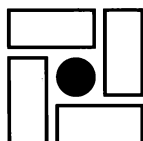# RUSSIAN JOURNAL OF ECOLOGY

Official English Translation of *Ekologiya*

Editor-in-Chief
Vladimir N. Bolshakov

Member of the Russian Academy of Sciences
Director of the Institute of Plant and Animal Ecology,
Ural Division of the Russian Academy of Sciences

A Journal of Original Papers and Reviews on Theoretical and Applied Ecology

Impact of Damaged Plants on the State of *Gonioctena pallidus* L. in the Course of an Outbreak of Its Numbers in the Polar Urals

I. A. Bogacheva

Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences,
ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia
Received November 30, 1995

Abstract—The state of larvae when fed by the foliage of severely and slightly damaged plants was studied experimentally during the peak and subsequent decline in numbers of *Gonioctena pallidus* L. A decrease in the individual weight (fecundity) and the growth rate, as well as an increase in mortality, led to the decrease in the numbers of *G. pallidus* L. in nature. It was shown that the processes under observation were the result of changes not only in the quality of food, but also in the phyllophagous insects themselves, and did not exhibit zonal specificity.

Most researchers presently acknowledge in some way the trophic theory of the dynamics of the numbers of phyllophagous insects that treats changes in the quality of food as the first cause of this phenomenon. This theory, however, is mainly based on the study of processes taking place in southern taiga and broadleaved forests. It was of interest to elucidate the situation on the northern border of the forest zone in the subarctic region, where, in the opinion of Haukioja and Hakala (1975), sharp rises in the numbers of phyllophagous insects should be observed particularly often, and to find out whether some specific features of phenomena observed in southern forest communities might be revealed there.

In addittion to well-known outbreaks in the numbers of *Epirrita autumnata* Bkh. in Fennoscandia (Tenow, 1963; Neuvonen, 1988), we found relatively few examples in the literature of manifestations of this phenomenon with respect to other Lepidoptera (Koponen, 1983), Chrysomelidae (Medvedev and Chernov, 1969), and Tenthredinidae (Koponen, 1981). The mass reproduction of phytophagous insects may escape notice because of the poor development of subarctic areas. It is also possible that the practical value of the mass reproduction of phyllophagous insects here, unlike in forests of the temperate zone, is not obvious for researchers and has not attracted their attention. However, mass reproduction in this area is most likely rare indeed. In any case, an outbreak of *Gonioctena pallidus* L. recorded in the lower reaches of the Ob in 1989–1990 was the first mass reproduction of a phyllophagous insect that we observed during our work in the area since 1970.

Even recorded outbreaks have been insufficiently studied. Only *E. autumnata*, whose cyclic fluctuations in numbers caused the extermination of forests in Fennoscandia over vast territories, attracted the attention of a large group of Finnish researchers; this made it possible to elaborate many aspects of the relations of the phyllophagous insect with the food plant. All the rest of the publications above typically concern noncyclic fluctuations in the numbers of phyllophagous insects and, at best, contain only very approximate assessments of diminished primary production due to their activity and the consequences of this impact on the food plant: usually, only the fact of the loss and the intense drying of plants is reported. How and by which mechanisms do decreases in the numbers of phyllophagous insects take place remained unknown. Therefore, having recorded an outbreak in the numbers of *G. pallidus* L., we set out to determine what were the consequences for the population of *G. pallidus* L. of their feeding on the foliage of plants damaged by them.

MATERIALS AND METHODS

Special experiments were performed in 1990 and 1992 in the polar Urals (the station Krasnyi Kamen', 50 km northwest of the city of Labytnangi) on the same plots used since 1984 for studying the biotopic variability of damage done to the willow (Bogacheva, 1990). In 1990, the numbers of *G. pallidus* L. were the highest; from 1991, they started to decrease, although they still remained higher than usual in 1992 (Fig. 1).

