ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. XLV, nr 3
1976

# Functional and structural changes in chloroplasts of senescent tobacco leaves

DANUTA WOLIŃSKA

Institute of Biology, Maria Curie-Skłodowska University, Lublin

(Received: January 29, 1976)

Abstract

The relationship between the structure and the function of chloroplasts of aging tobacco leaves was studied. From the observations of chloroplast structure in electron microscope, the results of other authors concerning earlier degradation of stroma lamellae in comparison with grana were confirmed. It was shown that this process is accompanied by changes in the content of galactolipids (in the first place MGDG) and earlier decomposition of chlorophyll-protein-complex I. This resulted in decrease of photosynthetic activity of leaves and earlier disappearance of Photosystem I activity.

Abbreviations:

DCIP — 2,6-dichlorophenolindophenol;
DCMU — (3,4-dichlorophenyl)-1,1-dimethylurea;
DGDG — digalactosyl diacylglycerol;
MGDG — monogalactosyl diacylglycerol;
PMS — phenazine metosulphate;
SDS — sodium dodecyl sulphate;
TMPD N, N, N, N-tetramethyl-p-phenylene diamine;
Tricine N-tris(hydroxymethyl)methylglicine;

## INTRODUCTION

Yellowing of leaves and loss of turgor are symptoms of their senescence (Mothes, 1960; Butler, 1967; Ljubešić, 1968). The outer changes are accompaniated by decomposition of the particular cellular organelles. From the studies of many authors (Butler, 1967; Dodge, 1970; Młodzianowski and Kwintkiewicz, 1973) it appears

that chloroplasts are the first cellular organelles which show senescent symptoms. It was also found that this process is associated with a decrease in the level of chlorophyll (Jeffrey and Griffith, 1947; Wolf, 1956; Birecka and Dakić--Włodkowska, 1966; Gej, 1966; Whitfield and Rowan, 1974), carotenoids (Chrastil, 1956; Goodwin, 1958; Chichester and Nakayama, 1965; Whitfield and Rowan, 1974) and galactolipids (Harnischfeger, 1973; Ferguson and Simon, 1973). However, the amount of lipophyllic plastoquinones in older leaves is much higher than in young ones (Tendille and Gervais, 1963; Wellburn and Hemming, 1966; Barr and Crane, 1967; Griffiths et al., 1968; Lichtenthaler, 1969). The above mentioned chemical compounds form a lipid fraction of chloroplasts.

The process of leaf senescence is also connected with a considerable decrease in the content of protein and nucleic acids (Fletcher and Osborne, 1965; Shaw et al., 1965; Woolhouse, 1967; Wollgiehn, 1967; Brady et al., 1971).

Attention was also drawn to the decrease in photosynthetic activity with the age of leaves (Singh and Lal, 1935; Freedland, 1952; Richardson, 1957; Šesták and Čatský, 1962; Smillie, 1962; Šesták, 1963; Hardwick et al., 1968; Larson and Gordon, 1969). Recently it has been shown that in the process of senescence both the efficiency of the membrane-bound ATP synthesizing system (Hernandez-Gil and Schaedle, 1973; Harnischfeger, 1974 b) and the activity of Hill reaction decrease (Harnischfeger, 1974 a).

The aim of the present work was to study the relationship between the structure and the content of some chemical compounds and photosynthetic activity of senescent chloroplasts in tobacco leaves.

## MATERIAL AND METHODS

The material used for the studies consisted of tobacco leaves *Nicotiana tabacum* L. of the variety 'Virginia Puławska 70802', seeds of which were obtained from the Institute of Soil Science and Plant Cultivation, Puławy. The seeds were initially germinated on wet lignin in petri dishes and then put into soil. The seedlings with 4—5 leaves were transplanted into Mitscherlich's pots filled with soil. The plants were kept in a greenhouse under 18 hrs light (4500 lx). About 4-month old plants in full blossom with leaves of all ontogenetic stages (young, mature, yellowing and dry) were taken for analyses.

Galactolipids analyses were carried out according to Pohl et al. (1970). They were assayed by determination of galactose according to Roughan and Batt (1968) and factors of 4.3 and 2.6 were used to

convert galactose to MGDG and DGDG respectively (Leech et al., 1973).

Chlorophyll was determined as described by Arnon (1949).

