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DYNAMICS OF NUMBERS OF THE LEAF-EATING INSECTS AND ITS EFFECT ON FOLIAGE PRODUCTION IN THE "GRABOWY" RESERVE IN THE KAMPINOS NATIONAL PARK*

ABSTRACT: Defoliation by leaf-eating insects was estimated. During a 4-years' series of investigations three basic phases of the dynamics of phytophagous insects were identified: a pre-outbreak period, an outbreak period and a post-outbreak period. The following features of the particular periods have been described: the dynamics of numbers and biomass of the leaf-eating insects during a growing season, the consumption of the phytophagous insects and the effect of the latter on the foliage production of the dominant tree species. A comparison of the leaf-fall, the foliage consumption by the phytophagous insects and the total foliage production in the particular years has shown that the possibilities to regenerate the photosynthetic system to compensate for the loss due to insect feeding are limited, being within the range of the expected foliage production under the particular conditions.

Contents

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1. INTRODUCTION

The leaf-feeding chain represents one of the most important channels of energy flow and matter circulation in a forest ecosystem. The quantity of foliage eaten over a many-year cycle is subject to considerable variations, from several to a hundred per cent of the vegetable mass produced. The defoliation caused by the leaf-eating insects thus determines the amount of organic fall progressing towards the detritus food chain. Through the production of faeces the phytophagous insects at the same time change the quality of the fall, accelerating its inclusion in the cycle.

An increase in the rate of leaf eating may thus on the one hand cause a considerable decrease in the increment of wood in a stand, and on the other hand it may accelerate the circulation of nutrients. Finally, without knowing the quantity eaten by the phytophagous insects it is impossible to assess the total foliage production. For this reason the investigation of the overall economy of the forest ecosystem, carried out in the "Grabowy" reserve for several years, required an assessment to be made of the effect of insects on the quantity of the plant mass produced in the form of foliage.

The studies presented in this paper included the dynamics of numbers and biomass of the leaf-eating insects in a mixed forest (*Pino-Quercetum*) during a period of 4 years, their consumption in the particular years, and the effect on the production of oak and hornbeam foliage whose weight proportion at the study site constituted over 80% of the vegetable biomass produced by all the broad-leaved tree species together. This paper represents part of a comparative study of the foliage economy in the various forest ecosystems of the Kampinos National Park near Warsaw.

2. STUDY AREA AND METHODS

The investigations were carried out in the south-eastern part of the Kampinos National Park. The study site selected was a mixed forest area (*Pino-Quercetum*), about 5 ha, surrounded by a moist alder-wood (*Carici elongatae-Alnetum*). The upper tree storey consisted of the pine (*Pinus silvestris* L.), the oak (*Quercus pedunculata* L.), the verrucose birch (*Betula verrucosa* Ehrh.); the lower storey – of the hornbeam (*Carpinus betulus* L.) (Table I). The thick shrub layer was made up mainly of the hornbeam and the oak, and to lesser extent of the birch, the hazel (*Corylus avellana* L.), the buckthorn (*Frangula alnus* Mill.) and the rowan (*Sorbus aucuparia* L.).

Table I. Tree stand structure at the study site

Dominant species	Trees			Shrub layer	
	age in years	number per 1 ha	per cent contribution	number per 1 ha	per cent contribution
Quercus pedunculata	150	64	27.1	152	16.6
Carpinus betulus	50–80	100	42.4	716	78.2
Pinus silvestris	100	64	27.1	0	0.0
Betula verrucosa	90	8	3.4	48	5.2

The method used was based on the comparison of the number and biomass of insects with the number and biomass of the leaves on which they occurred.

Samples were collected in the tree crowns by using a special catcher consisting of: (a) a metal ring 50 cm in diameter, (b) a thin nylon sack 53 cm in diameter and 1 m long, fastened to the metal ring by an elastic band strung through the margin of the sack (about 15 cm below its opening the sack had a cord strung through it; by pulling at the cord it was possible to constrict the sac on a branch), (c) a stick made up of a number of aluminium tubes fitted together (for this purpose tent masts were used) (Fig. 1). It was found that a stick above 8 m in length was too wobbly, making it impossible to collect a sample. The above-described catcher represents a modification of the catcher used for the same purpose by Palmgren (1932).

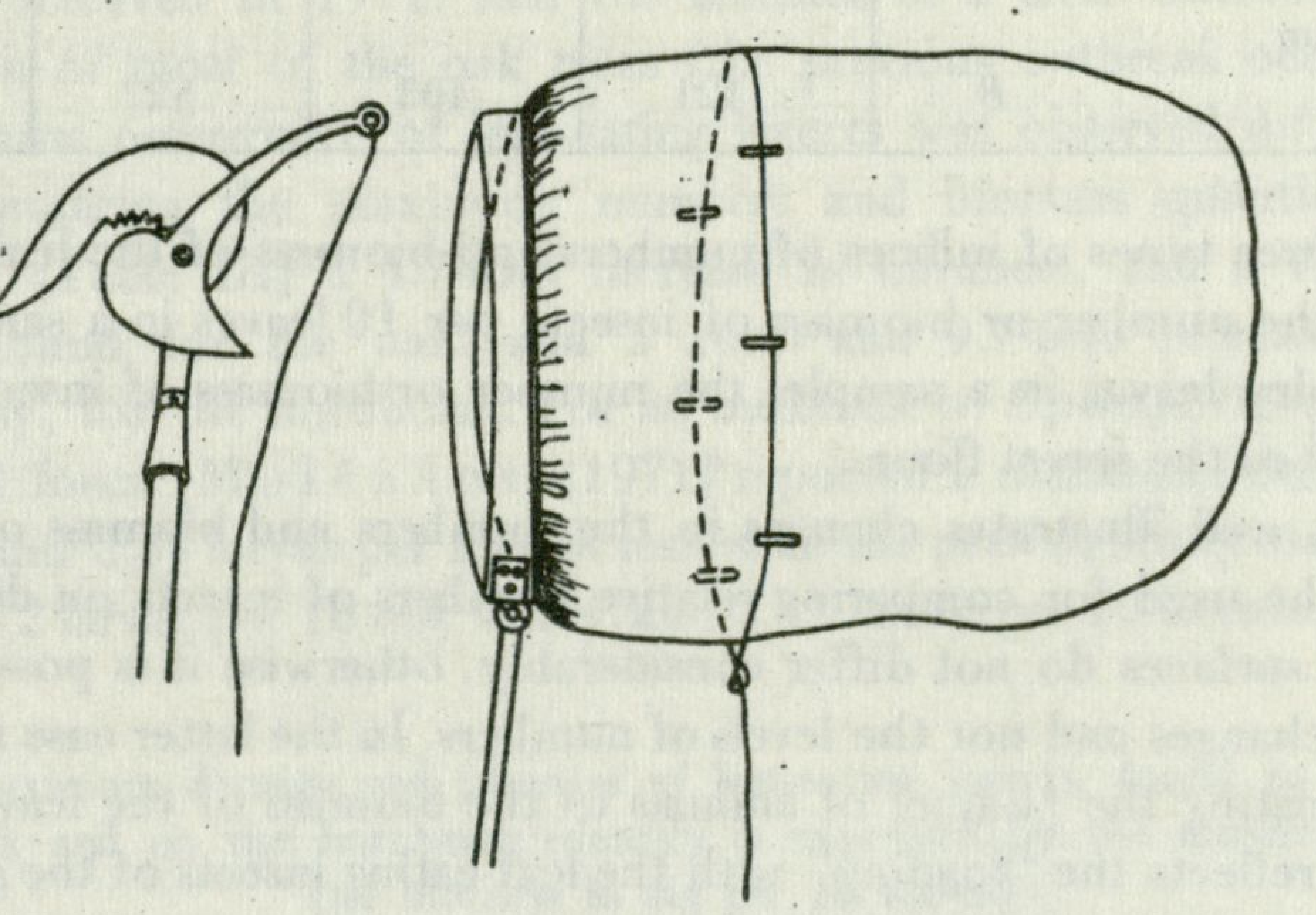

Fig. 1. Secateur and catcher sack for collecting samples from tree crowns

The catcher sack was first thrown onto a branch, then by pulling at the cord the sack was constricted, the branch was cut off with a secateur, also fitted on an appropriately long stick, and thus a sample was obtained. It consisted of a tree branch about 3/4 m long, from which the insects were extracted after carefully opening the sack and the leaves plucked. Each insect sample was divided into taxonomic groups, weighed and preserved in alcohol. The leaves of each sample were counted, dried to a constant weight at 60–70°C and weighed.

In order to investigate the variations in numbers of the insects of the tree crowns during a growing season, it was necessary to collect a relatively large number of samples evenly distributed over time. As the study site area was comparatively small (5 ha) and the cutting of branches slightly deformed and damaged the trees, the number of samples collected at a time was needs limited. Consequently, during the several years of study from each tree species the following numbers of samples were collected each time: 1968 – 2 up to 4 samples from the upper parts of the tree crowns and 2 from the lower tree crown parts, in 1969 – 3 from the upper and 2 from the lower, and in 1971 – 5 from the upper and 5 from the lower tree crown parts. In 1973, after reducing the diameter of the catcher ring, and of the sacks, to 25 cm, and of the length of the sacks to 50 cm, all the samples were collected at the average height of 7–10 m, each time 30 samples being collected. In Table II the numbers of samples collected each year and the average numbers of leaves in each sample are presented. The total number of leaf-eating insects collected by using the above method was 9,437.