In the experiments, we used larvae of *G. pallidus* L. collected in biotope 1, where, during 1989–1990, the leaves of *Salix phylicifolia* were almost completely eliminated, and in biotope 4, where the extent of damage to willow was fairly low (see Fig. 1). Biotope 1 represented a plot of meadow overgrown with shrubs on the rock bank of the River Sob'; biotope 4 was a plot of willow brushwood in the floodplain; a more detailed description of the vegetation of the plots was given earlier (Bogacheva, 1990).
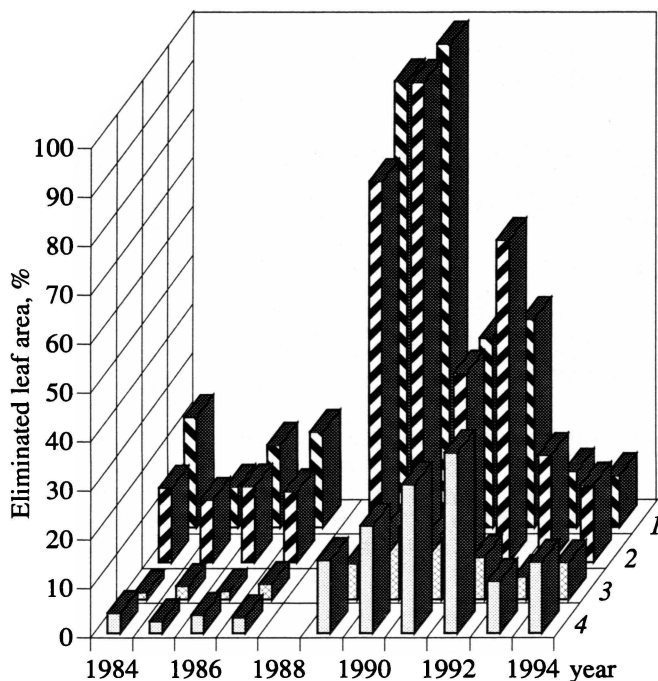
Fig. 1. Course of the consumption of *Salix phylicifolia* leaves by a complex of leaf-eating insects prior to and during an outbreak in the numbers of *Gonioctena pallidus*: (*1, 2*) severely damaged and (*3, 4*) slightly damaged biotopes.

Each collected sample of larvae was divided at random in two: half of the individuals were fed with plant leaves from biotope 1; the other, from biotope 4. Thus, in all, there were four variants of the experiments, each in ten replicates (a group of five individuals kept in a plastic container). The bottom of the container was covered with moistened filter paper or, when larvae attained the last instar, litter for pupation. As food, four or five foliated willow shoots were placed in the container, so that food was constantly in excess; the shoots were replaced daily simultaneously with moistening the litter. Food from each biotope was always collected from several plants, different plants being used each time. We also weighed larvae in these experiments daily, recorded all changes in their state, and, five to seven days after the final larvae were transferred to litter, we carefully examined the moss to weigh pupae. The next time the litter was studied was upon imago emergence (mid-August) in order to trace the fate of all individuals kept in the container. During experiments, we kept the containers outside, shaded from direct sunlight.

Hereafter, we shall name the four variants of experiments DD, DN, ND, and NN (control), where the first letter designates the origin of larvae (D—from biotope 1, i.e., from formerly damaged plants, and N—from biotope 4, i.e., from undamaged plants), and the second letter indicates the food origin (plant leaves from biotopes 1 and 4, respectively). The low locomotive velocity in this species (imagines do not fly, and larvae do not crawl far away) enabled us to state that larvae originated from individuals that fed in previous years on the same plant or on neighboring ones. We assessed the growth rate (*RGR*) in the experiment for the period of experiments, calculating it by the formula: $RGR = (\ln P_T - \ln P_0)/T$, where P_0 and P_T are the initial and ultimate weights of the larva for the period T (in days). We also assessed the loss of *G. pallidus* L. and, in 1992, the weight of individuals (by the pupal weight). When we needed to compare mean values, we used the Student's *t*-test.