Photosynthetic oxygen evolution was measured microrespirometrically according to Zurzycki (1955) using a light intensity of $3.4 \times 10^4$ ergs $\times$ cm$^{-2} \times$ s$^{-1}$.,

Chloroplasts were preparated according to Sane et al. (1970).

Photosystem I activity of chloroplasts was measured as oxygen uptake with Clark-type oxygen electrode at 24° C using sodium ascorbate and TMPD as electron donor and methylviologen as electron acceptor. The reaction mixture for measuring $O_2$ uptake contained the following components, in μmoles : Tricine-NaOH buffer (pH 8.0), 150; DCMU, 0.03; sodium ascorbate, 50; TMPD, 0.2; methylviologen, 0.4; chloroplast equivalent to about 30 μg of chlorophyll in a final volume of 1.9 ml. The reaction chamber was illuminated with red light at an incident intensity of $2.5 \times 10^5$ ergs $\times$ cm$^{-2} \times$ s$^{-1}$.

Photosystem II activity was measured spectrophotometrically at 600 nm by following the photoreduction of DCIP. The reaction mixture for Photosystem II measurements contained the following components, in μmoles: Tricine-NaOH buffer (pH 7.0), 150; DCIP, 0.125; chloroplasts containing about 30 μg of chlorophyll in a final volume of 3 ml. The optical density of the reaction was measured before and after illumination with $1.5 \times 10^5$ ergs $\times$ cm$^{-2} \times$ s$^{-1}$ of red light.

Cyclic photophosphorylation catalysed by PMS was measured according to the modified version of Avron (1960). The reaction mixture contained the following components, in μmoles : Tricine-NaOH buffer (pH 8.0), 50; KCl, 50; $MgCl_2$, 10; $Na_3PO_4$, 10; ADP, 4; PMS, 0.15; sodium ascorbate, 20; chloroplast equivalent to 50 μg of chlorophyll in a final volume of 3 ml. Illumination for 5 min was provided by light at an incident intensity of $1.2 \times 10^5$ ergs $\times$ cm$^{-2} \times$ s$^{-1}$. Inorganic phosphate analysis was measured by the method Fiske-Subbarow (1925).

Non-cyclic photophosphorylation was determined in the same way, in that PMS was replaced by 5 μmoles of $K_3Fe(CN)_6$ (Gyldenholm and Whatley, 1968).

Gel electrophoresis of lamellar chloroplast proteins was carried out according to Remy (1971).

For investigation of the structure of chloroplasts small leaf segments were fixed in 4% glutaraldehyde in 0.07 M phosphate buffer pH 7.2, for 12 h at 4° C and stained in 1% $OsO_4$. The fixed material was dehydrated through graded series of ethanol and propylene oxide washes and then embedded in Vestopal W. The polymerized material was cut on a Tesla ultramicrotome. The sections were counterstained with uranyl acetate and lead citrate. They were then photographed on Scientia Agfa-Gevaert plates at microscopic magnification $\times$ 9800.

## RESULTS

The relationship between the age of leaves and the amount of photosynthetically evolved oxygen from the discs cut out in the leaves is presented in Fig. 1. High intensity of photosynthesis in young leaves decrea-