Table II. Number of samples collected from the oak and the hornbeam (*A*) and the average numbers of leaves per sample (*B*) in particular study years

Species studied		Years			
		1968	1969	1971	1973
Oak	*A*	60	65	150	194
	B	240	219	427	78
Hornbeam	*A*	60	85	160	–
	B	421	403	527	–

In the paper three types of indices of numbers and biomass of the leaf-eating insect fauna have been used: the number or biomass of insects per 10 leaves in a sample; the number or biomass per 10 g dry leaves in a sample; the number or biomass of insects in tree crowns as projected per 1 m^2 of the forest floor.

The first index well illustrates changes in the numbers and biomass of the insects against time; it can also be used for comparing relative numbers of insects on different tree species, provided the leaf surfaces do not differ considerably, otherwise it is possible to compare the directions of the changes and not the levels of numbers. In the latter case it is better to use the second index – relating the number of animals to the biomass of the leaves. Apart from this, the second index reflects the "loading" with the leaf-eating insects of the green foliage mass of the different tree species at the particular points of time. However, it does not reflect the real variations in numbers and biomass against time, because of the increments in the leaf biomass during the growing season, or its losses due to an intensive pest feeding.

Both the above-described indices characterize the level of numbers or the biomass of insects relative to the existing quantity of foliage (surface area, biomass), but it would be difficult to use them directly for the estimation of foliage consumption. For this purpose a third index – the number (or biomass) of leaf-eating insects projected over 1 m^2 of the forest floor was used. These values are obtained by multiplying the mean number or biomass of individuals per 1 leaf in a sample by the average number of leaves fallen in the particular year per 1 m^2 of the forest floor. This was possible, because at the study site a simultaneous recording was carried out of the leaf-fall into standard bags 0.1 m^2 in surface area. Data on the quantity of leaf-fall and the number of leaves were kindly made available to the authors by W. Kaczmarek.

Because in 1971 there occurred a complete defoliation of the trees over a considerable area, and in the calculations it was necessary to use the initial number of leaves and not that of the leaves regenerated from the dormant buds, for 1971 the number of leaves in the preceding year (1970) was adopted as the initial number of leaves. The values of the oak and hornbeam foliage-fall in g/m^2 for the period 1968–1971 were calculated on the basis of the weight per cent contribution of the foliage or these species in 1973 and 1974. The average value for these years was 43.6% for the hornbeam, and 40.2% for the oak. The remaining quantities were calculated directly. Complete data on the fall of foliage in the period 1969–1975 can be found in the paper by W. Kaczmarek: "An analysis of foliage production and fall in 4 forest areas in the Kampinos National Park during the years 1964–1975" (in preparation). Information on the leaf-eating insects of the oak was gathered in the years 1968, 1969, 1971 and in 1973, and on those of the hornbeam – in 1968, 1969 and in 1971.

3. RESULTS

3.1. Dynamics of numbers and biomass of the leaf-eating insects

3.1.1. Dynamics over a many years' cycle

During the period 1968–1973, three distinctly different moments were identified in the variation of numbers of the leaf-eating insect fauna of the oak and hornbeam: a pre-outbreak period (1968 and 1969), an outbreak period (1971) and a post-outbreak period (1973). From 1968 onwards, the leaf-eating phytophagous insects increased in number, attaining the highest level in 1971, followed by a decrease in numbers (Table III). The increase in numbers of the leaf-eating insects, observed in 1971, had the features of a clear outbreak, and it led to a complete defoliation of most of the oak trees (the previous outbreak occurred at the study site in 1960). A mass occurrence of leaf-eating insects was observed on both the oak and the hornbeam. Comparing the maximum numbers and biomass quantities of the insects in 1968 and 1971 (Table III) a 4.7-fold increase in numbers, and a 7.2-fold increase in the biomass was found for the oak, and a 16.0- and 9.7-fold increase in numbers and biomass, respectively, for the hornbeam. For an outbreak of *Operophthera brumata* (L.) in a mixed broad-leaved forest Molčanov (1971) reported a maximum density of 1.84 larvae per 10 elm leaves, and 0.59 larvae per 10 oak leaves. In the present study much higher densities were recorded – 6.12 larvae per 10 oak leaves, and 2.53 larvae per 10 hornbeam leaves.

Table III. Maximum density and biomass of leaf-eating insects, found in the particular years on the oak and on the hornbeam (density is expressed by the number of individuals, and biomass in mg per 10 leaves)

Year	Oak		Hornbeam	
	density	biomass	density	biomass
1968	1.305	19.412	0.158	2.915
1969	1.541	22.409	0.201	3.873
1971	6.121	139.342	2.529	28.288
1973	1.509	13.508	–	–

Table IV. Maximum density and biomass of leaf-eating insects, found on the oak and the hornbeam in the particular years (density is expressed by the number of individuals, and biomass in mg wet weight per 10 g of dry leaf weight)

Year	Oak		Hornbeam	
	density	biomass	density	biomass
1968	20.019	218.471	3.483	62.029
1969	33.092	264.453	4.759	87.241
1971	296.972	3,036.426	107.058	1,010.382

In this case the number of insects was related to the number of leaves. As the average weight and the surface area of the leaves vary considerably from year to year, the relationship between the numbers and biomass of the phytophagous insects and the quantity of food available is better represented by an index showing the ratio of the number, or biomass of insects to the dry weight of the leaves (Table IV). Then the numbers and the biomass of the phytophagous insects in 1971, as compared with the year 1968, appear to be higher – 14.8 and 13.9 times on the oak, and 30.7 and 16.3 times on the hornbeam. V a r l e y (1970), who analysed similar groups of leaf-eating insects of the oak, found even 40-fold variations in numbers over a many years' cycle.

3.1.2. Dynamics during one growing season

Throughout the study period (1968–1973) a similar course of variations in numbers of the leaf-eating phytophagous insects could be observed during the growing season, characterized by

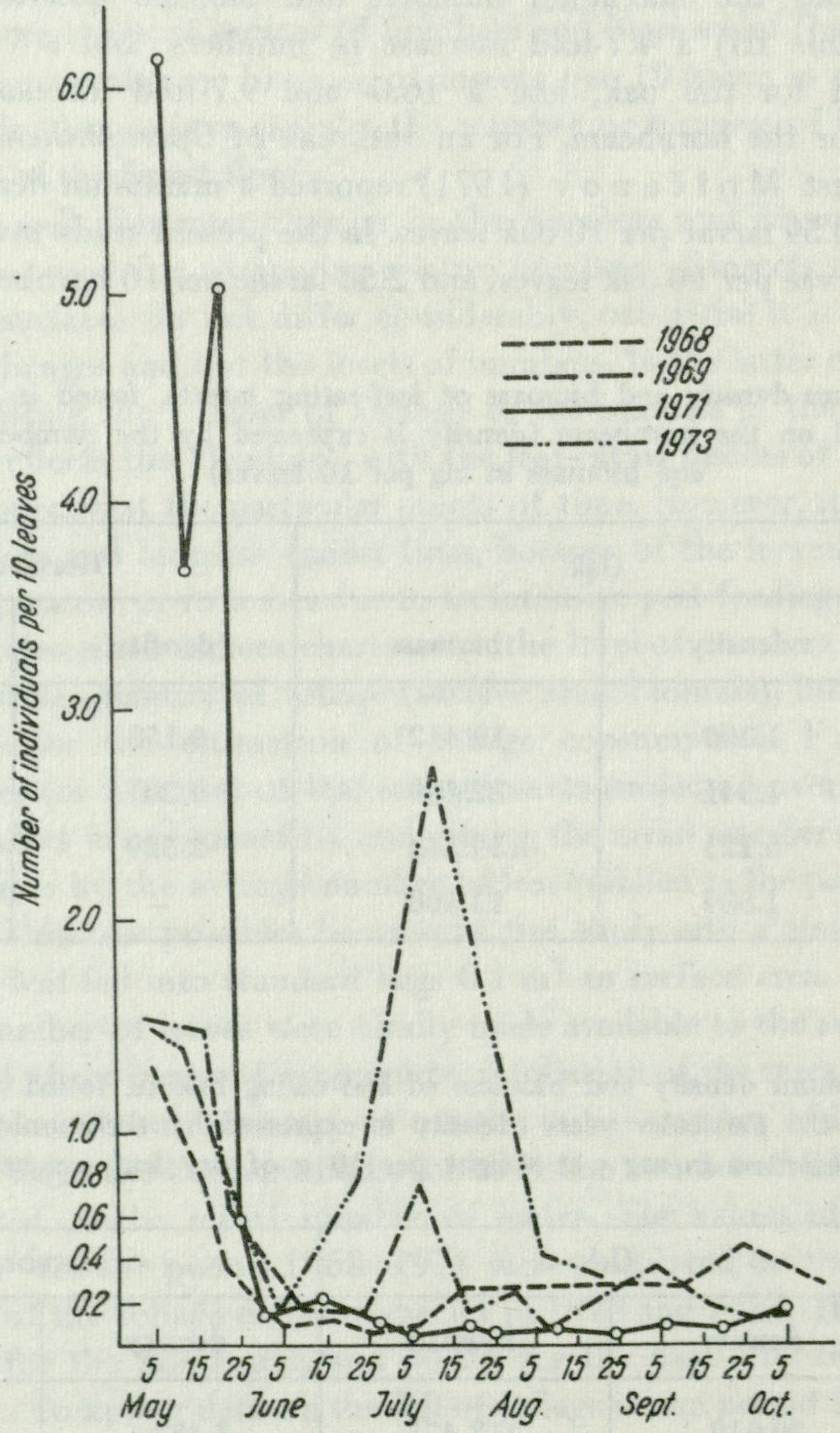

Fig. 2. Dynamics of numbers of leaf-eating insects on the oak during the growing season

the presence of a clear spring peak in May, followed by a relatively low level of numbers during the remainder of the growing season. The course of the variations in numbers appeared to be similar for the oak and hornbeam (Figs. 2, 3), except that during the pre-outbreak period the numerical peaks of the insects on the hornbeam occurred with a delay of about two weeks.

