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Ecophysiological studies on photosynthesis and respiration of some plant species in meadow ecosystem

Part I

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Little is known on the intensity of photosynthesis and respiration of meadow plants. The course of these physiological processes is somewhat different from the courses in plants of other ecosystems e.g. forests. This is due to the relatively high intensity of light, different thermal conditions corresponding to an open territory and to the relatively high humidity of the meadow ecosystem.

The present work is a continuation of research on the photosynthetic production of plants growing in natural ecosystems. The aim of this work was the determination of:

1) the rate of the assimilates' consumption in respiration process,

2) the compensation and light saturation points in relation to light and thermal conditions,

3) the maximum photosynthetic production under optimum light and thermal conditions.

On the basis of these data and of microclimatic measurements performed in the meadow ecosystem in the Ojców National Park, it became possible to establish the dynamics of assimilates accumulation during the growing season of 1965.

MATERIAL AND METHODS

The material for investigations was collected in the experimental plots of the Ojców National Park. The experiments were carried out on three plants characteristic of the investigated ecosystem, viz. *Plantago lanceolata*, *Rumex acetosa* and *Dactylis glomerata*. Measurements of the intensities of photosynthesis and respiration were performed at the beginning of every month during the whole growing season. The collected leaves were placed in large Petri dishes on filter paper moistened with water and transported to the laboratory. Two hours before proceeding with the measurements, discs (4 mm in diameter) were cut out of the middle part of the leaf blade between the larger veins. In order to prevent their drying the discs were placed on the bottom of a weighing bottle on moistened filter paper (Starzecki 1961).

The sources of error connected with the use of leaf discs in physiological research were investigated and discussed by Wassink 1946, Bartoš Kubin, Šetlik 1960, Starzecki 1961, 1962, Kubala 1961, Nakoneczna 1962 and Czopek 1964, 1967a.

For determination of the photosynthesis and respiration rates, the microrespirometric method was adopted (Zurzycki 1955, Starzecki 1961). This method enables us to determine the intensity of photosynthesis and respiration in dependence on the light intensity, thermal conditions and adequate CO_2 concentration.

Measurements were performed during 20 min. at 5 min. intervals at 10, 15, 20 and 25°C and light intensities of 2 100, 10 400, 31 800 and 64 000 ergs/cm^{2}sec (about 460, 2 300, 7 000 and 14 000 lux respectively). The above mentioned light intensities refer to photosynthetically active radiation (PAR) and were measured in absolute units (ergs/cm^{2}sec) by means of a Kipp and Zonen thermopile and a Kipp galvanometer (type A—7, Delft, Holland). A special filter (RG-8) was used to measure infrared radiation. A projection lamp 250 W, 220 V was used as the light source. Infrared radiation was absorbed by a 5-cm liquid filter obtained by dissolving 140 g of ferrous ammonium sulphate in 2% sulphuric acid (Withrow and Price 1953). The temperatures were maintained at a constant level by means of a Hoepler's ultrathermostat (±0.2°C).

The concentration of carbon dioxide in the gas phase in the micro-chambers of the microrespirometer was about 0.5% (volmue percent) at 20°C when using Warburg's carbonate buffer No. 10. The details of the measurement technique were described in previous papers (Czopek 1964, 1967b).

The rates of photosynthesis and respiration were expressed either in microlitres (μl) of oxygen produced or consumed or in milligrams (mg) of hexose produced or consumed by 1 dcm^2 of leaves during 1 hour.

RESULTS

The course of photosynthesis and respiration during the growing season does not only depend on the conditions prevailing in the investigated ecosystem, but equally on the plant species. Because of specific differences the results of experiments will be presented separately for *Plantago lanceolata* and *Rumex acetosa* on the one hand and for the grass *Dactylis glomerata*, on the other.

Plantago lanceolata and *Rumex acetosa*

Microrespirometric measurements have established that the course of photosynthesis and respiration is dependent not only on light and thermal conditions but also on the growing season. The curves representing the course of photosynthesis in relation to light intensity are undeniably of Blackman's type; they show however, variations depending on the season. They are more pronounced at the beginning and the end of the growing season. In May the intensity of photosynthesis is much higher than in October (at the same temperature), although the light saturation point has a similar value (Figs. 1 and 2).

