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Dynamics of Daily Changes in the Intensity of Photosynthesis and Starch Content in Lilac Leaves *(Syringa vulgaris* L.)

J. Pilarski

The Franciszek Górski Department of Plant Physiology, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland

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Abstract

Investigations were carried out in July on leaves of lilac variously situated in the head on the crown. Net photosynthesis was registered from 6 hr to 20 hr. The insolated leaves in the top part of the crown showed maximum photosynthesis between 8 hr and 11 hr, afterwards, the intensity of photosynthesis decreased in spite of the high intensity of irradiation in the midday hours. The insolated leaves located in the lower part of the crown showed maximum photosynthesis at the time of the greatest incident irradiation of the leaf. Shaded leaves inside the crown demonstrated the highest net photosynthesis between 8 hr and 15 hr. This amounted to about 20% of the maximum photosynthesis of insolated leaves.

Starch was present in the leaves both during the day and night. Before sunrise starch represented 6% of the dry weight of insolated leaves and 3% of the shaded leaves. In the insolated leaves its content quickly increased up to 13-14% since sunrise and remained at a slightly decreasing level till evening hours. Sunset was followed by a rapid decrease in starch content in the leaves. In the shaded leaves, throughout the day starch content remained at a constant level (3%).

Intensive photosynthesis of the lilac leaves causes a great accumulation of starch in the insolated leaves during the day. This is the main cause of reduction in the intensity of photosynthesis.

Keywords: leaves, photosynthesis, starch, irradiation, temperature

Introduction

Starch is one of the basic reserves of carbohydrates occurring in each part of the plant. High mobility of the changes in starch content in the plant is often used as an index value of the activity of the metabolic processes in the plant when determining the effect of various factors on metabolism [4, 9, 12, 13, 26, 27].

Investigations of the ultrastructure of chloroplasts in lilac have revealed great amounts of starch in the chloroplasts both in the leaves and in the bark. The filling of the chloroplasts with starch reached 90% of their surface area [16]. The content of starch in the leaves collected for investigations in the antemeridian hours amounted to 4-11% of their weight [18].

The great accumulation of starch in the chloroplasts may be due to difficulties in carrying away glucose from the chloroplasts [8, 23], and it is often observed, for example, in conditions of increased CO_2 concentration and the thus induced increased intensity of photosynthesis [5, 14]. Accumulation of starch may inhibit the intensity of photosynthesis. Investigations of starch content in lilac leaves were conducted from the point of view of the seasonal dynamics of changes in the starch content. Not taken into consideration were the dynamics of the twenty-four hour changes in its content and the relation between the intensity of photosynthesis and the accumulation of starch in the leaf. A question may be raised as to what extent the great filling of chloroplasts with starch affects the intensity of photosynthesis in lilac.

The aim of the study was to trace the intensity of photosynthesis and the starch content in the lilac leaves during the day.

Material and Methods

The investigations were carried out in July on the leaves of lilac *(Syringa vulgaris* L.) grown under field cultivation.

The experiments measured CO_2 exchange, air temperature, and PAR (photosynthetic active radiation) reaching the cultivated area and the leaves. Measurements of gaseous exchange were conducted using a transportable ADC infrared analyzer. Daily measurements of the gaseous exchange were started before sunrise and completed after nightfall. The presence of dew on the leaves frequently occurring before sunrise did not allow measurerement of the gaseous exchange, and in such cases the measurements were started after the dew had disappeared.

Solar irradiation in the PAR range was measured by means of an LI-COR sensor. Irradiation reaching the cultivated area was measured 3 m above the ground.

Leaves for the determination of the starch content (using the antron method described by Rose et al. [21]), were collected during the experiments. The content of starch was defined as the percentage of dry weight.

Results

Under laboratory conditions the lilac leaves from the top part of the crown attain photosynthetic light saturation at an irradiation of about 600 µmol(quantum) m^{-2} s^{-1} (Fig. 1), and when calculated as per hour integration in about 2160 µmol(quantum) m^{-2} s^{-1}. The intensity of photosynthesis under conditions of saturating irradiation was 16.8 µmol(quantum) m^{-2} s^{-1}.

