

CHANGES IN THE AREA AND WEIGHT  
OF LIGHT- AND SHADE-ADAPTED LEAVES  
AND SHOOTS OF QUERCUS PETRAEA  
AND QUERCUS CERRIS  
IN A HUNGARIAN OAK FOREST ECOSYSTEM\*

By

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The present paper deals with the growths of light- and shade-adapted shoots and leaves as expressed in area and dry weight of the two tree species, *Quercus petraea* and *Qu. cerris*, both study objects of the Síkfőkút Project. Biweekly or mensually collected data during the 1973 vegetation period were based on optical planimetric and dry weight measurements which permitted to trace the development of leaf and shoot production and the loss of material due to caterpillar feeding. Since the number of sampled leaves were known, the obtained data could be transposed per hectare.

Research in the field of ecosystems has always emphasized the importance of comprehensive investigation of green plant parts active in the photosynthetic process. Annual analyses of leaves and shoots most frequently focus on areal and weight measurements based on a suitable number of samples, allowing inferences on the development of leaf and shoot production respectively. But the same measurements point to the various growth parameters descriptive of the growth of individual green parts and to the interrelationship between the photosynthetic apparatus and production (BLACKMAN, 1919; BRIGGS—KIDD—WEST, 1920; WATSON, 1952; COOMBE, 1960; JARVIS, 1963; WILLIAMS, 1964; BLACKMAN, 1968; KVĚT—ONDOK—NEČAS—JARVIS, 1971 and others). In this study, the authors publish the results obtained during their research on leaves and shoots in the climate zonal *Quercetum petraeae-cerris* forest, near Eger, on the hilly land between the Great Hungarian Plain and the North Central Mountain Range of Hungary. The woodland was assigned to be the model of investigation (Síkfőkút Project), a part of the research programme "Man and Biosphere" (see JAKUCS, 1973; JAKUCS—HORVÁTH—KÁRÁSZ, 1975, B. PAPP, 1975, et al.). Measurements of area and weight were taken simultaneously on light- and shade-adapted shoots of the two dominant tree species. Investigations also included the temporal changes in site of whole leaves and of those damaged by caterpillars.

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## Sampling

The principles governing the sampling procedure was planned to have the data representing the entire forest of a rather homogeneous appearance. Three sample trees have been selected from each of the two species (each tree being 65 years old, of similar habit and of similar location within the environment, etc.). Sampling was made on ten occasions during the vegetation period. Ten shoots were gathered from the upperouter part of the crown (light-adapted shoots) and ten shoots from the lowerinner part of the crown (shade-adapted shoots). Since the majority of the single shoots had 5 to 9 leaves, each sampling yielded 120 shoots, i.e. 800 to 900 leaves.

## Material and method

The samples were grouped according to trees and light levels. The shoots were numbered, then the length of the shoot axis and the diameter at its middle measured, finally the number of leaves belonging to each shoot counted. The material was preserved in the pressed state.

### *Leaf area measurements*

According to international usage, the characterization of the assimilating capacity of the leaf is based not on the entire leaf surface; it suffices to present the measurements of only one side (the area) of the leaf. (CARLISLE—BROWN—WHITE, 1966). Leaf area was measured by electric optical planimeter. The device has been designed for this specific purpose (CZELLÁR and B. PAPP, 1975). Measurement precision is  $\pm 1\%$ .

### *Measurement of the damaged leaf area*

By the end of spring and the beginning of summer extensive caterpillar feeding could be observed in the forset (see Fig. 1). Calculation of the absent area was partly necessary to guarantee valid growth analysis and partly to estimate the area and weight of green assimilating organs already nonexistent.