EXPERIMENTAL RESULTS

In 1990, the larval growth rate was distinctly lower only in variant DD (0.119 g per g body weight per day); in the other three variants, it was actually equal (0.172, 0.196, and 0.193 g/g body weight per day in variants DN, ND, and NN). In Fig. 2a, this is clearly seen from the slope of the curves, i.e., feeding larvae with leaves from undamaged bushes made their state better in variant DN, but feeding larvae with leaves from damaged bushes did not decrease the growth rate in larvae collected from undamaged plants (note, however, that immature larvae in variant ND prior to the experiments fed on undamaged plants in nature). Similar results were obtained with respect to the mortality of *G. pallidus* L.: only variant DD, in which only 8.7% of the larvae yielded normal imagines, reliably differed from variant NN (48%); the other two variants, DN and ND, showed intermediate values of survival (37.5 and 28.0%) that did not reliably differ from either NN or DD (Fig. 3a). Finally, although pupal weight was not recorded in 1990, it is evident that the weight of individuals in variant DD was the lowest (Fig. 2a).

Experimental results obtained in 1992 exhibit a somewhat different pattern. Upon feeding with leaves collected from undamaged plants, the larval growth rate of *G. pallidus* L. in variant DN exhibited no greater increase and was actually equal in variants DD and DN (Fig. 2b) (0.277 g/g body weight per day), differing from variants ND and NN (about 0.355 g/g body weight per day). Mortality (Fig. 3b) was also almost equal in variants DD and DN (36 and 40% normal imagines emerged), noticeably differing from variants ND and NN (68 and 76%). Moreover, comparison of Figs. 3a and 3b revealed that *G. pallidus* L. perished at earlier stages, although their major portion was lost as before at the stage of larvae ready for pupation or pupae. It is unknown whether this loss was induced by disease or simply by physiological weakening of larvae as a result of their feeding on inadequate food. Larvae darkened and became inert, but, upon transferring to litter, did not exhibit clear evidence of bacterial or viral disease. It is true that pupae in the cradle were usually covered by mycelial down, but this was possibly of saprophytic fungi that might develop on the dead individual.
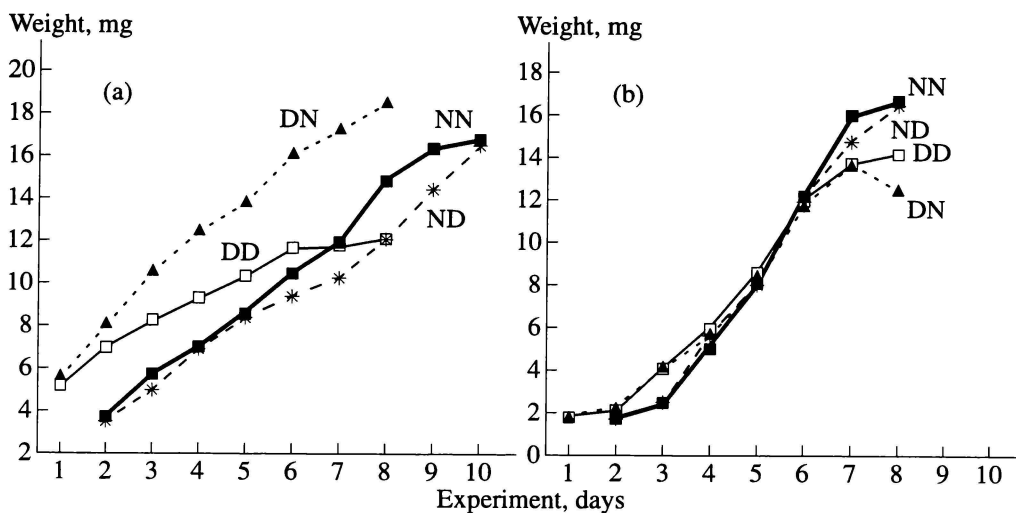
Fig. 2. Larval growth of *G. pallidus* in experiments of (a) 1990 and (b) 1992 (see text for explanations of the designations of the experimental variants).
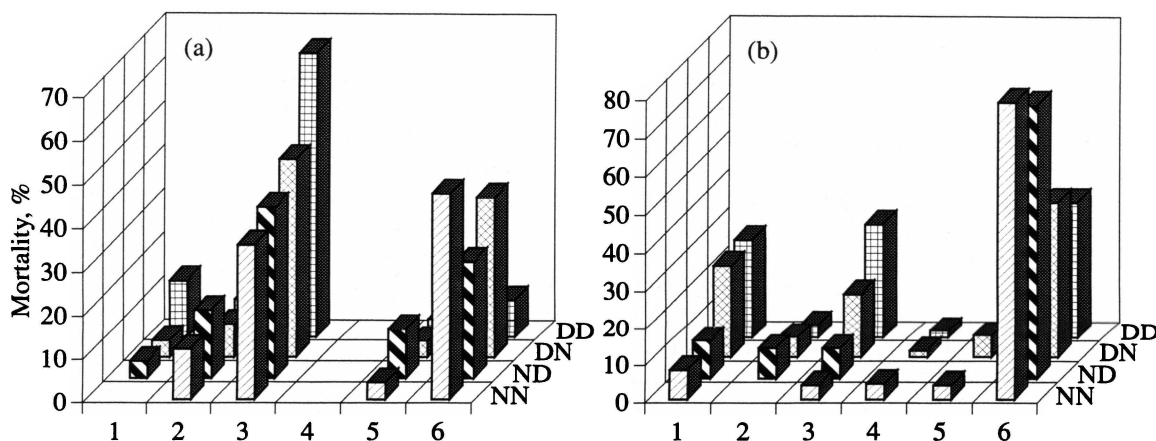

