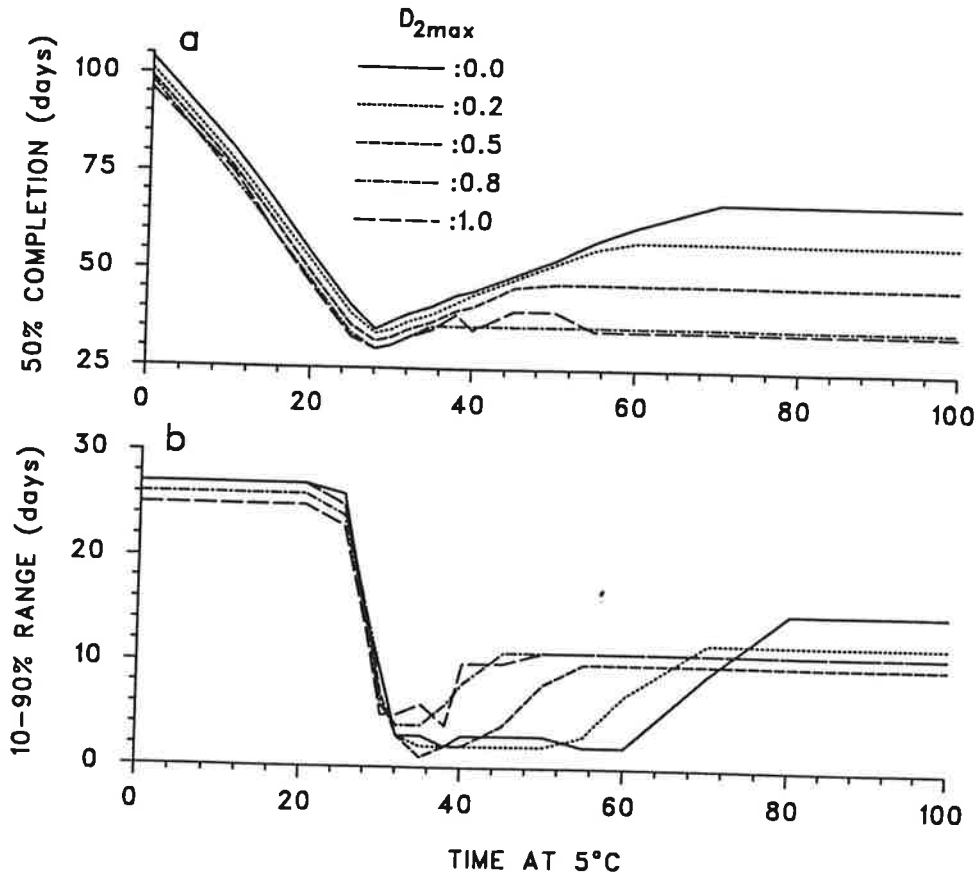


Figure 5. Relationship between the duration of cold storage (at 5°C) and completion of development after transfer to 20°C. (a) Time to completion by 50 percent of individuals. (b) Range in completion time (days) between 10 and 90 percent of the population. Results of experiment 1, changing the value of parameter  $D_{2,max}$ .

eventually in the queuing of insects in the early stages of Phase III, until transfer to 20°C (Fig. 6a-e). In a strictly simultaneous model ( $D_{2,max} = 1$ ), the response to short cold-storage periods is very similar to that of the sequential model, although Phase III is finished well before Phase II (Fig. 6f-h). As the cold storage period increases, however, Phase II tends to be completed before Phase III (Fig. 6h,i). Nevertheless, there is only a brief period during which synchronous development completion is achieved, because insects do not queue in the early stages of Phase III (much of Phase III development occurs simultaneously with Phase II). This reduces the ability of the simultaneous model to "hold" the insects in Phase III until transfer to warmer temperature and to synchronize their development (Fig. 6).