The daily course of the intensity of irradiation in the PAR range, reaching the cultivated area, and the intensity of net photosynthesis for 7 leaves are listed in Fig. 2. Leaves 1-6 were collected from the outer part of the shrub crown, and leaf 7 was taken from its inside part. On that day, from 7 hr until 17 hr, the intensity of irradiation reaching the lilac was close to or greater than the saturating intensity of photosynthesis. However, only leaves situated on the side facing east (leaves 4, 6), between 9 hr and 11 hr, attained high intensity of photosynthesis (16.8 µmol(CO_2) m^{-2} s^{-1}). In the other leaves, situated on the side facing south and west, the maximum intensity of photosynthesis did not exceed 15 µmol(CO_2) m^{-2} s^{-1}. Photosynthesis in a shaded leaf from the inner part of the crown was much smaller than that of the leaves from the outside.

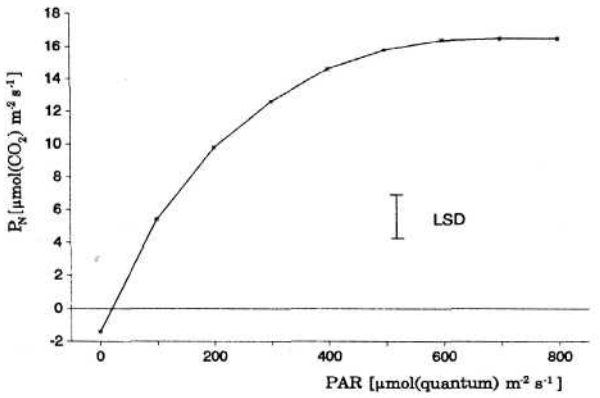

Fig. 1. Dependence of net photosynthesis (P_N) on irradiation intensity (PAR) of the lilac leaves, (n = 15)

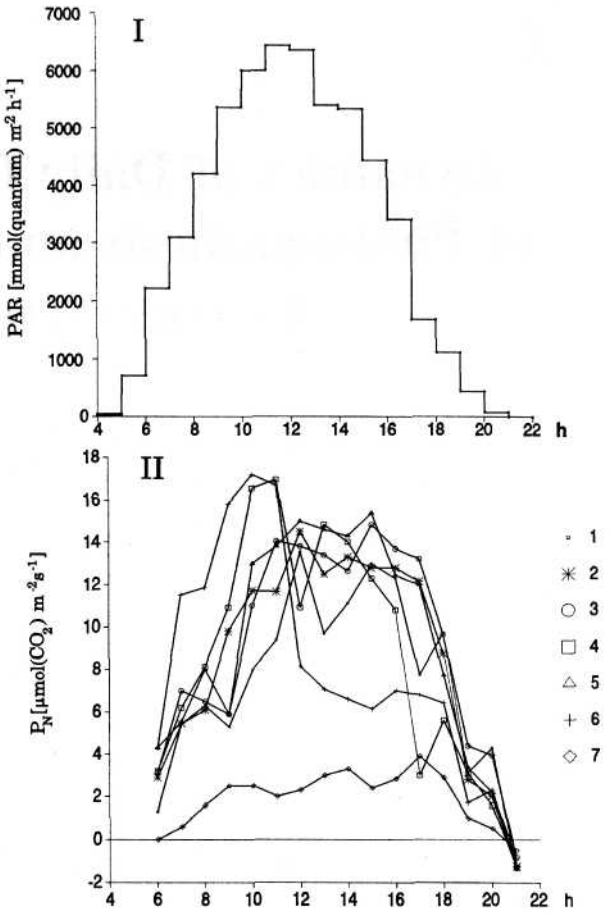

Fig. 2. Daily changes in the intensity of irradiation reaching the cultivated plants (PAR) (I) and the intensity of photosynthesis in lilac leaves situated differently on athe plant (P_N) (II). 1-6 leaves from the outer part of the shrub crown, 7 - leaf from the crown inside.