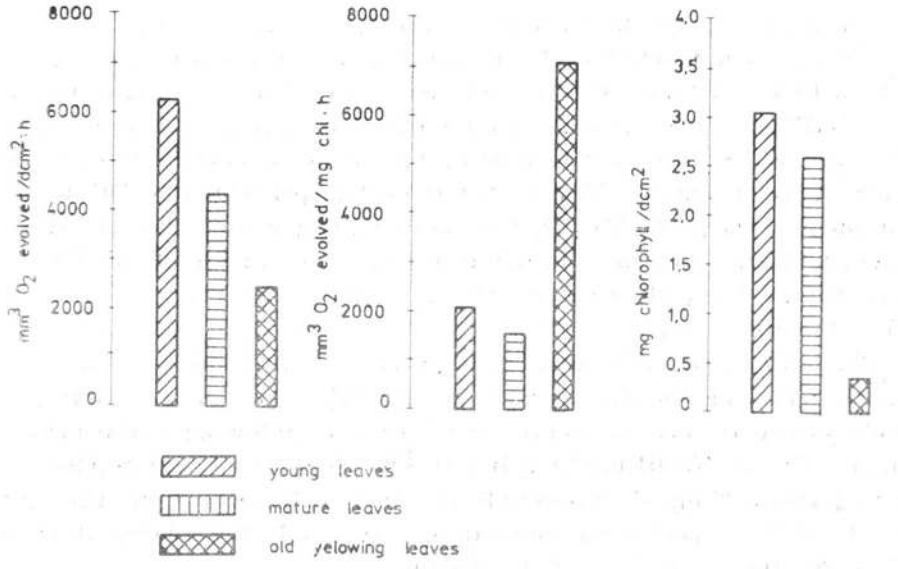



Fig. 1. Photosynthesis rate of tobacco leaves in different ontogenetic stages

ses in mature and yellowing ones. The amount of photosynthetically evolved oxygen expressed in terms of chlorophyll units also confirms this decrease. Just now at the last stage of senescence, when the amount of chlorophyll is very low, the result of this calculation increases. It appears from the studies of Šesták and Čatský (1967) and Aouni and Mousseau (1974) that "chlorophyll compensation point" (the amount of chlorophyll at which photosynthesis is equal zero) already occurs at 2.5 mg/dcm² in *Nicotiana sanderae* and 2.3 mg/dcm² in *Pinus nigra*. Thus at low concentrations of chlorophyll the rate of photosynthesis calculated per chlorophyll unit does not represent a real photosynthetic activity.

The dependence of Photosystem II and I activity on leaf age is presented in Table 1. As senescence of leaves develops, both Photosystem II activity measured by reduced DCIP/mg chl/h and Photosystem I activity measured by oxygen uptake/mg chl/h decreases. However, significant differences in both photosystems activity were found. In mature leaves already, at a relatively low decrease in Photosystem II activity, a very distinct decrease in Photosystem I activity can be observed. A rapid activity increase in both photosystems in the final phase of leaf senescence results

Table 1

Photosystem II and Photosystem I activities of tobacco leaves in different ontogenetic stages

| Physiological status of leaves | Photosystem II μmoles acceptor reduced per mg chl.·h $H_2O \rightarrow DCIP$ | Photosystem I μmoles $O_2$ uprake per mg chl.·h TMPD→meviol | Chlorophyll content in mg/g fr. wt |
|---|---|---|---|
| Young | 31.3 | 1503 | 1.97 |
| Mature | 30.4 | 348 | 0.89 |
| Old yellowing | 71.1 | 861 | 0.26 |

from a very low chlorophyll content at this time. This increase in the case of Photosystem II exceeds about twice the activity of young leaves, whereas Photosystem I does not reach the activity of young leaves. This fact would also point to a more rapid decrease in Photosystem I activity in comparison with that of Photosystem II as senescence of leaves proceeds.

Table 2 presents cyclic photophosphorylation catalysed by PMS and non-cyclic photophosphorylation catalysed by $K_3Fe(CN)_6$. The intensity of both photophosphorylations was higher in mature leaves than in young ones, whereas it gradually decreased in yellowing ones. Photophoshorylation was not found in yellow leaves by the method used.

Table 2

Cyclic and non-cylic photophosphorylation of tobacco leaves in different ontogenetic stages

| Physiological status of leaves | | μmoles Pi uptake/mg chloropyhll·h | |
|---|---|---|---|
| | | Cyclic photophosphorylation PMS catalysed | Non-cyclic photophosphorylation $K_3Fe/CN/_6$ catalysed |
| Young | | 50.4 | 24.1 |
| Mature | | 54.3 | 33.8 |
| Old yellowing | 1 | 33.2 | 21.0 |
| | 2 | 22.4 | 5.04 |
| | 3 | — | — |
| | 4 | — | — |

Fig. 2 shows densitometric tracings of polyacrylamide gels after electrophoresis of lamellar chloroplast protein of tobacco leaves. The quantitative and qualitative composition of the protein components changes with the age of leaves. In young leaves lamellar chloroplast protein is composed of 7 components (Fig. 2a). Lamellar protein of mature leaves lack of component 2, and components 1 and 3 occur in smaller quantities (Fig. 2b); however, in yellowing leaves further and very distinct decrease

in the content of component 1 can be observed (Fig. 2c). According to Remy (1971), components 1 and 4 belong to Photosystem II particles and components 2 and 3 to Photosystem I.