Under the conditions of experiment 1, intermediate values of  $D_{2,max}$  (.2, .4, .6) produced a behavior qualitatively similar to the strictly sequential model: the ability to prevent development completion under adverse conditions and consistent synchronization. In fact, varying  $D_{2,max}$  seems to be equivalent to changing the length of Phase III in a sequential model, as suggested by the results of experiment 2, in which the value of  $P_{2,1}$  was varied, keeping  $D_{2,max} = 0$  (Fig. 7).

Experiment 3 mimicked more closely the temperate-zone temperature regimes that an insect would experience when diapause is induced in late summer. There, the cold season is preceded by a period of warm temperatures during which Phase II is slowed and, in cases of simultaneity,

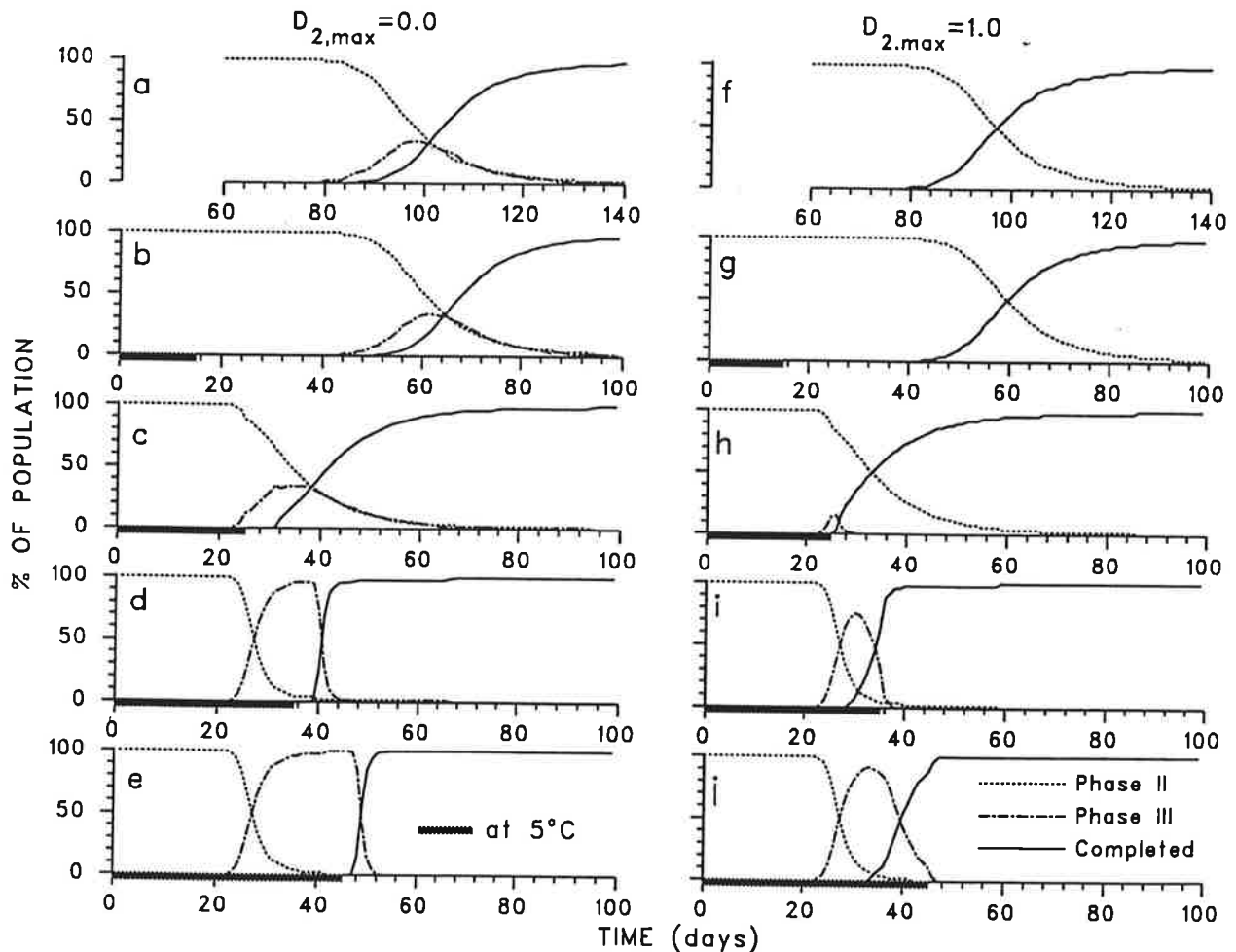


Figure 6. Percent of population in Phase II, Phase III or completing development as a function of time, with increasing durations of cold storage (at 5°C). (a)-(e): strictly sequential model ( $D_{2,max}=0$ ); (f)-(j): strictly simultaneous model ( $D_{2,max}=1$ ). Results of experiment 1.