Calculations were based on the correlations between leaf length and leaf area, leaf width and leaf area, length times width and area (see e.g. CARLISLE—BROWN—WHITE, 1966; KUBIČEK, 1971). In the case of both whole and damaged leaves area measurements were done parallel with leaf width and leaf length measurements as well. The whole leaf area of damaged leaves was computed by standard linear regression equations utilizing the measured data pairs. The obtained data were evaluated by the Computer Centre of the Kossuth Lajos



Fig. 1. Moderately damaged leaves on the shoots of *Quercus petraea* (photo: M. SZABÓ)

University, Debrecen. With respect to each category, equations expressing the closest relations (length times width—area) were applied to calculate the whole area of the damaged leaves. In some instances, were a parameter owing to caterpillar feeding was not available, we applied the equation pertinent to the measurable datum.\*

#### *Determination of the shoot area*

Based on the measured length and diameter, we calculated the cylindrical surface area by the formula  $2r\pi \cdot \text{length}$ .

#### *Weight measurements and the determination of the original weight of the damaged leaves*

The material was desiccated at 85°C for 48 hrs, then measured. In order to be able to reconstruct the original weight of the damaged leaves first the

\* It should be remarked that in order to obtain more concise values when computing regression equations close attention had been paid to the degree of development of the individual leaves on the various shoots, with reference to the light- and shade-adapted leaves of the two tree species. Accordingly, the leaves were grouped, counting from the shoot apex, into the groups 1—3, 4—6, 7—9, 10—18. Preliminary calculations gave significant differences between all groups.

weight of an area of 1 cm<sup>2</sup> was figured. With the aid of this calculation the weight of the sound leaf area for each leaf could be determined by the regression equation as well as the weight of the entire set of leaves produced on one shoot.

### Results and discussion

Seasonal changes in the average leaf area and weight of the reconstructed as well as of the damaged leaves for both oak species with respect to different light levels are given on Table 1 and illustrated in Fig. 2. Data displaying areal and weight variations of medium developed shoots (the mean of 30 shoots per

**Table 1**

*Seasonal changes in the mean value of whole reconstructed and damaged leaf areas and weights of Quercus petraea and Quercus cerris in 1973*

	Area in cm <sup>2</sup>				Weight in g			
	light		shade		light		shade	
	whole	caterpillar damaged	whole	caterpillar damaged	whole	caterpillar damaged	whole	caterpillar damaged
<i>Qu. p.</i>								
Apr. 18	2.25	—	3.13	—	0.0191	—	0.0202	—
May 4	17.93	16.07	30.50	27.90	0.0877	0.0863	0.1065	0.0964
10	24.72	17.83	27.26	22.41	0.1393	0.0975	0.1234	0.1020
24	26.05	21.62	35.61	32.08	0.1967	0.1630	0.1789	0.1581
June 13	22.70	15.42	29.99	23.67	0.2241	0.1515	0.2061	0.1806
27	20.33	15.06	30.71	26.27	0.2155	0.1573	0.2158	0.1834
July 27	21.24	16.49	28.84	22.26	0.2454	0.1914	0.2324	0.1775
Aug. 23	20.49	16.98	28.96	24.14	0.2207	0.1852	0.2004	0.1662
Sept. 26	19.47	15.43	28.86	22.66	0.2297	0.1838	0.2486	0.1890
Oct. 17	25.72	19.64	26.69	23.67	0.2578	0.1964	0.1743	0.1558
<i>Qu. c.</i>								
May 4	2.23	0.58	2.23	0.58	0.0172	0.0043	0.0172	0.0043
10	8.21	7.35	11.23	8.13	0.0586	0.0487	0.0520	0.0379
24	13.64	11.82	17.43	15.87	0.0925	0.0820	0.0931	0.0848
June 13	14.23	13.41	19.23	14.87	0.1298	0.1225	0.1211	0.0937
27	13.33	11.75	16.25	13.33	0.1523	0.1281	0.1042	0.0850
July 27	13.36	10.04	20.04	18.83	0.1684	0.1260	0.1338	0.1254
Aug. 23	13.50	11.37	18.04	14.47	0.1672	0.1411	0.1406	0.1136
Sept. 26	11.85	9.31	18.38	13.89	0.1482	0.1171	0.1417	0.1080
Oct. 17	16.16	13.02	18.89	14.62	0.1559	0.1253	0.1236	0.0974

tree) occurring during a given period are shown on Table 2 and illustrated in Fig. 3. The area of a single shoot represents the sum of the calculated area of the shoot axis and of the entire set of reconstructed leaves. The weight of the shoot equals the dry weight of the shoot axis and the dry weight of the sound leaf area.