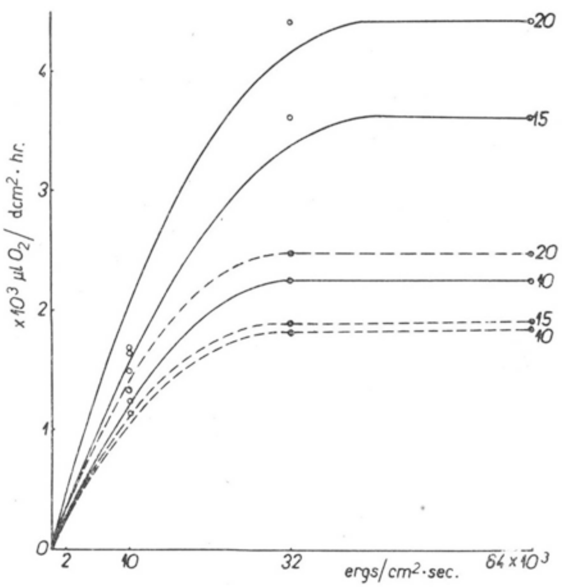

Fig. 1. Intensity of photosynthesis in leaves of *Plantago lanceolata* as a function of light intensity for various temperatures.

Abscissae — light intensity $\times 10^3$ ergs/cm² sec, ordinates — intensity of photosynthesis in $\mu l\ O_2/dcm^2$ hr. The figures on curves denote temperature. Solid line — true photosynthesis in May, broken line — true photosynthesis in November.

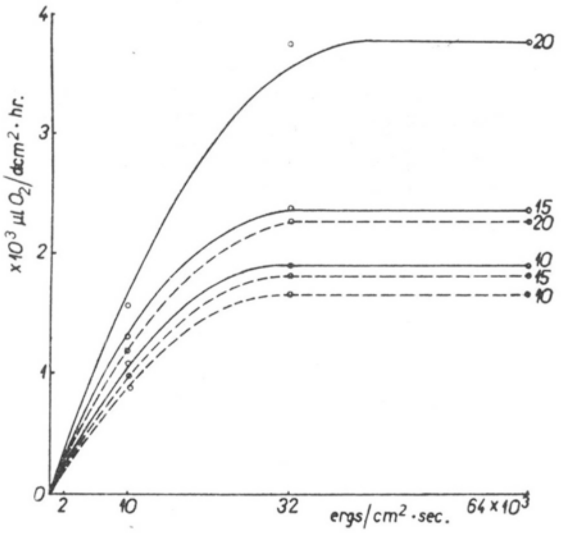

Fig. 2. Intensity of photosynthesis in leaves of *Rumex acetosa* as a function of light intensity for various temperatures. For explanations see Fig. 1.

The intensity of respiration attains the highest value at the beginning of the growing season; this is a consequence of the intensive growth of leaves in this period. A decrease in the respiratory rates is observed in June. In the following months this rate either remains at a steady level till the end of the growing season (*Rumex*) or is followed by an insignificant increase in September (*Plantago*) and a further fall. It appears from table 1 that the compensation points show some variations depending on the species and the developmental stage of the plant during the growing season. The light intensity required to compensate the respiratory process attains the highest values at the beginning of the season (May) viz. 7 500 ergs/cm^{2}sec for *Plantago* and 8 500 ergs/cm^{2}sec for *Rumex*. In the following months a decrease and a stabilization of the respiration rate occur especially for *Rumex*, followed by an insignificant increase (Table 1).

Table 1

Compensation (c.p.) and light saturation (s.p.) points in the meadow plants under investigation at 20°C in dependence on the growing season. The values are expressed in ergs/cm^2 sec (upper figures) and in lux (lower figures)

Plant species		Months						
		V	VI	VII	VIII	IX	X	XI
Plantago lanceolata	c.p.	7 500 1 630	5 000 1 090	4 700 1 020	2 000 440	3 600 780	2 000 440	4 000 870
	s.p.	32 000 7 000	32 000 7 000	40 000 8 700	30 000 6 500	28 000 6 100	32 000 7 000	27 000 5 900
Rumex acetosa	c.p.	8 500 1 850	8 500 1 850	4 300 940	2 000 440	2 000 440	2 200 480	4 100 890
	s.p.	32 000 7 000	30 000 6 500	42 000 9 100	32 000 7 000	27 000 5 900	30 000 6 500	28 000 6 100
Dactylis glomerata	c.p.	4 800 1 040	7 500 1 630	8 000 1 740	2 500 550	5 000 1 090	2 000 440	5 200 1 130
	s.p.	64 000 14 000	64 000 14 000	64 000 14 000	64 000 14 000	64 000 14 000	64 000 14 000	64 000 14 000