Phase III is accelerated. The results of the experiment indicate that the qualitative characteristics of the multiple-phase model are maintained with this type of temperature regime. Development is arrested in the early stages of Phase III, particularly in the strictly sequential model, whereas the strictly simultaneous model is even less apt to produce arrested development or synchronous completion of development (Fig. 8). Intermediate values of  $D_{2,max}$  produce intermediate results, but the higher the amount of simultaneity, the less the ability of the model to produce synchronous completion upon the return of favorable temperatures (Fig. 9). However, this decreasing efficiency of the multiple-phase diapause model is the result of an effective shortening of the sequential portion of Phase III development. It is interesting to note that a pre-storage

exposure to 20°C caused a net drop in total emergence time only in the strictly simultaneous model (Fig. 9,  $D_{2,max}=1$ ).

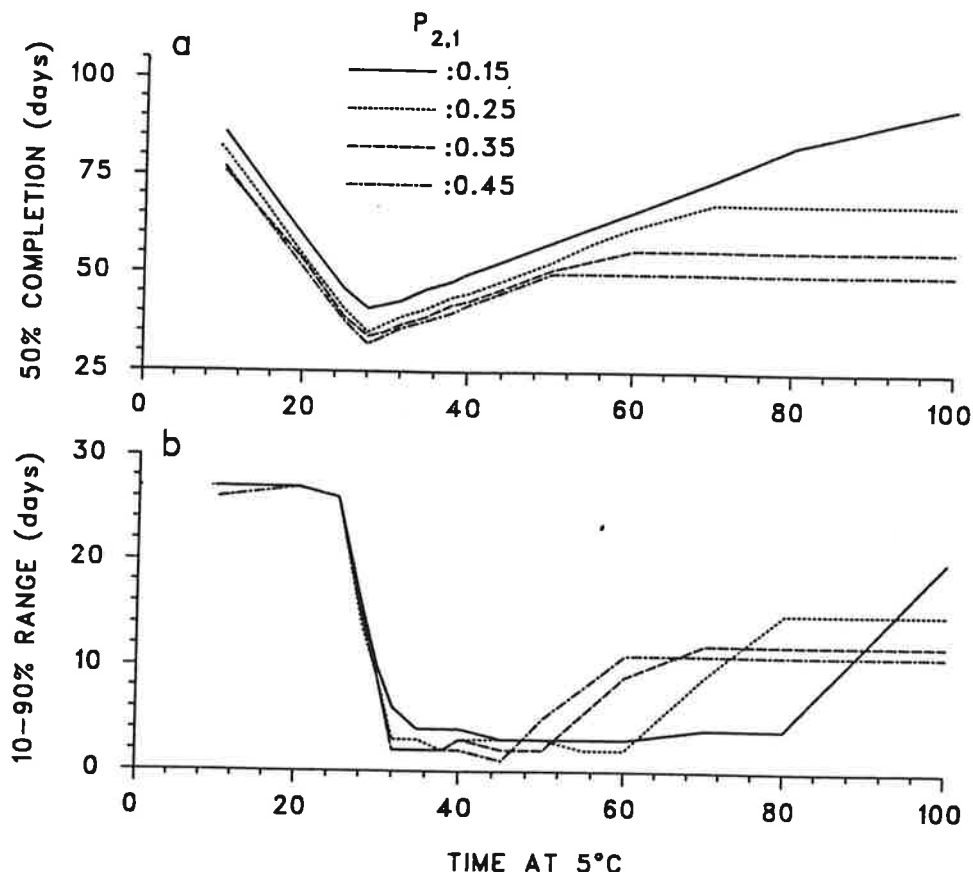


Figure 7. Relationship between the duration of cold storage (at 5°C) and completion of development after transfer to 20°C. (a) Time to completion by 50 percent of individuals. (b) Range in completion time (days) between 10 and 90 percent of the population. Results of experiment 2, changing the value of parameter  $P_{2,1}$ .

