

FROM WEEDS TO CROPS: CHANGING HABITATS OF PIERID BUTTERFLIES (LEPIDOPTERA: PIERIDAE)

FRANCES S. CHEW

Department of Biology, Tufts University, Medford, Massachusetts 02155, USA

ABSTRACT. Butterflies in the genus *Pieris* offer a model system for assessing the impact of agricultural expansion on the foodplant-linked biology of insects, notably why certain species become crop pests and others do not. Factors that influence the likelihood of attaining pest status when habitats change are reviewed, including hostplant density, climate, voltinism, larval diet breadth, and fecundity. The relative importance of these are explored in two now cosmopolitan species on agricultural crops, *Pieris rapae* and *P. brassicae*.

Anthropogenic changes to the landscape, particularly those associated with European colonization of the Americas, have brought numerous biological consequences. Some were intentional, such as clearing of forest in eastern North America (Cronon 1983); but others were not. For example, forest cutting brought into contact closely related species from opposite sides of the natural hardwood forest barrier in eastern Canada and the USA (Remington 1968). Anticipating unintended consequences of disrupting natural processes now applies to many human activities including agricultural control of insect pests. If we make agroecosystems more like natural ecosystems, we hope, we will promote effective natural regulation of potential insect pests.

One major challenge is the limited applicability of available information. Information obtained about one level of organization is not always sufficient to predict consequences at a higher level and vice versa (Power 1992, Vitousek 1994). For example, consumption rates of insect prey by predators may not enable us to predict predation's impact on prey population dynamics; similarly, knowing predation's impact on a prey population may not predict whether a predator population is sustained on that prey population (Hunter & Rice 1992). On one hand, most studies of insect ecology are case studies of populations or species in a restricted context, without necessarily accounting for the heterogeneity observed at each trophic level (Hunter & Rice 1992, Vitousek 1994). Limits of time and logistical support force us to focus on relatively small numbers of factors, interactions, populations, species or habitats. Few investigations of crop diversity effects on pest abundance examine mechanisms by which pest abundance changes (Risch et al. 1983, Andow 1988). On the other hand, the size of agroecosystems and the dispersal capacities of insects require that we view these systems at larger scales (Woiwod & Stewart 1990, Allen & Hoekstra 1992).

What lessons from natural populations and communities can we apply

to agroecosystems? Can we expect to alter dramatically the primary resource base of a community while controlling potential change at higher trophic levels? In this paper, I apply ecological research on pierid butterfly communities to speculate on the following questions: 1) What ecological traits enable some species to become pests when their resource base changes from "natural" to "agricultural;" and 2) What lessons from ecological work can we use to manage these pest species?

ECOLOGICAL PORTRAITS OF POTENTIAL PEST SPECIES

Of perhaps several dozen species or geographic subspecies of crucifer-feeding pierid butterflies studied by ecologists during the past several decades, only two species of Palearctic origin—*Pieris brassicae* L. and *P. rapae* L.—attain economic pest status on crucifer crops worldwide, particularly vegetables (Bonnemaison 1965, Oatman & Platner 1969, Takata 1962, Feltwell 1982, Thomas 1984, Finch 1988, Lamb 1989). *Pieris rapae* is now a cosmopolitan species. Figure 1 shows these two species as part of an indigenous community feeding on crucifers (Brassicaceae) in the High Atlas region of Morocco at one of the geographic centers of crucifer diversity (Tsunoda et al. 1980). Interactions among these species and between butterflies and potential hostplants were studied over several seasons (Courtney & Chew 1987, Chew & Courtney 1991). Comparable species richness occurs in pierid communities in the South American Andes and in California, USA. In these latter places, however, populations of *Pieris rapae* or *P. brassicae* are naturalized rather than indigenous. The Moroccan community thus represented an opportunity to observe these two pests in their native habitats where the resource base has not been converted to crucifer agroecosystems (although grain farming, fruit-tree orchards, evergreen tree farms, and grazing are conspicuous activities in some habitats). Further, these species could be observed together with other indigenous crucifer-feeding pierine and euchioline butterflies.

One general result is that we found no evidence that hostplant use was altered when butterfly species co-occurred. Diet breadth and specificity were unrelated to the composition of the pierid community and are better understood in terms of individual butterfly species adaptation to habitats and potential hostplants (Courtney & Chew 1987; Chew & Courtney 1991). In comparison with other species, *Pieris rapae* and *P. brassicae* differ in a number of traits that together promote rapid response to changes in hostplant abundance: 1) multivoltinism; 2) broad diet (euryophagy); 3) adult preference for mesic habitats with apparent crucifer populations; 4) potentially high fecundity. Euryophagy and fecundity correspond directly to two of four traits that contribute to



FIG. 1. Crucifer-feeding pierid community in the High Atlas region of Morocco, showing flight seasons of each species as white bars. Butterflies figured in top panel, clockwise from top left, the leaf-feeding guild includes *Pieris rapae* L., *P. napi segonzaci* Le Cerf, and *P. brassicae* L.; continuing clockwise, the inflorescence-feeding guild includes *Euchloe ausonia* Hubner, *E. belemia* Esper, and *Pontia daplidice* L. Lower panel, clockwise from top, *Elphinstonia charlontia* Donzel and *Anthocharis belia* L., both inflorescence feeders; *Colotis evagore* Lucas, a folivore on *Capparis spinosa* bushes, and the inflorescence feeders *Euchloe falloui* Allard and *Zegris eupheme* Lederer. Nomenclature follows Higgins & Riley (1980).

the major pest status of *Heliothis* species (Lepidoptera: Noctuidae) (Fitt 1989); multivoltinism and habitat selection are likely analogs of two traits named by Fitt for major *Heliothis* pests—facultative diapause and nocturnal migration between areas.

Multivoltinism Increases Outbreak Potential

The multivoltinism of both *Pieris* species in Morocco enables them to expand populations early in the season and to produce numerous offspring that colonize new habitats as the season progresses. In addition, multivoltinism together with euryophagy promotes local persistence of these species in years when other insects and their hostplants are asynchronous. We observed that sometimes univoltine butterflies and their hostplants were both abundant, but that the hostplants did not appear in a specific locality until after the butterflies had flown at that site (Chew & Courtney 1991)

Population expansion on alternative hosts in an earlier generation contributes to the rapid response of these *Pieris* species to crop hostplants and to their ability to exploit agricultural crops. This ecological trait also was noted for *Pieris rapae crucivora* Bdv. in Japan (Ohsaki 1982) and for *Pieris napi oleracea* Harris, a pierine that is locally extirpated in parts of the eastern USA, where it used to be an agricultural pest (Harris 1841). In northern Vermont, USA, this latter species occurs in low density early in the season, but flies with *P. rapae* in great abundance in July and August (Chew 1981).