As the leaves on the plant are situated differently in relation to the sun, they are in most cases exposed to direct irradiation only for a certain time during the day. In Fig. 3 there are listed the measurement results of PAR irradiation reaching the cultivated area and the leaves, air temperature and net photosynthesis obtained on various leaves. The measurements were carried out on two halves of the leaf (on both sides of the main nerve), since great differences in the intensity of irradiation often occur within a single leaf, e. g. in the case when it is bent along the main nerve (Fig. 3 D-F), which is responsible for considerable differences in the intensity of photosynthesis between the halves of the leaf. The intensity of irradiation reaching the cultivated area on that day between 7 hr - 18 hr was above the point of saturation of photosynthesis. The leaves from the east side attained maximum intensity of photosynthesis at 9 hr (Fig. 3 B), subsequently the intensity of photosynthesis rapidly decreasing in spite of the high intensity of irradiation reaching the leaf. A leaf situated on the side facing south showed maximum intensity of photosynthesis at 11 hr and 14 hr, and between those points of time being reduced (Fig. 3 D). Leaves on the side facing west did not reach the maximal intensity of photosynthesis until 17 hr - 19 hr (Fig. 3 E, F). As in the previous experiments, the

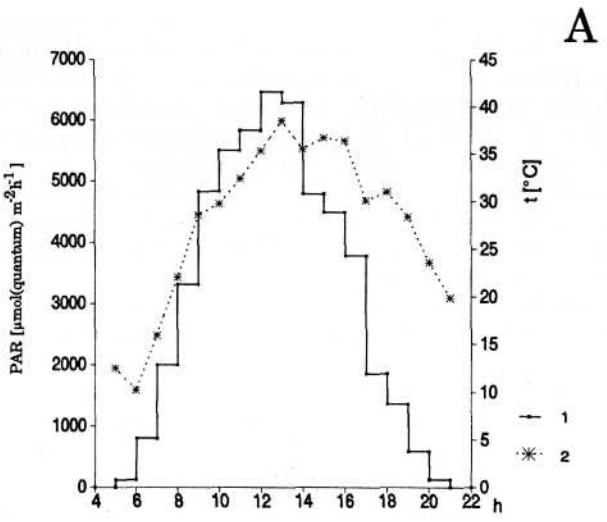

Fig. 3A. Explanation in Fig. 3.

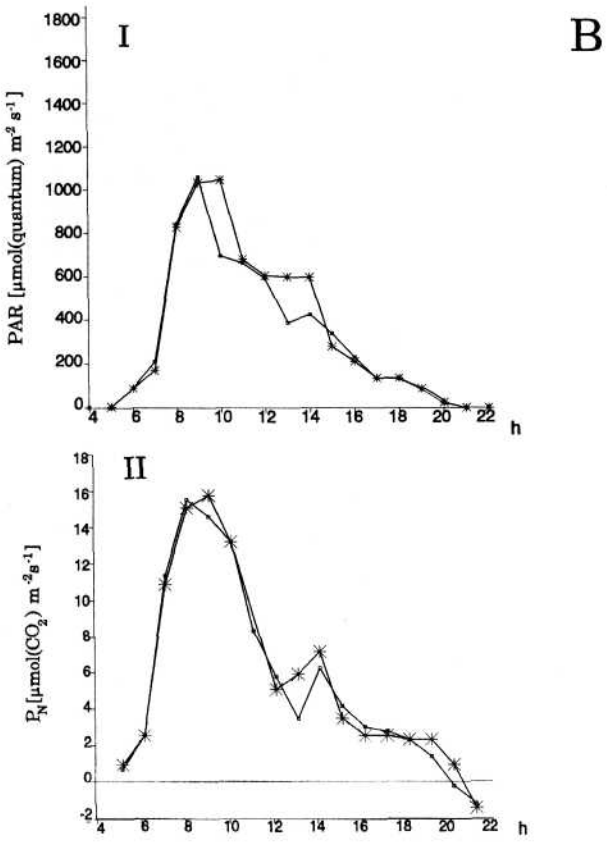

Fig. 3B. Expanation in Fig. 3.

leaves situated on the side facing east attained higher intensity of photosynthesis [16 µmol (CO_2) m^{-2} s^{-1}] than those situated on the sides facing south and west [12 µmol (CO_2) m^{-2} s^{-1}]. On that day the temperature reached up to 32°C. High intensity of photosynthesis was observed in the antemeridian hours, during which the temperature was below 20°C.