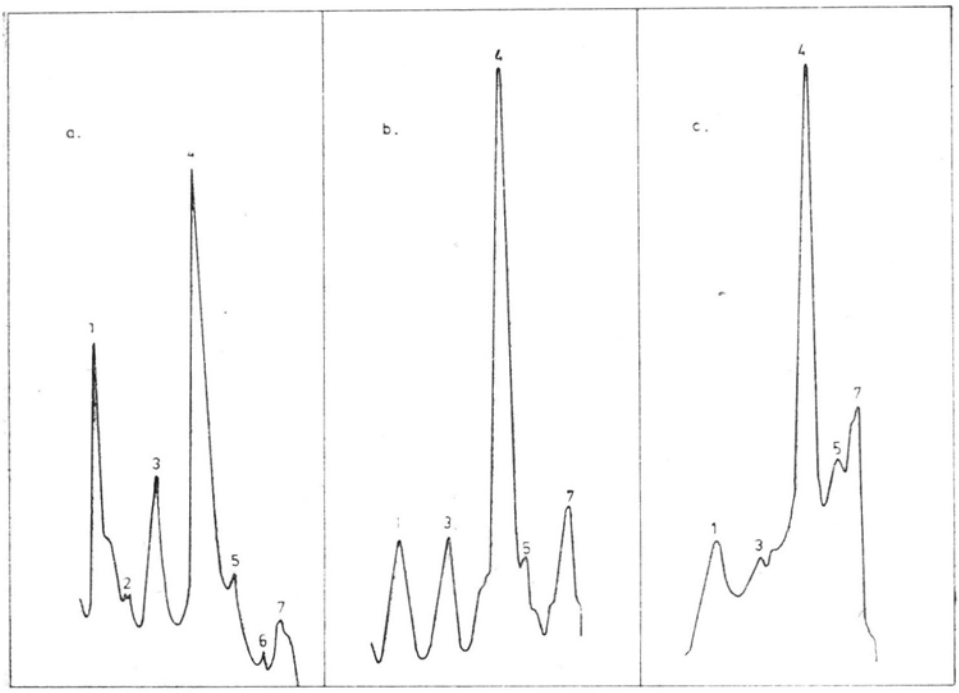


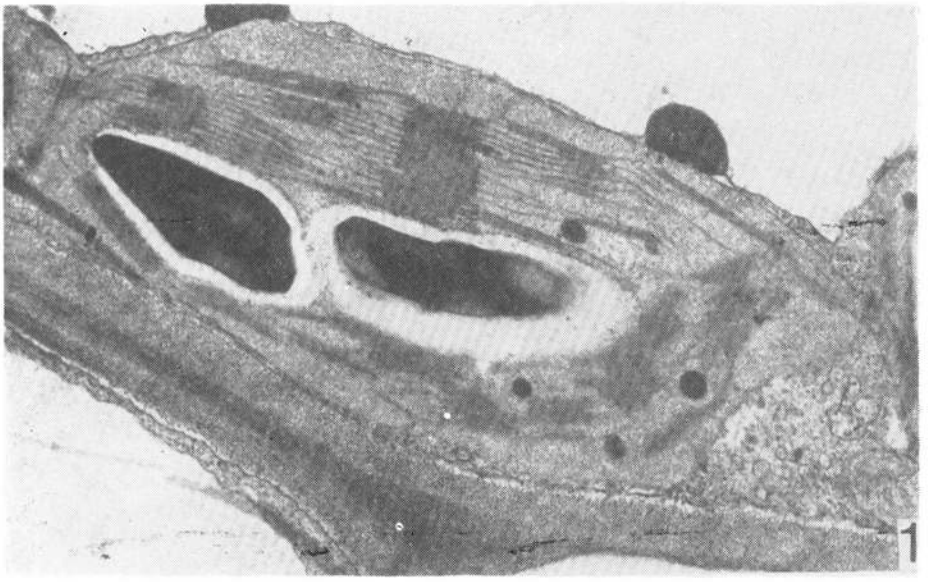

Fig. 2. Polyacrylamide gel electrophoresis of lamellar proteins of tobacco chloroplasts from leaves in different ontogenetic stages

