ACTA SOCIETATIS
BOTANICORUM POLONIAE
vol. 53, nr 1: 43-51
1984

Anatomical structure of moss leaves and their photosynthetic activity

JAN KRUPA

Institute of Biology, Department of Plant Physiology, Higher Pedagogical School, Podbrzezie 3, 31-054 Kraków, Poland

(Received: April 4, 1983. Revision accepted: August 1, 1984)

Abstract

The photosynthetic activity of the leaf area unit increases depending on the degree of differentiation of the anatomical structure of the leaves of six chosen moss species. There is a correlation between the leaf area and the degree of differentiation of the anatomical structure resulting in enlargement of the area of contact of the assimilating cells with air. The leaves of *Catharinea undulata* having a one-layer blade and provided with several lamellae show a higher photosynthesis per 1 cm^2 of their surface than the one-layer leaves of *Mnium* or *Funaria*. *Aloina* leaves are the smallest in area among those of the moss species discussed, however, their photosynthetic rate is almost 4.5 times higher than in *Funaria* leaves. By analogy to the structure of leaves and their function in vascular plants, these changes and correlations may be considered as attempts of primeval adaptation of mosses to terrestrial conditions of living.

Key words: crown-gall, transformation, hydroxyurea

INTRODUCTION

The structure of vascular plants, and especially the internal one, shows a considerable differentiation depending on many factors, among which light belongs to the external ones connected with the fundamental function of the leaf as an assimilation organ. The classification into sun and shade plants is based on the differentiation of the internal structure of the leaf. The light conditions, under which growth of leaves proceeds, influence the change of the relation between the adaxial surface of the leaf and its thickness (Starzecki 1967, Pieters 1974, Nobel et al. 1975). Leaves which grow in full light have better developed palisade and spongy parenchymas. These changes are reflected in an increase of the ratio between the internal and externel gas exchange (Nobel at al. 1975, T i c h a et al. 1980). Nevertheless, the differences in the thickness of the palisade parenchyma in sun and shade leaves may be an effect of the protective function of that parenchyma against the destructive influence of high light intensity (S t a r z e c k i 1967). This character is ascribed to the movement of chloroplasts (Z u r z y c k i 1957). The adaptational character of the movement of chloroplasts in the process of photosynthesis is especially well seen when plants pass from conditions of lower to higher light intensity (Z u r z y c k i 1962).

The anatomical structure of the leaves of mosses is comparatively simple and little differentiated. However, the leaves of some moss species show the presence of structure which differentiates them among themselves rather essentially. These differences concern mainly qualitative changes in the anatomical structure of the leaf, which, in turn are connected with the size of the assimilation area. The increase in the diffusion surface entails the extension of the transpiration area, which is of essential importance for these terrestrial plants having no structure to protect their leaves against an excessive loss of water (K r u p a 1977).

Mosses are classified among primitive terrestrial plants which depend very much on water. On the other hand, these plants, and especially some of their species, are distinguished by a high resistance to drying. When dehydrated, they can survive for a long period, and when again saturated with water they soon resume their physiological processes (B o w o l e y 1979).

Thus, the problem lies in the existence of relationships between the anatomical structure of moss leaves and their photosynthetic activity on the one hand, and their adaptation to terrestrial conditions of life on the other. For the reasons mentioned above, the adaptional character of the relationships between the structure of the leaf and the intensity of CO_2 uptake is particularly well seen if the photosynthesis is calculated in relation to a unit of area. For the present study, six moss species have been chosen differing in their anatomical structure and the ecological conditions under which these plants live.

MATERIALS AND METHODS

For the experiments, the leaves of six moss species were used. Their choice was based on the anatomical structure of their leaves (Fig. 1), as well as on the individual habitat conditions.

The measurments of gas exchange and chlorophyll content were performed on mature leaves growing at a distance of 0.8 cm from the apex of the stems of: *Polytrichum juniperinum, P. piliferum, Catharinea undulata,* and *Funaria hygrometrica.* In the experiments with *Aloina rigida* and *Mnium punctatum* mature leaves were used growing in apical part of the stems. The intensity of gas exchange was measured with the aid