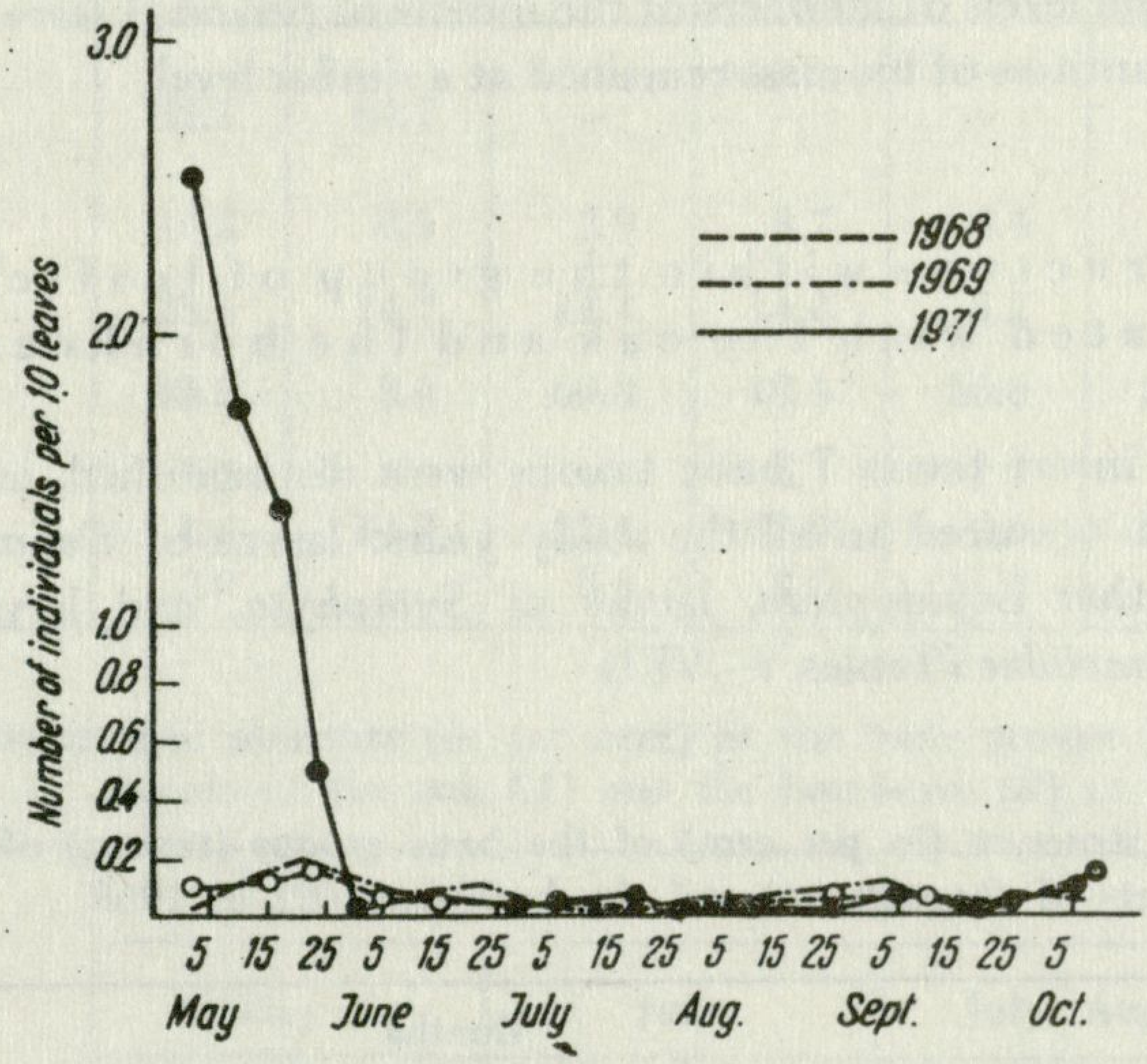

Fig. 3. Dynamics of numbers of leaf-eating insects on the hornbeam during the growing season

It is therefore possible in essence to distinguish two periods clearly differing by the level of numbers: a spring period (I) and a summer-autumn period (II). Differences between the individual years concern primarily the relationship between the numbers in period I and the numbers in period II during an outbreak year. The ratio of the maximum numbers of period I to the maximum numbers of period II was in the case of the hornbeam leaf-eating insects 1.15 and 1.73 for the pre-outbreak years. and 32.84 for the outbreak year. In the case of the oak leaf-eating insects the value of this ratio was: 4.48, 1.96 and 28.60, respectively. An exception was a considerable growth in numbers in July 1973. However, since this occurred at the expense of small insect forms, it did not significantly affect the course of biomass variations.

Similar regularities were found for the dynamics of the biomass during a growing season, except that biomass peaks occurred at a later time than the peaks of numbers. In the consecutive years the values of the ratio of the maximum biomass of period I to the maximum biomass of period II were as follows: 3.06, 4.18 and 28.9 for the hornbeam, and 8.11, 7.53 and 39.10, respectively, for the oak.

R a f e s (1970) reports that the autumn pest species are seldom active in the years of outbreaks of the spring pests. In the present study the outbreak that occurred in the spring of 1971 had no significant effect on the level of numbers of the leaf-eating insects in the autumn.

The mean values of numbers (N) and of biomass (B) (as adjusted to the per 10 leaves' basis) in the summer-autumn periods of the particular years were as follows:

		1968	1969	1971	1973
on the oak:	*N*	0.199	0.247	0.093	0.952
	B	1.189	1.256	1.026	2.448
on the hornbeam:	*N*	0.046	0.058	0.038	–
	B	0.407	0.505	0.419	–

In the outbreak year the levels of numbers of the insects of period II were in fact lower than in other years, but the quantities of biomass remained at a similar level.

3.2. Dominance structure within the group of leaf-eating insects associated with the oak and the hornbeam

Within the leaf-eating insect fauna 7 basic taxons were distinguished, including a variable number of species which occurred in all the study years: larvae of *Geometridae*, larvae of *Tortricidae*, larvae of other *Lepidoptera*, larvae of *Symphyta*, and larvae and adults of *Curculionidae* and *Chrysomelidae* (Tables V–VIII).

Table V. Dominance structure (in per cent) of the basic groups (taxons) of leaf-eating insects of the oak (*A*) and the hornbeam (*B*) in 1968

Taxons	Months							
	May		June		July, Aug.		Sept., Oct.	
	A	*B*	*A*	*B*	*A*	*B*	*A*	*B*
Operophthera brumata	25.1	29.9	–	–	–	–	–	–
Other *Geometridae*	3.4	2.1	–	5.0	8.1	9.1	–	–
Tortricidae	62.6	24.7	26.7	5.0	62.9	22.7	24.5	9.7
Other *Lepidoptera*	2.1	6.2	13.2	5.0	25.8	45.5	66.0	22.6
Symphyta	1.3	1.0	6.7	5.0	–	–	–	–
Curculionidae	3.8	25.8	46.7	55.0	1.6	13.6	9.4	67.7
Chrysomelidae	–	–	6.7	–	1.6	–	–	–

All the leaf-eating insect taxons distinguished were found on both the tree species: the oak and the hornbeam, but the contributions of the individual groups on either of them were different. During period I there was a larger proportion of *Tortricidae* in the phytophagous insect population on the oak than on the hornbeam, while on the hornbeam there was a higher dominance of *Geometridae* – mainly *Operophthera brumata*. During period II the following showed a higher degree of dominance on the oak than on the hornbeam: adults and larvae of *Chrysomelidae*, *Tortricidae* and other *Lepidoptera*, primarily *Tischeridae*, whereas on the hornbeam a higher proportion of *Curculionidae* was found.