During the growing season the light intensity of the saturation point shows also fluctuations (with the exception of *Dactylis*). It attains a maximum value in July for *Plantago* and *Rumex*, about 40 000 — 42 000 ergs/cm^{2}sec, and afterwards decreases to 27 000 — 28 000 ergs/cm^{2}sec until the end of the growing season. For *Dactylis* the light saturation point remains at a constant level during this period (Table 1).

The evaluation of the photosynthetic production during the growing season was based on the apparent photosynthesis (Figs. 3 and 4). It appears that at its beginning (May) the apparent photosynthesis attains the highest rate. In June there is a rapid fall of these rates which, however is followed by a slight increase. Since September (*Plantago*) or October (*Rumex*) the photosynthetic rate begins to decline visibly.

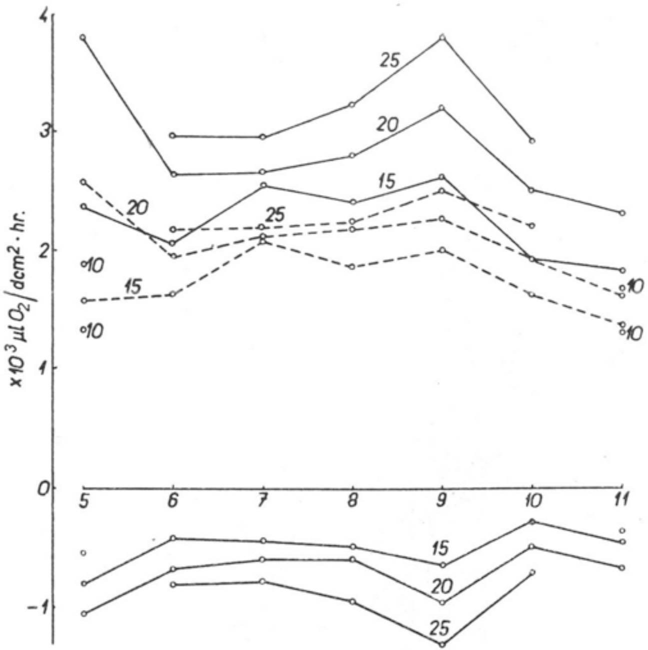

Fig. 3

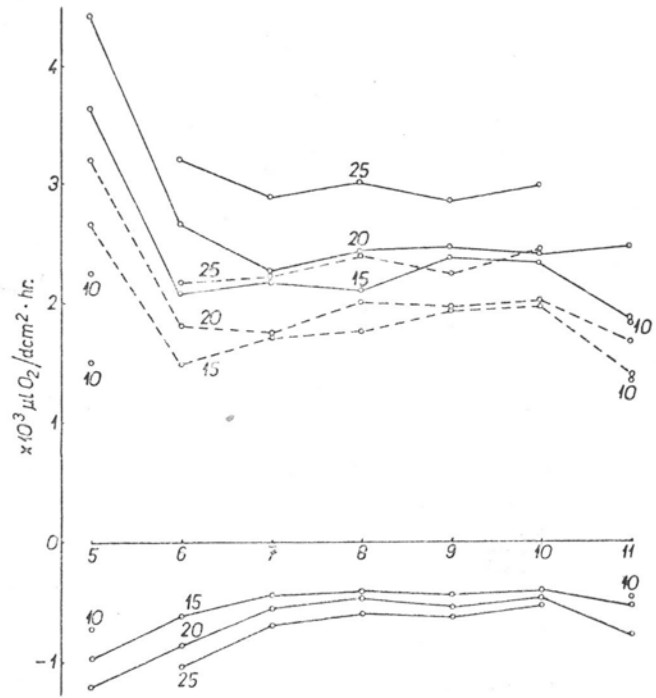

Fig. 4

Fig. 3. Course of photosynthesis and respiration intensity in leaves of *Plantago lanceolata* during the growing season for various temperatures at the light saturation point.