The results of the fourth experiment (Fig. 10) are strikingly similar to the observed reactions of spruce budworm to photoperiod during cold storage (unpublished). In the early stages of Phase II, photoperiod sensitivity is minimal, with a 3-day (10 percent) reduction in total development time for each 3-hour increase in daylength (Fig. 10a). However, after 18 days in cold storage (median Phase-II physiological age  $D_1=\alpha=0.65$ ), the effect of photoperiod was very pronounced (Fig. 10b). This sensitivity decreased with increasing cold-storage duration, as more and more insects completed Phase II and entered Phase III (Fig. 10c, d).

#### Model Performance Under Natural Weather Conditions

Simulations using parameter values suited for the spruce budworm, and air temperatures from Montreal (Quebec, Canada) produced highly realistic diapause-development patterns (Fig.

11). With all the values of  $P_{1,1}$  tested, the model predicted synchronous emergence over a 20-day period from late April to mid-May. These dates are quite realistic for that part of spruce budworm's area of distribution. The model's prediction was relatively insensitive to the value of parameter  $P_{1,1}$ . These results indicate that the multiple-phase hypothesis constitutes a robust diapause-development mechanism not very sensitive to Phase-II development rates. In the absence of photoperiod sensitivity, the best estimate of  $P_{1,1}$  was 0.020 (optimum: 65 days or 9.3 weeks at 1°C), because it predicted a shift between Phase II and Phase III in the period December-February (Fig. 11b), which reflects available information on spruce budworm diapause termination (Régnière 1990).