Flight season or multivoltinism alone do not promote attainment of pest status. *Pontia daplidice* L., a multivoltine species with the longest flight season in Morocco, is not usually a pest. However, multivoltinism may permit exploitation of otherwise unused resources and changes in host availability may favor multivoltinism. Native *Pieris napi* in California has extended its vernal flight season into summer near riparian habitats containing naturalized watercress (Shapiro 1975). Based on data showing that late emergence from overwintering puparia is controlled by a single gene locus, Finch (1988) suggests that trivoltine *Delia radicum* (cabbage root fly, Diptera: Anthomyiidae) evolved, in response to agricultural practices extending the season for cruciferous crops, from ancestors restricted to two generations per year.

Euryophagy Promotes Pre-adaptation to Crop Hosts

Both *Pieris rapae* and *P. brassicae* exploit a wide range of crucifers compared to other Moroccan pierids. They utilize all the hosts preferred by pierids with narrower diet breadth, and utilize additional hosts. Neither species exhibits strong negative or positive correlations in larval performance on hosts, a general finding for many herbivorous insects (Via 1990). Diet breadth maintains larval adaptation to a range of hostplants and increases the likelihood of successful colonization of a novel host. Available evidence suggests individual egg-laying pierid females oviposit on all the hostplants used by their population (*Pieris*

napi macdunnoughii Remington, Chew 1977a), but more extensive work on *Colias eurytheme* Bdv. (Pieridae) demonstrates heritable variation for oviposition preference among conspecific individuals of this family (Tabashnik et al. 1981).

Temporal variation in host availability between years is the most prominent correlate of diet breadth for Moroccan pierids. Some host species occur at nearly the same density in a given locality from year to year; in other species, some population densities may differ by several orders of magnitude from year to year. Crucifer species whose densities are numerically stable in a given locality are chosen by all the Moroccan pierids in this community. Exceptions are representatives of a few genera known to contain secondary compounds atypical of the Brassicaceae, some of which deter oviposition or larval feeding of *P. rapae* (Sachdev-Gupta et al. 1990, 1993). Thus pierids with narrow diet confine themselves to using numerically stable plant species in preference to less predictable species. Pierids with broader diet utilize these stable species, and add less predictable species. Only the most euryphagous pierid in this community, *Pontia daplidice*, uses highly unpredictable plant species, where population-level variation in crucifer density averages more than an order of magnitude from one year to the next. This pattern is similar to observations of three *Pieris* species living in the same region in central Japan (Ohsaki 1979).

Crucifer damage caused by unidentified herbivorous invertebrates shows the same pattern (Chew & Courtney 1991). Plant species with the least numerical stability from year to year have the least damage from unidentified invertebrate herbivores (by visual inspection of magnified photographs, $r = -0.66$, $p < 0.01$, $n = 19$ crucifer species); these plant species also accumulate fewer pierid eggs than species with more numerical stability. When the average population-level plant density varies more than four-fold (almost half an order of magnitude), only the most euryphagous pierid butterflies use that plant, and mean infestation rate (average number of eggs per host individual) drops from the range of 0.4–1.1 to less than 0.05–0.2.

Two exceptions to this general finding increase the likelihood that *Pieris rapae* and *P. brassicae* attain outbreak proportions on crops. First, despite its broad diet, *P. rapae* uses the most numerically stable populations of its hostplants. In this habit it resembles butterflies that exploit a much narrower range of hostplant species, except that *P. rapae* differentiates between more and less numerically stable populations within each hostplant species, while euechloines and pierines with more restricted diets differentiate between more and less numerically stable hostplant species. This adult behavior promotes consistent exposure of *P. rapae* larvae to a wide array of host species so larval adaptation to

these species is maintained by natural selection. This pattern of adult oviposition behavior is similar to the contrast observed by Ohsaki (1979, 1980) between the pest *P. rapae crucivora* and *P. melete* Menetries, which uses a wider range of hosts but does not specialize on crop hosts. When abundant, densely planted novel hosts occur in agricultural systems, *P. rapae* females exploit these resources as an extension of their behavior in natural habitats. Because their larvae are adapted to many natural hosts, there is high probability of larval success on the novel resource. In combination, adult and larval adaptation promote rapid, successful colonization. For *P. rapae crucivora*, however, Ohsaki and Sato (1994) also note that host use is a trade-off between the high quality of agricultural plants and the heavy parasitoid load encountered in agricultural situations. Possibly it is the only species sufficiently fecund to tolerate the exposure to parasitoids and still maintain local populations.

Pieris brassicae presents a second departure from the general findings about euryophagy and host numerical stability noted above, with consequences for numbers of larvae on individual hosts. *Pieris brassicae* uses hostplant populations with relatively less numerical stability compared to the host species averages. This occurs because some of its host species are annuals whose populations can attain high densities and very large individual size (>1.5 m) in wet years, but not during intervening dry years. Large individual hostplants support larval growth until *P. brassicae* must disperse from the plant they have consumed, so ovipositing on a large host increases the size larvae will attain before dispersal (Davies & Gilbert 1985). Typical cluster size on wild hosts in Morocco is a dozen eggs (Courtney 1986, personal observation), while in Europe egg clusters are several times that size (Davies & Gilbert 1985). The speculation that individual butterflies might adjust the size of egg clusters to the size of hosts is intriguing, but evidence is lacking (Courtney 1986). Selection may favor large cluster size where hosts are consistently large and dense because large clusters may increase female oviposition efficiency (Rothschild 1987) without negative consequences for dispersing larvae. *Pieris rapae* lay more eggs per alighting where climate limits flight activities (Jones 1987).

Pontia daplidice uses the broadest range of host species of any pierid in this community, yet it does not attain pest status. However, it differs from the two potential pests in two ways. First, it is an inflorescence feeder rather than a leaf feeder. It thus exploits resources that are individually short-lived in most crucifers; it is not pre-adapted to colonize (leafy) vegetable crops. Second, adults do not concentrate in dense crucifer populations (see habitat choice, below). Instead, *P. daplidice* occupies many habitats at very low density (Courtney & Chew 1987).

Euryophagy, like multivoltinism, may permit pest status, but is evidently not sufficient for pierid butterfly pest status.

