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Photosynthesis rate in moss leaves of various anatomical structure

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Abstract

On the basis of measurements of the rate of gas exchange in the leaves of mosses the value of the compensation and of the light saturation of photosynthesis points was determined. These points differentiate mosses into photo- and sciophilous ones.

Moss species such as: *Mnium punctatum, Catherinea undulata, Polytrichum juniperinum, Funaria hygrometrica, Polytrichum piliferum, Aloina rigida* were also classified according to differences in the anatomical structure of their leaves.

The morphological characters of the anatomical structure of leaves and their chlorophyll content are connected with photosynthetic activity. There is a correlation between the leaf surface and the degree of differentiation of the anatomical structure. This results in an enlargement of the contact surface of the cells assimilating from the air, and this in turn is associated with an increase in the photosynthetic activity per leaf surface area unit.

INTRODUCTION

Mosses belong to plants, the growth and development of which and their occurrence in nature are closely connected with light conditions. Mosses, like vascular plants, may be divided into photo and sciophilous ones. A basis for such a classification is frequently the value of the light compensation and saturation point. The values of these points reported by numerous authors are not constant even for the same species and depend on many factors, hence they may be expressed by a certain range of light intensity. The value of the compensation point for sciophilous mosses ranges from 20 to 400 lux (S t a l f e l t, 1937, 1960; B a z z a z et al., 1970). For the photophilous species, and particularly epiphytic mosses, the value of the compensation point is higher and lies between 1000 and 2000 lux (Miyata and Hosokawa, 1961). Mosses growing in shady places reach photosynthesis saturation at a light intensity of 4000 lux. The saturation point, the value of which lies usually between 10 000 and 20 000 lux for photophilous plants, may reach 50 klux for epiphytic mosses (Miyata and Hosokawa, 1961).

The multidirectional action of light on the photosynthetic apparatus is linked with certain properties of chloroplasts. Those of mosses are characterized by changes in their position in dependence on light intensity. The adaptive character of chloroplast movement in the photosynthesis process is most pronounced in the transition from light to high intensity conditions. In such circumstances there is a relation between the arrangement of chloroplasts and photosynthesis intensity (Zurzycki, 1962). On the other hand, under conditions of light radiation of high intensity the translocation of chloroplasts to the cell walls parallelly to the light incidence protects the photosynthetic apparatus from inactivation (Zurzycki, 1957). The monolayer structure of the assimilation organ in most species and the varying light conditions in the course of the day in natural habitats of these plants justify the attribution of an important role to this phenomenon as a rapid adaptative process.

Light conditions exert also a significant influence in the concentration and quantitative relations of chlorophyll. The character of these relations is similar as that described by many authors in vascular plants. Seasonal changes in chlorophyll concentration noted in the leaves of mosses are similar in their time course and character to analogous changes observed in evergreens and particularly in evergreen coniferous plants (Pisek, 1960; Miyata and Hosokawa, 1961). In the autumn and winter period the chlorophyll content in the leaves of epiphytic mosses increases, whereas in the summer months a marked decrease of the concentration of chlorophyll pigments is observed (Miyata and Hosokawa, 1961).

The anatomical structure of leaves and the structural characters of the assimilation organs show wide differences in dependence on the light conditions during their growth. The differences in the anatomical structure of the leaves in higher plants concern mainly the ratio of the surface area to the leaf thickness, this being associated in many plants with a change of the thickness of the palisade and spongy parenchyma (Starzecki, 1967; Pieters, 1970).

The anatomical structure of moss leaves is as compared with that of leaves of land vascular plants, much simpler and less differentiated. Nevertheless the leaves of some moss species have structures which result in wide differences between them. These differences involve mainly qualitative changes in the anatomical structure of leaves and are associated with the size of the assimilative surface and of the leaf blade. There should exist, therefore a relation between the anatomical structure of moss leaves and their photosynthetic activity. In order to reveal this, measurements were performed of the intensity of gas exchange in the leaves of 6 moss species differing from each other by their anatomical structure and by the light conditions prevailing during the growth of the assimilative organs in their natural habitats.