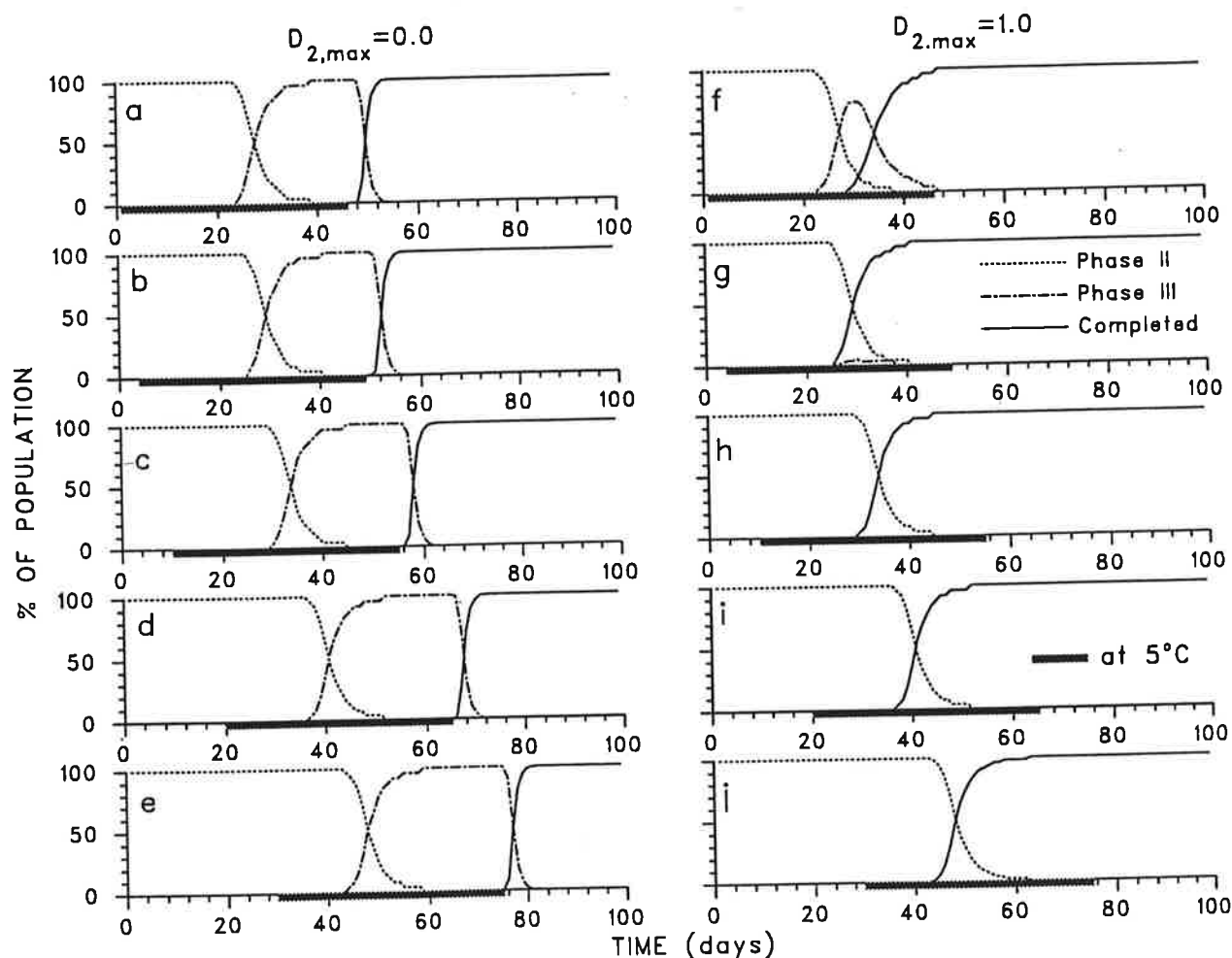


Figure 8. Percent of population in Phase II, Phase III or completing development as a function of time, with increasing durations of pre-storage at 20°C (cold storage: 45 days at 5°C). (a)-(e): strictly sequential model ( $D_{2,max}=0$ ); (f)-(j): strictly simultaneous model ( $D_{2,max}=1$ ). Results of experiment 3.

Photoperiod sensitivity in late Phase II ( $\alpha=0.65$ ) increased model robustness by further reducing its sensitivity to Phase-II development rates (Fig. 11d-f). With the parameter values used (equation [11]), the best value of  $P_{1,1}$  was 0.015 (optimum: 87 days or 12.5 weeks at 1°C).