Abscissae – months, ordinates – intensity of photosynthesis and respiration in $\mu l\ O_2/dcm^2$ hr. The figures on curves denote temperature. True photosynthesis – solid line, apparent photosynthesis – broken line.

Fig. 4. Course of photosynthesis and respiration intensity in leaves of *Rumex acetosa* during the growing season for various temperatures at the light saturation point. For explanation see Fig. 3.

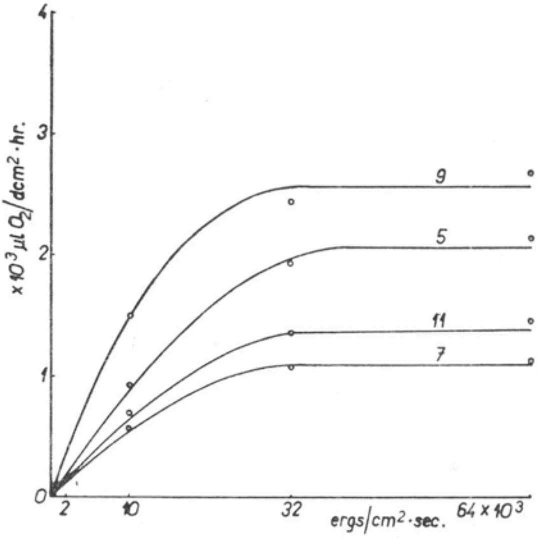

Fig. 5. Intensity of photosynthesis in leaves of *Dactylis glomerata* as a function of light intensity for various months at 20°C.

Abscissae — light intensity $\times 10^3$ ergs/cm² sec, ordinates — intensity of true photosynthesis in $\mu l\ O_2$/dcm² hr. The figures on curves denote months.

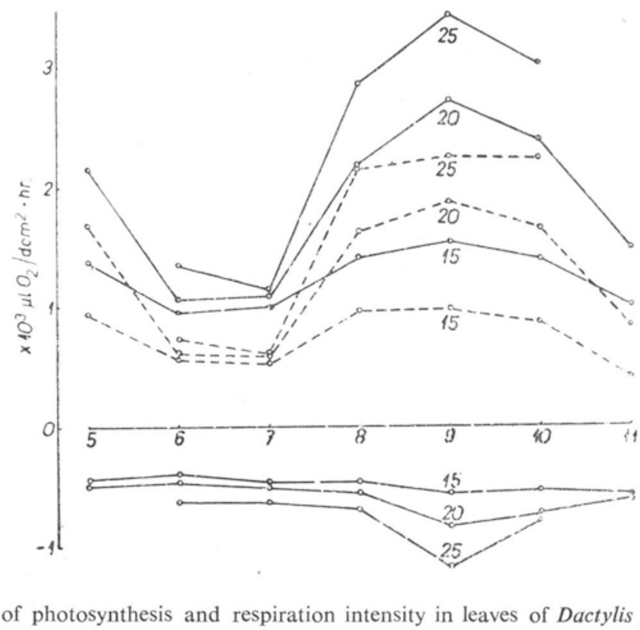

Fig. 6. Course of photosynthesis and respiration intensity in leaves of *Dactylis glomerata* during the growing season for various temperatures at the light saturation point.
For explantaion see Fig. 3.

True photosynthesis attains maximum values (similarly as apparent photosynthesis) in May, subsequently it decreases and either remains at an almost constant level (*Rumex*) or attains a second maximum in September (*Plantago*), which however is much lower than the maximum in May.

When the vegetative growth of leaves was over (July) measurements of the leaf areas and the dry weights were performed. A photographic and planimetric method was used for the measurement of the leaf area. The dry weights of 1 dcm^2 of leaves were 361 and 203 mg for *Plantago* and *Rumex* respectively. These values are the means of measurements on 20 leaves of average size.

Dactylis glomerata

During the growing season the intensity of photosynthesis in relation to light intensity shows some variations (see Fig. 5 for the temperature of 20°C). It is interesting that the respiration rate of *Dactylis glomerata* at the beginning of the growing season in spite of the rapid growth of leaves, is not low in comparison with that in the other investigated plants. This rate remains at a constant level, while in September the respiration shows a tendency to rise and then returns to the previous level (Fig. 6).