Pests Prefer Dense Hosts in Mesic Habitats

Of all Moroccan pierids, *Pieris rapae* occurs most abundantly in a wide range of habitats. Populations of *P. rapae* are widespread, although not ubiquitous at high latitudes, high elevations or islands (missing, for example, from Alaska, USA; K. Philip, pers. comm.). With the exception of wooded areas, it is a habitat generalist in Morocco, as well as in Japan and eastern North America (e.g., Takata 1962, Cromartie 1975, Ohsaki 1979). Given the open population structure of *P. rapae* in Japan and North America (Chew 1981, Yamamoto 1981, Ohsaki 1982, Thomas 1984), this butterfly's dispersal capabilities permit rapid spread to new sites (Scudder 1889) and reduce local genetic differentiation (Vawter & Brussard 1983) that might restrict adaptation to its many hosts. Because it favors open areas and is euryophagous, multivoltine and fecund, its frequent colonization of agroecosystems is not surprising.

Pieris rapae prefers open, sunny habitats, in contrast with *P. napi nesis* and *P. melete* in Japan (Ohsaki 1986) and *P. napi macdunnoughii* (Chew 1977a), *P. napi oleracea* (Chew 1981), and *P. virginiensis* Edw. (Klots 1951, Cappuccino & Kareiva 1985) in eastern North America. When ambient temperatures are too high, *P. rapae* adults intercept solar radiation by closing the wings over the body (Ohsaki 1986; cf. *Cotias*, Watt 1968). By contrast, *P. melete* and *P. napi nesis* adults regulate body temperature by flying in and out of shaded areas (Ohsaki 1986). Because the oviposition sites of these two butterflies are in shaded areas, Ohsaki (1986) concluded that adults sought sunlight in order to elevate body temperatures above the minimum needed for flight activities such as oviposition. However, these observations raise the possibility that of the three *Pieris* species examined, only *P. rapae* adults are able to prevent overheating in open, sunny areas. Rates and spatial patterns of oviposition in *P. rapae* have diverged adaptively among British, western Canadian and eastern Australian populations (Jones 1977, 1987). Populations in cool or cloudy climates where temperature limits flight activities tend to dump eggs to reduce egg shortfall while butterflies in sunny Australia disperse eggs more widely (Jones 1987).

Pieris rapae's preference for sunlit habitats extends to choosing sunlit oviposition sites, where elevated ambient temperatures reduce the time required to complete larval development to only two-thirds the requirement of larvae growing in shaded habitats (Ohsaki 1982). Elevated temperature of the larval habitat appears to be a key factor in increasing the number of generations achieved in central Japan by *P. rapae crucivora* in comparison with *P. napi nesis* and *P. melete* (Ohsaki 1982;

cf. *Euphydryas gillettei* Barnes, Williams 1981). Similar developmental acceleration could result from females choosing only those hosts that support the most rapid development (Scriber & Lederhouse 1992, van der Reijden & Chew 1992). By choosing a narrow range of microhabitats, *P. rapae* crucivora exploits a large range of hosts evidently without compromising rapid larval development (Ohsaki 1979, 1980, 1982). Curiously, when faster growing female *P. rapae* larvae from Australia and Britain developed into adults, they laid more eggs per alighting than adults from more slowly developing larvae (Jones 1987). Under lab conditions, higher ambient temperatures result in increased forewing length, pupal weight, and subsequent adult fecundity in *P. rapae* (Jones et al. 1982, Kimura & Tsubaki 1986), but possible trade-off between these measures of fitness and the advantage of short generation time in a multivoltine population with overlapping generations (Ohsaki 1982, Jones 1987), and the relation of fecundity to tolerance of parasitoid load (Ohsaki & Sato 1994) is not known.

Pieris brassicae is most frequently associated with fertile open sites where individual crucifers attain great size and density in mesic years (Courtney & Chew 1987). Because larvae of *P. brassicae* leave individual plants after defoliating the plant (Davies & Gilbert 1985), high hostplant density increases likelihood of larvae locating alternative hosts. Crucifer agroecosystems mimic these natural conditions of abundance, soil moisture, and fertility to which *P. brassicae* are attracted. Davies and Gilbert (1985) argue that *P. brassicae* more efficiently uses larval resources than does *P. rapae*, a trait they attribute to the gregariousness of *P. brassicae* caterpillars, which frequently use hosts to which they've dispersed. These latter host individuals are not oviposition sites, but their use permits higher larval survival than if the population were restricted to host individuals that receive eggs. A similar theoretical argument by King (1971), adapted by Chew (1975) for pierid butterflies that disperse to novel hosts in late instars, proposes that additional novel resources increase the equilibrium population size.

Where *P. brassicae* and *P. rapae* co-occur, encounter rates between the two species may be reduced by two mechanisms. First, *P. brassicae* may occupy large plants while *P. rapae* chooses smaller plants or species. In Morocco *P. rapae* often oviposit on tiny individual crucifers (<2 cm height). In the USA, *P. rapae* also sometimes oviposit on tiny crucifers, as do other Nearctic pierine species (*P. napi macdunnoughii*, *P. napi oleracea*, *P. virginiensis*). Second, oviposition deterrent pheromones (ODPs) have been isolated from eggs of both *P. brassicae* and *P. rapae*. Tarsal and antennal receptors of both species responded to the ODPs from their own as well as the other species' eggs (Klijnstra & Roessingh 1986, Schoonhoven et al. 1990a), so it is possible that these pheromones

influence the local distribution of eggs where the two species fly together. Chemical studies show the active compounds are water soluble, relatively non-volatile, and relatively stable (Schoonhoven et al. 1981); they are identified as novel cinnamic acid derivatives (J. J. A. van Loon, personal communication). While laboratory studies of behavior and electrophysiology of European and North American *P. rapae* show that both populations produce and respond to extracts containing ODP (Schoonhoven et al. 1990b), field studies of *P. rapae* behavior and eggs distribution in Australia and the USA have cast doubt on the importance of ODP in oviposition behavior of *P. rapae* (Ives 1978, Root & Kareiva 1984). These results leave unanswered the possible role of ODPs in interspecific interactions under field conditions.

Unlike both *Pieris brassicae* and *P. rapae* in Morocco, *Pontia daplidice* is everywhere, but never dense or abundant anywhere. While both other species are abundant as adults in their preferred habitats, we observed *P. daplidice* in the widest range of habitats, but always in very low numbers. This low-density population structure, combined with lack of preference for mesic habitats or high densities of crucifers, is probably one factor that prevents this insect from reaching pest status in densely planted agroecosystems.