MATERIAL AND METHODS

The intensity of gas exchange in 6 moss species was measured by the microspirometric method (Zurzycki, 1970). The conditions of moss culture and the measurement technique have been described earlier (Krupa, 1977). For the measurement of photosynthesis and respiration leaves were used from the same position on the stem. Leaves from *Polytrichum juniperinum, P. piliferum, Catherinea undulata* and *Funaria hygrometrica* were taken at a distance of about 0.8 cm from the shoot apex. In experiments with *Aloina rigida* and *Mnium punctatum* well developed and full grown leaves were used.

The leaf surface area was calculated as follows. The leaves were photographed under the microscope and after enlarging the negative in a photographic enlarger their countours were circumscribed. The enlarged drawings were planimetred and their surface area was calculated. Determination of chlorophyll was done by the method described by Goodwin (1965) by means of Arnon's formula (1949) and converted to several reference units: dry weight (mg) and leaf surface area (cm^2).

RESULTS

The leaves used for measurement of gas exchange were fully hydrated and during the experiments were in constant contact with water. The net photosynthesis values expressed per milligramme of dry weight per 1 square centimetre of surface area or per 1 mg of chlorophyll show differences in dependence on the moss species.

The rate of gas exchange in the leaves of *Mnium punctatum* is lowest among the examined species when converted to the above mentioned parametres (Fig. 1).

The compensation point is reached by the leaves of this species at a light intensity of about 0.6 W/m^2. Within the range from the compensation point to 15 W/m^2 a distinct increase in photosynthesis rate occurs. After reaching the saturation point at 15 W/m^2 a decrease in the rate of gas exchange is noted. Above an intensity of 32.5 W/m^2 the rate of net photosynthesis remains at an almost constant level

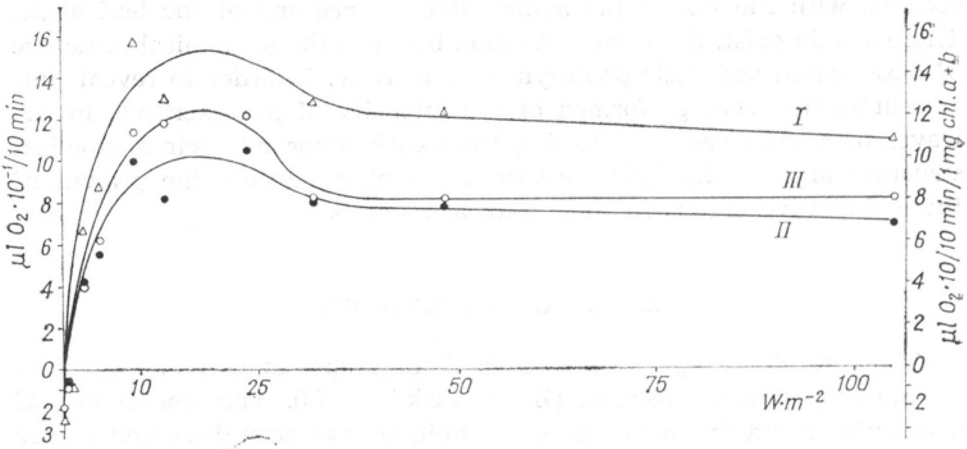

Fig. 1. Net photosynthesis rate in leaves of *Mnium punctatum* as converted to: 1 cm² cf leaf surface area — curve I

Curve I (scale on left side of diagram), 1 mg of chlorophyll a and b; curve II (scale on right side of diagram), 1 mg of dry weight; curve III (scale on left side of diagram). x axis — light intensity, W/m2