Table VI. Dominance structure (in per cent) of the basic groups (taxons) of leaf-eating insects of the oak (*A*) and the hornbeam (*B*) in 1969

Taxons	Months							
	May		June		July, Aug.		Sept., Oct.	
	A	*B*	*A*	*B*	*A*	*B*	*A*	*B*
Operophthera brumata	41.1	64.7	–	–	–	–	–	–
Other *Geometridae*	10.8	0.9	2.9	3.7	3.4	9.3	2.3	–
Tortricidae	23.6	14.7	11.4	14.8	5.2	7.0	9.1	8.3
Other *Lepidoptera*	19.2	3.9	60.0	18.5	56.0	39.5	38.6	4.2
Symphyta	1.2	–	–	3.7	1.7	–	1.1	–
Curculionidae	1.5	14.7	17.1	51.9	2.6	37.2	32.9	83.3
Chrysomelidae	2.0	–	8.6	3.7	31.0	7.0	15.9	4.2

Table VII. Dominance structure (in per cent) of the basic groups (taxons) of leaf-eating insects of the oak (*A*) and the hornbeam (*B*) in 1971

Taxons	Months							
	May		June		July, Aug.		Sept., Oct.	
	A	*B*	*A*	*B*	*A*	*B*	*A*	*B*
Operophthera brumata	74.3	83.8	–	–	–	–	–	–
Other *Geometridae*	2.6	10.2	5.4	4.5	12.1	8.8	5.7	1.8
Tortricidae	18.1	2.8	7.8	6.0	–	–	1.9	2.7
Other *Lepidoptera*	3.6	1.2	13.9	12.1	23.5	47.5	45.9	16.1
Symphyta	0.2	–	–	–	1.5	–	0.6	–
Curculionidae	0.6	2.0	18.7	36.4	27.3	40.0	35.7	78.6
Chrysomelidae	0.2	–	54.2	39.4	35.6	3.8	10.2	–

Table VIII. Dominance structure (in per cent) of the basic groups (taxons) of leaf-eating insects on the oak in 1973

Taxons	Months		
	May	June	July, Aug.
Operophthera brumata	31.6	–	–
Other *Geometridae*	5.3	–	1.3
Tortricidae	34.5	7.8	1.9
Other *Lepidoptera*	16.5	19.5	14.0
Symphyta	0.5	0.4	0.4
Curculionidae	6.3	4.0	1.6
Chrysomelidae	5.3	67.9	80.7

In general, one may state that during the spring (May) larvae of *Tortricidae* and *Geometridae*, mainly *Operophthera brumata*, dominated on both the tree species studied, during the summer (June, July, August) adults and larvae of *Curculionidae* and *Chrysomelidae* (only on the oak), and during the autumn (September, October) *Curculionidae* and larvae of *Lepidoptera* (Tables V–VIII). Exceptionally in 1968, one of the groups dominating during the summer and autumn was *Tortricidae* (Table V), the spring group and the summer-autumn group consisting of different species.

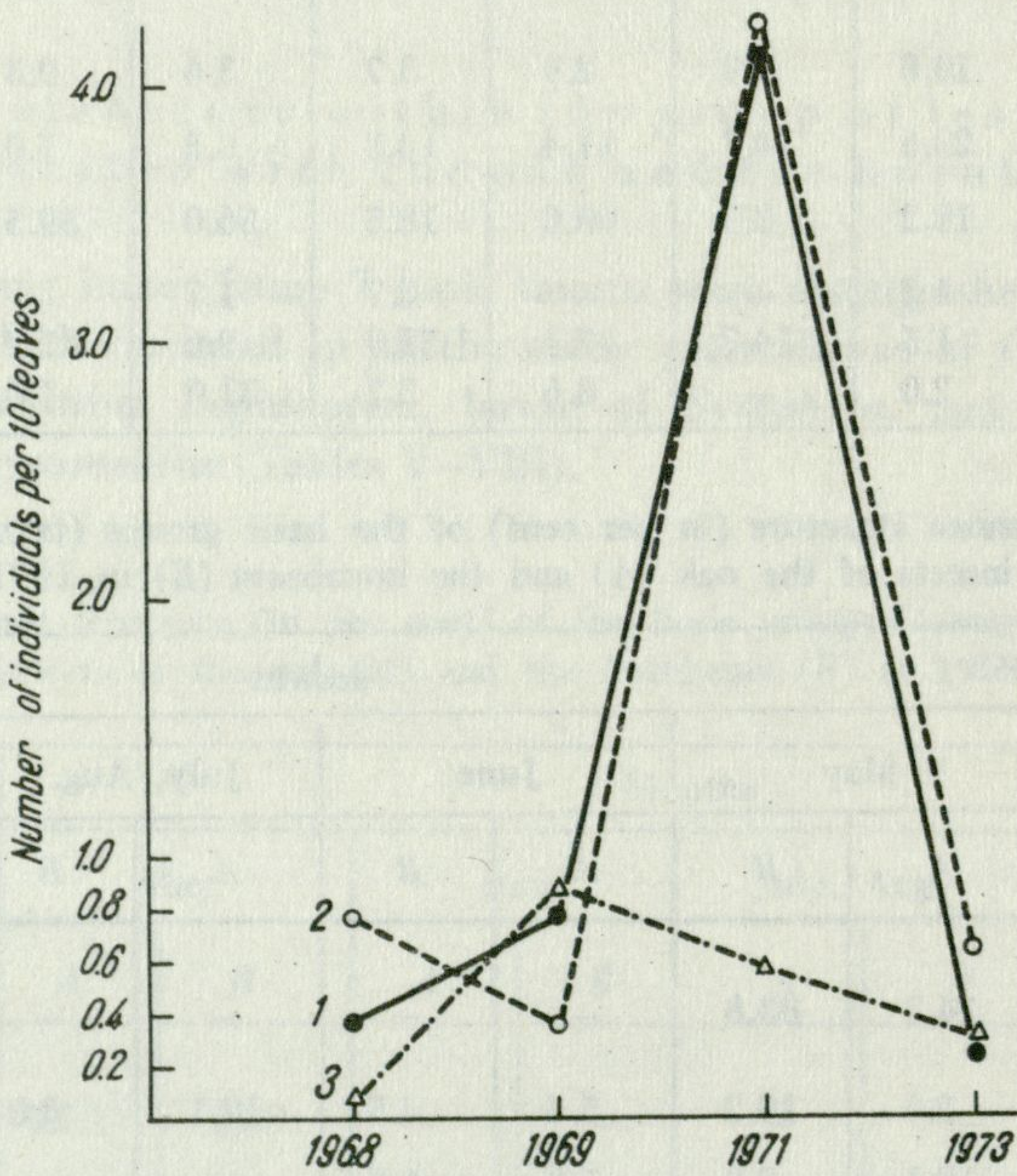

Fig. 4. Variations in numbers of *Operophthera brumata* (*1*), *Tortricidae* (*2*) and of the remaining *Lepidoptera* (*3*) on the oak during the period 1968–1973

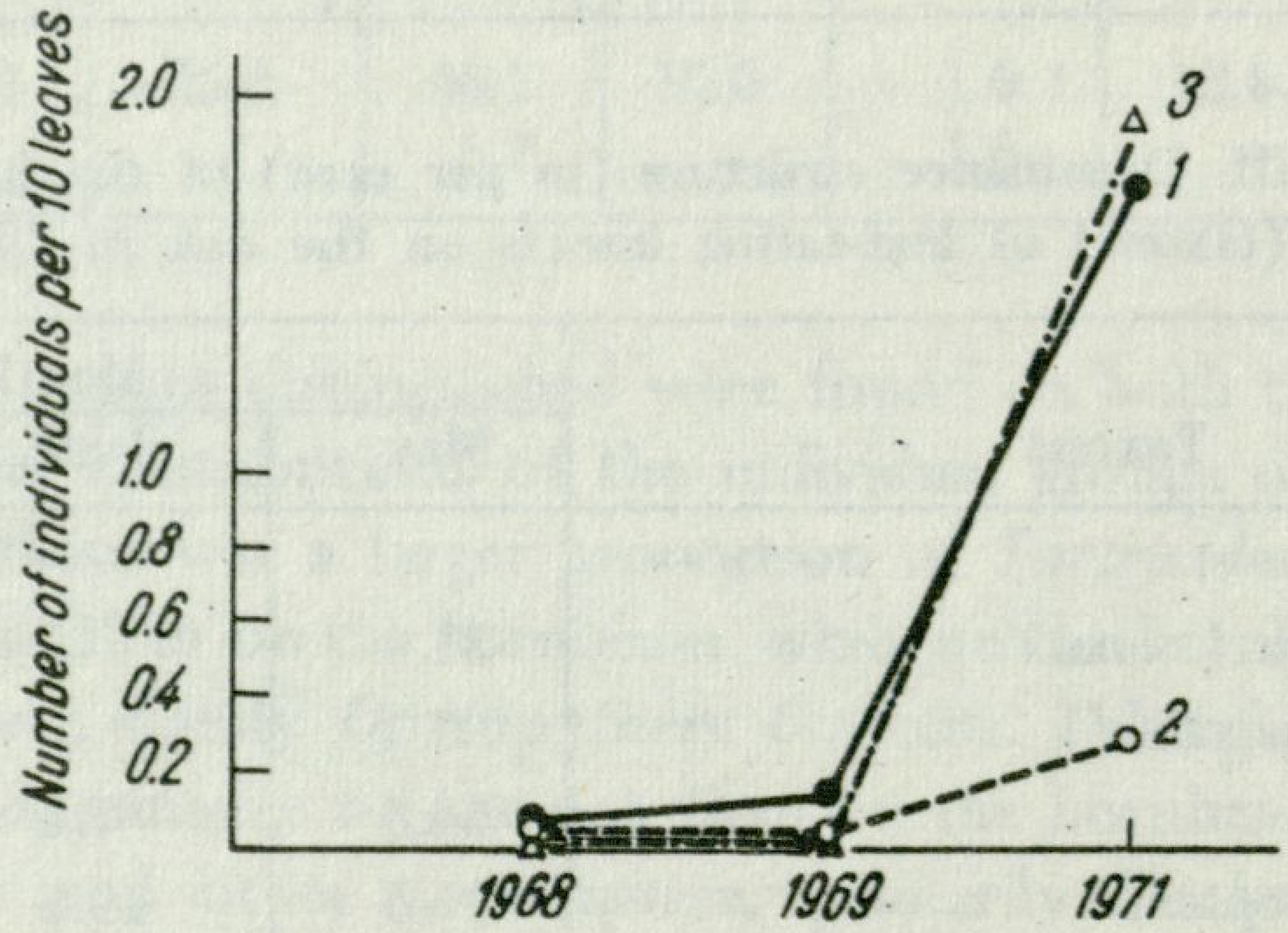

Fig. 5. Variations in numbers of *Operophthera brumata* (*1*), *Tortricidae* (*2*) and of the remaining *Lepidoptera* (*3*) on the hornbeam during the period 1968–1971

Species belonging to the spring groups as a rule occur in larger numbers than those occurring during the summer and autumn (Figs. 2, 3). As they are at the same time large-bodied forms (mainly *Geometridae* and other *Lepidoptera*), the differences in biomass between the spring period and the summer-autumn period were much more marked than the differences in the levels of numbers.