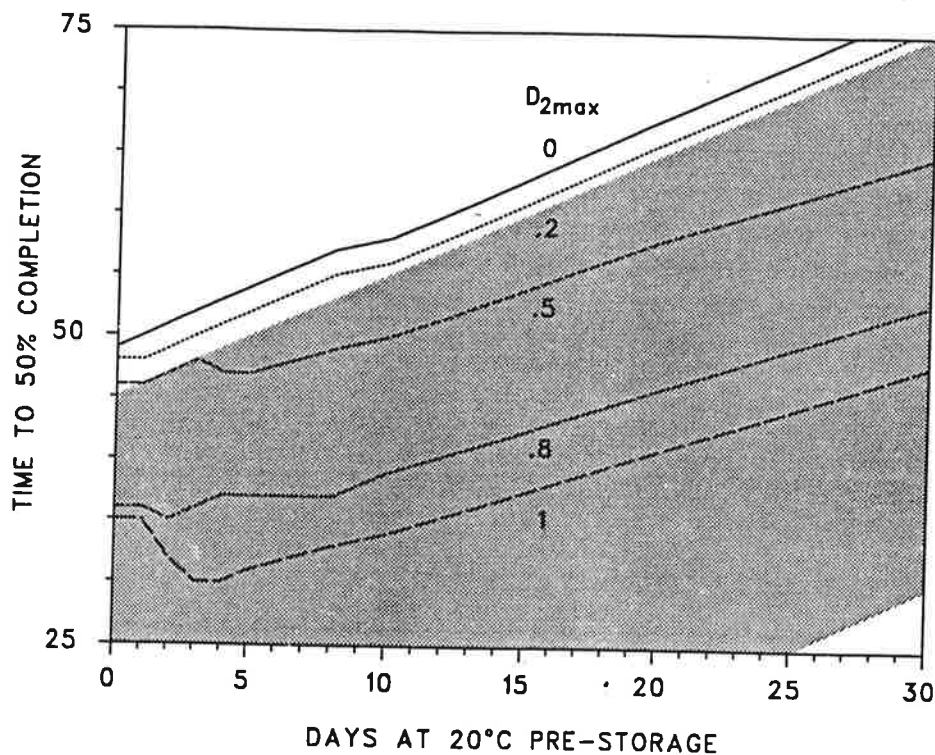


Figure 9. Relationship between the duration of pre-storage at 20°C and time to development completion by 50 percent of the population, with increasing values of  $D_{2,max}$ . Shaded area: development completion in cold-storage. Results of experiment 3.

## CONCLUSION

The simulation experiments conducted with this multiple-phase model of diapause development indicate that phase simultaneity decreases the ability of the diapause process to prevent development completion under adverse conditions and to produce synchronous development. It has an effect similar to a reduction in the duration of postdiapause development. For these reasons, strictly simultaneous phases ( $D_{2,max}=1$ ) probably are not common in nature. Hilbert et al. (1985) proposed the idea of phase simultaneity to explain results obtained under controlled conditions with eggs of the migratory grasshopper, *Melanoplus sanguinipes* (Parker 1930, as cited in Hilbert et al. 1985). It is possible that a sequential multiple-phase model of diapause development could explain Parker's observations if thermal responses during Phase III were not assumed constant, but gradually changing, as was found in the spruce budworm (Régnière 1990). The partly simultaneous model ( $D_{2,max}=0.8$ ) of Hilbert et al.'s (1985) adequately predicted the occurrence or absence of diapause in various geographical locations. From the present analysis, however, it seems that similar results could be obtained with a sequential-phase model with a short second phase. It also seems likely that modeling the occurrence of facultative diapause in insects will require consideration of diapause-induction processes, which undoubtedly are involved in determining diapause intensity, defined in terms of Phase-II development rates. Important developments have been made in modeling the endocrine processes involved in diapause induction and maintenance (Zaslavski 1988).