Fig. 3. Mortality of *G. pallidus* individuals in experiments of (a) 1990 and (b) 1992 (see text for explanations of the designations of the experimental variants). (*1–5*) Individuals that perished at the stage of (*1*) immature larvae, (*2*) the last instar larvae, (*3*) larvae in the litter prior to pupation, (*4*) pupae, (*5*) developing imagines, and (*6*) normal imagines.

Both the growth rate and mortality show that the origin of larvae exerts a greater impact upon their state than does the food they use. The third criterion, that of pupal weight, behaves differently. Variant DD significantly differed from DN (13.72 ± 0.43 and 15.16 ± 0.51 mg, respectively; $p < 0.05$); and ND, from NN (14.24 ± 0.30 and 15.42 ± 0.29 mg; $p < 0.01$). In comparing larvae that had different origins and fed on similar food, we did not reveal significant differences, i.e., when larvae could attain greater weight when fed on leaves of undamaged plants, irrespective of its origin.

DISCUSSION

The experimental results showed that feeding on the foliage of formerly damaged plants was unfavorable for a phyllophagous insect, i.e., increased larval mortality and decreased weight (and consequently, the fecundity of future imagines) were observed. The developmental period was lengthened, which, in nature, increases the danger of the phyllophagous insect's death from predators or parasites. All the above were usual phenomena repeatedly shown earlier in studies of the feeding of phyllophagous insects on leaf remains that were left intact on trees from the secondary foliage or foliage grown on trees in the year following an outbreak (Verzhutskii, 1969; Verzhutskii *et al.*, 1971; Rafes, 1974, 1981; Pleshanov, 1981; Haukioja and Niemelä, 1976; Werner, 1979; Niemelä *et al.*, 1980; Baltensweiler, 1984). As a rule, these phenomena are attributed to the increase in the concentration of secondary metabolites in leaves and a decrease in the nitrogen and water contents; the entire complex of changes occurs simultaneously.