The relatively low rate of respiration in this period may be attributed to the fact that the discs used in the experiments were cut out not from the base, but from the middle parts of the leaf blade, on both sides of the midrib (it is well known that the base of a grass leaf is the zone of the most intensive growth and respiration).

During the growing season the value of the compensation point changes. In May it attains 4 800 $ergs/cm^2sec$, in June and July it increases almost to 8 000 $ergs/cm^2sec$, and then decreases with insignificant fluctuations.

On the contrary the light saturation point is relatively high (64 000 $ergs/cm^2$ sec) and remains at a constant level during the growing season. This probably is related to the type of structure shown by the assimilatory tissue of *Dactylis* leaves, which requires a notable amount of radiation energy for ensuring light saturation.

The course of photosynthesis during the growing season presents some interesting features. The maximum rate of photosynthesis is attained in spring and decreases in June and July (Fig. 6). Then follows an new increase leading to a second maximum which is significantly higher than that in spring. Since September there is at first a slow and then a more rapid fall of photosynthesis until the end of the growing season.

The notable decrease of the rates of photosynthesis in June and July may be attributed to a partial and transitory inactivation of the assimilatory apparatus caused by the intensive sunlight on the open territory of the investigated ecosystem. In the later months as if a regeneration of the assimilatory apparatus is observed reflected in the rise of the photosynthetic rates.

The decrease observed in autumn may be ascribed to the waning thermal and light conditions prevailing then in environment and to the age of the plant.

The dry weight per unit area of *Dactylis glomerata* leaves is relatively high; it amounts to 452 mg for 1 dcm^2.

DISCUSSION

The values of the compensation and light saturation points depend on the plant species and developmental conditions; for this reason these points can be used to characterise the ecological type of plants. A detailed analysis of this problem was made by Rabinowitch (1951), Starzecki (1958, 1959), Mooney and Billings (1961), Hadley and Bliss (1964) and Czopek (1967a). In the investigated meadow plants (*Plantago* and *Rumex*) the compensation and light saturation points change more or less during the growing season. The compensation point show a certain tendency to decrease. The light saturation intensity for *Dactylis glomerata* is relatively high (64 000 ergs/cm^{2}sec) and hardly changes steady during the whole growing season. The leaves of this grass required higher light intensities for saturation of the photosynthetic apparatus independently of the developmental stage.

Table 2

Measurements of sunlight intensity performed in the middle of March 1966 from 12 noon to 1 p.m. in Cracow (50° 04′ nothern latitude). 1 impulse for PAR = 0.12 cal/cm^2

Weather conditions	Solar radiation		Photosynthetically active radiation			
	cal/cm^2 min	lux (mesured)	cal/cm^2 min	lux (calculated)	Percentage of total radiation	Time interval betw. two impulses of integrator in sec.
Clear cloudless sky	1.32	60 000	0.5	54 000	38	12
Sun hardly visible through the clouds	0.685	28 500	0.3	32 200	44	27
Rainclouds	0.057	3 100	0.033	3 600	58	220

In June and July the intensity of photosynthesis showed a distinct fall, which was most marked for *Dactylis glomerata*. In this period the rapid development of grasses in the meadow causes a partial shading of the leaves of *Plantago* and *Rumex*. On the contrary the leaves of *Dactylis* were all the time exposed to intensive insolation. It is known, that excessive light energy can lead to a transitory or even irreversible inactivation of chloroplasts (Johansson 1923; Schoder 1932; Emerson 1935; Gessner 1940; Steemann Nielsen 1949, 1952; Zurzycki 1957; Sironval and Kandler 1958). In our opinion the decrease of the intensity of photosynthesis observed in the following months is ascribable to a transitory inactivation of the assimilatory apparatus.

The following discussion concentrates on the evaluation of photosynthetic and respiration rates on the basis of microclimatic conditions in the Ojców National Park. On this account it is necessary to give a short characteristic of these conditions prevailing in the investigated ecosystem.