High Fecundity Increases Colonization Potential

Because temperate butterfly population sizes are limited by recruitment into the population (number of eggs laid) (Wiklund & Åhrberg 1978, Hayes 1981, Courtney & Duggan 1983, Courtney 1986), high fecundity in the field enables butterflies to respond rapidly to new abundant resources. *Pieris rapae* is the most fecund butterfly I have ever reared; laboratory and field fecundities of 800+ eggs per female are reported (Norris 1935, Richards 1940, Yamamoto 1978, Yamamoto & Ohtani 1979). High fecundity is achieved partly by allocation to small eggs. In central Japan, *P. rapae* eggs are half the volume of eggs from *P. napi* and *P. melete* (Ohsaki 1982). In the northeastern USA, measurements of egg heights (Scudder 1889, Chew 1981) suggest conservatively that *P. napi oleracea* eggs are 25% larger than those of *P. rapae*. *Pieris rapae* pupae are also larger than many pierines, and its larvae develop faster than *P. napi oleracea* on a wide range of Palearctic crucifers if grown at 20–25°C (van der Reijden & Chew 1992). Developmental rates may constrain the voltinism of species like *P. napi oleracea*, by limiting it to two or three discrete generations, while *P. rapae* occurs continuously from late spring to hard frost in the same areas of eastern North America, a pattern also observed for *P. rapae crucivora* in comparison to *P. napi* and *P. melete* in Japan (Ohsaki 1982). *Pieris rapae*'s overlapping generations may favor individuals

that develop quickly enough to produce an additional generation (Ohshaki 1982, van der Reijden & Chew 1992), further improving *P. rapae*'s ability to respond rapidly to increased availability of host resources. *Pieris brassicae* lays up to 500 eggs per female (Gardiner 1963), a higher lifetime fecundity than the 240–400 eggs per female recorded for *P. napi nesis* (Yamamoto & Ohtani 1979).

In addition to high lifetime fecundity, *Pieris rapae* females are successful colonists because their age-specific fecundity, dispersal behavior, and oviposition behavior permit them to increase fecundity in response to increased resources. First, age-specific fecundities peak early during adult life in *P. rapae crucivora* compared to *P. napi nesis* (Yamamoto 1978, Yamamoto & Ohtani 1979). Age-specific fecundity peaks the third or fourth day of adult life, about the time when adult female dispersal often occurs (Root & Kareiva 1984), often as emigration from locally dense populations (Shapiro 1970, Ohtani & Yamamoto 1985). Second, egg-laying rates of *P. rapae crucivora* in the field increase with increasing ambient temperature (from 20 to 25°C) and hours of sunny weather. Thus improved conditions result in higher realized fecundity for this species.

For many other crucifer-feeding pierid butterflies including *Pontia daplidice*, larval cannibalism and the accompanying pierid "red-egg syndrome" may limit the egg density (Shapiro 1981, Courtney 1986) even in areas with dense host populations. By contrast, ample rain may reduce activity of the water-soluble oviposition deterrent pheromones of *P. rapae* and *P. brassicae*, permitting greater density of eggs where available hostplants and mesic conditions will support more larvae.

FROM NATURAL TO AGROECOSYSTEMS

Agroecosystems mimic environments where crucifers flourish—vernal conditions in fertile habitats. In addition, most agricultural practices do not promote plant symbiosis with vesicular-arbuscular mycorrhizal fungi (VAM) because VAM establishment retards early crop growth (Bethlenfalvey et al. 1982) and its later benefits are neutralized by fertilizer and water. Unlike more than 80% of other angiosperm taxa, crucifers do not support symbiosis with VAM (Tommerup 1984, Glenn et al. 1985, 1988), perhaps because they have evolved specialized nutrient uptake capacity (Nye 1981) to exploit lush, but temporary, conditions (Grime 1977). Thus crucifer agroecosystems very closely resemble natural habitats preferred by *P. brassicae* and *P. rapae*.

Multiple Infestation Occurs in Crops and Apparent Plants

Multiple infestation by different pierid species and species from other orders occurs for many crucifer crops (e.g., Bonnemaïson 1965, Williams

& Free 1979, Andow et al. 1986, Andow 1988, Lamb 1989) and for the most apparent and heavily utilized crucifers in the Moroccan pierid-crucifer community. For a multiply infested plant, it is not obvious which herbivores have greater impact. First, infestation by one herbivore species may make host individuals more vulnerable to damage by others e.g., *P. brassicae* damage makes *Brassica oleracea* hosts more susceptible to subsequent aphid damage (Mitchell 1977); however, herbivore damage also may attract parasitoids (Keller 1990). Second, herbivore effects on plants may be unpredictably severe; for example, in a study of herbivore impact on *Solidago altissima* (Asteraceae), Meyer (1993) found that of three herbivores—a xylem-sap feeding spittlebug (*Philaenus spumarius*; Homoptera: Ceropidae), an aphid (*Uroleucon caligatum*; Homoptera: Aphididae), and a leaf-chewing beetle (*Trirhabda* spp.; Coleoptera: Chrysomelidae)—the spittle bug had by far the greatest impact on growth because its activities reduced water transport needed for leaf expansion in growing plants.

Any species under selection from multiple sources and directions will be constrained evolutionarily. Partly for this reason, Moroccan pierid larvae are best adapted to the plants they are most likely to encounter—the same plants with the heaviest herbivore loads. These are conspicuous crucifers whose populations are persistent and numerically stable (Chew & Courtney 1991). This general finding completes the partial picture explored by earlier apparency theory (Feeny 1975). Inverse relationships between palatability and apparency may occur in depauperate communities where a hostplant is under strong directional selection from only one species (Courtney 1982) because these frequently encountered (apparent) plants evolve unpalatability under strong directional selection from a single herbivore source. But in the species-rich Moroccan community there is a stalemate: the most heavily utilized plants cannot respond evolutionarily to directional selection from multiple sources—a situation that applies to crucifer crops in agroecosystems (Andow 1988) as well as to apparent crucifer species in natural habitats.

The Resource Base is the Primary Factor

Even if no evolutionary response is desired (crop plants), frequent encounter enables insect pests to track more easily any changes in resistance of the cultivar. Lamb (1989) reports that the expansion of canola (oilseed brassicas) has been accompanied by vast expansion of the insect fauna attacking these plants. Recent introduction of zero-glucosinolate Canola varieties to large scale cultivation in Canada should have presented brassica pests with hosts lacking this major chemical class of oviposition and feeding stimulants (reviewed by Chew 1988).