It is likely that these impacts caused a sharp decline in the numbers of the phyllophagous insect. It was cal-

culated for *Epirrita autumnata* that the decrease in the weight (and, consequently, in fecundity) of individuals and the survival of caterpillars leads to a decrease in the total number of eggs produced by the generation of *Epirrita autumnata* in the year following the outbreak of its numbers by 70–80%. If we take into account the effect of retarded growth, the actual decrease in fecundity in nature comprises about 90% (Haukioja *et al.*, 1985). The above is supplemented by direct starvation, interference, and cannibalism, observed in caterpillars at high population densities (Rafes, 1968, 1974), as well as predators, parasites, and diseases, "finishing off" the phyllophagous insect in the phase of its decline in numbers. The numbers of the phyllophagous insect *G. pallidus* L. likewise decreased in our study (see Fig. 1). It is likely that this was mostly accounted for by direct larval mortality due to deterioration of the food quality. An increase in larval weight with feeding on undamaged leaves in 1992 (variant DN) suggests that, with gradual improvement in the quality of food, i.e., willow leaves, the restoration of the level of numbers of *G. pallidus* L. will start with an increase in fecundity.

Experimental results showed that the growth rate of larvae was lower in 1990 than in 1992, whereas their mortality was higher. This phenomenon was present both in the experiment and in the control; hence, it would be incorrect to relate it to the deterioration of the food quality as a result of the mass reproduction of *G. pallidus* L. Instead, this is likely to be related to the change in weather: the extremely high temperatures and unusually small amount of precipitation in late June and July of 1990 not only affected the quality of leaves, but accelerated their development as well; as a result of this, indices of food moistening dropped by mid-July to values usually corresponding to those at the end of the growing season. Undoubtedly, the low moisture concentration was accompanied by other changes in the chemical composition of leaves. However, it is probable, that, in 1990, high temperatures affected the phyllophagous insects directly as well.

Against the background of distinctions caused by the different weather situation, we recorded additional changes in 1992 that require another explanation. The relative roles of two parameters changed in our experiments, i.e., the food quality and the factor complex called "larval origin" (this includes the feeding of immature larvae in nature prior to the experiment, the feeding of their parents at the beginning of the current season and of their more distant ancestors in former years), was different in 1990 and 1992. Indeed, larval mortality in 1990 was an average of 24.4% lower with "good food" (comparison of variants DD with DN and ND with NN, (Fig. 3a)) than on leaves of damaged plants. At the same time "good origin" added only 14.8% to the survival of larvae (comparison of variants DD with ND and DN with NN). In 1992, "good food" added only 6.3% to the survival of larvae; and "good origin," 36.9% (Fig. 3b, the same comparisons). We derived the same conclusion on the basis of analysis of

the growth-rate data: in 1990 with "good food," the growth rate of larvae collected from damaged plants increased, but there was no such response in 1992. Hence, it may be concluded that, by 1992, feeding on damaged plants changed the insects themselves. There is nothing unusual in this fact: similar changes in phyllophagous insects at different stages of dynamics in their numbers have been already predicted and shown (Rafes, 1968; Haukioja and Hakala, 1975). No specific features exclusively inherent to the subarctic region were found in the aforementioned phenomena.

ACKNOWLEDGMENTS

REFERENCES

Baltensweiler, W., The Role of Environment and Reproduction in the Population Dynamics of the Larch Bud Moth, *Zeiraphera diniana* Gn. (Lepidoptera, Tortricidae), *Adv. Invertebr. Reprod.*, 1984, vol. 3, pp. 291–302.

Bogacheva, I.A., *Vzaimootnosheniya nasekomykh–fitofagov i rastenii v ekosistemakh Subarktiki* (Relationships between Phytophagous Insects and Plants in Subarctic Ecosystems), Sverdlovsk: Ural. Otd., Akad. Nauk SSSR, 1990.

Haukioja, E. and Hakala, T., Herbivore Cycles and Periodic Outbreaks: Formulation of a General Hypothesis, *Rep. Kevo Subarct. Res. Stn.*, 1975, vol. 12, pp. 1–9.

Haukioja, E. and Niemelä, P., Does Birch Defence Itself Actively against Herbivores?, *Rep. Kevo Subarct. Res. Stn.*, 1976, vol. 13, pp. 44–47.