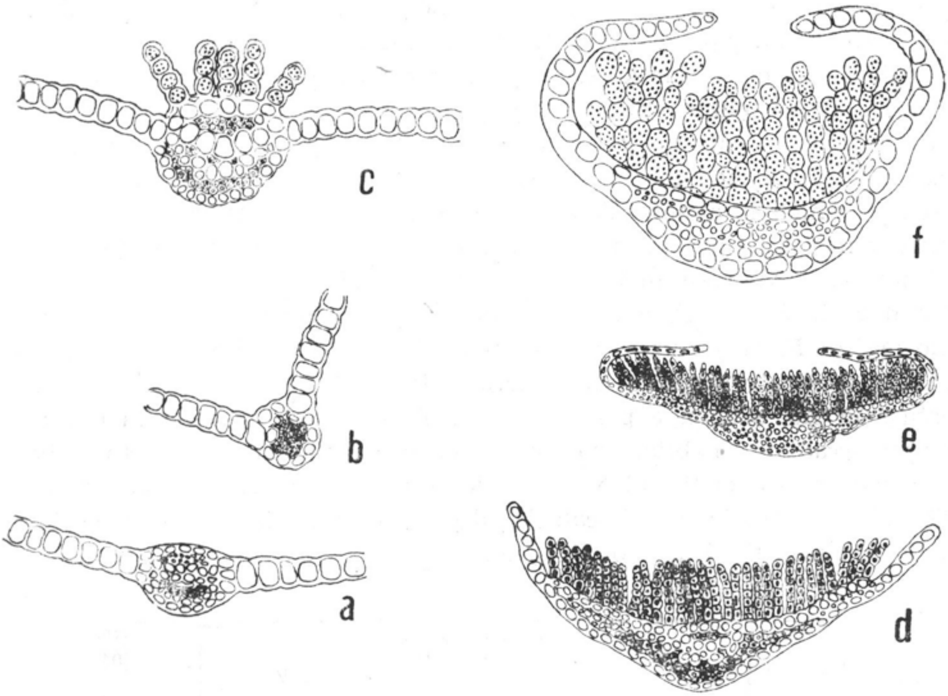

Fig. 1. Cross sections of leaves (a scheme): a — *Mnium punctatum*, b — *Funaria hygrometrica*, c — *Catharinea undulata*, d — *Polytrichum juniperinum*, e — *Polytrichum piliferum*, f — *Aloina rigida*. × 1.3

of the microrespirometric method (Zurzycki 1962). Photosynthesis was determined under light from a wolfram lightbulb (Tungsram 1000 W) within the range of optimum intensities for each moss species (Krupa 1977). Experiments were caried out at 25°C. Determination of chlorophyll was done by the method described by Goodwin (1965) and converted to several reference units: dry weight (mg), and leaf surface area (cm^2). Gas exchange and chlorophyll content determinations were replicated 5-7 times for each species.

RESULTS

The differentiation in anatomical structure of the moss leaves used for the experiments is connected with their photosynthetic activity calculated in relation to one reference system (Fig. 2). If a unit of area is taken as basis in calculation of the photosynthetic rate, it may be established that there exists a corelation between the leaf size and the photosynthetic rate of 1 cm^2 of the leaf area (the projected leaf surface). The lowest rate is characteristic of the *Mnium* leaves, the photosynthetic rate of which constitutes about 27% of the rate of gas exchange calculated per 1 cm² of *Aloina* leaves. As the leaf area decreases, the photosynthetic activity of its unit area increases. The leaves of *Catharinea undulata* having a one-layer blade and provided with several lamellae show a higher photosynthesis per 1 cm² of their surface than the one--layer leaves of *Mnium* or *Funaria*. Further increase of the number of lamellae established in the leaves of *Polytrichum juniperinum*, the leaf area of which is almost identical with that of *C. undulata*, leads to greatly increased photosynthesis calculated per 1 cm² of area. The growth of net photosynthesis in the leaves of *Polytrichum juniperinum* as compared with that of *C. undulata* amounts to 3.6 $mm^3 O_2 \cdot h^{-1}$. The area of the leaf of *P. piliferum* is much smaler than that of the former species; having a similar anatomical structure, these leaves show a greater increase in gas exchange per area unit. This species growing in dry and highly irradiated habitats has leaves curved in so much that their borders partly protect the photosynthetic apparatus in the form of lamellae. The photosynthetic rate, if calculated per area unit, is almost three times higher than in the leaves of *Funaria*.