Densitometric tracings at 600 nm. Migration was from the origin (left) to the anode (right). *a* — young leaves, *b* — mature leaves, *c* — old yellowing leaves

The content of galactolipids in various ontogenetic stages of tobacco leaves has been presented in Fig. 3. The highest concentration of MGDG and DGDG occured in young leaves and decreased with age of leaves. A reverse direction of these changes can be seen when the content of galactolipids is expressed in terms of chlorophyll units (Fig. 3a). This results from the fact that the rate of chlorophyll decrease in the process of senescence is much higher than decomposition of galactolipids. The ratio of MGDG to DGDG decreasing with the age of leaves indicates that MGDG underwent a faster decomposition.

Chloroplasts of young leaves had a typical ellipsoidal shape and a well developed thylakoid system. Small plastoglobuli and large starch grains occur between the lamellar system (Plate I, photo 1). Chloroplasts of mature leaves differ from those previously described by slightly greater dimensions of plastoglobuli and starch grains (Plate I, photo 2).

The characteristic feature of chloroplasts of yellowing leaves is swell-



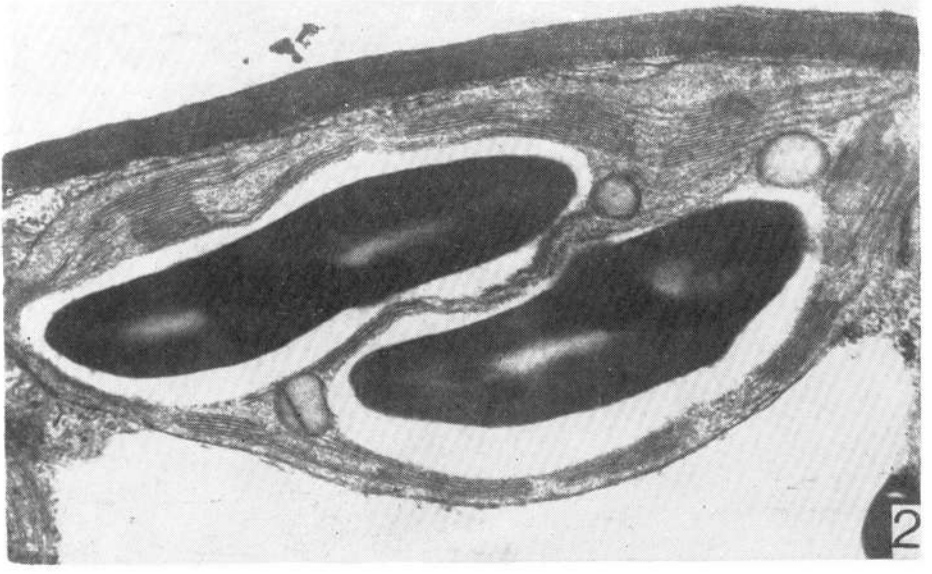
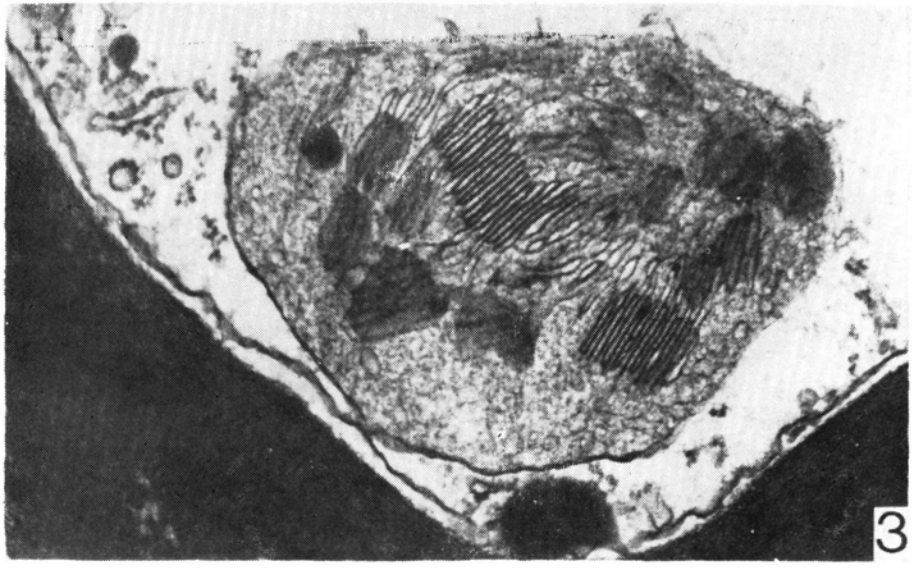