The daily course of intensity of net photosynthesis from the top parts of the crown and the measurement results of solar irradiation reaching the cultivated area are shown in

Fig. 3. Daily changes in the intensity of irradiation reaching the cultivated plants (PAR)(A 1) and air temperature (A 2), the irradiation reaching the leaf (PAR) (I) and intensity of photosynthesis (P_N)(II) in lilac leaves situated differently on the plant (B-F). Measurements I and II were made on the two halves of each leaf.

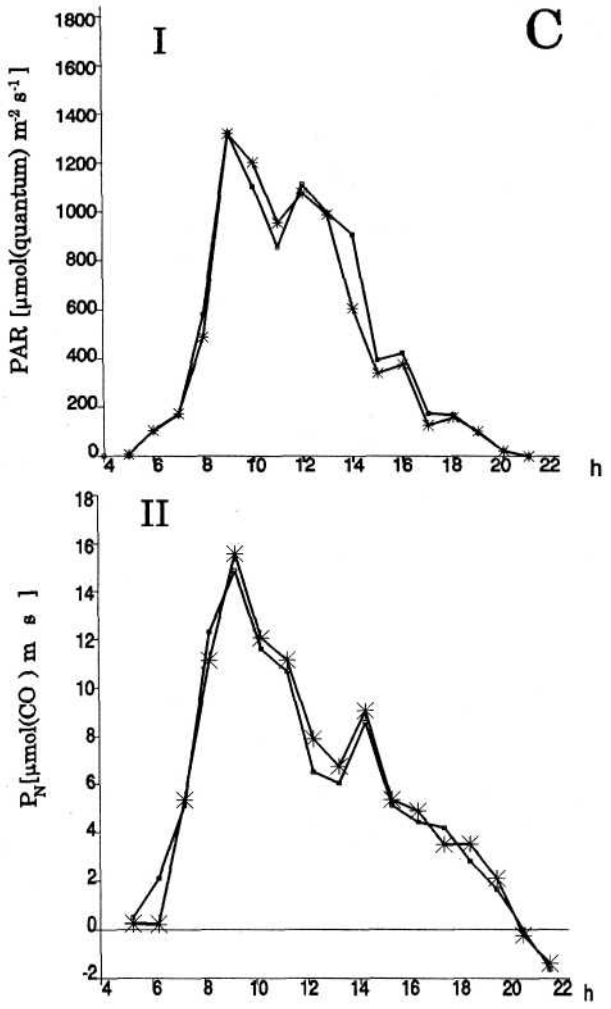

Fig. 3C. Explanation in Fig. 3.

Fig. 4. For the whole day the leaves were not shaded. During the measurements (every two hours) one measurement leaf was cut off for determination of starch content. Net photosynthesis on that day was recorded from 6 hr until 20 hr. From 7 hr to 18 hr the intensity of irradiation reaching the cultivated plants was the saturating irradiation of photosynthesis, but the leaves demonstrated maximum intensities of photosynthesis only between 8 hr - 11 hr. It was about 10 times higher than with dark respiration. After 11 hr the intensity of net photosynthesis gradually diminished.

The results of determination of the starch content in the measured leaves showed that from the morning hours its content in the leaves increased till 12 hr (13% d.w.) (Fig. 4); subsequently, it slowly decreased until 20 hr (11%). After sunset the starch content in the leaves was rapidly decreased, and at 22 hr it resembled that before sunrise.