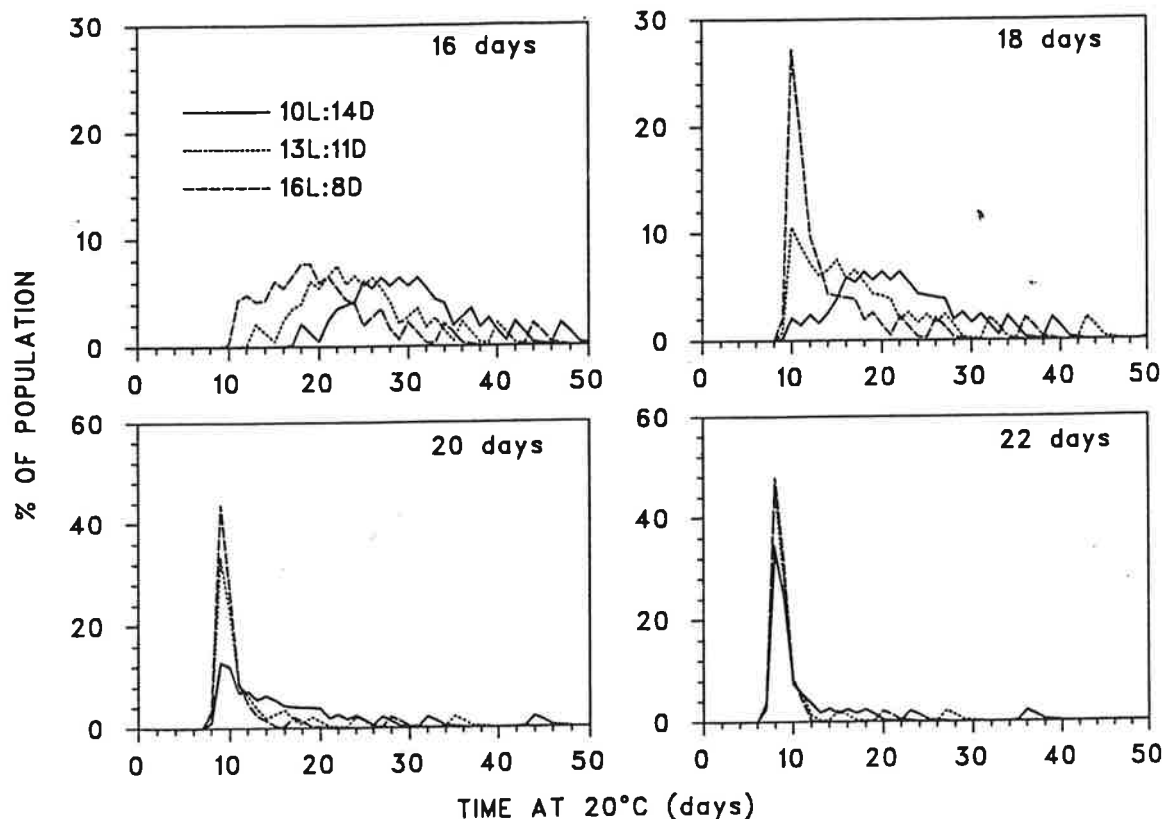


Figure 10. Relationship between time at 20°C and the rate of development completion ( percent of population) at three photoperiods, after (a) 16, (b) 18, (c) 20 and (d) 22 days storage at 5°C. Results of experiment 4.

A multiple-phase model of diapause processes can produce highly realistic simulations of diapause development, even when Phase-II parameter values are not accurately estimated. In the case of spruce budworm, these values were arrived at with relatively simple experiments in which cold-storage duration, temperature and photoperiod were varied (unpublished). More accurate estimation would require observation of the shift between phases in individuals under diverse environmental conditions. In cases where there is no clear morphological or behavioral sign of such a change in individuals, this observation may require the use of more sophisticated experimental methods such as the measurement of metabolic rates and thermal responses through respirometry. Based on the results of the simulation experiments reported here, it would be difficult to distinguish partially simultaneous from strictly sequential phases on the basis of measurements of development duration under various temperature regimes. Again, analysis of changes in metabolic rates and responses to temperature throughout diapause would provide an appropriate basis for this distinction.

A multiple-phase model of diapause development seems to produce generally valid predictions of diapause-development completion times. These predictions were relatively insensitive to Phase-II development parameters. Photoperiod sensitivity in late Phase II further increased the model's robustness by reducing optimal Phase-II development rates. Such a

reduction diminished the likelihood that insects enter Phase III in the fall and complete development under adverse conditions. Photoperiod sensitivity would then allow the insects to enter Phase III in early spring, bypassing further Phase-II development. However, the simulations done here reflected a cold-winter climate. To simulate diapause development in milder areas (e.g. southern United States), where winter temperatures often exceed postdiapause development thresholds, more precise parameter estimates would be required for Phase-II development rates, variability and photoperiod sensitivity. It would seem adaptive for insects living in such environments to display wider separation in the ranges of temperatures at which each phase can proceed, and to avoid phase simultaneity. Photoperiod sensitivity also would enhance the likelihood of a timely switch between phases, although variation in daylength is less pronounced at lower latitudes.