*Development of the area*

The data unambiguously indicate that the area of the shade-adapted leaves is significantly larger than that of the light-adapted leaves. The primary cause is presumably also the inhibitive action of the light exerted on the leaves exposed to the more intense and direct radiation in the upper levels.

**Table 2**

*Seasonal changes in the mean value of reconstructed area and weight of light- and shade-adapted shoots of Quercus petraea and Quercus cerris and the percentual extent of caterpillar induced damage calculated for shoot leaves in 1973*

	Area in cm <sup>2</sup>		Weight in g		Extent of damage in %	
	light	shade	light	shade	light	shade
<i>Qu. petraea</i>						
Apr. 18	17.64	21.14	0.1754	0.1539	—	—
May 4	110.04	169.96	0.6341	0.6273	11.55	7.71
10	153.61	157.19	0.8994	0.8882	27.11	16.84
24	157.18	222.64	1.2426	1.1941	18.07	9.72
June 13	162.79	160.61	1.7061	1.2781	38.41	19.09
27	160.39	174.90	1.9133	1.2932	19.56	12.85
July 27	164.08	178.49	2.1063	1.5380	22.90	23.03
Aug. 23	145.22	170.05	1.7319	1.2811	17.71	11.07
Sept. 26	141.15	168.74	1.9160	1.4947	21.55	21.47
Oct. 17	157.80	150.45	2.1161	1.0472	21.98	12.37
<i>Qu. cerris</i>						
May 4	17.42	17.42	0.1431	0.1431	1.95	1.95
10	51.43	64.68	0.3708	0.3263	5.58	1.93
24	89.52	92.03	0.6093	0.5293	3.76	5.60
June 13	94.33	104.50	0.9257	0.7131	6.34	9.58
27	85.37	89.43	0.9317	0.6279	8.56	14.60
July 27	81.25	104.09	1.0969	0.7552	8.21	5.80
Aug. 23	98.66	91.09	1.3656	0.7712	12.82	11.53
Sept. 26	116.03	118.91	1.7574	1.1184	8.62	12.86
Oct. 17	79.31	104.76	0.8417	0.8238	6.69	8.72