However, after introduction of these cultivars, the fauna of oilseed brassicas did not change. Lamb notes that major changes have accompanied shifts in the resource base and cultural management, rather than changes in phytochemical traits of the cultivars (Lamb 1989).

Another observation supporting this view is that many heavily infested crops are not preferred by their pests in laboratory tests where alternative hosts are equally available. Experimental assessments of *P. rapae* oviposition and larval preference conclude that agricultural crops e.g., cabbage (*Brassica oleracea* cultivars), are not preferred by either butterflies (Renwick & Radke 1985) or larvae (Chew, unpublished observations), although some *Brassica* cultivars contain specific glucosinolates that are strong stimulants for ovipositing *P. rapae*. Similarly, cotton is severely damaged by several *Heliothis* species but is not a preferred host of any *Heliothis* species (Fitt 1989); and cranberry plants are not preferred hosts of a major pest, cranberry weevil (*Anthonomus musculus*; Coleoptera: Curculionidae) (Mechaber & Chew 1991). These findings argue that outbreak populations occur on crops because of their abundance and phenology, not because of their intrinsic palatability to the potential pest.

The crucial role of phenology in resource base management is illustrated by what occurred in the United Kingdom after widespread introduction of Canola® (oilseed brassica). Cabbage root fly (*Delia radicum*; Diptera: Anthomyiidae) is a major pest. Finch (1989) reports that only serendipity averted a potentially serious pest situation that might also have provided a crucifer reservoir for increased pest problems on cruciferous vegetable crops. Because the harvest of spring-sown oilseed brassica crops coincided with cereal harvests, oilseed brassicas were sown in the fall so that harvesting machinery could be used on both cereals and oilseed crops. Nearly all of the British crop of oilseed brassicas, which now totals about five times the acreage planted with vegetable crucifers, is sown in the fall (Finch 1989). Because *D. radicum* cannot easily attack seedlings in the fall, it cannot become established on overwintering oilseed crops. Finch notes that if oilseed brassicas were rotated in Canada, similar phenology management could be useful in controlling *Delia* species, which in Canada have a single midsummer generation (Finch 1989).

Could Wild Crucifers Harbor Potential Pest Populations?

Do weedy or indigenous crucifers act as reservoirs for crucifer crop pests? Finch (1988, 1989), in a detailed commentary on *Delia radicum*, calculates the proportion of infestation likely to arise from weedy crucifers in hedgerows. He concluded it is trivial because hedgerow cru-

cifers are sporadic and rare, and because *D. radicum* develops poorly on these weeds.

In the case of the crucifer-feeding Moroccan butterfly community, most are unable to respond to increased host resources by rapidly increasing population density. In the case of *Pieris napi oleracea*, prior to cutting of hardwood forest and destruction of the herbaceous understory, native *Cardamine* and *Dentaria* species supported the vernal brood of *P. napi oleracea*. *Pieris napi oleracea* propagated on these wild hosts and then emerged in large numbers as pests on summer cole crops near wooded areas. But unlike hedgerows, these wooded areas were extensive and their crucifer stands were large. Earlier observers supposed that *P. napi oleracea* was victim to competition with its naturalized congener *P. rapae* (Scudder 1889, Klots 1951). More recent evidence shows the two species use similar resources, but the forest is a vernal refugium for *P. oleracea*. Where woods or native herbaceous understory have been destroyed and supplanted by naturalized weeds unsuitable for *P. oleracea* larvae, this species has disappeared (Chew 1981). Local extirpation occurs when *P. oleracea* are deprived of a vernal host. Nearly all hosts now available in urban and suburban areas where *P. oleracea* used to fly are naturalized crucifers on which females oviposit and larvae die (Bowden 1971, Chew 1977b). A possible exception is the garlic mustard *Alliaria petiolata*, which grows at woodland edges, to which larvae of some *P. oleracea* appear to be adapting (Courant et al. 1994). Were *P. virginiensis* larvae able to adapt to this weed, it would gain a large larval resource (Porter 1994) and perhaps become multivoltine (Courant & Chew 1995). Where habitat change has eliminated suitable native hostplants, other indigenous North American pierids, *P. virginiensis* and *Anthocharis midea* Hubner, oviposit on naturalized crucifers, but many of these support larval growth poorly if at all (Chew 1977b). When native vegetation in their wooded and rock ledge habitats is destroyed or severely reduced, they likewise disappear locally.

From a viewpoint of promoting biodiversity, destroying native herbaceous understory is an ecologically unacceptable mechanism for regulating an agricultural insect pest (Gilpin, Gall & Woodruff 1992). But since most wooded areas of the world have been cut at least once, and their understories—including native crucifers—are often destroyed, populations of *Pieris oleracea* and its many relatives in the *P. napi* complex are now reduced compared to earlier periods (Ohsaki 1979, Chew 1981, Yamamoto 1981). Even if these crucifer-feeding pierid populations were not reduced by suburbanization, their inability to tolerate broad expanses of open habitat (pierines) and egg dispersion (especially among euschloeines, Shapiro 1981) make it extremely un-

likely that these species would attain pest status in open agricultural habitats.

CONCLUSIONS

Conspicuous, dense, numerically stable crucifer stands support the largest herbivore loads (Root 1973, Chew & Courtney 1991). If these stands happen to be crops, pierids and other herbivorous invertebrates are only exhibiting the same behavior observed in indigenous habitats. Changing plant defense mechanisms may be ineffective or result in rapid adaptation to plant resistance, a concern expressed about broad-scale applications of some biological control methods (Altman, 1992, Abbot 1994). By manipulating the numerical stability of the crop, for example by rotation in different seasons or years, we may reduce attainment of outbreak proportions by these insects. But these large-scale manipulations of the resource base—the only kind of change that seems likely to control these two pierid pests and other crucifer pests in large agroecosystems, requires implementation at landscape scales (Allen & Hoekstra 1992). On a local scale, manipulating the apparency of the stand, for example by small scale (single row) intercropping (Tahvanainen & Root 1972, Vandermeer 1990), may reduce colonization by crucifer herbivores including *Pieris brassicae* and *P. rapae*. But as Finch (1988) observes, inexpensive, short-term floating row covers have superseded intercropping for many vegetable crops. These row covers directly reduce crop apparency and butterfly access to oviposition sites and thus are very effective at controlling pierid colonization.

