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Factors Limiting Northward Expansion of Phyllophagous Insects: The Example of *Pieris napi* L. and *Pieris brassicae* L.

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Abstract—In the southern Subarctic, including forest-tundra of the lower Ob region, *Pieris napi* L. is common, but *P. brassicae* L. is not found. It was demonstrated that this could not be related to the air temperature during the growing season, because both growth rate and the duration of molting in *P. napi* and *P. brassicae* were equal. It is suggested that the northward expansion of *P. brassicae* is limited by the food plant. Crucifers, on which *P. brassicae* caterpillars feed, are widespread in the lower Ob region but do not form natural patches. These patches, however, are necessary for *P. brassicae*, because this species is characterized by gregarious egg laying. In addition, agriculture in this region does not employ the single-crop system.

INTRODUCTION

It was suggested that the expansion of phytophagous insects to the north is mainly limited by abiotic factors (primarily, temperature), rather than by food plants. As evidence in favor of this hypothesis, many authors indicate that plants usually expand to the north farther than the insects that feed on them (Shtakel'berg, 1944; Downes, 1964; MacLean and Hodkinson, 1980; MacLean, 1983; Danks, 1986). Apparently, the example of *Pieris napi* L. confirms this hypothesis.

Pieris napi is widespread in the temperate zone and expands northward to forest–tundra and southern tundra. It is a common species in the lower Ob and polar Ural regions. *Pieris napi* is an oligophage feeding on crucifers. Apparently, it has a good food supply in this region, although I have been finding and rearing *P. napi* larvae only on *Hesperis matronalis*. In 1978, I revealed that *P. napi* larvae developing to the fourth to fifth instar ate virtually nothing throughout August, when the air temperature was low (about 8°C). They could not reach the pupal stage, at which this species winters, and perished. In any case, these butterflies were not observed during the following several years and became common again only in 1983 (Bogacheva, 1990). At that time, I did not elucidate the specific factors that prevented larvae from reaching the pupal stage (this might be a decreased growth rate and/or a prolonged period of molting); however, it was clear that the primary cause was the weather factor (specifically, air temperature), affecting the phytophage directly. In critical years, therefore, the populations of phytophagous insects become unstable even in the lower Ob region, although the crucifers occur much farther to the north.

Pieris brassicae L. shares most biological characteristics and food preferences with *P. napi*. It was demonstrated that this species occurs and even harms agricultural plants at 63° north latitude (Korshunov, 1966; Sedykh, 1974), but its northward expansion is limited to the northern Urals. It was interesting to elucidate the factors responsible for this restriction of the *P. brassicae* range. Although *P. brassicae* is larger than *P. napi* (the final weight of larvae is approximately 600 mg vs. 180–190 mg in *P. napi*), it is unlikely that the body size is crucial. For example, even large insects, such as *Celerio galii,* whose larvae weigh as much as 5 g, have succeeded in completing their development during summer in the lower Ob region.

This study was aimed at revealing the adaptations of *P. napi* to the conditions of southern Subarctic and elucidating why *P. brassicae* could not live there. For this purpose, I estimated the growth rate and the duration of molt in these two species in the southern taiga, where they are abundant (Korshunov and Gorbunov, 1995) and often occur on the same plant species in the same biotopes. The study was performed in 1995.

MATERIALS AND METHODS

In early September 1995, I collected caterpillars of *P. brassicae* and *P. napi* in different biotopes of the city of Yekaterinburg (parks, lawns, and wasteland). They were found only on *Sysimbrium loeselii,* while *P. napi* lived also on *Bunias orientalis, Turritis glabra*, and *Thlaspi arvense*. During the experiments, I kept larvae of both species on *S. loeselii*. In addition, *P. brassicae* larvae were kept on *Rorippa sylvestris,* penny-cress, and white cabbage (*Brassica oleracea* var. *capitiata*). I tried to feed the larvae with other crucifers available in this season,

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both cultivated (celery cabbage and leaves of cauliflower and radish) and wild (*Erysimum cheirantoides* and *Capsella bursa-pastoris*). Caterpillars of *P. brassicae* ate all these plants except the latter species (*P. napi* did not eat this plant either).

In experiments, I used standard methods. Larvae were kept in Petri dishes lined with filter paper, two larvae per dish. Larvae were daily weighed on a torsion balance with the accuracy of 1 mg. Larvae received an excessive amount of food, which was replaced daily. I recorded all changes in the state and behavior of larvae. At the end of the study, I found that many larvae were infested; these experimental series were rejected.

To perform experiments at different temperatures, the sets of Petri dishes were kept in a refrigerator and in the laboratory room. In the room, daily variations of temperature were small (2–3°C). The temperature was recorded permanently with the use of a thermographer. The data on temperature, to which I refer below, are the average temperatures for the given period (molting or growth).