The group of spring species – mainly *Geometridae* and *Tortricidae* – also played an important role in the outbreak that occurred in 1971.

The increase in numbers of the leaf-eating insects, observed between 1968 and 1971, applied to both these groups, as well as to the remainder of *Lepidoptera*. *O. brumata* and *Tortricidae* (Fig. 4) then attained maximum levels of numbers on the oak, and *O. brumata* and other *Lepidoptera* on the hornbeam (Fig. 5). This tendency of the different leaf-eating insect species to synchronize the growth in numbers has been pointed out by Varley and Gradwell (1963), but on the other hand Moeller and Lotz (1968) found higher levels of numbers of *O. brumata* at a site where at the same time *Tortricidae* did not occur in large numbers.

However, in the study area the main role in the outbreak that took place in 1971 was played by *O. brumata*. The contribution of this species increased from 25.1% on the oak and 29.9% on the hornbeam in 1968 (Table V) to 74.3 and 83.8%, respectively, in 1971 (Table VII). As the outbreak progressed, the percentage of *Tortricidae* fell, although in fact their numbers increased (Figs. 4, 5). This seeming contradiction resulted from the fact that the contribution of the particular group, relative to other groups, was calculated for the whole spring period, while the detailed analysis of the variations in numbers of the particular groups during the spring of 1971

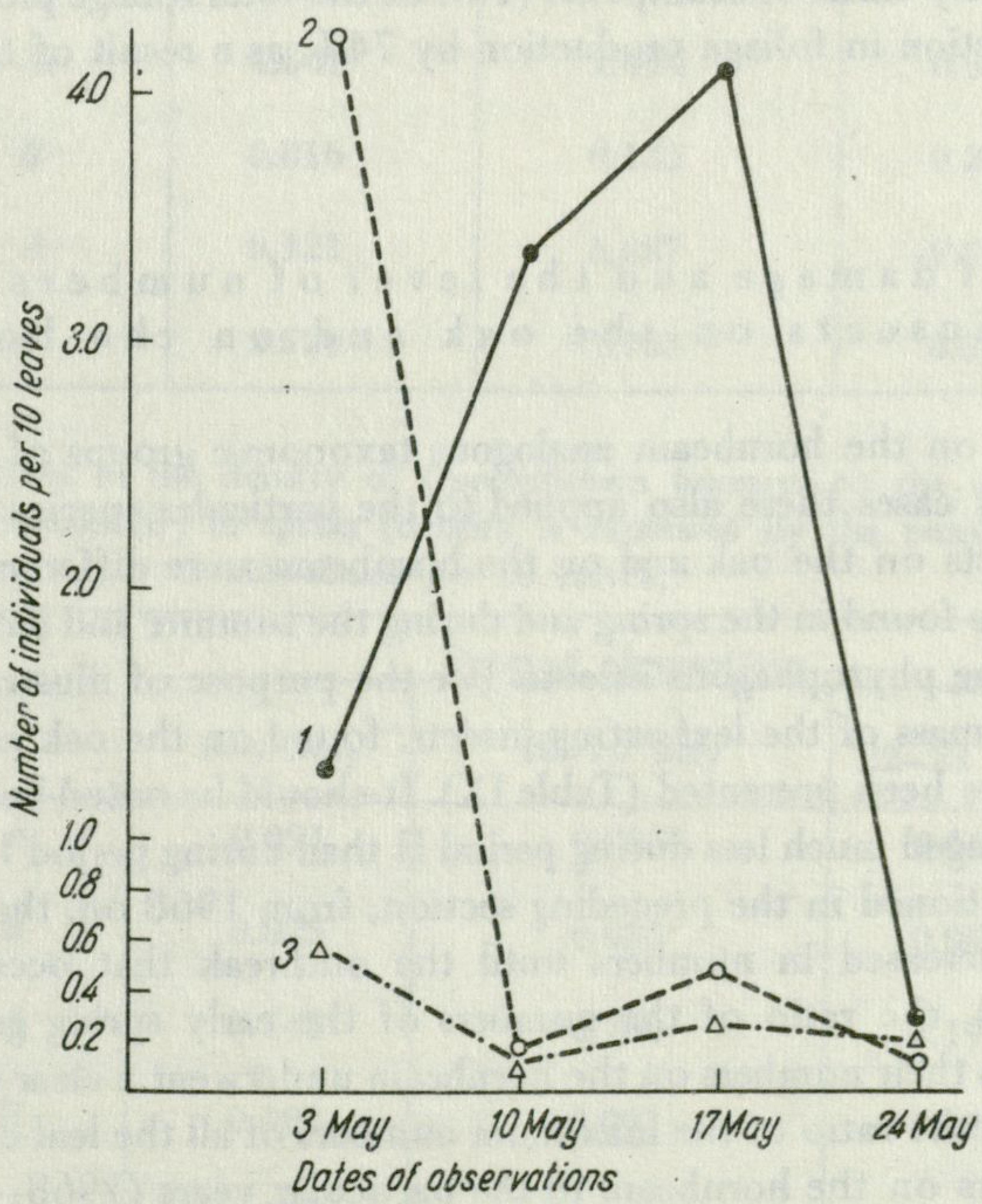

Fig. 6. Variations in numbers of *Operophthera brumata* (*1*), *Tortricidae* (*2*) and of the remaining *Lepidoptera* (*3*) on the oak in the spring of 1971

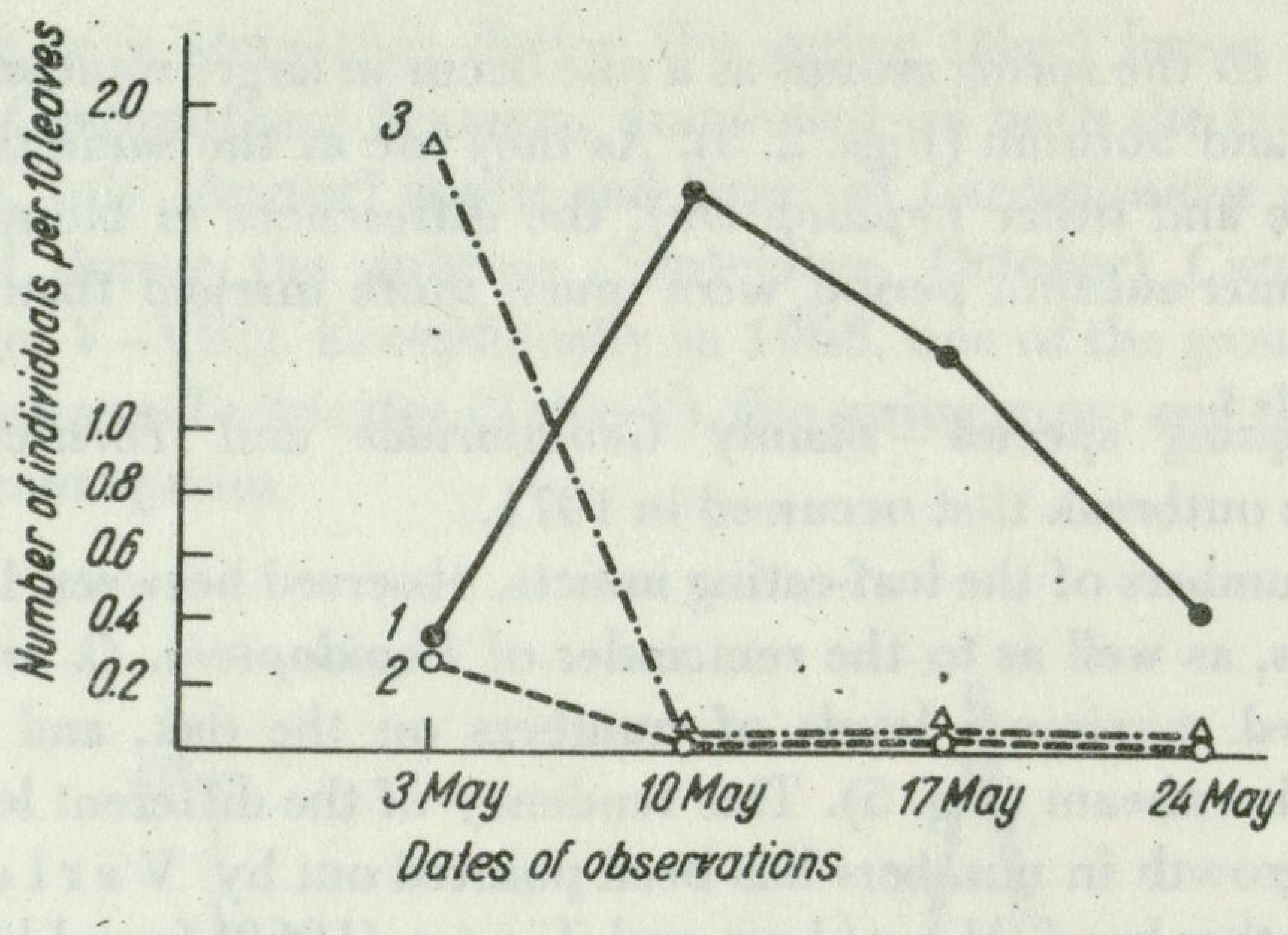

Fig. 7. Variations in numbers of *Operophthera brumata* (*1*), *Tortricidae* (*2*) and of the remaining *Lepidoptera* (*3*) on the hornbeam in the spring of 1971

(Figs. 6, 7) indicated that although the *Tortricidae* on the oak and other *Lepidoptera* on the hornbeam attained even higher densities than those of *O. brumata*, the numerical peaks of these groups preceded, phenologically, the maximum of numbers of *O. brumata* and they lasted a shorter time.