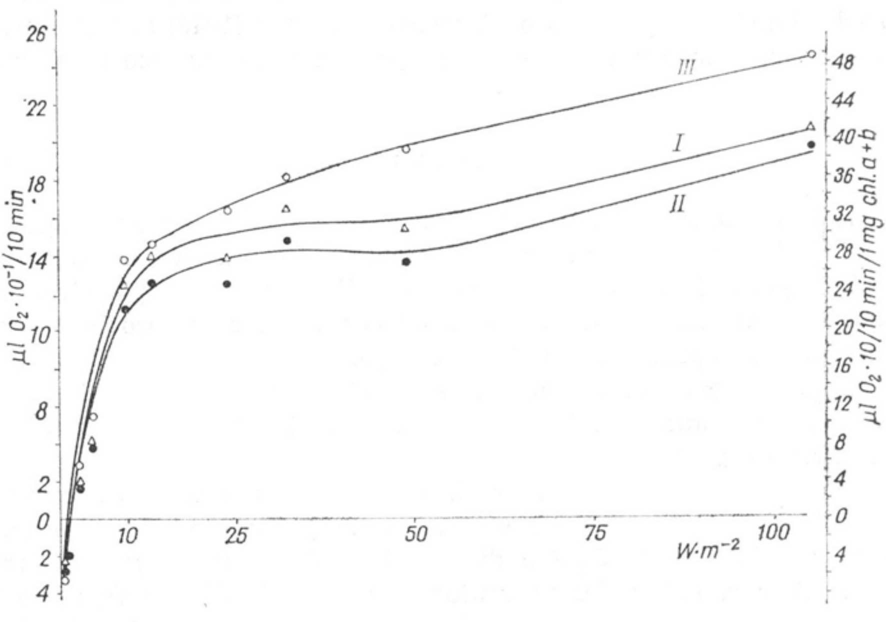

Fig. 2. Gas exchange rate in leaves of *Funaria hygrometrica*
(notations as in fig. 1)

and is lower when converted to 1 mg dry weight by 4 μl O_2/10 min than at the saturation point. Although the leaves of *Funaria hygrometrica* also have a monolayer structure of the leaf blade, the rate of photosynthesis is in this plant much higher than in the previously discussed species (Fig. 2). The compensation point for the leaves of *Funaria* lies around 1.4 W/m². Illumination of the leaves with radiation within the range of photosynthetically active light up to 15 W/m² intensity produces a very rapid increase in net photosynthesis up to about 15×10^{-1} μl O_2/10 min in conversion to 1 mg dry weight or to one surface area unit. The leaves of *Funaria* placed under light of intensity exceeding 25 W/m² exhibit a much weaker dynamics of the increase in photosynthesis rate, in dependence on light intensity. This situation does not change up to values above 100 W/m². Thus, there is no distinctly limited light intensity range, the transgression of which would produce no changes in the rate or gas exchange. It is true that in the range of 25-50 W/m² light intensity applied the occurring enhancement of photosynthesis is slight when converted to one surface area unit or to 1 mg of chlorophyll, but a certain increasing tendency is noticeable in the conversion of the photosynthesis value to one unit of dry weight. On account of the very low value of dry weight per 1 cm² of leaf surface the photosynthesis rate as converted to this unit is higher only in this species than the rate of this process converted to 1 cm² surface area.

An increase of the surface area of gas exchange by the development of assimilation lamellae leads to an increase in photosynthesis rate as converted to one surface area unit.

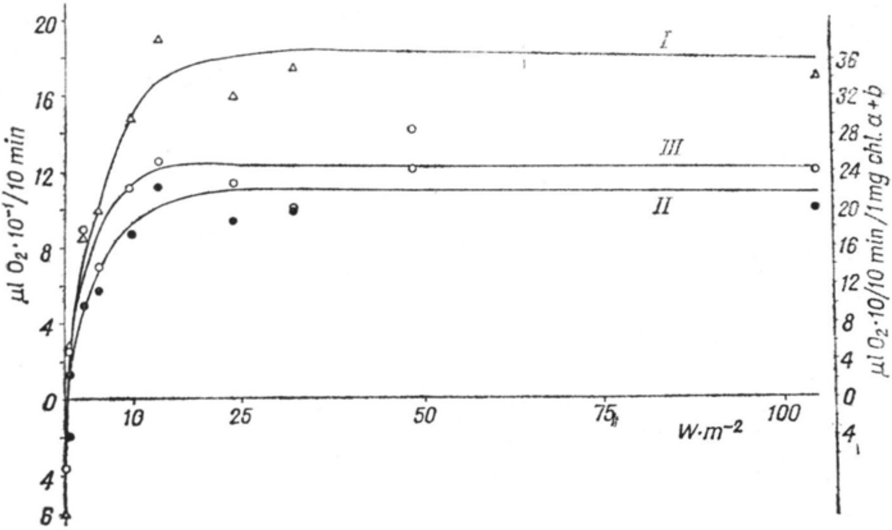

Fig. 3. Influence of white light intensity on photosynthesis rate in *Catherinea undulata* leaves. Light of various intensities applied