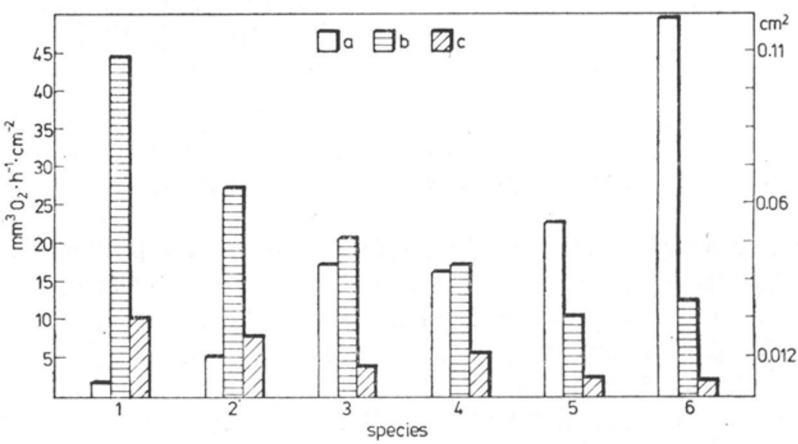

Fig. 2. Net photosynthetic rate expressed in units of leaf area: 1 — *A. rigida*, 2 — *P. piliferum*, 3 — *P. juniperinum*, 4 — *C. undulata*, 5 — *F. hygrometrica*, 6 — *M. punctatum*. a — leaf area (scale on right side of diagram), b — photosynthetic rate (scale on left side of diagram), c — dark respiration

Aloina leaves are the smallest in area among those of the moss species discussed, their net photosynthetic rate, however, is almost 4.5 times higher than in *Funaria* leaves, and reaches 44.4 $mm^3 O_2 \cdot h^{-1} \cdot cm^{-2}$. The assimilation filaments developed in the leaf considerably increase the area of gas exchange, and their partial shielding by the leaf borders protects them against quick drying up in certain conditions. The rate of photosynthesis calculated per 1 mg of chlorophyll a+b shows the highest efficiency of the chlorophyll unit in that species. This value is

Table 1

Morphological characteristics of leaves, chlorophyll (Chl) content and photosynthetic rate

Species	Area of 1 leaf, cm^2	Fresh matter of 1 leaf, mg	Dry matter of 1 leaf, mg	Dry weight of 1 cm^2 of leaf, $mg \cdot cm^{-2}$	Chl (a+b) content in 1 leaf, 10^{-4}mg	Chl (a+b), $mg \cdot g^{-1}$ dry weight	Chl (a+b), $10^{-3} mg \cdot cm^{-2}$	Level of irradiance ($W \cdot m^{-2}$) in the points of		Net photosynthetic rates at saturating irradiance, $mm^3 O_2 \cdot h^{-1}$		
								compensation	saturation	cm^{-2}	mg^{-1} d.w.*	mg^{-1} Chl
Aloina rigida	0.0038	0.039	0.016	4.21	0.84	5.24	22.11	2.4	25	44.4	10.8	2011
Polytrichum piliferum	0.0125	0.15	0.067	5.36	2.43	3.63	16.24	1.8	55	27.6	5.4	1622
Polytrichum juniperinum	0.041	0.295	0.120	2.93	9.4	7.83	22.93	1.3	27.5	20.4	7.2	889
Catharinea undulata	0.039	0.210	0.088	2.26	6.19	7.03	15.87	0.9	17.5	16.8	7.8	1067
Funaria hygrometrica	0.053	0.216	0.045	0.85	5.94	13.2	11.19	1.4	52.2	10.2	12.0	927
Mnium punctatum	0.113	0.578	0.180	1.59	25.2	14.0	22.3	0.6	15.0	7.2	7.2	532

* d.w. — dry weight.

almost twice that obtained from similar calculations for the leaves of *F. hygrometrica*. The concentration of photosynthetic pigments per area unit of the leaves of *Polytrichum juniperinum* is almost the same as that of the leaves of *Mnium*, but the photosynthetic rate calculated per 1 mg of chlorophyll is much higher in the leaves of *Polytrichum*. Thus, there is no definite correlation between the amount of chlorophyll calculated per 1 cm^2 of the leaf area and the photosynthetic rate (Table 1). The pigment contained in the shaded leaves of *M. punctatum* exhibits the lowest efficiency of the chlorophyll unit.

