

## Coevolution of Pierid Butterflies and Their Cruciferous Foodplants

### I. The Relative Quality of Available Resources

Frances S. Chew

Department of Biology, Yale University, New Haven, Connecticut, and  
The Rocky Mountain Biological Laboratory, Crested Butte, Colorado

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*Summary.* Two Colorado populations of *Pieris* butterflies show a spectrum of larval growth responses to potential foodplant crucifer species growing in montane habitats. Analysis of larval growth responses to this array suggests potential selection for differential utilization of these species: 1) available crucifers vary considerably in the rates of larval survival and growth they support; 2) climatological factors favor larvae which develop rapidly. Food-related larval mortality and climatological factors may provide selection for utilization of crucifer species on which larvae develop rapidly.

#### Introduction

Although there is abundant evidence that most phytophagous insect species restrict their feeding activity to limited arrays of plant taxa containing biochemically similar secondary compounds, evidence for variation in resource quality within these arrays is only beginning to emerge. This study examines the relative qualities of potential foodplants available to an insect population in a natural community. From an assessment of insect growth responses to these plants in relation to climatological factors, the possible adaptive value of differential utilization among potential foodplant species will be explored.

Caterpillars of two pierid butterflies (Lepidoptera: Pieridae) native to the southern Rocky Mountains, *Pieris napi macdunnoughii* Remington and *P. occidentalis* Reakirt, were reared on crucifer species abundant near the Rocky Mountain Biological Laboratory at Gothic, Colorado. These butterflies, like other *Pieris* whose behavioral and neurophysiological responses to plants and their secondary compounds have been studied (Verschaffelt, 1910; David and Gardiner, 1966; Schoonhoven, 1967), choose as egg-laying sites and larval food only those plants which contain glucosinolates (mustard oil glucosides) (Remington, 1952). In montane meadows near Gothic the only plants which contain glucosinolates are members of the Cruciferae which therefore represent potential larval foodplants to these species. In examining the growth responses of these pierid larvae to potential crucifer foodplants, two questions are of particular interest: 1) which of the available crucifer species are in fact suitable as larval food? 2) How might the relative quality of larval foods be related to selection on the patterns of food resource utilization in these butterfly populations?

## Materials and Methods

1. *Biological Materials.* *Pieris napi macdunnoughii* flies in moist montane meadows (elev. 2750–3450 m), while *P. occidentalis* flies in drier meadows at slightly lower elevation in the Gothic area. Both butterfly species are facultatively univoltine in this area, emerging from pupal diapause in late June and early July. Both species lay eggs singly on the leaves of crucifers. Larvae complete development during the summer before entering pupal diapause, the stage in which they pass the winter. All larvae of *P. n. macdunnoughii* entered larval diapause when reared outside under natural photoperiod. While *P. occidentalis* were not reared outside, these larvae and those of *P. n. macdunnoughii* emerged several days after pupation when reared under long-day (L15:D9) laboratory conditions.

Five native crucifer species abundant in meadow areas where adult *P. n. macdunnoughii* fly were used in rearing experiments on this butterfly species: *Arabis drummondii* Gray, *Descurainia richardsonii* (Sweet) Schulz, *Draba aurea* Vahl, *Thlaspi montanum* L., and *Erysimum asperum* (Nutt.) DC. *Cardamine cordifolia* Gray, which grows abundantly in willow swales adjacent to meadows, was also tested. *Pieris occidentalis* larvae were reared on three native crucifers abundant where these adults fly: *Arabis drummondii*, *Descurainia richardsonii*, and *Lepidium densiflorum* Schrad. *Thlaspi arvense* L., an introduced crucifer which is locally abundant where *P. occidentalis* flies, was tested on larvae of both species.