(notations as in fig. 1)

The leaves of *Catherinea undulata* have on their upper side a relatively small number of lamellae, yet they show a photosynthesis rate higher by 2.7×10^{-1} μl O_2/10 min/1 cm^2 at the saturation point than the leaves of *Mnium* and those of *Funaria*.

The compensation point for the leaves of *C. undulata* lies at 0.5 W/m^2. Its value is characteristic for sciophilous plants, therefore this species may be considered as belonging to this category. Saturation of photosynthesis occurs under white light of 17.5 W/m^2 intensity. The value of net photosynthesis in conversion to 1 cm^2 of leaf surface area is higher by 30 per cent than under analogous light intensity in conversion to one dry weight unit. Photosynthesis rate after reaching the saturation point does not undergo any changes and remains at an almost constant level within the remaining light intensity ranges. It results from the data shown in diagram (Fig. 3) that the net photosynthesis value at the saturation point is only about 3 times higher than respiration in darkness and this value is lower than the similar relation in the leaves of *Mnium*.

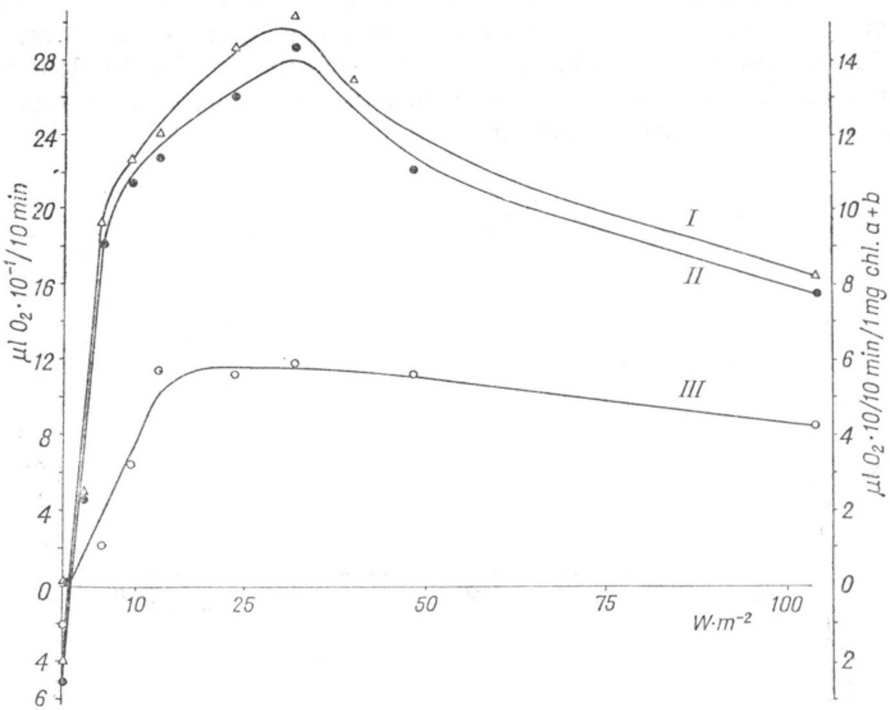

Fig. 4. Gas exchange in *Polytrichum juniperinum* leaves exposed to light of various intensity

(notations as in fig. 1)