ACKNOWLEDGMENTS

To Charles Remington: I offer these musings in your honor, with deep gratitude for your encouragement. I was inspired by your enthusiasm for life and for terrestrial arthropods. Exploration, speculation, and debate, combined with rigorous attention to natural history observations and biological principles, occurred on many an afternoon around your third floor tea table in Osborn Laboratories. I benefited from your care for students meeting the challenges of research: for me, not the least of these was a lost suitcase containing one-third of the data in my dissertation! Long after I had passed the point of desperation, you got the airline to find the lost luggage. For these gifts, and for your role as a "keystone mutualist" in the scientific community (one who facilitates access to resources, promotes connections among community members, and provides structure for community activities), I tender my heartfelt and affectionate appreciation.

The Ecology Reading Group at Tufts listened to early versions of these ideas. Research was supported by the National Geographic Society (81-2305), National Science Foundation (IBN 9108987), and the Arabis Fund. I thank R. Bryan for abiding faith. The figure was produced by Katherine Brown-Wing.

LITERATURE CITED

- ABBOTT, R. J. 1994. Ecological risks of transgenic crops. *Trends Ecol. Evol.* 9:280-281.
ALLEN, T. F. H. & T. W. HOEKSTRA. 1992. *Toward a unified ecology*. Columbia Univ. Press, New York. 384 pp.

- ALTMANN, M. 1992. "Biopesticide" turning into new pests? Trends Ecol. Evol. 7:65.
- ANDOW, D. A. 1988. Management of weeds for insect manipulation in agroecosystems, pp. 265-301. In Altieri, M.A. and M. Liebman (eds.), Weed management in agroecosystems: ecological approaches. CRC Press, Boca Raton, Florida.
- ANDOW, D. A., A. G. NICHOLSON, H. C. WIEN & H. R. WILLSON. 1986. Insect populations in cabbage grown with living mulches. Environ. Entomol. 15:293-299.
- BETHLENFALVEY, G. J., M. S. BROWN & R. S. PACOVSKY. 1982. Parasitic and mutualistic associations between a mycorrhizal fungus and soybean: development of the hostplant. Phytopathol. 72:889-893.
- BONNEMAISON, L. 1965. Insect pests of crucifers and their control. Ann. Rev. Entomol. 10:233-256.
- BOWDEN, S. R. 1971. American white butterflies (Pieridae) and English food-plants. J. Lepid. Soc. 25:6-12.
- CAPPUCCINO, N. & P. M. KAREIVA. 1985. Coping with a capricious environment: a population study of the rare woodland butterfly *Pieris virginiensis*. Ecology 66:152-161.
- CHEW, F. S. 1975. Coevolution of pierid butterflies and their cruciferous foodplants. I. The relative quality of available resources. Oecologia 20:117-127.
- . 1977a. Coevolution of pierid butterflies and their cruciferous hostplants. II. The distribution of eggs on potential hostplants. Evolution 31:568-579.
- . 1977b. Introduced plants as food resources for native cabbage butterflies. Atala 5:13-19.
- . 1981. Coexistence and local extinction in two pierid butterflies. Am. Nat. 118: 655-672.
- . 1988. Biological effects of glucosinolates, pp. 155-181. In Cutler, H.G. (ed.), Biologically active natural products. Am. Chem. Soc. Symp. 380, Washington, D.C.
- CHEW, F. S. & S. P. COURTNEY. 1991. Plant apparency and evolutionary escape from insect herbivory. Am. Nat. 138:729-750.
- CHEW, F. S. & J. A. A. RENWICK. 1995. Host plant choice in *Pieris* butterflies, pp. 214-238. In Bell, W. J. & R. Cardé (eds.), Chemical ecology of insects II. Chapman and Hall, New York.
- COURANT, A. V., A. E. HOLBROOK, E. D. VAN DER REIJDEN & F. S. CHEW. 1994. Native pierine butterfly adapting to naturalized crucifer? J. Lepid. Soc. 48:168-170.
- COURANT, A. V. & F. S. CHEW. 1995. Latent polyphenism and direct development in *Pieris virginiensis* (Pieridae). J. Lepid. Soc. 49:84-87.
- COURTNEY, S. P. 1982. Coevolution of pierid butterflies and their cruciferous foodplants. IV. Hostplant apparency and *Anthocharis cardamines* oviposition. Oecologia 52:258-265.
- . 1986. The ecology of pierid butterflies: dynamics and interactions. Adv. Ecol. Res. 15:51-131.
- COURTNEY, S. P. & F. S. CHEW. 1987. Coexistence and host use by a large community of pierid butterflies: habitat is the templet. Oecologia 71:210-220.
- COURTNEY, S. P. & A. DUGGAN. 1983. The population of the orange-tip butterfly, *Anthocharis cardamines* in Britain. Ecol. Entomol. 8:271-281.
- CROMARTIE, W. J. 1975. Influence of habitat on colonization of collard plants by *Pieris rapae*. Environ. Entomol. 4:783-784.
- CRONIN, W. 1983. Changes in the land. Hill and Wang, New York. 241 pp.
- DAVIES, C. R. & N. GILBERT. 1985. A comparative study of the egg-laying behavior and larval development of *Pieris rapae* L. and *P. brassicae* L. on the same host plants. Oecologia 67:278-281.
- FEENY, P. 1975. Biochemical coevolution between plants and their insect herbivores, pp. 3-19. In Gilbert, L. E. & P. H. Raven (eds.), Coevolution of animals and plants. Univ. Texas Press, Austin.
- FELTWELL, J. 1982. The large white butterfly, the biology, biochemistry and physiology of *Pieris brassicae* (Linnaeus). Dr. W. Junk, The Hague.
- FINCH, S. 1988. Entomology of crucifers and agriculture—diversification of the agroecosystem in relation to pest damage in cruciferous crops, pp. 39-71. In Harris, M.