A. Light conditions. An electronic integrator was used to measure the photosynthetically active radiation, in the spectral range 350—750 nm; the range of equal sensitivity being 400—700 nm (Kubin and Hladek 1963, Šetlik 1965). The radiation energy was expressed in cal/cm²min. The integrator was calibrated by means of a thermopile and a galvanometer (see methods) for various illumination of sunlight conditions. The results of measuring light during calibration of the integrator are presented in Table 2. On the average one impulse of the integra-

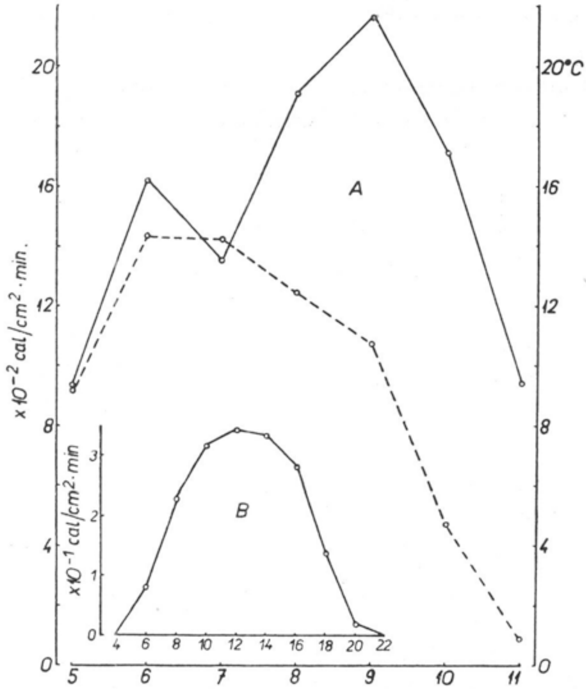

Fig. 7. A. Intensities of photosynthetically active radiation (PAR, solid line) falling on an open area in the Ojców National Park and temperatures (broken line) 20 cm above the ground level in the meadow ecosystem during the growing season 1965.

Abscissae — months, ordinates: left axis — PAR intensity in cal/cm² min, right axis — temperature.

B. Intensity of PAR during a cloudless day in July.

Abscissae — hours, ordinates — PAR intensity in cal/cm² min. Microclimatic data after J. Klein.

tor i.e. one unit of the counter corresponds to 0,12 cal/cm² for the photosynthetically active radiation (PAR). The time elapsing between two successive impulses depends on the light intensity.

„Luminous efficiency may be expressed in various units, but those commonly used are lumens per watt (radiated watts, not electrical) and lux or foot-candles per calorie per minute per square centimeter. The foot-candle per cal $min^{-1}cm^{-2}$, also referred to as the illumination equivalent of 1 cal $min^{-1}cm^{-2}$, has been used by the Weather Bureau for the evaluation of solar energy (Klimball 1924, *cit. acc.* to Withrow and Withrow 1956). Solar radiant flux has a luminous efficiency of about 100 lumens w^{-1}, or 6 500 ft-c per cal $min^{-1} cm^{-2}$. The maximum solar visible irradiance is then about 10 000 ft-c" (Withrow and Withrow 1956) i.e. 108 000 lux. Thus supposing that 1 cal/cm²min of visible irradiance corresponds to 108 000 lux it is easy to express the energy units PAR in photometric units. Table 2 shows that the intensities of sunlight measured with a luxmeter differ only slightly from the theoretical values.

In spite of the differences occurring in the spectral sensitivity and the spectral regions of the integrator and the luxmeter the measurements of the photosynthetically active radiation falling on an open surface presented only slight differences.

It follows from the measurements that the photosynthetically active radiation involves 38 to 58 percent of total irradiance. This percent depends upon the

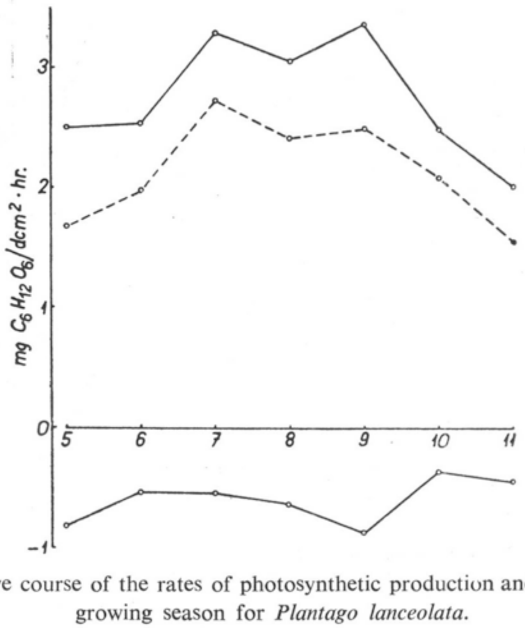

Fig. 8. Approximative course of the rates of photosynthetic production and respiration during the growing season for *Plantago lanceolata*.