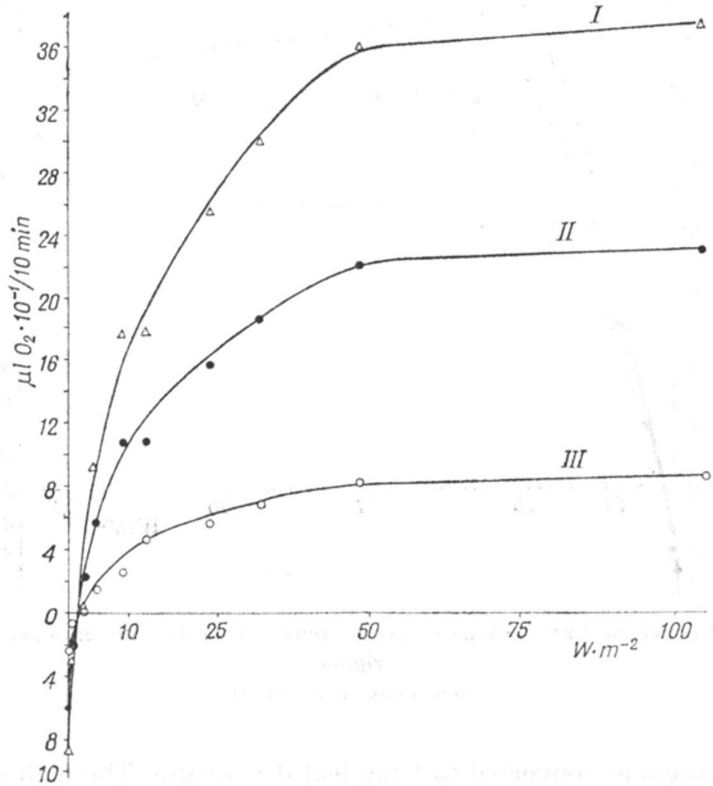

Fig. 5. Gas exchange in leaves of *Polytrichum piliferum* in dependence on light intesity
(notations as in fig. 1)

An increased surface area of gas exchange and assimilation, the leaf surface area remaining almost the same in *Catherinea undulata,* is observed in the leaves of *Polytrichum juniperinum.* The leaves of this moss species are covered on almost their whole surface with assimilation lamellae. This species growing on moderately shaded places is characterised by a higher value of the compensation point amounting to 1.25 W/m^2 than that of the previously described species. The data in fig. 4 show that apparent photosynthesis reached its maximal value when the leaves of *P. juniperinum* were illuminated with light of about 27.5 W/m^2 intensity. A further increase of the latter leads to a decrease in net photosynthesis, particularly when converted to one chlorophyll or surface area unit. The photosynthesis value under light of 100 W/m^2 intensity is lower by almost 40 per cent than that at the saturation point. Maximal gross photosynthesis intensity per surface area unit reaching a value of nearly 36×10^{-1} µl O_2/10 min is the highest of those for the so far discussed moss species. The value of maximal gross photosynthesis rate in conversion to one surface area unit exceeds almost 2.5 times the rate

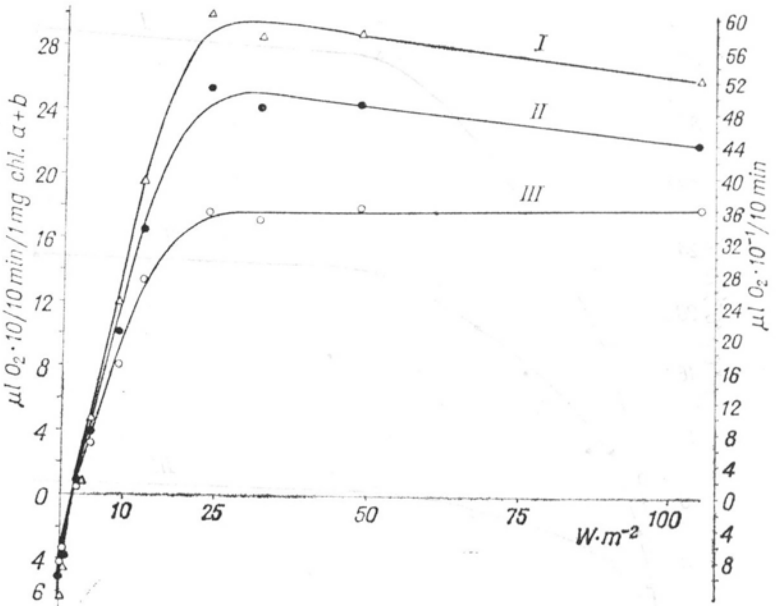

Fig. 6. Influence of light intensity on net photosynthesis rate in leaves of *Aloina rigida*
(notations as in fig. 1)