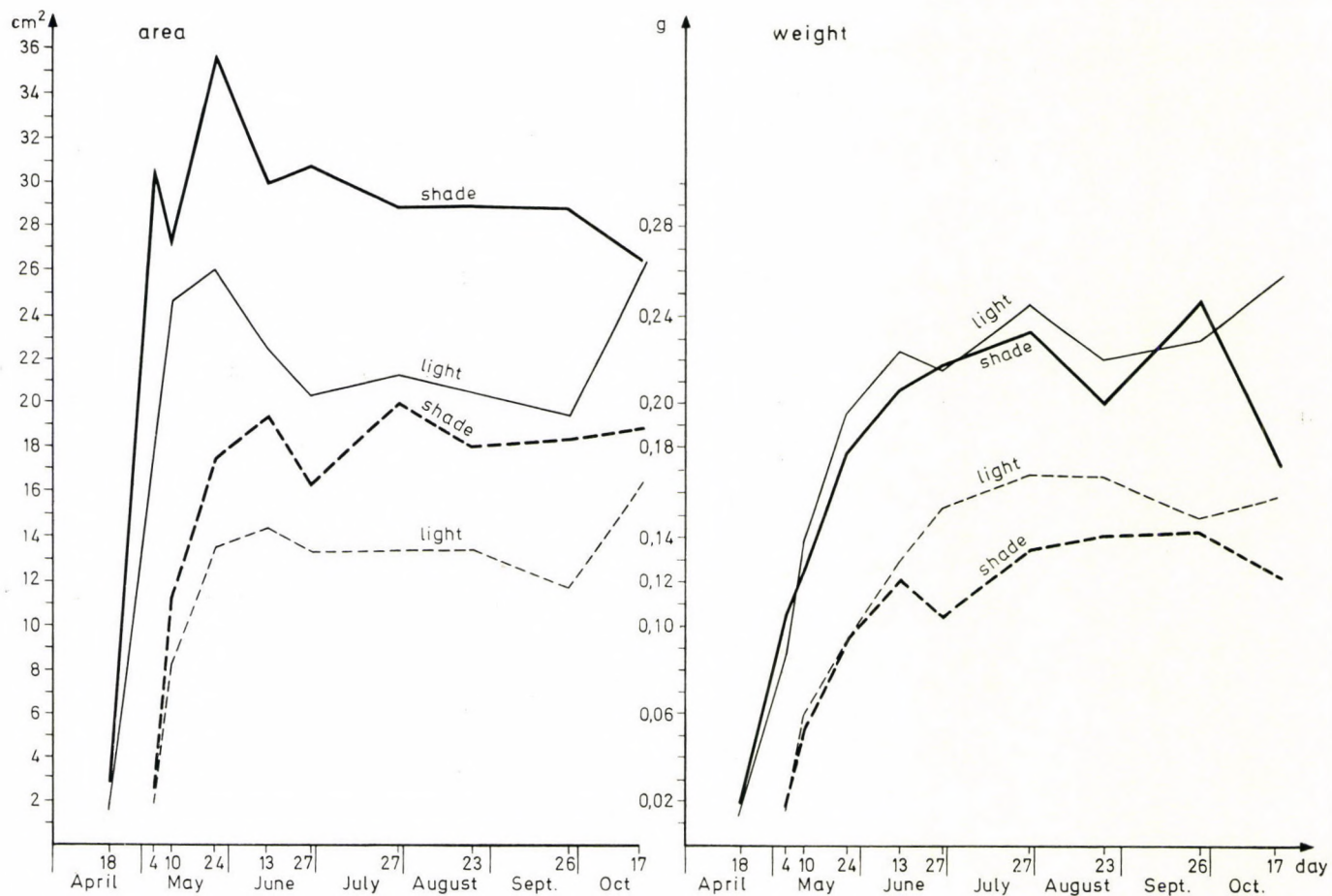


Fig. 2. Seasonal modification of reconstructed area and weight of light- and shade-adapted leaves of *Quercus petraea* (solid line) and *Quercus cerris* (dotted line)