The particular groups of leaf-eating insects may be of variable importance, depending on the magnitude of the damage to the foliage, even if the amounts of food eaten by the individual species are similar. Z l o t i n and C h o d a š o v a (1974) have found, for instance, that in spite of their relatively small consumption (13% of the total foliage production), the leaf roller moths cause a reduction in foliage production by 74%, as a result of the damage to the apical meristem.

3.3. Advance of damage and the level of numbers of the leaf-eating insects on the oak and on the hornbeam

On the oak and on the hornbeam analogous taxonomic groups of leaf-eating insects were found, and in many cases these also applied to the particular species. However, the levels of density of the insects on the oak and on the hornbeam were different. On the oak, a higher level of numbers was found in the spring and during the summer and autumn. The same applied to the biomass of the phytophagous insects. For the purpose of illustration, the average levels of numbers and biomass of the leaf-eating insects, found on the oak and on the hornbeam in particular years, have been presented (Table IX). It should be noted here that both the density and the biomass changed much less during period II than during period I.

As has been mentioned in the preceding section, from 1968 on, the species present during period I (spring), increased in numbers until the outbreak that occurred in 1971. As the outbreak progressed, the ratio of the numbers of the early spring groups of phytophagous insects on the oak to their numbers on the hornbeam underwent a clear change in the successive years. The values of the ratio of the maximum numbers of all the leaf-eating insects on the oak to the total numbers on the hornbeam in the particular years (1968–1971) were as follows: 8.26, 7.67, 2.42. The corresponding ratio of the biomass was: 6.64, 5.79, 4.93 (here the indices of numbers and biomass as per 10 g dry leaf weight were used).

Table IX. Average numbers and biomass (in mg) of leaf-eating insects on the oak (*A*) and the hornbeam (*B*) in periods I and II (numbers and biomass are expressed by the number of individuals and by mg per 10 g of leaves)

Year		Period I		Period II	
		numbers	biomass	numbers	biomass
1968	*A*	10.025	151.741	1.281	8.195
	B	2.985	50.704	0.675	6.295
1969	*A*	18.637	133.923	1.669	8.588
	B	3.285	42.479	0.936	8.254
1971	*A*	146.244	1,054.354	1.199	14.065
	B	61.692	477.193	1.452	12.144

Table X. Variations in the density of leaf-eating insects on the oak (*A*) and the hornbeam (*B*) during spring period (density is expressed by the number of individuals per 10 leaves)

Year		Dates of observations		
		3–4 May	10–16 May	22–24 May
1968	*A*	1.305	0.755	0.359
	B	0.101	0.112	0.158
1969	*A*	1.541	1.494	0.641
	B	0.016	0.135	0.201
1971	*A*	6.121	3.687	0.594
	B	2.529	1.763	0.505

Table XI. Variations in the density of *Operophthera brumata* on the oak (*A*) and the hornbeam (*B*) in spring (density is expressed by the number of individuals per 10 leaves)

Year		Dates of observations		
		3–4 May	10–16 May	22–24 May
1968	*A*	0.391	0.085	0.029
	B	0.025	0.035	0.051
1969	*A*	0.141	0.780	0.199
	B	0.000	0.091	0.128
1971	*A*	1.280	3.352	0.276
	B	0.330	1.706	0.435

As indicated by the above figures, corresponding to the lowest densities of the phytophagous insects in the particular years were the greatest density differences between the oak and the hornbeam; with the growth in the overall level of numbers these differences decreased, being the lowest in the year of the outbreak.

Similar relationships of numbers on the oak and on the hornbeam were recorded for *O. brumata*, a species which, as has been shown in the preceding section, played the main role in the outbreak that took place. The values of the ratio of the numbers of *O. brumata* on the oak to its numbers on the hornbeam in the years 1968, 1969 and 1971 were: 7.67, 6.09, 2.40, respectively.

The leaf-eating insects on the oak and on the hornbeam not only differed in density, but their growth in numbers on each of these tree species was different as well (Table X). In the years of low density (1968, 1969) the highest level of numbers on the hornbeam occurred much later than on the oak; in the outbreak year – simultaneously.

The same regularity of the course of seasonal variations in numbers on the oak and on the hornbeam in the particular years concerned also *O. brumata* (Table XI).

At least with regard to *O. brumata* we may say that it is a relatively polyphagous species. Although it can feed on almost 100 plant species, in the environment studied it only uses several species,showing a distinct food preference. In the light of the data presented in this section and in the preceding one, it is possible to state that in the given habitat the preferred species is the oak. The growth of *O. brumata* on the hornbeam is considerably retarded (unpublished data of L. Andrzejewska and G. R. Gradwell, and the authors' own data). Hence it may be concluded that the parallel course of the seasonal variations of numbers on the oak and on the hornbeam in 1971, as well as the much equalized level of numbers, as compared with the preceding years, may at least in part have been caused by a migration of larvae from the oak, on which complete defoliation had taken place earlier, to the surrounding hornbeam trees.

By analogy it may be presumed that the above statements apply to the remainder of the species of *Lepidoptera*.

3.4. Oak and hornbeam foliage consumption by leaf-eating insects

The quantity consumed by the leaf-eating insects was calculated from the data on the mean level of their biomass (B) per 1 m^2 in the period between two measurements at point of time i:

$$\bar{B} = \frac{1}{2} \sum_{i=1}^{2} Bi \qquad (1)$$

The mean biomass values thus obtained were multiplied by the coefficient of daily food ingestion – 0.75 $W^{1.0}$. The 0.75 constant was adopted according to Schwerdtfeger (1957) (after W. Kaczmarek 1967), and Reichle and Crossley (1967). The proportion between the amount of food ingested and the biomass of the individuals $W^{1.0}$ was adopted according to Gere (1957) (after W. Kaczmarek 1967). The values thus obtained of the daily rations of food ingested by the leaf-eating insects expressed in mg of the wet plant weight were multiplied by the number of days between the consecutive measurements.

In order to compare the value of consumption on particular tree species with the leaf-fall, the consumption was ultimately expressed im mg of dry leaf weight. For this purpose, taking into account the content of water in the leaves of the individual species, the value of consumption in mg of wet weight was multiplied by the coefficient 0.50 in the case of the oak phytophagous insects, and 0.36 – in the case of those of the hornbeam.

In the pre-outbreak period of both years (1968 and 1969) the annual consumption of the leaf-eating insects on the oak and on the hornbeam did not differ considerably (Table XII). In the outbreak period (1971) it attained a 3.3 times higher value than in 1968 on the oak, and 3.2 times higher on the hornbeam. If only period I (May-beginning of June) was taken into account, the values of consumption in the outbreak year appeared to be higher 4.0 and 4.3 times, respectively.

Table XII. Foliage consumption by leaft-eating insects of the oak (*A*) and the hornbeam (*B*) in mg dry leaf weight per 1 m^2 (in brackets – consumption in the particular periods in per cent of the consumption for the whole growing season)

Year		Consumption in mg dry leaf weight per 1 m^2				
		for the whole growing season	in period I (3 May–6 June)		in period II (7 June–9 Oct.)	
1968	*A*	11,307.3	84,418.8	(74.7)	2,865.5	(25.3)
	B	6,662.9	4,334.7	(65.1)	2,328.2	(34.9)
1969	*A*	13,566.3	9,877.7	(72.8)	3,688.6	(27.2)
	B	5,830.3	3,044.5	(52.2)	2,785.9	(47.8)
1971	*A*	37,321.3	34,170.1	(91.6)	3,151.2	(8.4)
	B	21,398.0	18,528.1	(86.6)	2,869.8	(13.4)
1973	*A*	17,288.6	7,583.8	(43.9)	9,704.8	(56.1)
	B	–	–	–	–	–

Table XIII. Consumption of the oak and the hornbeam foliage by *Operophthera brumata* and its proportion in the consumption of all leaf-eating insects together (in per cent)

Year	Oak foliage consumption		Hornbeam foliage consumption	
	in mg dry weight per 1 m^2	in per cent	in mg dry weight per 1 m^2	in per cent
1968	1,204.5	10.7	1,190.9	17.9
1969	6,585.0	48.5	2,029.5	34.8
1971	27,765.6	74.4	16,145.3	75.5
1973	4,263.9	24.7	–	–

The proportion of the phytophagous insect consumption during period I, relative to the annual consumption, increased from 74.7 in 1968 to 91.6% in 1971 on the oak, and from 65.1 to 86.6%, respectively, on the hornbeam. The percentages of consumption during period II decreased accordingly, although the real values of consumption by the phytophagous insects in this period remained for three years at a relatively constant level, with a tendency to grow in the case of the hornbeam leaf-eaters (Table XII). In 1973, following the decline of the outbreak, the value of the spring consumption of the oak leaf-eaters remained at a level similar to that of the pre-outbreak period, whereas the summer consumption was much higher. Unfortunately, in 1973 no material was collected from the hornbeam.