I calculated the relative growth rate (*RGR*) by the following formula: $RGR = (\ln P_T - \ln P_0)/T$, where P_0 and P_T are, respectively, the initial and final weights of a larva during the period T (measured in days). The growth rates are indicated for the last larval instar (from its beginning to the moment of achieving the maximum weight). The duration of molting was estimated by the method of calculation that assumed molt to be a temporary cessation of larval growth (Ayres and MacLean, 1987). The results of this study performed in southern taiga (56°N) were compared with the results of similar studies performed in 1991 in northern forest–tundra (66°N, the town of Labytnangi in the lower Ob region) on the local *P. napi* population. The results were published earlier (Bogacheva, 1993; 1995).

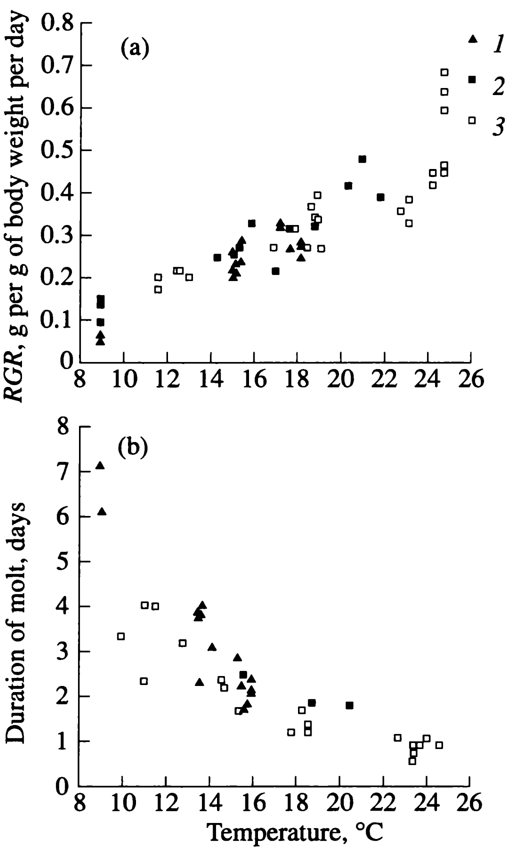

Fig. 1. Developmental rate (a) and duration of molt (b) in caterpillars of (1) *Pieris brassicae* from southern taiga, (2) *P. napi* from southern taiga, (3) *P. napi* from forest–tundra.

RESULTS AND DISCUSSION

The growth rate of *P. napi* caterpillars from the Subarctic population (Fig. 1a) was not higher than that for the southern-taiga population. This conclusion should be made with caution, because these groups of caterpillars were fed with different plants; however, the content of dry matter in *S. loeselii* and *H. matronalis* was almost the same (approximately 23%). The data on growth rate of *P. brassicae* caterpillars fed with different plants were similar, although their growth was slightly retarded at lower temperatures.

The data on the rate of molting exhibited a similar pattern. In caterpillars of *P. napi* from the Subarctic population, the molt proceeded slightly more rapidly than in larvae from the southern-taiga population (Fig. 1b); however, the data on the Yekaterinburg population are insufficient for a definite conclusion. The data on *P. brassicae* were also similar to those on *P. napi*, although the duration of molt in the former species increased at lower temperatures.

Many authors note that Arctic insects exhibit some physiological changes resulting in decreased thresholds and optimums of activity. However, the researchers usually draw these conclusions from the averaged data on sets of species that are different for different geographic zones. It remains unknown whether or not these changes are adaptations that have appeared in northern populations of widespread species expanding to Subarctic. Some species do not display differences in their growth rates in different climatic zones (Ritland and Scriber, 1985; Gilbert, 1988; Haukioja *et al.*, 1990). These are, e.g., *Papilio glaucus, P. rapae*, and *Epirrita autumnata*. I obtained similar data on *Aglais urticae* (Bogacheva, 1995). In addition, this species exhibits no changes in the rate of molting. In *P. napi*, I also did not find a visible increase in the rate of larvae development. Its expansion to the north was not accompanied by any substantial changes in the growth rate and the duration of molt. However, the number of generations per season decreased as the species expanded northward, so that in the northern Ob region, even one generation could not survive in some years.

The data obtained do not allow us to answer the main question of this study, i.e., why *P. brassicae* is absent from the northern Ob region. It is true that, at a low temperature, the development (both growth and molting) of larvae in this species was somewhat slower than in *P. napi*, while the body weight at the end of development was considerably greater. This suggests that the development of *P. brassicae* requires more time. Near Oktyabr'skii, this species produces only one generation per season, whereas *P. napi* at least attempts to yield the second generation, judging from the swarming of the butterflies during the last two-thirds of August (Korshunov, 1966). In addition, the swarming of *P. brassicae* in the beginning of the season usually occurs later than that of *P. napi* (Korshunov, 1966), leaving less time for the development of larvae. However, *P. brassicae* is not completely unable to develop at low temperatures. On the contrary, a group of larvae developed in a refrigerator at 8–9°C from the early second instar to pupation, whereas this was impossible for some other lepidopterans and phyllophages because of considerably retarded molting and a high larval mortality. Moreover, *P. brassicae* caterpillars are known to bask in the sun, which should accelerate their growth. Caterpillars of *P. brassicae* have a darker color than those of *P. napi*, which also facilitates their warming.