2. *Tests of Single Foodplant Species.* Female butterflies of both *Pieris* species were captured near Gothic. These adults were maintained on honey and water (1:3 solution). They were caged with cultivated *Raphanus* (Early Scarlet Globe, Ferry-Morse Seed Co.) either in natural sunlight or under incandescent lighting to elicit egg-laying. Eggs were gently teased off the plants with fine glass needles and placed on aluminium foil in petri dishes, where they were allowed to hatch. Newly hatched caterpillars were placed on intact crucifers which had been transplanted from the field and supplied with Hyponex "7-6-19" (total nitrogen, available phosphoric acid, potash) and Transplantone (naphthaleneacetamide 0.018% and naphthaleneacetic acid 0.002%). While the possible effects of plant growth hormones on glucosinolate metabolism in crucifers have not been tested directly, available evidence suggests there is probably little *in vivo* catabolism of glucosinolates (Skytt-Andersen and Muir, 1966; Marquand *et al.*, 1968; Joseffson, 1971), and relatively slow loss of glucosinolates from the green vegetative parts of plants which have been stored for weeks (Skytt-Andersen and Muir, 1966). The time from hatching to pupation (to the nearest half-day) was recorded for each surviving individual. This measurement represents the time spent feeding and pupating. Because larval diseases and non-specific factors may contribute to larval mortality, survival and growth of *P. n. macdunnoughii* larvae on the various crucifer species were compared with growth on cultivated *Raphanus*, which supports 95–100% survival and rapid larval growth outside and under optimal conditions in the laboratory. This control permitted mortality or retarded growth observed on other crucifers to be attributed directly to the foodplant treatments. Some pupae reared in the laboratory at  $22^{\circ}\text{C} \pm 2$  were weighed to the nearest 5 mg within 12 hrs of pupation. Larvae of *P. n. macdunnoughii* were reared at three temperatures: in the laboratory at  $22^{\circ}\text{C} \pm 2$  and  $19^{\circ}\text{C} \pm 2$ ; and outside under diurnally fluctuating temperatures with a mean daily temperature of  $14.5^{\circ}\text{C}$  (SD = 8.1). *Pieris occidentalis* larvae were reared in the laboratory at  $22^{\circ}\text{C} \pm 2$ . For rearing experiments on both species of larvae, the progeny of three to six females, each represented approximately equally, were combined. The probable diversity of female age at the time of capture and the necessity of synchronizing larvae used in each foodplant treatment by combining progeny of several females made it possible to effectively randomize any systematic effects due to variation in maternal age. In addition to these composite broods, small numbers of *P. n. macdunnoughii* larvae from each of five females were reared separately on each of five crucifers (25 lots). These broods were segregated to compare the growth responses of progeny from different females. In addition, records of oviposition choices of these butterflies in the field, obtained just prior to capture, permit examination of larval growth responses in relation to maternal oviposition choices. These five females oviposited as follows: 1) consecutive ovipositions on *Thlaspi montanum* and *Draba aurea*; 2) two successive ovipositions on *Draba aurea* plants; 3) two successive ovipositions on *Descurainia richardsonii* plants; 4) consecutive ovipositions on *Draba aurea* and *Arabis drummondii*; 5) four successive ovipositions on *Descurainia richardsonii* plants.

3. *Tests of Mixed-Species Diets.* Extensive observations of oviposition behavior in these butterflies (Chew, in preparation) suggest that eggs are often laid on crucifers too small to support complete larval development. Individuals exhausting the initial food supply selected by their mothers might survive if they locate another foodplant. Because individuals of different crucifer species sometimes occur in close proximity (Chew, in preparation), some preliminary tests were made to explore the consequences of larval feeding on two foodplant species. Larvae were reared initially on one crucifer species and were subsequently transferred to another to complete development. The developmental times for these individuals were determined and compared with those of larvae which completed development on a single crucifer species. In these transfer experiments (whose design is shown in Table 4), *P. n. macdunnoughii* larvae were initially reared on *Draba aurea*, *Thlaspi montanum*, and *Descurainia richardsonii*. Some larvae from each of these groups were then transferred in the fourth instar to new plants of the same species to complete development. With the remaining larvae, six pair-wise reciprocal transfers were made among the three crucifer species. These larvae completed development on a different crucifer from the species on which they had been initially reared. There were thus six foodplant treatments in which larvae were reared on two crucifer species, and three control groups in which larvae completed development on the food on which they were initially reared. Reciprocal transfer experiments were also conducted on both *Pieris* species using *Thlaspi arvense* and native crucifers. Similar experiments using *Pieris rapae* L., the introduced cabbage butterfly, were carried out in New Haven, Connecticut using *Barbarea vulgaris* R.Br. transplanted from the field, hydroponically grown cultivated *Raphanus*, and *Thlaspi arvense* grown hydroponically from seed collected near Gothic.