Haukioja, E., Suomela, J., and Neuvonen, S., Long-Term Inducible Resistance in Birch Foliage: Triggering Cues and Efficacy on a Defoliator, *Oecologia*, 1985, vol. 65, no. 3, pp. 363–369.

Koponen, S., Outbreaks of *Dineura virididorsata* (Hymenoptera) and *Eriocrania* (Lepidoptera) on Mountain Birch in Northernmost Norway, *Not. Entomol.*, 1981, vol. 61, no. 1, pp. 41–44.

Koponen, S., Phytophagous Insects of Birch Foliage in Northernmost Woodlands of Europe and Eastern North America, *Tree-Line Ecology: Proc. of the Northern Quebec Tree-Line Conf.*, Quebec, 1983, pp. 165–176.

Medvedev, L.N. and Chernov, Yu.I., New Species of *G. pallidus* L. of the Genus *Chrysomela* (Coleoptera, Chrysomelidae) as an Important Component of Taimyr Biocenoses, *Zool. Zh.*, 1969, vol. 48, no. 4, pp. 532–537.

Neuvonen, S., Interactions between Geometrid and Microtine Cycles in Northern Fennoscandia, *Oikos*, 1988, vol. 51, no. 3, pp. 393–397.

Niemelä, P., Ojala, H., Ojala, M.-L., and Haukioja, E., Retarded Growth of Lepidopteran Larvae after Mechanical Damage to Leaves of Tamarack and Dwarf Birch near Shefferville, Central Quebec–Labrador Peninsula, *McGill Subarct. Res. Rep.*, 1980, vol. 30, pp. 52–56.

Pleshanov, A.S., Ecological–Physiological Aspects of Larch Resistance to Defoliating Insects, in *Rol' vzaimootnoshenii rastenie–nasekomoe v dinamike chislennosti populyatsii lesnykh vreditelei* (Role of the Plant–Insect Relationship in the Population Dynamics of Forest Pests), Irkutsk, 1981, pp. 40–41.

Rafes, P.M., *Rol' i znachenie rastitel'noyadnykh nasekomykh v lesu* (Role and Significance of Phytophagous Insects in Forests), Moscow: Nauka, 1968.

Rafes, P.M., Research on the Population Dynamics of Competitive Species of Leaf-eating Birch Pests, *Dokl. Akad. Nauk SSSR*, 1974, vol. 214, no. 6, pp. 1431–1433.

Rafes, P.M., *Vzaimodeistvie lesnykh nasekomykh, povrezhdayushchikh list'ya s kormovymi derev'yami* (Interaction of Leaf-damaging Forest Insects with Forage Trees), in *Itogi Nauki Tekh., Ser. Entomol.*, 1981, vol. 5, pp. 140–202.

Tenow, O., Leaf-eating Insects in the Mountain Birch at Abisco (Swedish Lapland) with Notes on Bionomics and Parasites, *Zool. Bidr. Uppsala*, 1963, vol. 35, pp. 545–568.

Verzhutskii, B.N., Feeding of Saw Flies Hymenoptera, Symphyta on Secondary Larch Needles and Evolution of the Plant–Host Relationship, *Izv. Vost. Sib. Otd. Geogr. O-va. SSSR*, 1969, vol. 66, pp. 153–154.

Verzhutskii, B.N., Dokiichuk, T.A., and Zhivotova, M.M., Biochemical Changes in Larch Regrowth Needles Damaged by *Pristiphora wesmaeli* (Tischb.) and the Significance of These Changes for Insects Eating Coniferous Needles, *Izv. Sib. Otd. Akad. Nauk SSSR, Ser. Biol.*, 1971, vol. 2, no. 10, pp. 88–93.

Werner, R.A., Influence of Host Foliage on Development, Survival, Fecundity, and Oviposition of the Spear-marked Black Moth, *Rheumaptera hastata* (Lepidoptera: Geometridae), *Can. Entomol.*, 1979, vol. 111, no. 3, pp. 317–322.