Abscissae – months, ordinates – photosynthetic and respiratory rates in mg of hexose/dcm² hr. True photosynthesis – solid line, apparent photosynthesis – broken line.

absorbtion of the near infrared radiation by the water vapour and carbon dioxide in the atmosphere, and therefore depends on the weather conditions (Table 2).

The reading of the integrator-counter was performed thrice a day. The number of impulses was expressed as the average intensity of light per day or per month. The average day lengths for the particular months were taken from climatologic data (Klein 1965). Fig. 7 shows the intensities of photosynthetically active radiation during the growing season. The mean daily total radiant energy falling on a horizontal area in the Ojców National Park (50°12′ nothern latitude) during the summer months varies between 260 and 400 cal/cm² day, depending upon climatic conditions. The daily mean corresponding to the photosynthetically active radiation vary from 120 to 200 cal/cm^2. day. The global energy PAR during the growing season of 1965 (May – November) amounts to about 35 000 cal/cm^2 season.

Since in laboratory measurements the light intensities (PAR) were expressed in ergs/cm^{2}sec, it became necessary to express them in cal/cm^{2}min.

$$1 \text{ erg/cm}^2\text{sec} = 1.43 \times 10^{-6} \text{ cal/cm}^2\text{min}$$

$$1 \text{ cal/cm}^2\text{min} = 6.98 \times 10^5 \text{ ergs/cm}^2\text{sec}$$

Thus the light intensities used in the microrespirometric measurements, viz. 2 100, 10 400, 31 800 and 64 000 ergs/cm^{2}sec correspond to 0.0030, 0.0149, 0.0455 and 0.0915 cal/cm^{2}min, respictively.

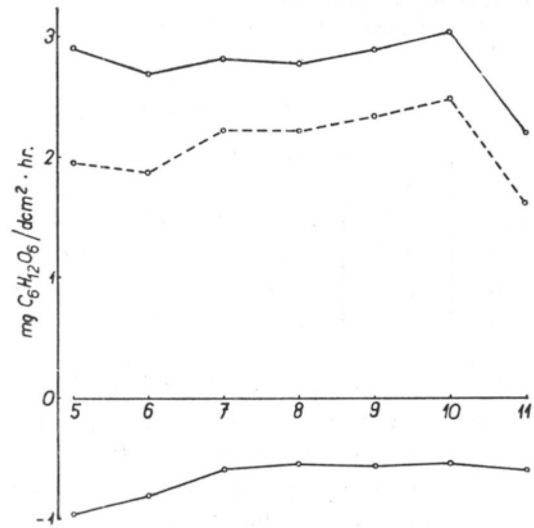

Fig. 9. Approximative course of the rates of photosynthetic production and respiration during the growing season for *Rumex acetosa*. For explanations see Fig. 8.

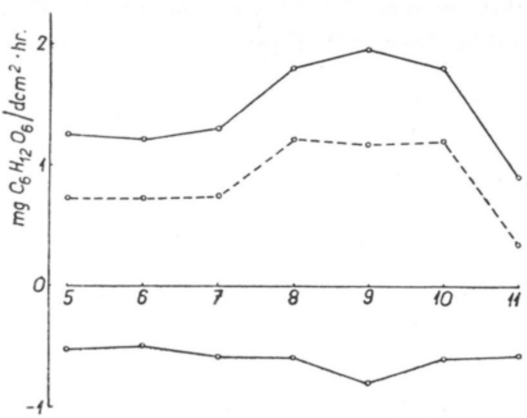

Fig. 10. Approximative course of the rates of photosynthetic production and respiration during the growing season for *Dactylis glomerata*. For explanations see Fig. 8.

B. The thermal conditions were calculated from microclimatic data (Klein 1965). The average monthly temperature in the meadow ecosystem (20 cm above the ground level) attained the highest values in June and July (Fig. 7). Some climatic data for Ojców and Cracow for the year 1963 were published by Rajchel (1965).