## Results

### 1. *Effects of Single Crucifer Species*

The effects of potential foodplant species on the survival, pupal weights, and developmental times of both *Pieris* species are summarized in Table 1. Survival data were analyzed using the G-test. Analysis of variance was performed on larval developmental times and pupal weights to test the effect of foodplant treatments. Measurements of larval developmental time for *P. n. macdunnoughii* were also analyzed by two-way analysis of variance to test the effects of foodplant treatments, possible differences between broods, and effects of different rearing temperatures.

For *P. n. macdunnoughii*, all crucifer species tested were suitable for rearing larvae except *Erysimum asperum*, which was refused by larvae of all instars, and *Thlaspi arvense*, which was eaten, but on which larvae subsequently died (Table 1). The number of larvae which survived on each of the other crucifers varied significantly ( $P < 0.05$ ) only in the case of larvae reared at  $22^{\circ}\text{C} \pm 2$ . Pupal weights of larvae reared on the four native meadow species did not vary significantly ( $P > 0.14$ ). Since pupal weight and adult size have been positively correlated with both the number of ovarioles (potential reproductive capacity) and fecundity in a variety of Lepidoptera (e.g. Labine, 1966; Engelmann, 1970; and references therein), this observation suggests that foodplant treatments cause no substantial differences in fecundity. The four meadow species can be ranked, although the differences in pupal weight are not significant: *Descurainia richardsonii*, *Thlaspi montanum*, *Arabis drummondii*, and *Draba aurea*. However, individuals reared on these meadow crucifers weighed less than those reared on either cultivated *Raphanus* or the willow swale species, *Cardamine cordifolia*.

Larval developmental times varied significantly ( $P < 0.001$ ). Of the native meadow species, *Descurainia richardsonii* supported the shortest developmental

Table 1. Effects of single crucifer species on the growth of *Pieris* larvae

Crucifer <sup>a</sup>	Temp- erature	Pupated <sup>b</sup>	Mean <sup>c</sup>	S.D.	Weighed <sup>d</sup>	Mean <sup>e</sup>	S.D.
<i>Pieris napi macdunnoughii</i>							
<i>A. drummondii</i>	22° C ± 2	47/61	16.47	0.88	14	98.2	9.73
<i>D. richardsonii</i>		52/64	14.37	0.87	20	105.0	11.70
<i>D. aurea</i>		43/102	17.19	1.16	14	92.5	12.82
<i>T. montanum</i>		53/98	17.66	1.18	21	99.3	12.38
<i>C. cordifolia</i>		14/15	17.79	0.58	14	124.6	9.89
<i>Raphanus</i> cultivar		48/51	13.45	0.58	15	132.3	9.61
<i>A. drummondii</i>	19° C ± 2	16/18	20.50	1.03			
<i>D. richardsonii</i>		16/21	19.56	1.09			
<i>D. aurea</i>		13/24	21.62	1.26			
<i>T. montanum</i>		17/21	23.18	1.59			
<i>C. cordifolia</i>		17/17	18.50	0.62			
<i>Raphanus</i> cultivar		10/10	17.10	0.32			
<i>E. asperum</i>		0/26					
<i>T. arvense</i>		0/40					
<i>A. drummondii</i>	outside	13/28	51.54	1.33			
<i>D. richardsonii</i>		26/51	41.81	2.32			
<i>D. aurea</i>		21/33	49.57	1.72			
<i>T. montanum</i>		23/38	48.04	1.55			
<i>C. cordifolia</i>		35/36	40.46	1.69			
<i>Raphanus</i> cultivar		12/13	41.67	1.44			
<i>Pieris occidentalis</i>							
<i>A. drummondii</i>	22° C ± 2	16/38	16.75	0.86	16	118.8	11.76
<i>D. richardsonii</i>		10/45	17.70	1.64	10	123.5	18.72
<i>L. densiflorum</i>		9/12	14.67	0.87	9	118.3	9.68
<i>T. arvense</i>		0/46					

<sup>a</sup> Crucifer species: *Arabis drummondii*, *Descurainia richardsonii*, *Draba aurea*, *Thlaspi montanum*, *T. arvense*, *Erysimum asperum*, *Cardamine cordifolia*, *Lepidium densiflorum*.