The importance of dry weight as reference unit in comparisons of that type is fairly relative and connected with the mean mass of the leaf used for the measurements. For this reason there is no correlation between the values of photosynthesis calculated per unit of dry weight. The highest rate of the maximum net photosynthetic rate calculated per 1 mg of dry weight was established in the leaves of *Funaria hygrometrica*. The dry weight of 1 cm^2 of the leaf of that moss species is almost six times smaller than that of leaves of *Polytrichum piliferum*, while the net photosynthetic rate is 2.2 times higher in the leaves of *Funaria*. Similar comparisons made with the leaves of *Mnium* and *Catharinea* indicate that the dry weight of 1 cm^2 of the latter species is by 29% greater and shows a net photosynthetic rate higher by 0.6 $mm^3O_2 \cdot h^{-1} \cdot mg^{-1}$ dry weight. The dependences quoted above are still more distinctly marked if we compare the dry weight of the leaf area units of *Funaria* and *Aloina* (Table 1). These species belong to typical light-loving plants. The dry weight of 1 cm^2 of the *Aloina* leaf is almost five times higher than that of the *Funaria* leaf, while its net photosynthesis shows a value lower by 1.2 $mm^3O_2 \cdot h^{-1} \cdot mg^{-1}$ dry weight than in leaves built of one layer.

It results from comparison of the data submitted above that the differentiation of the leaf structure (which influences the increase of the surface area of gas exchange and, at the same time, the assimilation surface) is in fairly close connection with the photosynthetic rate.

DISCUSSION

In the comparison of the photosynthetic activity of the leaves of various plant species, and especially of those differing in anatomical structure, there are considerable difficulties resulting from various reasons. This seems understandable when we consider the complexity of the process of photosynthesis and the many-level dependence on external factors. Detailed analysis of similar problems is the object of the papers of Ticha and Čatsky (1981), as well as in that by Żelawski (1968). A comparison of the photosynthetic activity of leaves calculated per unit of dry weight, unit of area of the leaf blade, amount of chlorophyll, or the derivatives of these units, contains, of necessity, an element of relativity. In the anatomical structure of the leaf as an assimilation organ it is the ratio of area to the leaf volume, and the quantitative percentage of assimilation tissues in the general mass of the leaf, which plays an essential role from the physiological and ecological point of view. Modifications in these relationships encountered in the leaves of terrestrial plants show tendency towards extension of the assimilation area (by an increase of the external or internal area) which, however, is conditioned by light or water relationships prevailing in the habitat of a given plant (Nobel et al. 1975). Similar dependences may by traced in the differentiation of the anatomical structure of some moss species. The leaves of *Funaria hygrometrica* and *Mnium punctatum* have a one-layer structure, but in spite of that similarity in the anatomical structure, they differ in certain morphological characters. First of all, the area of the leaf blade of *M. punctatum* is almost twice larger than of *F. hygrometrica*. The dry weight of the leaf area unit of *Funaria* is much smaller than that of *Mnium*, their fresh weights being similar. These data indicate that the *Mnium* leaf contains greater amounts of less hydrated elements, and that, on the whole, a part of the leaf blade is formed of dead elements.

On the other hand, the amount of chlorophyll a+b, if calculated in relation to the parameters mentioned above and concerning the shaded leaf of *Mnium*, is much higher than in *Funaria* leaves. The lower activity of the unit of chlorophyll found in the leaves of *Mnium*, as well as other physiological differences between the sun and shade leaves, may be the cause of the differences in the photosynthetic activity of the leaf area unit (Krupa 1978). The extension of assimilation area by means of creating additional structural elements leads to an increase of the leaf weight, and consequently, of the dry weight of the area unit. On the other hand, for lack of morphological elements protecting the leaf against excessive transpiration and because of the lack of other elements sufficiently stabilizing the water content, the total leaf area is diminshed and is the area of evaporation.

The rate of gas exchange calculated per area unit increases greatly in leaves which have a more complex structure in comparison with the moss leaves built of one layer and living in habitats having similar light conditions. The increase of the leaf assimilation area proceeds by way of an increase of the number of lamellae and, consequently, of the area of evaporation. The leaves of *Catharinea undulata, Polytrichum juniperinum* and *P. piliferum* are examples of these tendencies. At the same time there follows an increase of the photosynthetic rate of the area unit, which attains its maximum value in the leaves of *Aloina*. The leaves of that species have on their surface a great number of single, often branched, filaments which no doubt increase the area of gas exchange. Both the assimilation filaments and the lamellae are partly shielded by the folded borders of the leaves (Dominick et al. 1967, Bazzaz et al. 1970), especially in *P. piliferum*. After a longer period of drying the leaves of the latter two species lose similar amounts of water, as other moss species (Krupa 1977), but if constantly provided with water and at a lower saturation deficiency of the air immediately above the surface of humid soil, they are able to show some photosynthetic activity, and the presence of anatomical structures which partly shield the lamellae and filaments, may for some time delay their drying up. The presence of the anatomical structures discussed above increases the photosynthetic activity of the leaf area unit. If we accept these assumptions as justified, we may conclude that the differentiation of the anatomical structure of moss leaves is a result of their adaptation to terrestrial conditions of living.