Photo 1. Chloroplast of a young leaf. Well developed thylakoid system. Small plastoglobuli and starch grains are present between the lamellar system. × 30.000

Photo 2. Chloroplast of a mature leaf. In comparison with the chloroplast in Photo 1 slightly larger plastoglobuli and starch grains. × 30.000



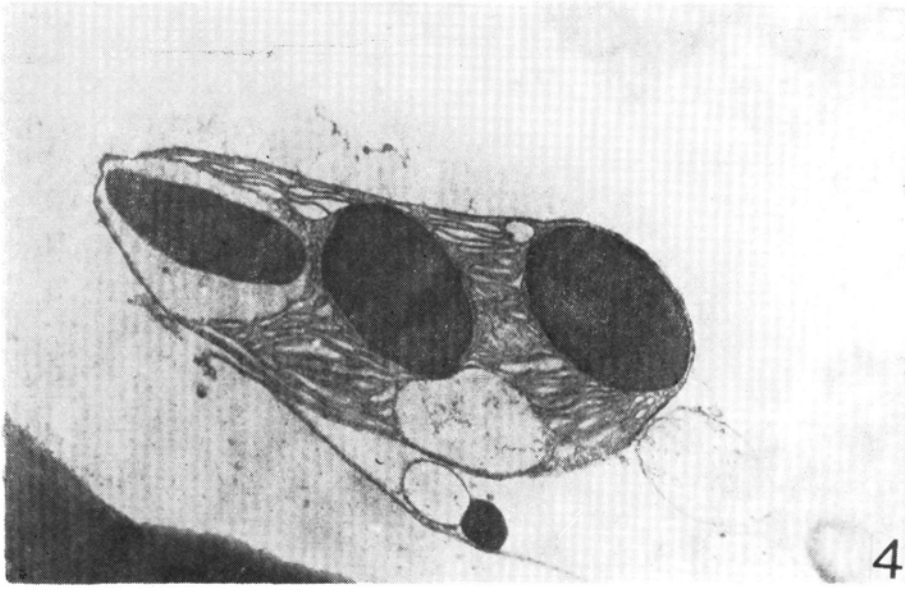




Photo 3. Chloroplast of a yellowing leaf. Visible swelling and destruction of stroma lamellae. Grana stacks are still present. × 30.000

Photo 4. Chloroplast of a yellow leaf. A completely disorganized lamellar system, very large plastoglobuli. × 30.000