<sup>b</sup> Number (as fraction) of larvae which pupated, of those initially placed on plant.

<sup>c</sup> Mean time to pupation, in days.

<sup>d</sup> Number of pupae weighed.

<sup>e</sup> Mean pupal weight, in mg.

time. Scheffé analysis (Scheffé, 1953; Snedecor and Cochran, 1966) of the developmental times shows that at the three temperatures used for rearing *P. n. macdunnoughii*, larval growth on *D. richardsonii* was significantly faster than on any of the other three meadow species ( $P < 0.01$ ). At outdoor temperatures, all larvae growing on *D. richardsonii* pupated before any larvae reared on the other meadow crucifers began to pupate. Two-way analysis of variance to test the effects of temperature and foodplant treatments showed a significant interaction between foodplant and temperature effects ( $P < 0.001$ ). Some crucifer species, including *Cardamine cordifolia* which at outdoor temperatures supports a very rapid larval growth rate, supported relatively slower growth at higher temperatures.

*Pieris occidentalis* larvae ate all four of the meadow crucifers offered, and completed larval development on all but *Thlaspi arvense*, which larvae ate but on

Table 2. Developmental rates of larvae from different *P. n. macdunnoughii* females

Crucifer	Female					Composite brood
	1	2	3	4	5	
<i>Arabis drummondii</i>						
Pupated successfully <sup>a</sup>	7/9	9/11	6/8	6/9	9/11	10/13
Mean days to pupation	16.43	16.33	16.33	16.83	16.33	16.82
SD	1.39	0.71	1.03	0.75	0.71	1.33
<i>Descurainia richardsonii</i>						
Pupated successfully	5/7	8/10	8/9	6/9	5/6	20/23
Mean days to pupation	14.20	14.29	14.13	14.67	14.60	14.40
SD	0.84	0.49	0.99	1.03	1.14	0.83
<i>Draba aurea</i>						
Pupated successfully	4/8	5/12	3/10	10/16	6/13	14/43
Mean days to pupation	17.00	16.71	17.00	17.20	16.83	17.36
SD	0.82	1.80	1.00	0.92	1.17	1.59
<i>Thlaspi montanum</i>						
Pupated successfully	6/9	5/9	7/12	8/12	6/10	21/46
Mean days to pupation	16.57	17.20	17.43	17.50	17.40	18.00
SD	2.30	0.84	0.98	0.76	1.14	1.41
<i>Raphanus cultivar</i>						
Pupated successfully	5/5	7/8	9/10	7/7	5/6	15/15
Mean days to pupation	13.25	13.43	13.67	13.71	13.40	13.27
SD	0.50	0.54	0.71	0.76	0.55	0.46

<sup>a</sup> Number (as fraction) of larvae which pupated, of those initially placed on plant.

which they subsequently died. The number of larvae surviving on the other three crucifers did not vary significantly ( $P > 0.1$ ). The weights of pupae reared on the three crucifers (Table 1) did not vary significantly ( $P > 0.63$ ), but larval developmental times did ( $P < 0.001$ ). These results, although difficult to interpret because the sample sizes are quite small, suggest that variation in *P. occidentalis* growth responses is similar to that observed in *P. n. macdunnoughii*.

## 2. Intrapopulation Variation

The possibility of brood-specific differences in growth rate was tested by two-way analysis of variance of developmental times for the progeny of five females reared separately on each of five crucifers (Table 2). This analysis showed that while foodplant treatments resulted in significant differences in the developmental times of larvae ( $P < 0.001$ ), differences between broods were not evident ( $P > 0.24$ ). The responses of larvae from these five females corresponded closely with those of composite broods (Tables 1 and 2). Larvae did not necessarily develop more rapidly on plant species chosen as oviposition sites by their mothers. This limited result suggests no substantial genetic differences in growth response characters, but does not permit assessment of the degree to which these responses vary genetically.

Table 3. Effect of *Thlaspi arvense* on larval survival: Reciprocal transfers between *T. arvense* and native crucifers at different larval instars

Transfer	Instar of transfer			
	II	III	IV	V
<i>T. arvense</i> to native crucifer <sup>a</sup>				
<i>P. n. macdunnoughii</i> Pupated successfully <sup>b</sup>	0/45	0/25		
<i>P. occidentalis</i> Pupated successfully	0/22	0/12		
Native crucifer to <i>T. arvense</i>				
<i>P. n. macdunnoughii</i> Pupated successfully		0/11	1/27	25/34
<i>P. occidentalis</i> Pupated successfully			0/20	19/25

<sup>a</sup> Native crucifers were *Descurainia richardsonii* and *Thlaspi montanum*; cultivated *Raphanus* also used.