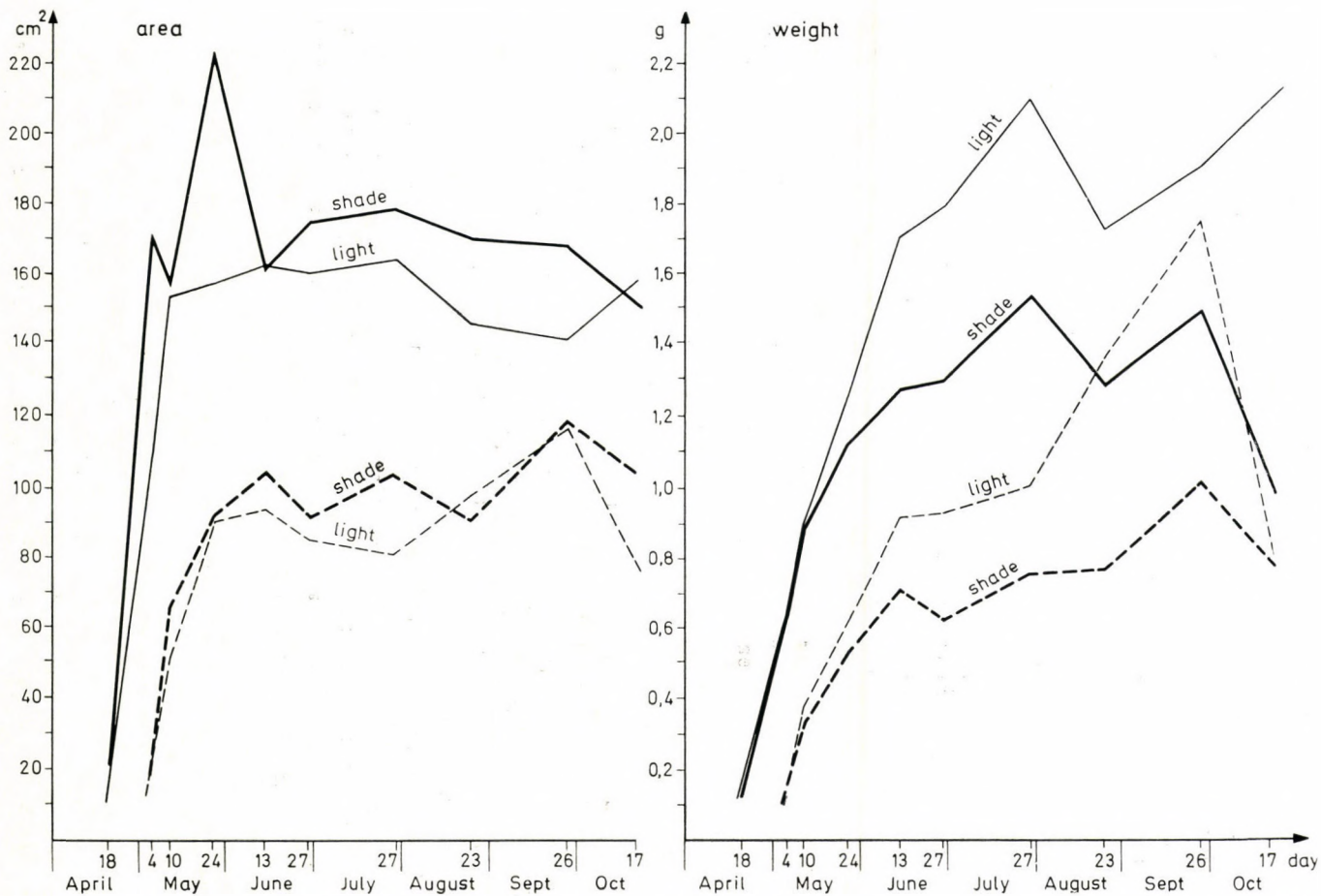


Fig. 3. Seasonal change of reconstructed area and weight of light- and shade-adapted shoots of *Quercus petraea* (solid line) and *Quercus cerris* (dotted line)

However, in the cited case one may also assume that not only radiation effects but the xerothermic character of the microenvironment also plays a role in the retarded development of leaf area.

Leaf growth of *Quercus petraea* is very rapid during the spring and by the end of May both the light- and shade-adapted leaves have almost reached full development. A later difference of size between the light- and shade-adapted leaves appears at the end of May when foliage is completely developed and its stratifications according to light intensity levels becomes more pronounced. Leaves which have reached their fully developed and maximum area by the end of May experience an abrupt decrease of average dimensions in June, and this state scarcely alters during the subsequent vegetation period. This regression is significant primarily in the case of shade-adapted leaves and could be observed only in the case of *Quercus petraea*. The reason obviously lies in the fact that the average area of the great number of fresh and young leaves, developing in May and June after the extensive caterpillar damage, is rather small.

From June till autumn the leaf area showed little variation in size; their areal growth had been essentially completed. Nevertheless, in the uppermost stratum a sudden increase of leaf area for both species could be noticed in October. To identify the principle underlying this phenomenon further research is necessary.

Leaf development in *Quercus cerris* started approximately two weeks later. Maximum areal values were reached only by the middle of June. In the case of shade-adapted leaves a regression in the areal growth process has set in at the end of June and the maximum was reached in July, a fact perhaps related to the second leafing following damages caused by caterpillars. The leaf area of *Qu. cerris* is considerably smaller than that of *Qu. petraea*, a characteristic of this species.

The shoot area has reached its maximum in the middle of May and June, respectively, for both tree species. Nearing the end of the vegetation period areal regression becomes noticeable. At summer's beginning, the areal loss of shade-adapted shoots associated with caterpillar damage was perhaps more extensive than in the case of leaves.

### *Changes in weight*

Changes in dry weight of the leaves and shoots in the course of time showed an entirely different picture than areal modifications. During the spring season gain in weight was slighter, more gradual. Generally the maximum in both light levels was reached by the representatives of the two different species by the end of July and the beginning of August. Deferment of leaf development had considerably less influence on weight regardless of the species.