On both the oak and the hornbeam with the progress of the outbreak the proportion of *O. brumata* consumption, relative to the annual consumption, increased steadily. The share of this species in the annual consumption of oak foliage increased from 10.7 in 1968 to 74.4% in 1971, and from 17.9 to 75.5%, respectively, in the consumption of hornbeam foliage (Table XIII). As can be seen from the above data, as regards the quantity of foliage eaten, *O. brumata* played the main role in the outbreak, although other groups – *Tortricidae* on the oak, and other *Lepidoptera* on the hornbeam attained even higher density levels (Figs. 4, 5). This was determined by both the relatively high biomass of *O. brumata* and the time of feeding on the foliage (Figs. 6, 7).

3.5. Effect of leaf-eating insect consumption on the production of oak and hornbeam foliage

The total annual production of oak and hornbeam foliage at the study site represented a sum total of the foliage fall, recorded simultaneously with the present research, and of the consumption of the leaf-eating insects (Table XIV).

Table XIV. Leaf fall (*LF*), foliage consumption by leaf-eating insects (*C*) and the total foliage production (*P* = *LF* + *C*) of the oak (*A*) and the hornbeam (*B*), and the percentage of total leaf production consumed by insects

Year		Leaf fall in mg dry weight per 1 m^2 (*LF*)	Consumption in mg dry leaf weight per 1 m^2 (*C*)	Total foliage production in mg dry weight per 1 m^2 (*P*)	Percentage of production consumed
1968	*A*	86,030	11,307	97,337	11.6
	B	93,300	6,663	99,963	6.7
1969	*A*	84,820	13,566	98,386	13.8
	B	92,000	5,830	97,830	6.0
1971	*A*	64,320	37,321	101,641	36.7
	B	69,760	21,398	91,158	23.5
1973	*A*	86,430	17,289	103,719	16.7

In the pre-outbreak period, the quantity eaten by the insects represented 11.6 up to 13.8% of the annual production of oak foliage, and 6.0 to 6.7% of the annual production of hornbeam foliage. In the outbreak year, insect consumption attained a level of 36.7% of the annual production of oak foliage, and 23.5% of the annual production of hornbeam foliage. In the post-outbreak period, the quantity eaten by the leaf-eating insects amounted to 16.7% of the annual production of oak foliage.

Noteworthy was the comparison of the variations in the quantity of the leaf fall of the particular species with the variations in the total production. In the outbreak year, most of the oak trees and a large percentage of the hornbeam trees became completely defoliated. Therefore, in 1971, the leaf fall consisted mainly of foliage regenerated from the dormant buds. The quantity of the fall was much smaller than that recorded for the years preceding the outbreak, in the case of both the oak trees and the hornbeam trees, and smaller also than the oak-foliage fall in the year following the outbreak year. This allows the conclusion to be made that the production of the regenerated foliage was much below the level it would have attained if the outbreak had not occurred. If the maximum quantity of leaf fall for the period 1968–1973 is taken as 100%, then the difference between the maximum value and the minimum value (for the outbreak year) amounts to 25.6% for the oak foliage fall, and 25.2% for that of the hornbeam.

On the other hand – the values of total foliage production (consumption + fall) of both the oak and hornbeam were maintained at an almost unchanged level from 1968 to 1973 (Table XIV). In this case the difference between the maximum and the minimum values of total foliage production was as small as 5.2% in the case of the oak, and 8.7% in the case of the hornbeam.

Table XV. Leaf fall (*LF*), foliage consumption by leaf-eating insects (*C*) and the total production ($P = LF + C$) of the oak and the hornbeam foliage jointly in the particular years, and the percentage of total leaf production consumed by insects

Year	Leaf fall in mg dry weight per 1 m^2 (*LF*)	Consumption in mg dry leaf weight per 1 m^2 (*C*)	Total production of oak and hornbeam foliage in mg dry weight per 1 m^2 (*P*)	Percentage of production consumed
1968	179,330	17,970	197,300	9.1
1969	176,820	19,396	196,216	9.9
1971	134,080	58,719	192,799	30.5

If both the leaf fall and the total production of the oak and of the hornbeam are considered jointly (Table XV), the reduction in the aggregate quantity of the fall of both species, due to insect feeding, amounts to 25.2%, whereas the maximum difference between the aggregate values of total foliate production appears to be 2%.

The above data would indicate that the regenerative capability of the oak and of the hornbeam, offsetting the losses sustained by the photosynthetic system due to the feeding of the phytophagous insects, are limited, being within the range of the foliage production value expected under the given conditions. In other words, regeneration offsets consumption to the value of foliage production that would be attained if insect feeding did not exist. This conclusion is confirmed by the data reported by M o l č a ň o v (1971), who compared oak foliage fall in areas affected by the outbreak of *Ocneria dispar* L. with the quantity of fall in control areas, where no outbreak foci were found. In the case of stands of older age-classes the sum total of the fall and of the leaves consumed by the pests was equal to the value of the foliage fall in the control areas, and was higher only in the case of young stands (28–32 years).

According to the data reported by many authors, summarized by S e m e v s k i j (1971), the complete defoliation of the oak trees, which took place due to an outbreak of *Tortricidae* and *Operophthera brumata* in 1971, might have caused losses in wood increment of the order of 50%. However, this complete defoliation did not noticeably affect the value of foliage production in the two years following the outbreak of the pests.

4. SUMMARY

Within the frame of team researches into the economy of the foliage in various forest ecosystems the quantity was estimated of the foliage consumed by the leaf-eating insect fauna of the tree crowns. The investigations were carried out in the "Grabowy" reserve in the north-eastern part of the Kampinos National Park, in the years 1968–1973. The study area represented a patch of mixed forest (*Pino-Quercetum*), about 5 ha in area, surrounded by a moist alder wood (*Carici elongatae-Alnetum*). The research covered the dynamics of numbers and biomass of the insect fauna of the crowns of the dominant tree species – the oak, and the hornbeam – during a 4-years' period, estimation of the foliage consumption by this insect fauna in the particular years, and its effect on the production of foliage.

The method used was based on the comparison of the number and biomass of the insects with the number and biomass of the leaves on which they lived. The picture of the dynamics of numbers and biomass of the insects in the tree crowns was obtained by collecting foliage samples by means of a special catcher sack (Fig. 1). By recording the quantities of leaf fall at the end of the growing season, it was possible to calculate the number and biomass of the insects in the samples and represent these quantities in a projection per 1 m^2 of the forest floor. In Table II the number of samples collected each year and the average number of leaves per sample are presented. The total number of insects collected in 774 samples amounted to 9,437 individuals.

On the basis of the data gathered the following conclusions have been drawn:

1. In the period 1968–1973 there occurred three clearly different stages in the dynamics of numbers of the oak and hornbeam leaf-eating insects: the pre-outbreak stage (1968, 1969), the outbreak stage (1971) and the post-outbreak stage (1973) (Table III). The maximum levels of the numbers and of biomass of the phytophagous insects in the outbreak year were higher than the numbers and biomass in the years preceding the outbreak, 4.7 and 7.2 times in the case of the oak, and 16.0 and 9.7 times, respectively, in the case of the hornbeam. When considered in relation to the amount of the food available (insect numbers and biomass related to leaf biomass), the increase in numbers and biomass of the insects appeared to be higher: 14.8 and 13.9 times on the oak, and 30.7 and 16.3 times on the hornbeam (Table IV).

2. On both the oak and hornbeam maximum densities of leaf-eating insects during the growing season occurred in the spring (Figs. 2, 3); in the summer-autumn period much lower numbers were observed than in the spring – on the hornbeam 1.15 to 1.73 times, prior to the outbreak, and 32.84 times, during the outbreak. On the oak – 1.96 up to 4.48 times, respectively, prior to the outbreak, and 28.6 times, in the oubreak year.

3. Similar relationships were recorded for the biomass: the maximum values of the biomass in the spring each year were greater than the maximum biomass values in the summer-autumn period: 3.06, 4.18 and 28.9 times on the hornbeam, and 8.11, 7.53 and 39.10 times on the oak.

4. During the period 1968–1971, variations in numbers occurred in the spring; the outbreak did not appreciably affect the level of numbers of the phytophagous insects in the summer-autumn period.

5. In the spring period the dominant groups on the oak consisted of larvae of the families *Geometridae* and *Tortricidae*, whereas those on the hornbeam included *Geometridae* and larvae of other *Lepidoptera*. During the summer and autumn, dominating on the oak trees were adults and larvae of *Chrysomelidae*, larvae of *Tortricidae* and of other *Lepidoptera*, and on the hornbeam – mainly *Curculionidae* (Tables V–VIII). In the outbreak year, the dominating group on the oak consisted of larvae of *O. brumata* and of *Tortricidae*

(Fig. 4), and those on the hornbeam – of *O. brumata* and larvae of other *Lepidoptera* (Fig. 5). There were the groups of the spring species that played the main role in the outbreak that occurred. The greatest importance in the outbreak must be attributed to *O. brumata:* as the outbreak progressed the contribution of this species increased from 25.1% on the oak, and 29.9% on the hornbeam in 1968 to 74.3 and 83.8%, respectively, in 1971 (Tables V, VII). Although during the outbreak the *Tortricidae* on the oak, and other *Lepidoptera* on the hornbeam, attained a higher level of density than *O. brumata*, the maximum numbers of these groups phenologically preceded the highest level of numbers of *O. brumata* and lasted a shorter time (Figs. 6, 7).