<sup>b</sup> Number (as fraction) of larvae which pupated, of those initially placed on plant.

### 3. Effects of Mixed-Species Diets

In reciprocal transfers of both *P. occidentalis* and *P. n. macdunnoughii* between *Thlaspi arvense* and other crucifer species, larvae feeding for one instar on *T. arvense* at any time prior to the fifth (last larval) instar died before pupating (Table 3). However, more than two-thirds of the larvae of both species pupated and successfully emerged when transferred to *T. arvense* during the fifth instar. Interestingly, *Pieris rapae*, the introduced cabbage butterfly, is able to develop successfully from hatching on *T. arvense*.

The main effect of reciprocal transfers of larvae among crucifers which all support complete larval development (Table 4) is increased variation in developmental time, at least in some cases. Comparison of mean developmental times across each row of Table 4 (larvae in each row were initially reared on the same crucifer species) shows that larvae which complete development on an alternate food may grow more rapidly or slowly than their counterparts (controls) which complete development on the same crucifer. Thus the effect of between-species transfers on a group of larvae initially reared on the same crucifer (groups arranged in rows in Table 4) is to increase the range and variance of developmental times compared to control groups (diagonal groups in Table 4) for which such transfers were not made. This increased variance is significant ( $P < 0.05$ ) in two of three groups (rows) of *P. n. macdunnoughii* (Table 4), and three of six such groups of *P. rapae* (Chew, 1974). Larvae initially placed on small plants by their mothers may thus increase variation in growth rates if they complete development on alternate food resources.

### Discussion

The diversity and profusion of secondary metabolic compounds in higher plants have been used widely to investigate systematic relationships among plant

Table 4. Effect of single and mixed-species diets on developmental rate of *P. n. macdunnoughii* larvae

		Crucifers used to complete development		
		<i>D. richardsonii</i>	<i>D. aurea</i>	<i>T. montanum</i>
Crucifers used to initiate development <sup>a</sup>	<i>D. richardsonii</i>			
	Pupated <sup>b</sup>	20/23	11/16	14/18
	Mean <sup>c</sup>	14.40	14.82	14.21
	SD	0.88	0.87	0.70
	<i>D. aurea</i>			
	Pupated	10/18	14/43	9/20
	Mean	16.50	17.36	17.56
	SD	0.85	1.60	1.01
	<i>T. montanum</i>			
Pupated	12/18	10/20	21/46	
Mean	17.67	17.30	18.00	
SD	1.37	0.82	1.41	

<sup>a</sup> Rows are groups of larvae initially reared on the same crucifer; off-diagonal groups were transferred to other plants; diagonal groups (controls) completed development on the same foodplant species.

<sup>b</sup> Number (as fraction) of larvae which pupated, of those initially placed on plant.

<sup>c</sup> Mean developmental time, in days.

taxa at many levels (see *e.g.* Hegnauer, 1962–1969; Gibbs, 1974). Elucidation of synthetic pathways for these compounds has in many cases permitted derivation of metabolic relationships among secondary products and presumptive phylogenetic relationships among the taxa in which they occur. More recently, from these data and extensive published records of butterfly larval foodplants, Ehrlich and Raven (1964) have argued persuasively that products of secondary metabolism in plants have been the foci of coevolution between higher plants and phytophagous insects. They argue that because the primary function of these compounds is defensive (see *e.g.* Fraenkel, 1959), the resulting evolution of mechanisms for tolerance, detoxification, and recognition of specific groups of compounds has produced the extreme specialization observed among contemporary insects. The food-related activities of most of these insects (*e.g.* food-seeking, feeding, egg-laying) are dependent on the presence of specific stimulatory compounds whose occurrence is restricted to certain plant taxa. To a lesser extent, these specialized feeders also respond to more generally occurring chemical deterrents (see *e.g.* Brues, 1924; Dethier, 1954; Thorsteinson, 1960; Burnett *et al.*, 1974). This restriction of food habits along chemosystematic lines facilitates precise identification of potential food resources for a particular insect species. It is with this chemically and systematically defined array that an insect species must coevolve. The degree to which these potential food resources vary in suitability provides some measure of how much farther selection for mechanisms of tolerance, detoxification, or recognition of unsuitable resources may proceed. The crucifer species which represent potential foodplants for these two montane *Pieris* species are not equivalent food sources in terms of larval survival and growth rate.