The data presented above as the first attempt to elucidate the connections between the structure of moss leaves and their function indicate that the evolutionary tendencies aiming at adaptation of that group of plants to terrestrial conditions of living are realized by way of an increased photosynthetic activity of the leaf area unit, with a simultaneous decrease of the whole leaf surface, which results from the requirements of water economy in these plants.

REFERENCES

Bazzaz F. A., Dominick J., Paolillo J., Jagels R. H., 1970. Photosynthesis and respiration of forest and alpine populations of *Polytrichum juniperinum*. The Bryologist 73: 579-585.

Bowoley J. D., 1979. Physiological aspects of desiccation tolerance. Ann. Rev. Plant Physiol. 30: 195-238.

Dominick J., Paolillo J., Reighard J. A., 1967. Ultrastructural features of some polytrichaceous moss leaves. The Bryologist 70: 61-69.

Godwin T. W., 1965. Chemistry and Biochemistry of Plant Pigments. Acad. Press, London-New York.

Krupa J., 1977. The interdependence between transpiration intensity and the anatomical structure of moss leaves. Acta Soc. Bot. Pol. 46: 57-68.

Krupa J., 1978. Photosynthesis rate in moss leaves of various anatomical structure. Acta Soc. Bot. Pol. 47: 391-402.

Nobel P. S., Zaragoza L. J., Smith W. K., 1975. Relation between mesophyll surface area, photosynthetic rate, and illumination level during development for leaves of *Plectrenthus parviflorus*. Plant Physiol. 55: 1067-1070.

Pieters G. A., 1974. The growth of sun and shade leaves of *Populus euramericana* in relation to age, light intensity and temperature. Medelingen Landbou Whogeschool, Wageningen.

Starzecki W., 1967. Protection of the palisade parenchyma against the harmful action of light intensities on leaves. Acta Soc. Bot. Pol. 36: 171-180.

Ticha I., Čatsky J., Peisker M., 1980. Ontogenic changes in the internal limitations to bean leaf photosynthesis. 6. CO_2 dependence of net photosynthetic rate. Photosynthetica 14: 489-496.

Ticha I., Čatsky J., 1981. Photosynthetic characteristics during ontogenesis of leaves. 5. Carbon dioxide compensation concentration. Photosynthetica 15: 401-428.

Zurzycki J., 1957. The destructive effect of intense light on the photosynthesis apparatus. Acta Soc. Bot. Pol. 26: 157-175.

Zurzycki J., 1962. The action spectrum for the light dependent movements of chloroplasts in *Lemna trisulca*. Acta Soc. Bot. Pol. 31: 498-538.

Żelawski W., 1968. Wymiana gazowa i bilans wodny igliwia. In: Zarys fizjologii i ekologii sosny zwyczajnej. SGGW, Warszawa.

Budowa anatomiczna liści mchów a ich aktywność fotosyntetyczna

Streszczenie

Aktywność fotosyntetyczna jednostki powierzchni liścia wzrasta zależnie od stopnia zróżnicowania w budowie anatomicznej liści sześciu wybranych do doświadczeń gatunków mchów. Liście *Catharinea undulata* zbudowane z jednowarstwowej blaszki i posiadające kilka lamell wykazują większą fotosyntezę przeliczoną na 1 cm² powierzchni niż jednowarstwowy liść *Mnium* lub *Funaria*. Powierzchnia liścia *Aloina* jest najmniejsza spośród omawianych gatunków mchów zaś natężenie fotosyntezy jest prawie 4.5 raza wyższe niż liści *Funaria*. Przez analogie do budowy liści i ich funkcjonowania u roślin wyższych można uznać te zmiany i istniejące korelacje jako próby pierwotnej adaptacji mchów do lądowych warunków życia.