After maximum weight had been reached, no significant change occurred. At the end of the vegetation period, in October, weight decrease has set in which can be explained by the translocational processes of the fall season. Decrease of weight was most significant in the case of the shade-adapted shoots, in contrast to even a slight growth of light-adapted leaves of *Quercus petraea* (where also an areal increase occurred).

The weight of the light-adapted leaves was always more considerable than that of the shade-adapted leaves, with the exception of the early spring period when the density and shading effect of the canopy is less prominent. The collected data reflect the pattern that despite their smaller area the accumulation of organic matter is more intense in the light-adapted leaves — although their area is smaller — than in the shade-adapted leaves (this can be especially expressed in the case of *Qu. cerris*). Thus photosynthetic activity decreases in the lower stratum of the crown (according to DYLLIS—KARPOV—TZELNIKER, 1966, it is occasionally merely one tenth of that occurring in the light level). There can be no doubt, however, that no complete and precise explanation can be given without regard to respiration and translocation “losses”. The greater average weight of light-adapted leaves can be related also with the more advanced development of the assimilating tissues, of the palisade parenchyme layer, and thus of their thickness. One may also assume that excess weight is due to inclusions, mainly of the presence of Ca-oxalate crystals. This, however, is contradicted by the analysis of the mineral content of light-adapted leaves which indicates that more Ca is always detectable in shade-adapted leaves (B. PAPP, ined.).

Seasonal changes in shoot weight show a tendency similar to that of leaves. Based on the total number of leaves, the reconstructed total leaf and shoot area, respectively, and their dry weights per hectare are summarized below. (The number of leaves has been supplied by B. PAPP, for September 1973; the authors have calculated areal and weight data based on the mean values obtained in the light and shade levels also for September).

		Number/hectare	m <sup>2</sup> /ha	kg/ha
<i>Quercus petraea</i>	leaf	27 897 000	67 427	6 673
	shoot	4 649 500	72 044	7 929
<i>Quercus cerris</i>	leaf	5 481 250	8 288	795
	shoot	783 000	9 198	1 126

### Extent and effect of caterpillar feeding

Based on whole leaf area and the reconstructed area of caterpillar-eaten leaves on the shoots 30 shoots per light levels we computed the percentage of damage for each sampling period and for both tree species (see Table 2).

The data point to the fact that especially in the case of *Qu. petraea* damages caused by caterpillars were considerable (Fig. 4). Furthermore, caterpillar damage reached its climax twice during the vegetation period in the forest ecosystem; the first climax at the beginning of May, the second in the middle of June. Damage induced in the spring was due chiefly to *Tortrix viridana* and to a lesser extent to *Hybernia defoliaria*. Maximum damage in June was caused by the caterpillar of *Lymantria dispar* (VARGA, personal communication).

The maximum is always a function of weather conditions as well. The caterpillars of *Tortrix viridana* hatch at the beginning of April, but damage on