### 1. Food-Related Mortality

*Pieris occidentalis* individuals (or *P. n. macdunnoughii*) initially placed on *Thlaspi arvense* by their mothers will almost certainly die from food-related causes if they do not first encounter other sources of mortality. The lethality of this plant would provide a powerful advantage to ovipositing females which discriminated against *T. arvense*. The lethality of *Erysimum asperum* to *P. n. macdunnoughii* larvae (whether from starvation, effects of plant toxins, or both is unknown) would similarly favor discriminating females. Because *T. arvense* elicits feeding behavior from both species of larvae, any variation permitting larvae to develop successfully on this plant would have a chance to be favored. Larvae may also successfully exploit *T. arvense* if they develop initially on other crucifer species, and utilize *T. arvense* during the final larval instar. King (1971) suggests that populations whose component individuals do not specialize on one of a number of food resources may support a greater number of individuals on a given set of food resources than populations whose component individuals specialize. In this case, the use of two foodplant species by individual larvae may permit successful exploitation of a crucifer which could not otherwise be used, and may permit the survival of individuals which might otherwise exhaust their initial food supply.

### 2. Climatological Interaction with the Spectrum of Larval Growth Rates

The advantage of using a foodplant which supports faster larval growth is less obvious. More rapid development reduces the period of exposure to larval predators and parasites; however, the effects of these potential selective agents and their possible association with different foodplant species have not been assessed. Examination of climatological records from the Gothic area suggests strongly that rapid larval development may be advantageous. Air temperature minima, shown in Fig. 1 (U.S. Department of Commerce, 1949-1974), show that a growing season arbitrarily defined by the last spring frost and the first severe autumn frost ( $0^{\circ}\text{C}$  in spring,  $-4.4^{\circ}\text{C}$  in autumn) is variable in onset as well as duration. Data used in this analysis are conservative; both temperature and precipitation are more variable and more extreme near Gothic than at the Crested Butte weather station, 14 km south and 240 m. lower (Ehrlich *et al.*, 1972; Langenheim, 1962; W. A. Calder, unpublished data). Further, Ehrlich *et al.* (1972) have documented the effects of severe late spring storms on some Lepidoptera in this region.

The time available to larvae developing in the field is shown in Fig. 2, which places frosts, droughts, and butterfly emergence along a calendar axis. The mean date of the last spring frost ( $0^{\circ}\text{C}$ ) appears to be a reasonable predictor of the first emergence of female *P. n. macdunnoughii*, and at  $-4.4^{\circ}\text{C}$ , severe frost and the accompanying lower daytime maximum temperatures may substantially retard larval or plant growth. Sherman and Watt (1973) have shown for example, that montane *Colias* larvae do not feed actively at temperatures below  $15^{\circ}\text{C}$ . It is likely that similar thermal requirements exist for *Pieris* larvae although the critical temperatures may differ.

Females emerge over several weeks during the summer so that only a relatively small proportion of the adult population risks exposure to late frost. The results of rearing *P. n. macdunnoughii* outside show that larvae placed on *Descurainia*