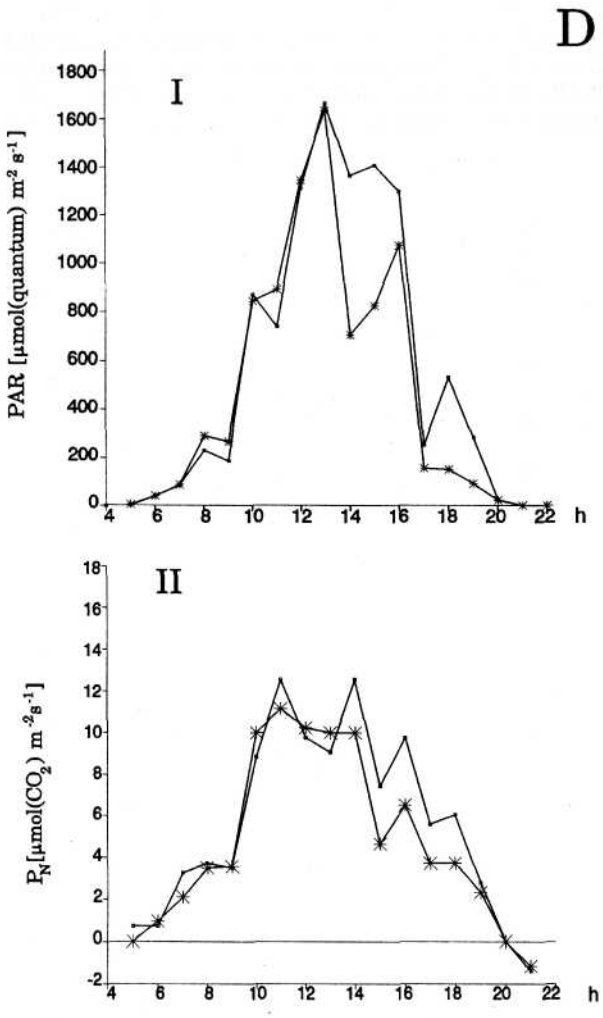

Fig. 3D. Explanation in Fig. 3.

The results from Fig. 4 indicate that an intensive progress of photosynthesis is accompanied by an increase in the starch content in the leaf, the high content of starch in turn causing a reduction in the intensity of photosynthesis.

For comparison, Fig. 5 presents the results obtained on shaded leaves situated in the lilac shrub crown. Direct solar irradiation did not reach those leaves, and the intensity of dispersed irradiation was rather small in comparison with the direct irradiation reaching the cultivated area, which is illustrated, by way of example, by the results obtained for a single leaf. For the other leaves the intensity of irradiation was similar. Net photosynthesis of shaded leaves was on a similar level from 7 hr to 18 hr. It was about four times higher than the dark respiration, being equal to about one fifth of the intensity of photosynthesis of insolated leaves. The starch content in the shaded leaves remained at a constant level during the whole day. It was smaller nearly by half than the minimal starch content in the insolated leaves, and 4-5 times smaller when compared with the maximal starch content in the insolated leaves.

Discussion

In the daily course of photosynthesis of the leaves, in many species there can be observed a depression in the midday hours and often a renewed increase in the intensity of photosynthesis in the afternoon hours. [15, 25]. The drop in photosynthesis may be as great as 80% [24]. This may be due to ecological, physiological or biochemical factors [3, 7, 11, 15, 20, 24, 25, 29]. Accumulation of assimilates, for example, is one of the biochemical factors [14, 29]. The results presented in this study indicate that the reduction in intensity of photosynthesis of *Syringa vulgaris* leaves is caused by the accumulation of assimilates in the form of a great amount of starch.

Glucose formed in the chloroplasts in the process of photosynthesis is in most cases carried away, and only small amounts of assimilates become deposited in the chloroplasts in the form of starch. Accumulation of greater amounts of starch in the chloroplasts during the day is the result of their intensive photosynthesis and difficulties with the outflow of assimilates. This takes place, for example, in the case of disturbances in sucrose synthesis in the cytosol and its transportation to the vacuoles and to vascular bundles [23]. Great accumulation of starch in the chloroplasts was observed, for example, at prolonged illumination [1, 12] or in plants growing at increased CO_2 concentration [5, 14], i. e. under conditions favoring increased intensity of photosynthesis. In the tomato, at normal CO_2 concentration in the atmosphere, the starch content varied from 1% at night to 2% in the afternoon hours; at increased CO_2 concentration in the atmosphere the starch content increased to 10% at night and 14% in the afternoon hours [14].