6. For the oak higher levels of numbers and biomass of the leaf-eating insects were recorded than for the hornbeam (Table IX). In the case of *O. brumata* this was due to a stronger food preference towards oak leaves; the same was probably true of the remaining groups of the leaf-eating insects. With the progress of the outbreak the differences between the level of numbers of the phytophagous insects on the oak and on the hornbeam became reduced several times (Tables X, XI). This was probably partly caused by the spreading of the outbreak focus already at the time of egg laying, and partly by the migration of larvae from the oak trees, which had become completely defoliated at an earlier time, on to the surrounding hornbeam trees.

7. During the pre-outbreak period, the contribution of the consumption of the phytophagous insects in the spring to the consumption for the whole growing season represented 74.7 on the oak and 65.1% on the hornbeam. In the outbreak year – 91.6 on the oak, and 86.6% on the hornbeam. In the outbreak year the spring consumption, as compared with 1968, was 4 times higher on the oak and 4.3 times higher on the hornbeam. In the summer-autumn period in all the study years the consumption was maintained at a similar level (Table XII).

8. With the progress of the outbreak the contribution of *O. brumata* to the annual consumption of foliage increased steadily: on the oak it increased from 10.7 to 74.4%, and on the hornbeam – from 17.9 to 75.5% (Table XIII).

9. In the pre-outbreak period the quantity consumed by the insects represented 11.6–13.8% of the total annual production of oak foliage, and 6.0–6.7% of the hornbeam foliage production. In the outbreak year – 36.7% of the annual foliage production of the oak, and 23.5% of that of the hornbeam (Table XIV).

10. The capabilities of the oak and of the hornbeam to regenerate the foliage and compensate for the losses sustained by the photosynthetic system, due to insect feeding, appeared to be limited, being within the range of foliage production expected under the given conditions. This was indicated by the relative stability of the total foliage production in the particular years, despite the considerable variations in the consumption of foliage by the phytophagous insects (Table XV).

5. POLISH SUMMARY (STRESZCZENIE)

W ramach zespołowych badań nad gospodarką listowiem w różnych ekosystemach leśnych dokonano oceny wielkości spasania listowia przez liściożerną entomofaunę koron drzew. Badania przeprowadzono w latach 1968–1973 w płn.-wsch. części Kampinoskiego Parku Narodowego, w rezerwacie „Grabowy". Teren badań stanowił płat boru mieszanego (*Pino-Quercetum*), o powierzchni około 5 ha, otoczony wilgotnym lasem olsowym (*Carici elongatae-Alnetum*). Badania objęły dynamikę liczebności i biomasy entomofauny koron dominujących gatunków drzew – dębu i grabu – w okresie czterech lat, ocenę konsumpcji listowia przez tę entomofaunę w poszczególnych latach oraz wpływ na produkcję listowia.

Podstawę metody stanowiło odniesienie liczby i biomasy owadów do liczby i biomasy liści, na których one występowały. Obraz dynamiki liczebności i biomasy owadów w koronach drzew uzyskano poprzez pobieranie próbek listowia za pomocą specjalnego czerpaka (fig. 1). Rejestracja wielkości opadu liści pod koniec sezonu umożliwiła przeliczanie liczby i biomasy owadów z próbek, na liczbę i biomasę owadów w projekcji na 1 m^2 dna lasu. Liczbę pobranych w poszczególnych latach próbek i przeciętne liczby liści w próbce zawiera tabela II. Łączna liczba zebranych w 774 próbkach owadów wynosi 9437 osobników.

Na podstawie zebranego materiału stwierdzono:

1. W okresie 1968–1973 wystąpiły trzy wyraźnie różne okresy w dynamice liczebności liściożernej entomofauny dębu i grabu: pregradacyjny (1968, 1969), gradacyjny (1971) i postgradacyjny (1973) (tab. III). Maksymalna liczebność i biomasa fitofagów w roku masowego pojawu przewyższały liczebność i biomasę w latach poprzedzających gradację 4,7 i 7,2 razy na dębie i odpowiednio 16,0 i 9,7 razy na grabie. W stosunku do zasobów pokarmowych (liczba i biomasa owadów odniesiona do masy liści) wzrost

liczebności i biomasy owadów jest odpowiednio wyższy: 14,8 i 13,9 razy na dębie oraz 30,7 i 16,3 razy na grabie (tab. IV).

2. Maksymalne liczebności liściożernej entomofauny w ciągu okresu wegetacji wystąpiły zarówno na dębie jak i na grabie wiosną (fig. 2, 3); w okresie letnio-jesiennym liczebność jest znacznie niższa niż wiosną – na grabie 1,15 do 1,73 razy przed gradacją i 32,84 razy podczas gradacji. Na dębie – odpowiednio 1,96 do 4,48 przed gradacją i 28,6 razy w roku gradacji.

3. Analogicznie kształtowały się relacje biomas: maksymalne wartości biomasy wiosną przewyższały w kolejnych latach maksymalne biomasy w okresie letnio-jesiennym 3,06, 4,18 i 28,9 razy na grabie i 8,11, 7,53 i 39,10 razy na dębie.

4. Zmiany liczebności w okresie 1968–1971 następowały w okresie wiosennym; masowy pojaw nie wpłynął w sposób widoczny na poziom liczebności fitofagów w okresie letnio-jesiennym.

5. W okresie wiosennym dominujące grupy na dębie stanowiły larwy *Geometridae* i *Tortricidae*, a na grabie *Geometridae* i larwy innych *Lepidoptera*. W okresie lata i jesieni na dębie dominowały imago i larwy *Chrysomelidae*, larwy *Tortricidae* i innych *Lepidoptera*, na grabie – głównie *Curculionidae* (tab. V–VIII). W roku masowego pojawu na dębie dominowały larwy *O. brumata* i larwy *Tortricidae* (fig. 4), na grabie – *O. brumata* i larwy innych *Lepidoptera* (fig. 5). Te właśnie grupy wiosennych gatunków odegrały główną rolę w zaistniałej gradacji. Największe znaczenie w masowym pojawie należy przypisać *O. brumata*: w miarę rozwoju gradacji udział liczebności tego gatunku rośnie z 25,1 na dębie i 29,9% na grabie w 1968 r. do odpowiednio: 74,3 i 83,8% w 1971 r. (tab. V, VII). Podczas gradacji *Tortricidae* na dębie a inne *Lepidoptera* na grabie osiągały wprawdzie nawet wyższe liczebności niż *O. brumata*, lecz szczyty liczebności tych grup wyprzedzają fenologicznie maksima liczebności *O. brumata* i są bardziej krótkotrwałe (fig. 6, 7).

6. Liczebności i biomasy liściożernych fitofagów na dębie są wyższe niż na grabie (tab. IX). W przypadku *O. brumata* jest to rezultatem większej preferencji pokarmowej w stosunku do liści dębu; to samo dotyczy prawdopodobnie pozostałych grup liściożernych owadów. W miarę rozwoju gradacji różnice pomiędzy liczebnością fitofagów na dębie i grabie ulegają jednak kilkakrotnemu zmniejszeniu (tab. X, XI). Częściowo jest to prawdopodobnie wynikiem rozprzestrzeniania ogniska gradacyjnego już w momencie składania jaj przez imagines, a częściowo wynikiem migracji larw z dębów, na których wcześniej nastąpił gołożer, na otaczające graby.

7. W okresie pregradacyjnym udział konsumpcji fitofagów w okresie wiosennym w konsumpcji za cały okres wegetacji wynosił 74,7 na dębie i 65,1% na grabie. W roku masowego pojawu – 91,6 na dębie i 86,6% na grabie. W roku gradacji konsumpcja w okresie wiosny, w porównaniu z 1968 r., była 4-krotnie wyższa na dębie i 4,3 razy wyższa na grabie. W okresie letnio-jesiennym konsumpcja we wszystkich latach badań utrzymywała się na podobnym poziomie (tab. XII).

8. W toku rozwoju gradacji coraz wyższy udział w całorocznej konsumpcji listowia przypada *O. brumata*: na dębie wzrasta on z 10,7 do 74,4%, na grabie – z 17,9 do 75,5% (tab. XIII).

9. W okresie pregradacyjnym żer owadów stanowił 11,6–13,8% całkowitej rocznej produkcji listowia dębu i 6,0–6,7% produkcji listowia grabu. W roku masowego pojawu – odpowiednio 36,7% rocznej produkcji listowia dębu i 23,5% – grabu (tab. XIV).

10. Możliwości regeneracji listowia dębu i grabu, kompensujące straty aparatu asymilacyjnego wskutek żeru owadów, są ograniczone i mieszczą się w zakresie oczekiwanej w danych warunkach wielkości produkcji listowia.. Wskazuje na to względna stabilność całkowitej produkcji listowia w poszczególnych latach, mimo znacznych wahań wielkości konsumpcji listowia przez fitofagi (tab. XV).

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