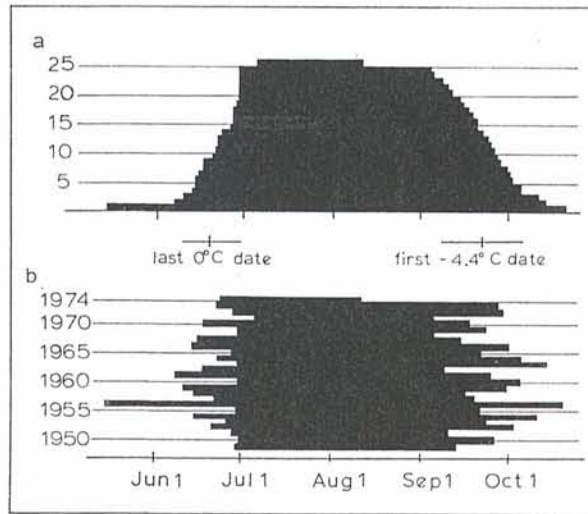


Fig. 1 a and b. Number of days between last spring frost and first severe autumn frost. (a) Cumulative frequency distribution showing the number of times a given date was included in the past 26 growing seasons. (b) Black bars show duration and placement of growing season between air temperature minima, last spring  $0^{\circ}\text{C}$  ( $\pm$  SD) and first autumn  $-4.4^{\circ}\text{C}$  ( $\pm$  SD). Data from U.S. Department of Commerce

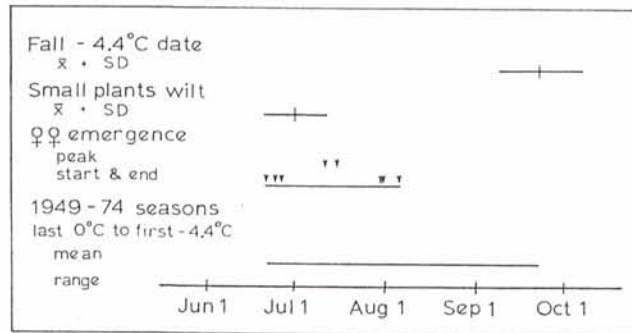


Fig. 2. Flight season of female *Pieris napi macdunnoughii* in relation to air temperature minima and drought periods. Temperature data from Fig. 1; drought date is the 14th day ( $\pm$  SD) of nine drought periods (1949–1974) of more than 17 days' duration. Butterfly emergence data are for 3 years (1971–1973) (Watt *et al.*, in preparation)

*richardsonii* or *Cardamine cordifolia* spend an average of 5–6 weeks in the larval stage, while those reared on *Arabis drummondii* require about seven and one-half weeks to develop (Table 1). With the addition of 5–6 days' developmental time spent in the egg under natural conditions, pre-pupal developmental times on this array of crucifers range from  $6\frac{1}{2}$  weeks to 8 or 9 weeks. Given the observed flight emergence-pattern of *P. n. macdunnoughii* (Fig. 2), a substantial proportion of eggs laid by females emerging at the peak of the flight season may have insufficient time to complete larval development if they are placed on crucifers on which growth is slow. Larvae of females emerging late in the season which do not succumb to autumn frost may pupate earlier during their development. The decreased pupal weight may contribute to pupal mortality or to reduced fecundity.

Offspring of females which emerge early during the flight season appear to have ample time to develop. However, periods of severe drought early in the summer cause irreversible wilting of some crucifer individuals. *Thlaspi montanum* plants appear to be particularly susceptible (Rochow, 1970; Chew, 1974). Periods of drought with elevated temperatures (daily maxima above 24° C) for longer than 2 weeks occurred during nine of 26 years for which climatological data were examined. Because ovipositing females place some of their eggs on plants small enough to succumb to drought under these conditions, some larvae will be forced to seek other foodplants. Prolonged drought periods are rare (one in 26) after early July. One consequence of the effect and timing of these drought periods is that larvae which grow rapidly during the initial part of their development will be favored. Larger larvae (fourth and fifth instar) travel faster, more quickly locate alternative crucifers, and tolerate starvation for longer periods than young larvae (Chew, 1974). Thus climatological factors favor larvae which develop rapidly.

Whether selection favoring rapid larval development is a mechanism by which foodplant utilization patterns can be modified depends on the magnitude of genetic variation in larval growth responses to the different crucifer species. The data presented here do not exclude the possibility of small amounts of variation sufficient to allow selection for intrapopulational specialists which excel on particular crucifers, or the possibility that crucifer species other than *Descurainia richardsonii* (in the meadow) and *Cardamine cordifolia* (in willow swales) may be superior foodplants under conditions not yet examined. Neither, however, do these data suggest such possibilities. Given the experimentally determined spectrum of larval growth responses (Table 1), the selective pressures of food-related mortality, and those of the climatological pattern (Fig. 2), these butterfly populations may be expected to differentially utilize members of these crucifer arrays.

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Dr. Frances S. Chew  
Department of Biology  
Tufts University  
Medford, Massachusetts 02155, USA