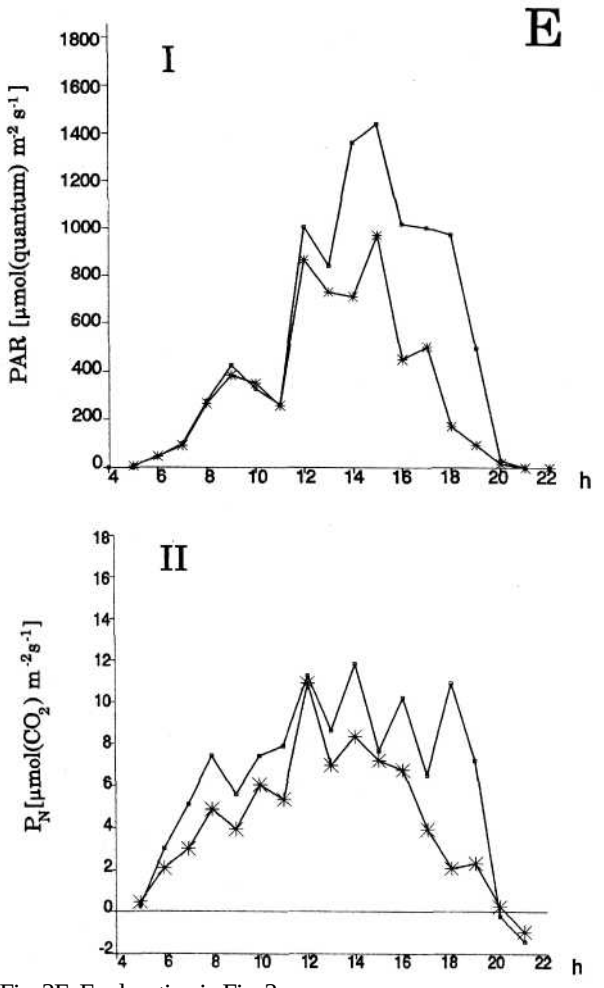

Fig. 3E. Explanation in Fig. 3.

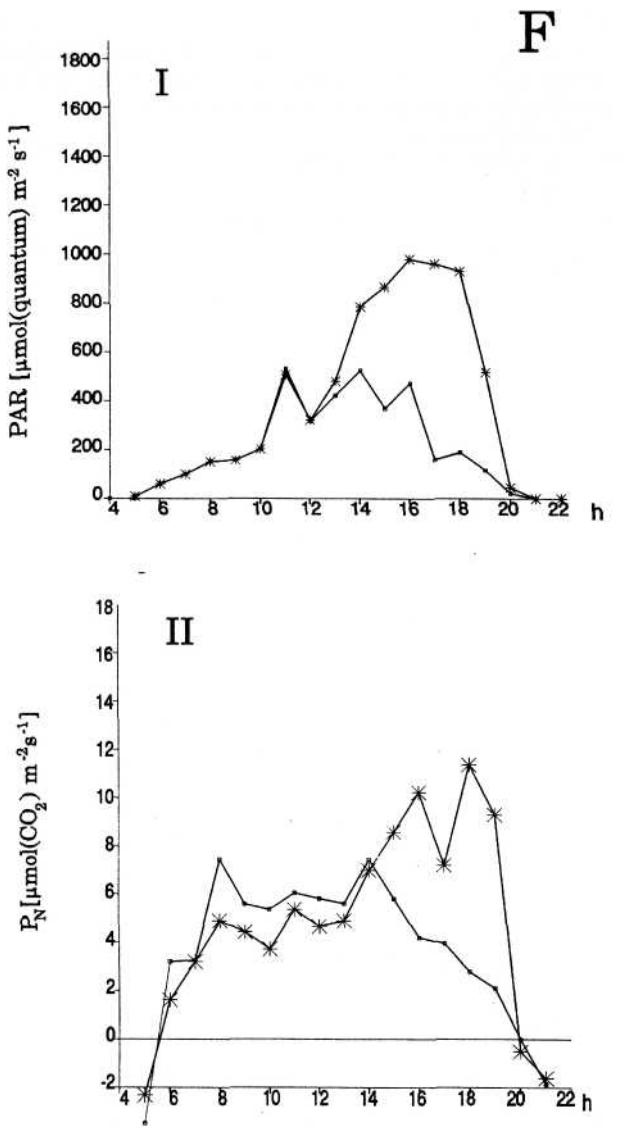

Fig. 3F. Explanation in Fig. 3.