Retardation of development at low temperatures is not the only mechanism of the temperature effect on *P. brassicae*. However, this mechanism was revealed in *P. napi*; therefore, it was also suggested for *P. brassicae*. In addition, *P. brassicae* and *P. napi* share other biological characteristics that may be disadvantageous for *P. brassicae* in the northern Ob region (e.g., the open wintering of pupae). Nevertheless, *P. brassicae* could have settled temporarily in the northern Ob region, as many other species do. These settlements, disappearing after an unfavorable growing season or excessively cold winter, would have been restored again due to migrations. This restoration would be easier, as *P. brassicae* is considered a good migrant (Henriksen and Kreutzer, 1982). However, *P. brassicae* was not observed in the region of Labytnangi–polar Urals, although the local butterflies have been studied in detail by the Institute of Plant and Animal Ecology over the last 25 years. Therefore, to elucidate the reasons for the absence of *P. brassicae* from the studied region, we should consider other factors.

In our opinion, the greatest biological difference between *P. napi* and *P. brassicae* is the fact that clutches of *P. brassicae* are considerably larger (up to 300 eggs). Even in the case of the smallest clutch (20–30 eggs), caterpillars would need a large amount of vegetable food to reach the last instar. Therefore, butterflies are not attracted by single (even large) plants, during the period of egg laying; they prefer natural patches of plants or "single-crop cultures," including both weeds on arable and ruderal lands and agricultural plants in fields and garden plots. Other researchers (Kellner and Shapiro, 1983; Davis and Gilbert, 1985) who studied *P. brassicae* and the Pieridae species that lay single eggs came to the same conclusion. In early September 1995, I found clutches of *P. brassicae* eggs only on large *S. loeselii* plants that formed patches; other wild plants that belonged to the species readily eaten by the caterpillars, but were small or grew separately, had no clutches on them.

Now consider the lower Ob region from this point of view. Until recently, crucifers were cultivated neither in fields nor on garden plots in this region. Ruderal crucifers, which expand over deteriorated lands in temperate zones, do not constitute the background for this type of vegetation in the northern Ob region. Only *Sisymbrium* and *Erysimum* are sometimes found along the roads and around the landfills, especially on the elevations warmed by the sun. In Labytnangi, single *Rorippa* plants and small patches of low *Capsella* have recently begun to grow as weeds in garden plots and near houses. Some crucifers, primarilly *Cardamine* spp. and sometimes *Hesperis matronalis*, are widespread in meadow biotopes, but their plants are usually scattered. In the polar Ural region, *Cardamine macrophylla* is abundant in some forests, where it grows in considerably shaded places. However, Korshunov (1966) especially noted that *P. brassicae* does not inhabit forest biotopes at the northern boundary of the range. In the polar Ural region, *Draba* spp. and *Parrya* sp. form patches; however, they grow at considerable elevations and in the biotopes where *P. brassicae*, apparently, cannot live. Therefore, although the food plants of *P. brassicae* grow in the lower Ob region, *P. brassicae* cannot live in this region for reasons related to the food plants.

Consider once again the common notion of the obstacles to the northward expansion of phytophages. The history of emergence of *A. urticae* in the northern Ob region demonstrates that the factor limiting the northward expansion of phytophagous species may be the absence of their food plant (at least, this is true for monophages). In the 1970s, nettle has yet been absent from this region. It appeared only in the 1980s and gradually occupied the favorable territories (primarily, with the soils rich in organic matter), growing in patches characteristic of this species. This allowed *A. urticae* to live there and even to become abundant in the early 1990s; neither growth rate nor the duration of molting limited its expansion to these high latitudes (Bogacheva, 1995). As a result of the warming of climate during the recent years, many plants have expanded from the temperate zone to the North and settled there. Along with them, some monophagous insects might have also expanded to this region.

The example of *P. brassicae* is less self-evident: the plants that this butterfly could eat grow in the northern Ob region; however, the butterfly itself is absent. Nevertheless, I consider this situation to be also related to the food plant. It is possible that the obstacles to northward expansion of phytophages are more often related to food plants than it is generally assumed. The plants may prove to be inappropriate as a food because of the characteristics of their growth, phenology, etc. If densely growing crucifers emerge in appropriate biotopes, *P. brassicae* will be able to expand to the lower Ob region. The most probable prospective habitats are garden plots in settlements and patches of crucifers along railroads, which have recently begun to appear in the polar Ural region.

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