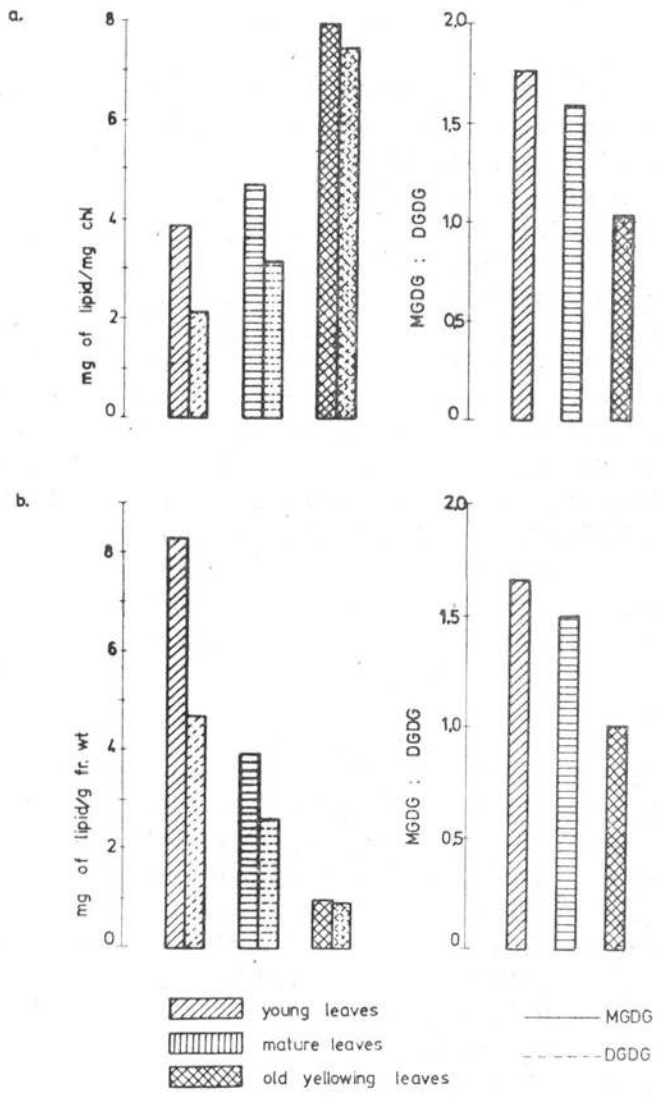



Fig. 3. Galactolipids content of tobacco leaves in different ontogenetic stages *a* — in mg/mg chlorophyll, *b* — in mg/g fresh weight.

ing and destruction of stroma lamellae and increase in the volume of plastoglobuli (Plate II, photo 3).

Chloroplasts of yellow leaves possess a completely disorganized lamellar system. The are filled with large plastoglobuli and swollen grana lamellae (Plate II, photo 4).

## DISCUSSION

Changes occuring in the ultrastructure composition and photosynthetic activity of chloroplasts in senescence of tobacco leaves have been presented in this paper. The present studies concerning the process of senescence do not give a clear picture of correlation of the occuring changes. The reason of it seems to be the variety of the plant material used in different and often unspecified growth periods of leaves, as well as different ways of expressing the results of the studies. The changes in the ultrastructure of chloroplasts of tobacco leaves do not basically differ from those described for the leaves and cotyledons of other plants. One of the symptoms of chloroplast degeneration in senescence is their volume shrinkage. This was stressed by Dodge (1970) in the case of senescent chloroplasts of birch leaves, Młodzianowski and Ponitka (1973) for chloroplasts of parsley leaves and Ljubešić (1968) for chloroplasts of *Nicotiana rustica*. At the same time decomposition of the lamellar system and volume increase of plastoglobuli takes place, as found by other authors. Stroma lamellae breakdown first, then grana stacks. This kind of decomposition of the lamellar system of chloroplasts corresponds to type A of the thylacoid decomposition distinguished by Młodzianowski (1974). The formation of a temporaly different membrane system is characteristic for two other types distinguished by this author. Volume increase of plastoglobuli accompanying the degradation is, as suggested by Ikeda and Ueda (1964), Barton (1966), Lichtenthaler and Sprey (1966), connected with accumulation of lipids occurring as a result of the breakdown of the plastid membrane system. Morphological changes in the organization of the lamellar system are reflected in the chemical composition of the membranes. Proteins constitute 50% of lipoproteids of chloroplast lamellae (Lichtenthaler and Park 1963). Beside structural proteins in chloroplasts there occur soluble proteins. They are largely represented by the so-called fraction 1, which is characterized by ribulose-1,5-diphosphate carboxylase activity and which catalize photosynthetic carboxylation (Lyttleton and Ts'o 1958). Protein fraction 1 was distinguished as one of two soluble protein fraction of spinach leaves (Wildmann and Bonner 1947, after Woolhouse, 1967). Part of fraction 2 components are also localized in chloroplasts and they contain ferredoxin (Brady et al., 1971). Brady et al. (1971) showed that the decrease of protein synthesis during senescence of chloroplasts proceeds gradually starting with fraction 1 through lamellae protein to fraction 2. Remy's (1971) studies showed that lamellar protein of chloroplasts is heterogenic. This author separated it gelelectrophoretically into a number of components and showed that some of them are related to Photosystem I and others to Photosystem II. Similar preparation of proteins was also obtained in this paper. Moreover,