- K. & C. E. Rogers (eds.), The entomology of indigenous and naturalized systems in agriculture. Westview Press, Boulder and London.
- . 1989. Ecological considerations in the management of *Delta* pest species in vegetable crops. *Ann. Rev. Entomol.* 34:117-137.
- FITT, G. P. 1989. The ecology of *Heliothis* species in relation to agroecosystems. *Ann. Rev. Entomol.* 34:17-52.
- GARDINER, B. O. C. 1963. Genetic and environmental variation in *Pieris brassicae*. *J. Res. Lepid.* 2:127-136.
- GILPIN, M., G. A. E. GALL & D. S. WOODRUFF. 1992. Ecological dynamics and agricultural landscapes. *Agric. Ecosyst. Environ.* 42:27-52.
- GLENN, M. G., F. S. CHEW & P. H. WILLIAMS. 1985. Hyphal penetration of *Brassica* (Cruciferae) roots by a vesicular-arbuscular mycorrhizal fungus. *New Phytol.* 99: 463-472.
- . 1988. Influence of glucosinolate content of *Brassica* (Cruciferae) roots on growth of vesicular-arbuscular mycorrhizal fungi. *New Phytol.* 110:217-225.
- GRIME, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111:1169-1194.
- HARRIS, T. W. 1841. Report on the insects of Massachusetts, injurious to vegetation. Folsom, Wells & Thurston, Cambridge, Massachusetts.
- HAYES, J. L. 1981. The population ecology of a natural population of the pierid butterfly *Colias alexandra*. *Oecologia* 49:188-200.
- HIGGINS, L. G. & N. D. RILEY. 1980. A field guide to the butterflies of Britain and Europe. Collins, London. 380 pp.
- HUNTER, M. D. & P. W. PRICE. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73: 724-732.
- IVES, P. M. 1978. How discriminating are cabbage butterflies? *Austral. J. Ecol.* 3:261-276.
- JONES, R. E. 1977. Movement patterns and egg distribution in *Pieris rapae*. *J. Anim. Ecol.* 46:195-212.
- . 1987. Behavioural evolution in the cabbage butterfly (*Pieris rapae*). *Oecologia* 72:69-76.
- JONES, R. E., J. R. HART & G. D. BULL. 1982. Temperature, size and egg production in the cabbage butterfly, *Pieris rapae* L. *Austral. J. Zool.* 30:223-232.
- KELLER, P. M. 1990. Responses of the parasitoid *Cotesia rubecula* to its host *P. rapae* in a flight tunnel. *Entomol. Exp. Appl.* 57:243-249.
- KIMURA, K. & Y. TSUBAKI. 1986. Female size and age specific fecundity in the small white butterfly *Pieris rapae crucivora* Boisduval (Lepidoptera; Pieridae). *Res. Popul. Ecol.* 28:295-304.
- KING, C. E. 1971. Resource specialization and equilibrium population size in patchy environments. *Proc. Natl. Acad. Sci. (USA)* 68:2635-2637.
- KLIJNSTRA, J. W. & P. ROESSINGH. 1986. Perception of the oviposition deterrent pheromone by tarsal and abdominal contact chemoreceptors in *Pieris brassicae*. *Entomol. Exp. Appl.* 40:71-79.
- KLOTS, A. B. 1951. A field guide to the butterflies of North America east of the Great Plains. Houghton Mifflin, Boston. 349 pp.
- LAMB, R. J. 1989. Entomology of oilseed *Brassica* crops. *Ann. Rev. Entomol.* 34:211-229.
- MECHABER, W. L. & F. S. CHEW. 1991. Rewriting the natural history of cranberry weevil. *Cranberries* 55:5-8.
- MEYER, G. A. 1993. A comparison of the impacts of leaf and sap-feeding insects on growth and allocation in goldenrod. *Ecology* 74:1101-1116.
- MITCHELL, N. D. 1977. Differential host selection by *Pieris brassicae* (the large white butterfly) on *Brassica oleracea* subsp. *oleracea* (the wild cabbage). *Entomol. Exp. Appl.* 22:208-219.
- NORRIS, M. D. 1935. A feeding experiment on adults of *Pieris rapae* L. (Lepidoptera, Rhopalocera). *Entomol.* 68:125-127.

- NYE, P. H. 1981. Changes in pH across the rhizosphere induced by roots. *Plant Soil* 61: 7-26.
- OATMAN, E. R. & G. R. PLATNER. 1969. An ecological study of insect populations on cabbage in southern California. *Hilgardia* 40(1):1-40.
- OHSAKI, N. 1979. Comparative population studies of three *Pieris* butterflies, *P. rapae*, *P. melete*, and *P. napi*, living in the same area. I. Ecological requirements for habitat resources in the adults. *Res. Popul. Ecol.* 20:278-296.
- . 1980. Comparative population studies of three *Pieris* butterflies, *P. rapae*, *P. melete*, and *P. napi*, living in the same area. II. Utilization of patchy habitats by adults through migratory and non-migratory movements. *Res. Popul. Ecol.* 22:163-183.
- . 1982. Comparative population studies of three *Pieris* butterflies, *P. rapae*, *P. melete*, and *P. napi*, living in the same area. III. Difference in the annual generation numbers in relation to habitat selection by adults. *Res. Popul. Ecol.* 24:193-210.
- . 1986. Body temperatures and behavioral thermoregulation strategies of three *Pieris* butterflies in relation to solar radiation. *J. Ethology* 4(1):1-9.
- OHSAKI, N. & Y. SATO. 1994. Food plant choice of *Pieris* butterflies as a trade-off between parasitoid avoidance and quality of plants. *Ecology* 75:59-68.
- OHTANI, T. & M. YAMAMOTO. 1985. The adult behavior of the Japanese cabbage white (Lepidoptera, Pieridae) in the field. II. Ecological aspects of major behavior patterns. *Tyo to Ga* 36(2):43-76.
- PORTER, A. H. 1994. Introduced garlic mustard (*Alliaria petiolata*), a new host for *Pieris virginianensis*. *J. Lepid. Soc.* 48:171-172.
- POWER, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* 73:733-746.
- REMYINGTON, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. *Evol. Biol.* 2:321-428.
- RENWICK, J. A. A. & C. D. RADKE. 1985. Constituents of host and non-host plants deterring oviposition by the cabbage butterfly *Pieris rapae*. *Entomol. Exp. Appl.* 39: 21-26.
- RICHARDS, O. W. 1940. Biology of *Pieris rapae* with special reference to factors controlling abundance. *J. Anim. Ecol.* 9:243-288.
- RISCH, S. J., D. ANDOW & M. A. ALTIERI. 1983. Agrosystem diversity and pest control: data, tentative conclusions, and new directions. *Environ. Entomol.* 12:625-629.
- ROOT, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43:95-120.
- ROOT, R. B. & KAREIVA, P. M. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of Markovian movements in a patchy environment. *Ecology* 65:147-165.
- ROTHSCHILD, M. 1987. Speculations concerning the large white butterfly (*Pieris brassicae* L.): do females assess the number of suitable host plants present?, pp. 175-192. In Chapman, R. F., E. A. Bernays & J. G. Stoffolano (eds.), *Perspectives in chemo-reception and behavior*. Springer-Verlag, New York.
- SACHDEV-GUPTA, K., J. A. A. RENWICK, C. D. RADKE. 1990. Isolation and identification of oviposition deterrents to the cabbage butterfly, *Pieris rapae*, from *Erysimum cheiranthoides*. *J. Chem. Ecol.* 16:1059-1067.
- SACHDEV-GUPTA, K., C. D. RADKE, J. A. A. RENWICK & M. B. DIMOCK. 1993. Cardenolides from *Erysimum cheiranthoides*: Feeding deterrents to *Pieris rapae* larvae. *J. Chem. Ecol.* 19:1355-1369.
- SCHOONHOVEN, L. M., T. SPARNAAY, W. VAN WISSEN & J. MEERMAN. 1981. Seven weeks persistence of an oviposition-deterrent pheromone. *J. Chem. Ecol.* 7:583-588.
- SCHOONHOVEN, L. M., E. A. M. BEERLING, R. BRAAKSMA & Y. VAN VUGT. 1990a. Does the imported cabbageworm, *Pieris rapae*, use an oviposition deterring pheromone? *J. Chem. Ecol.* 16:1649-1655.
- SCHOONHOVEN, L. M., E. A. M. BEERLING, J. W. KLIJNSTRA & Y. VAN VUGT. 1990b. Two related butterfly species avoid oviposition near each other's eggs. *Experientia* 46: 526-528.