of this process as converted to 1 mg leaf dry weight. The high coefficient expressing the relation of photosynthesis to respiration indicates an important superiority of synthesis processes over dissimilative ones. The anatomical strucutre of *Polythichum piliferum* leaves is in many respects similar to that of *P. juniperinum* leaves. The different habitat of the former species and certain differences in the morphology of its leaves find their reflection in the rate of gas exchange. The compensation point for this species has a value of 1.8 W/m². Photosynthesis saturation is reached under light intensity of about 55 W/m². An increase of light intensity above the saturation point does not lead to a decrease in photosynthetic activity within the range of intensities applied in the experiments. The net photosynthesis value in conversion to a 1 cm² surface area of the leaf is 35.5×10^{-1} μl O_2/10 min and it is 6×10^{-1} μl O_2/10 min higher than in the leaves of *P. juniperinum*. The relatively low photosynthesis value when converted to one dry weight unit indicates a high proportion of dead elements in the leaf structure. Net photosynthesis in conversion to 1 mg dry weight is here the lowest among all the examined moss species, amounting to 8.6×10^{-1} μl O_2/10 min. The maximal gross photosynthesis value is almost 5 times higher than the respiration rate in darkness.

The leaves of *Aloina rigida* have a somewhat different anatomical structure than the above discussed species. The different structure and other characteristics result in differences in gas exchange. This species is distinctly photophilous, as indicated by the high value of its compensation point amounting to 2.4 W/m². Photosynthesis saturation occurs at light of 25 W/m² intensity. When this point is exceeded, the photosynthesis rate is only slightly depressed, this being most pronounced on the curves corresponding to conversion to one surface area and one chlorophyll unit. Net photosynthesis rate at the point of saturation and gross maximal synthesis converted to one surface area unit greatly exceed the values reached by the leaves of the remaining moss species studied in the present paper. The net photosynthesis value converted to one dry weight unit is almost two times higher than that in the leaves of *P. piliferum* and reaches values similar to those for the leaves of *F. hygrometrica*. Maximal gross photosynthesis rate is almost 6 times higher than that of respiration in this species.

DISCUSSION

Similarly as in the case of higher plants, species can be distinguished among mosses which are markedly scio- or photophilous. As basis for this classification serve the values of the compensation point and of light saturation in photosynthesis. These values for mosses are similar as those for vascular plants. The division into photo- and sciophilous plants cannot be strictly applied to all plants. Some of them, for instance the moss *Fontinalis*, exhibit variability in the saturation and compensation points in dependence on the preliminarily prevailing light conditions (Harder, 1933). The saturation point value changes in dependence on light distribution within the assimilation organs and its fluctuations are also season-dependent. This seasonal variability is particularly pronounced in evergreen plants. It results from the detailed discussion of this problem by Żelawski (1968) that it is difficult to establish a strict limit for the values of these points even for one genus, namely the pine. The dependence of photosynthesis on light intensity is similar in mosses to that in vascular plants. The compensation point value at optimal temperature is for most moss species about 400 lux (Stålfelt, 1937; Plantefol, 1927; Tallis, 1959; Miyata and Hosokawa, 1961; Hosokawa, Odani and Tagawa, 1964; Rastorfer and Higinbotham, 1968). The photophilous and mainly epiphytic species reach their compensation point at a light intensity of 1000 or even 2000 lux (Miyata and Hosokawa, 1961), while the values of this point are widely variable (1—4 klux) depending also on temperature. Comparison of the values of this point in the examined mosses shows significant differences between photo- and sciophilous species. The value of the compensation point for *Mnium*, a typical sciophilous plant, is 4 times lower than that determined for *Aloina*. Within the group of photophilous mosses to which belong *Polytrichum piliferum* and *Funaria hygrometrica* there are differences in the value of the compensation point depending on the anatomical structure of the leaves. The highest value of this point was found in the case of leaves of *Aloina*, it was lower for *Polytrichum piliferum* and for the monolayer leaves of *F. hygrometrica* the value was by 150 lux lower than the maximal value of about 500 lux. On the other hand, the leaves of *P. juniperinum* reach an equilibrium between respiration and photosynthesis under light with intensity somewhat lower than the values mentioned for the previously discussed species, but the compensation point is almost two times that for the sciophilous mosses — *Mnium punctatum* and *Catherinea undulata*. Although the data concerning the position of the compensation point lie within the limits of the values reported by various authors, however, their direct comparison is rather difficult on account of the different, and frequently unspecified, conditions, of the experiments in which the measurements were done. Moreover, most data concerning the values of the compensation point were determined for methodical reasons for whole stems or their parts, whereas the present data refer to single directly exposed leaves. It is for this reason perhaps that the values of the photosynthesis saturation point lie within the lower range of light intensities given by various authors for this plant group.