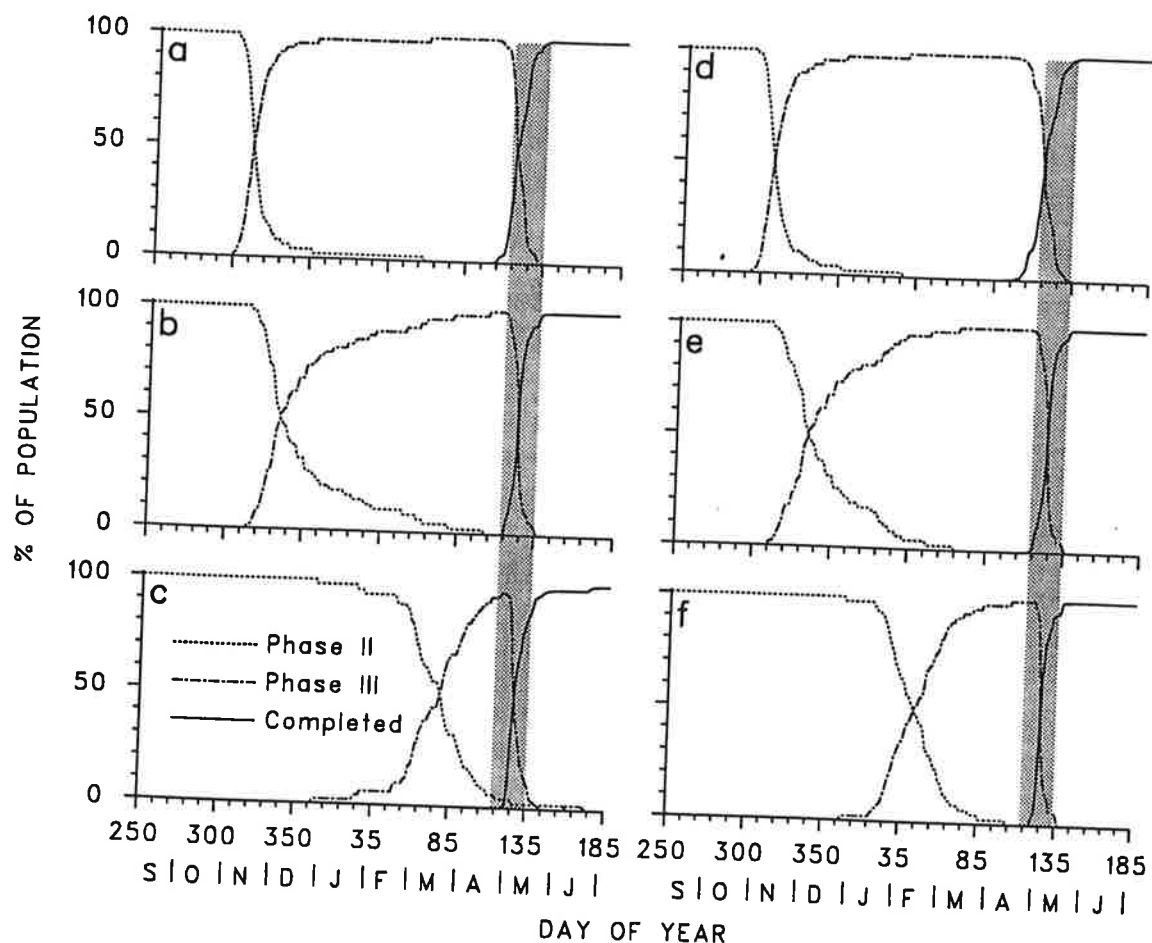


Figure 11. Percent of a simulated population in Phase II, Phase III, or completing development as a function of day of the year, under a natural air-temperature regime from Montreal (Quebec, Canada), with decreasing values of  $P_{2.1}$ : (a) 0.035, (b) 0.025, (c) 0.02 and (d) 0.015. Shaded area: 20-day period from late-April to mid-May during which emergence of spruce budworm can be expected to occur at that latitude.

Several insects have evolved additional mechanisms by which the diapause process can be fine tuned to insure that development resumes in a timely fashion. Photoperiod sensitivity early in postdiapause would increase the likelihood that postdiapause development proceeds only as



daylength increases in the spring (McNeil and Stinner 1983, McNeil and Fields 1985). A gradually changing response to temperature during postdiapause probably also constitutes such a mechanism (Régnière 1990). It is not known at this time whether such changes are common. They would best be detected, once again, through direct measurement of metabolic rates during postdiapause.

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