- SCRIBER, J. M. & R. C. LEDERHOUSE. 1992. The thermal environment as a resource dictating geographic patterns of feeding specialization of insect herbivores, pp. 429-466. In Hunter, M. R., T. Ohgushi, & P. W. Price (eds.), Effects of resource distribution on animal-plant interactions. Academic Press, New York.
- SCUDDER, S. H. 1889. The butterflies of the eastern United States and Canada. Vol. 1. Published by the author. Cambridge, Massachusetts. 748 pp.
- SHAPIRO, A. M. 1970. The role of sexual behavior in density-related dispersal of pierid butterflies. *Am. Nat.* 104:367-372.
- . 1975. Ecological and behavioral aspects of coexistence in six crucifer-feeding pierid butterflies in the Central Sierra Nevada. *Am. Midl. Nat.* 93:424-433.
- . 1981. The pierid red-egg syndrome. *Am. Nat.* 117:276-94.
- TABASHNIK, B. E., H. WHELOCK, J. D. RAINBOLT & W.B. WATT. 1981. Individual variation in oviposition preference in the butterfly *Colias eurytheme*. *Oecologia* 50: 225-230.
- TAHVANAINEN, J. O. & R. B. ROOT. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10:321-346.
- TAKATA, N. 1962. Studies on the host preference of the common cabbage butterfly *Pieris rapae crucivora* (Bdv.) XIV. General consideration. *Physiol. Ecol.* 10:79-97.
- THOMAS, J. A. 1984. The conservation of butterflies in temperate countries: past efforts and lessons for the future, pp. 333-335. In Vane-Wright, R. I. & P. R. Ackery (eds.), The biology of butterflies. Academic Press, London.
- TOMMERUP, I. C. 1984. Development of infection by a vesicular-arbuscular mycorrhizal fungus in *Brassica napus* L. and *Trifolium subterraneum*. *New Phytol.* 98:497-502.
- TSUNODA, S., K. HINATA & C. GOMEZ-CAMPO (eds). 1980. *Brassica* crops and wild allies. Japan Scientific Societies Press, Tokyo. 354 pp.
- VAN DER REIJDEN, E. D. & F. S. CHEW. 1992. Assessing host-plant suitability in caterpillars: is the weight worth the wait?, pp. 69-70. In Mencken, S. B. J., J. H. Visser & P. Harrewijn (eds.), Proc. 8th Intl. Symp. Insect-Plant Relationships. Kluwer Academic Publishers, Dordrecht.
- VANDERMEER, J. H. 1990. Intercropping, pp. 481-516. In Carroll, C. R., J. H. Vandermeer & P. M. Rosset (eds.), Agroecology. McGraw-Hill, New York.
- VAWTER, A. T. & P. F. BRUSSARD. 1983. Allozyme variation in a colonizing species: the cabbage butterfly *Pieris rapae* (Pieridae). *J. Res. Lepid.* 22(3):204-216.
- VIA, S. 1990. Ecological genetics and host adaptation in herbivorous insects: the experimental study of evolution in natural and agricultural systems. *Ann. Rev. Entomol.* 35:421-446.
- VITOUSEK, P. M. 1994. Beyond global warming: ecology and global change. *Ecology* 75:1861-76.
- WATT, W. B. 1968. Adaptive significance of pigment polymorphism in *Colias* butterflies. I. Variation of melanic pigment in relation to thermoregulation. *Evolution* 22:437-458.
- WIKLUND, C. & C. AHRBERG. 1978. Host plants, nectar source plants and habitat selection of males and females of *Anthocharis cardamines*. *Oikos* 31:169-183.
- WILLIAMS, E. 1981. Thermal influences on oviposition in the montane butterfly *Euphydryas gilletti*. *Oecologia* 50:342-346.
- WILLIAMS, J. B. & I. H. FREE. 1979. The distribution of insect pests on crops of oil-seed rape (*Brassica napus* L.) and the damage they cause. *J. Agric. Sci., Camb.* 92: 139-149.
- WOIWOD, J. P. & A. J. A. STEWARD. 1990. Butterflies and moths—migration in the agricultural environment, pp. 189-202. In Bunce, R. (ed.), Species dispersal in agricultural habitats. Bellhaven Press, London.
- YAMAMOTO, M. 1978. Number of eggs laid by *Pieris napt nesis* Fruhstorfer (Lepidoptera: Pieridae) in Sapporo, northern Japan. *New Entomol.* 27 (3):1-6.
- . 1981. Comparison of the population dynamics of two pierid butterflies, *Pieris rapae crucivora* and *P. napt nesis*, living in the same area and feeding on the same

plants in Sapporo, northern Japan. J. Fac. Science Hokkaido Univ. Ser. VI, Zool. 22: 202-249.

YAMAMOTO, M. & T. OHTANI. 1979. Number of eggs laid by *Pieris rapae cructivora*, compared with *P. napi nests* in Sapporo (Lepidoptera: Pieridae). Kontyu 47:530-539.