The value of the photosynthesis saturation point in the group of photophilous mosses examined in the present study varies from 25 W/m^2 (ca. 6250 lux) to about 55 W/m^2 (ca. 13 750 lux) and for sciophilous ones it is about 4000 lux. All the examined moss species with the exception on *F. hygrometrica* attain photosynthesis saturation within the range of light intensities applied in the experiments. In the course of the curves illustrating gas exchange in the leaves of *Mnium* and *P. juniperinum*, and partly also *Aloina*, a certain decrease of apparent photosynthesis rate can be observed at higher light intensities. High doses of light radiation have a destructive effect on the photosynthetic apparatus (Zurzycki, 1957; Björkman and Holmgren, 1963). Zurzycki (1957) found that shoots of *Lemna trisulca* exposed to light of high intensity show after several hours of exposure a reduced chlorophyll amount, and the process of decolorisation progresses from the edge of the monolayer part of the shoot. The noxious effect of high intensity light observed also by Stalfelt (1937) and Rastorfer (1970) indicates that light in this aspect of its activity may be the determining factor in the distribution of the particular moss species. The destructive effect of high light intensities is particularly pronounced when the leaves are fully hydrated. A decrease of water content up to their drying reduces or eliminates completely their sensitivity to light of high intensity. (Tallis, 1959). The verification of this finding on the results obtained in photosynthesis measurement after rehydration cannot be considered as direct evidence, since, as demonstrated by Zurzycki (1957), the noxious effect of excessive light intensity is partly reversible in dependence on the time of exposure.

The relation between the rate of gas exchange and the degree of hydration of the leaves of these plants is particularly pronounced because they lack anatomical structures which would protect the leaves from excessive transpiration and too high light intensities (Krupa, 1977). For these reasons the increase of the assimilation surface by increasing the surface area of direct contact of the leaves with the surrounding air must increase the risk of greater water loss. Therefore the increase of the area of gas exchange is associated with a reduction of the total leaf surface area. The tendency to differentiation of the leaf structure in mosses is connected with the increase in photosynthetic activity and with the influence of leaf transpiration on these processes. The increase of the assimilation surface by formation of assimilative lamellae or filaments, as in the leaves of *Aloina*, leads to an increased photosynthesis rate. This is particularly marked when the intensity of this process is converted to one surface area unit (see Krupa, 1979).

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Natężenie fotosyntezy liści mchów o różnej budowie anatomicznej

Streszczenie

Określona na podstawie pomiarów intensywności przemiany gazowej liści mchów wartość punktu kompensacyjnego i wysycenia świetlnego fotosyntezy wyraźnie różnicuje te rośliny na światłolubne i cieniolubne.

Doboru takich gatunków mchów jak: *Mnium punctatum, Catherinea undulata, Polytrichum juniperinum, Funaria hygrometrica, Polytrichum piliferum, Aloina rigida* dokonano również na podstawie zróżnicowania w budowie anatomicznej ich liści.

Morfologiczne cechy struktury anatomicznej liści oraz zawartość chlorofilu pozostają w związku z aktywnością fotosyntetyczną. Istnieje korelacja między powierzchnią liścia a stopniem zróżnicowania w budowie anatomicznej, której efektem jest powiększenie powierzchni kontaktu komórek asymilujących z powietrzem, co wiąże się ze wzrostem aktywności fotosyntetycznej jednostki powierzchni liścia.