In lilac leaves a great accumulation of starch in the chloroplasts was observed in plants growing in natural conditions [16]. Evidence indicating difficulties in the transportation of assimilates in lilac may be supplied by the results of investigations on the effect of CO_2 concentration on the intensity of photosynthesis [17]. They showed that maximum intensity of photosynthesis was obtained at a concentration of 400-550 µmol(CO2) mol^{-1}, while higher concentrations inhibited the intensity of photosynthesis. In other plant species, the inhibition of the intensity of photosynthesis was not observed even at 1000 µmol(CO2) mol^{-1} [2, 22]. Further evidence may also be the fact that as a result of two weeks long shading of leaves (reducing irradiation by 50%), starch content in the chloroplasts was reduced by 80% in comparison with the control leaves [16].

In the needles from the outer part of the crown of *Pseudotsuga menziesii* during the day, two maxima of starch content were observed, one at 9 hr (7%), and the other at 18 hr (6%); at 12 hr the content of starch in the needles was the lowest during the day, being equal to 4% [28].

In the lilac leaves the variations in starch content are much greater than those of *Pseudotsuga menziesii* and are similar to the values obtained on tomato leaves at increased CO_2 concentration, amounting from 5 to 14% in the in-solated leaves [14]. No changes were observed in the shaded leaves, which receive a rather small amount of irradiation, and the intensity of photosynthesis in these leaves is equal only to about 20% of the intensity of insolated leaves. A high content of starch was observed in the lilac for a long time during the day, from 10 hr to 20 hr. This is an indication that the production of assimilates, after the chloroplasts have been filled with starch, is limited by the possibility of outflow of the assimilates from them.

Czopek and Starzecki [6], who investigated the gaseous exchange in lilac for the entire 24 hours period, also observed the maximum of photosynthetic activity in the early morning, at 9 hr.

At the time of the investigations carried out on lilac the air temperature during the day reached 32°C. For most plants growing in a moderate climate the optimal temperature falls in the range 25-30°C, higher temperatures reducing the intensity of photosynthesis [10, 12]. There are no data available in literature on the effect of temperature on photosynthesis in lilac. Investigations carried out on chloroplasts isolated from lilac leaves have shown that they demonstrate their highest activity at a temperature of 35°C [19]. Since the reduction of photosynthetic activity in lilac

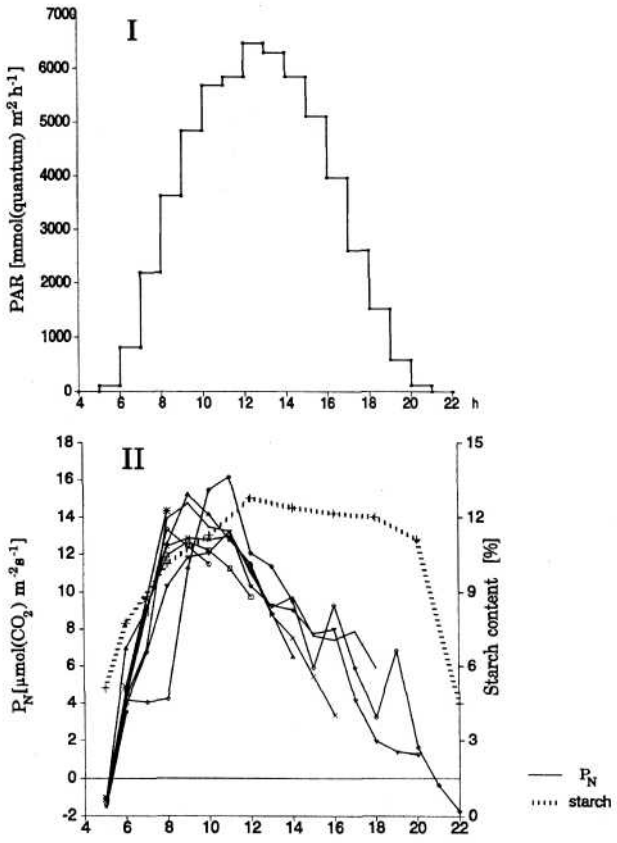

Fig. 4. Daily changes in the intensity of irradiation reaching the cultivated plants (PAR) (I), intensity of photosynthesis (P_N) of the leaves and the starch content in leaves (II). Measurements were carried out on leaves from the top part of the crown.