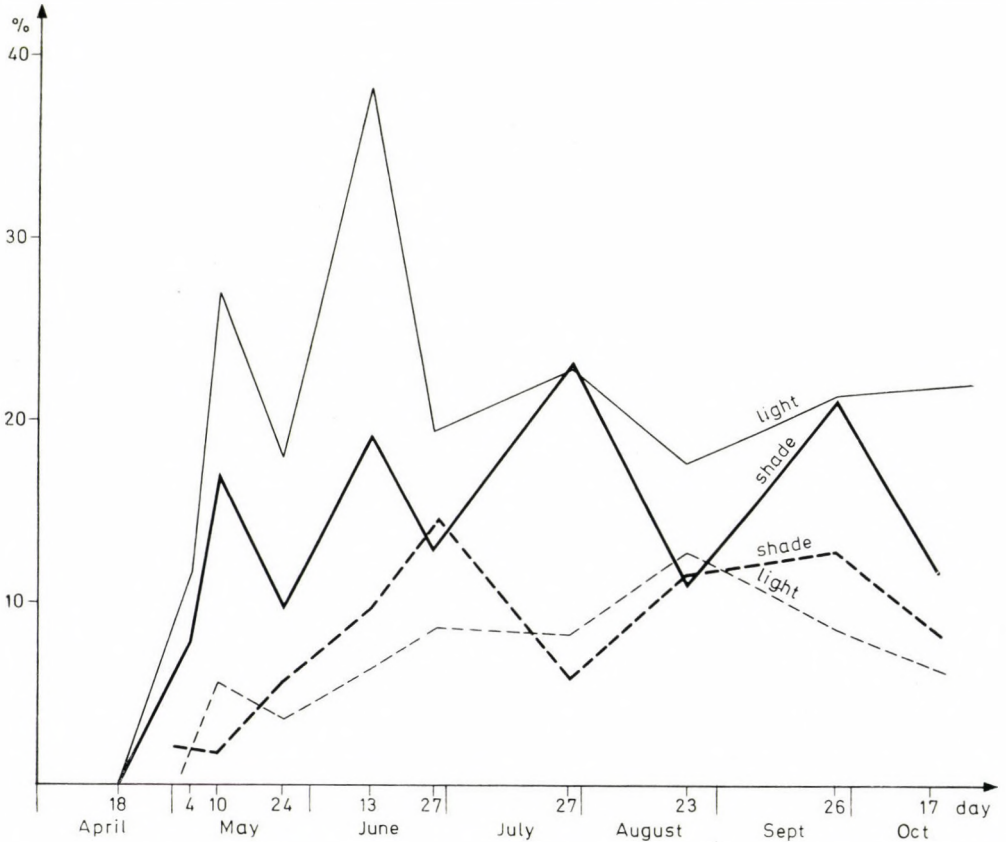


Fig. 4. Extent of caterpillar induced damage of the light- and shade-adapted leaves of *Quercus petraea* (solid line) and *Quercus cerris* (dotted line)

a large scale could be observed only at the beginning of May. This shift was due to the coolish but dry spring. Field surveys indicated that the light-adapted leaves and shoots suffered heavier damage than the shade-adapted leaves and shoots, respectively. Shade-adapted leaves and shoots exhibited a damage peak at the end of July, but the degree of damage, as compared with the first two maxima measured in the light level, was notably less. The most likely explanation is that young leaves developing during the second leafing period were more favoured by the caterpillars than the older, larger well-developed ones. Furthermore it may be connected also with the destruction wrought by the gradation of *Calymnia trapezina* around the end of July and the beginning of August.

If the damages, expressed in percentage, are compared for both oak species, it can be stated that *Quercus cerris* suffered considerably less than *Qu. petraea*. The main reason is probably that *Qu. cerris* starts to unfold its foliage about 2 weeks later, and this brief phenological difference offers a significant protective advantage for the Turkey oak against *Tortrix*. Hatched by this time, the caterpillars of this species were feeding on the young leaves of *Qu. petraea* and migrated to trees of another species (e.g. to *Qu. cerris*) only in want of food.

As a last remark, attention must be called to the fact that the authors have practically no data at hand on the damaging affect, and the extent of the damage which larvae exert on buds. For it is evident that the first enormous damage is caused in the buds by the minute caterpillars emerging from the eggs. Accordingly, the real loss of potential assimilating area is considerably greater than measurements have indicated. Bearing in mind that numerous leaves were completely devoured by the caterpillars (in some cases even the midrib was left in mutilated condition), it is justified to maintain that the real loss for one hectare is at least 10% greater than actually measured.

Calculating the loss of assimilating area and weight, respectively, for one hectare the measurement data are as follows:

	%	m <sup>2</sup> /hectare	kg/hectare
<i>Qu. petraea</i>	30.72	26 421	2 047
<i>Qu. cerris</i>	13.71	1 257	114

In cognizance of the reconstructed areal and weight data of the total leaf number, the above values were calculated on the basis of the respective damage percentages (the means of the light and shade level maxima!).

The given m<sup>2</sup>/ha and kg/ha values and the percentage of material loss (the extent of damage expressed in percentage) were probably 10% higher owing to the reasons mentioned above (i.e., 41 and 24%, respectively).

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