C. The relatively high humidity of the meadow ecosystem was accepted as optimum value for the physiological processes.

Table 3

Maximum photosynthetic production under optimum conditions based on experimental data (Ph. op.) and approximate rate of photosynthetic production based on microclimatic data (Ph. mc.) expressed in mg $C_6H_{12}O_6/dcm^2$ hr.

Plant species		Months						
		V	VI	VII	VIII	IX	X	XI
Plantago lanceolata	Ph. op.	4.80	3.74	3.67	4.16	4.72	3.62	2.88
	Ph. mc.	2.50	2.52	3.27	3.04	3.55	2.47	2.00
Rumex acetosa	Ph. op.	5.57	4.00	3.63	3.72	3.50	3.72	3.14
	Ph. mc.	2.92	2.70	2.82	2.77	2.90	3.04	2.21
Dactylis glomerata	Ph. op.	2.71	1.70	1.47	3.58	4.25	3.88	1.89
	Ph. mc.	1.25	1.22	1.29	1.80	1.96	1.78	0.90

Basing on the results of measurements performed in laboratory conditions and on the microclimatic data for the Ojców National Park, the author calculated approximately the mean rates of photosynthetic production and respiration for the investigated plant species during the growing season. The results of calculation were expressed in milligrams of hexose produced or consumed by 1 dcm^2 leaf area during 1 hour (1 μl O_2 corresponds to 0.001356 mg hexose, Czopek 1967a). The results of the calculations are presented in Table 3 and Fig. 8 — 10.

These results do not give the global production of organic matter (as hexose); on the contrary they present the rates of photosynthetic hexose accumulation and its consumption in dissimilation processes occurring in leaves during the growing season.

SUMMARY

This work is a continuation of research on the photosynthetic production of plants growing in natural ecosystems.

1. Three plant species were investigated in a meadow ecosystem of the Ojców National Park, viz. *Plantago lanceolata*, *Rumex acetosa* and *Dactylis glomerata*.

2. The object of the studies was the intensity of photosynthesis and respiration in relation to light and thermal conditions.

3. The compensation and light saturation points were determined. Their values change depending on the species and developmental stage of the plant during the growing season.

4. Maximum photosynthetic production under optimum light and thermal conditions was determined (Table 3).

5. The highest respiration rates were observed in spring. They are connected with the intensive growth of leaves.

6. The intensity of photosynthesis shows variations during the growing season. The decrease of its rates observed in June may be ascribed to a transitory inactivation of the assimilation apparatus.

7. On the basis of the results of microrespirometric measurements and of microclimatic data for the Ojców National Park the rates of photosynthetic production and respiration for three plant species growing in the meadow ecosystem during the growing season of 1965 were approximatively determined.

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Ekofizjologiczne badania nad fotosyntezą i oddychaniem niektórych gatunków roślin ekosystemu łąkowego

Część I

Streszczenie

Powyższa praca stanowi kontynuację badań nad produkcją fotosyntetyczną roślin rosnących w naturalnych ekosystemach.

1. Przedmiotem badań były liście trzech gatunków roślin ekosystemu łąkowego w Ojcowskim Parku Narodowym jak: *Plantago lanceolata, Rumex acetosa* i *Dactylis glomerata.*

2. U powyższych gatunków przebadano intensywność fotosyntezy i oddychania w zależności od warunków termicznych i świetlnych.

3. Wyniki doświadczeń wykazują, że punkt kompensacyjny i punkt wysycenia świetlnego zmieniają się zależnie od gatunku i etapu rozwojowego roślin w ciągu sezonu wegetacyjnego.

4. Określono maksymalną produkcję fotosyntetyczną w optymalnych warunkach (tabela 3).

5. Najwyższa wartość oddychania w okresie wiosny była związana z intensywnym wzrostem liści.

6. Natężenie fotosyntezy wykazuje zmiany podczas sezonu wegetacyjnego. Obniżenie tych wartości w czerwcu może być związane z przejściową inaktywacją aparatu asymilacyjnego.

7. Opierając się na wynikach pomiarów mikrospirometrycznych i danych mikroklimatycznych Ojcowskiego Parku Narodowego, określono przybliżony przebieg produkcji fotosyntetycznej i wartości oddychania dla trzech gatunków roślin ekosystemu łąkowego podczas okresu wegetacyjnego w 1965 r.