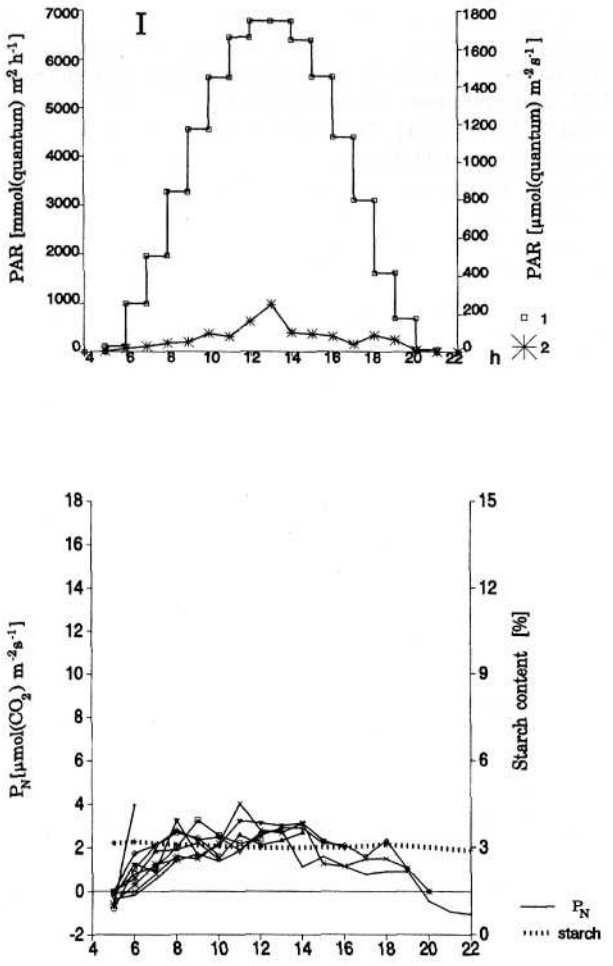

Fig. 5. Daily changes in the intensity of irradiation reaching the cultivated plants (1) and the leaf (2), intensity of photosynthesis (P_N) of the leaves and the starch content in leaves (II). Measurements were carried out on leaves from the crown inside of the lilac. 1 - PAR [mmol(quantum) m^{-2} h^{-1}], 2 - PAR ^mol(quantum) m^{-2} h^{-1}].

already began at a temperature below 20°C, this observation indicates that temperature is a the factor responsible for the reduction of photosynthesis in lilac.

On the basis of the presented results it was assumed that starch occurs in the lilac leaves throughout the twenty-four hours. In the insolated leaves, as a result of the intensive progress of photosynthesis, starch content increases, and its great accumulation reduces the intensity of photosynthesis. High intensity of photosynthesis is attained only by leaves exposed to intensive irradiation in the morning hours. These leaves are better able to make use of their potential possibility, attaining a high intensity of photosynthesis. Leaves exposed to irradiation of high intensity during the midday or afternoon hours begin to accumulate the starch earlier, before they become subjected to strong irradiation. The accumulated starch prevents full utilization of the potential possibility of the photosynthetic apparatus of these leaves. The photosynthetic intensity of leaves situated in the crown of the shrub is limited by the poor irradiation reaching them.

In lilac leaves there takes place an accumulation of starch during the day probably caused by the difficulties in transport of assimilates from the leaf. Filling of chloroplast with starch is responsible for diminishing the intensity of photosynthesis and for the small utilization of the potential possibilities of the photosynthetic apparatus.

It is not possible, however, to exclude the effect of other factors on the reduction of photosynthetic activity in lilac, e.g. high temperature, strong solar irradiation. Nevertheless, it seems that the effect of these factors is of less importance.

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