it was found that first of all protein components connected with Photosystem I disappear with progressing senescence of chloroplasts. Degradation of grana stacks and simultaneous disappearance of stroma lamellae is also strictly connected with changes occuring in the content of galactolipids. They constitute about 80% lipids in lipoproteid lamellae of chloroplasts (Wintermans, 1960; Park and Pon, 1963). The content of these compounds both MGDG and DGDG decreases with senescence of leaves, while MGDG undergoes a faster degradation. A decrease in the content of both galactolipids and a change in their proportion was also found by Ferguson and Simon (1973) in senescent discs cut out from cucumber cotyledons as well as by Harnischfeger (1973) for pumpkin cotyledons. Anderson et al. (1974) found that galactolipase decomposes MGDG faster than DGDG, which may be the reason of the change of their relationship. The distribution of the individual galactolipids in thylakoid is still controversial. In the opinion of Kenyon and Stanier (after Wintermans, 1971) DGDG is connected with Photosystem II activity, so it should be localized in grana stacks (Anderson and Boardman 1966). Slower DGDG decomposition would thus be connected with longer preserved grana than stroma lamellae during aging. Changes in the ultrastructure and chemical composition of chloroplasts occuring during senescence were corelated with the decrease in photosynthetic activity of these organelles. The dependence of photosynthetic rate on the age of leaves was described for many plant species. Singh and Lal (1935) had already shown that young leaves of wheat, sugar cane and flax are characterized by higher photosynthesis activity than old ones. This was then confirmed for tobacco, maize, beet, and barley (Šesták and Čatský, 1962; Šesták, 1963; Thorne, 1963; Kisaki et al., 1973). It appears from the studies of Freedland (1952), Richardson (1957), Hardwick et al. (1968), Wada (1968), Jewiss and Woledge (1967) and Hernandez-Gil and Schaedle (1973) that photosynthetic activity begins to decrease after reaching full maturity by leaves. The studies presented in this paper showed that photosynthetic rate decrease resulted from a decrease in Photosystem I and II activity with the progress of senescence. It was also shown that Photosystem I undergoes an earlier degradation. Attention to a decrease of Photosystem I particles, as compared with the amount of Photosystem II particles along with maturing and aging of spinach and radish leaves, was already drawn by Šesták (1968). This author also suggested that this fact was the reason of the decrease in photosynthetic rate with the age of leaves. A decrease in Photosystem II activity (Hill reaction) in senescence of pumpkin cotyledons was earlier found by Harnischfeger (1974). A more rapid decrease in Photosystem I activity in comparison with that of Photosystem II, as shown in this paper, is correlated with faster decomposition of chlorophyll-protein-complex I than of chlo-

rophyll-protein-complex II. This is closely connected with earlier degradation of stroma lamellae observed in electron microscope, as compared with grana lamellae. The obtained results confirm therefore the generally known fact (Anderson and Boardman 1966) of Photosystem I localization in stroma lamellae, whereas that of Photosystem II in grana, although the studies from recent years (Park and Sane 1971) suggest that grana also demonstrate a slight Photosystem I activity. A decrease in photosynthetic activity, as suggested by Hernandez-Gil and Schaedle (1973), also results from decreased capacity to ATP synthesis. These authors observed a gradual decrease in the amount of ATP formed on the way of cyclic photophosphorylation as early as full leaf expansion of cottonwood leaves. The studies of this paper have given similar results. Moreover, it was shown that the amount of ATP formed on the way of non-cyclic photophosphorylation was also reduced with senescence. However, no correlation between ATP formation and the activity of the individual Photosystems was observed.

The author wish to thank Dr J. Bednara for preparing the electron micrographs.

## REFERENCES

Anderson J. M., Boardman N. K., 1966. Biochim. Biophys. Acta 112: 403—421.
Anderson M. M., McCarty R. E., Zimmer E. A., 1974. Plant Physiol. 53: 699—704.
Aouni M. H. El., Mousseau M., 1974. Photosynthetica 8: 78—86.
Arnon D. J., 1949. Plant Physiol. 24: 1—15.
Avron M., 1960. Biochim. Biophys. Acta 40: 257—272.
Barton R., 1966. Planta 71: 314—325.
Barr R., Crane F. L., 1967. Plant Physiol. 42: 1255—1263.
Birecka H., Dakić-Włodkowska L., 1966. Acta Soc. Bot. Pol. 35: 637—662.
Brady C. J., Patterson B. D., Heng Fong Tung, Smillie R. M., 1971, [in]: Autonomy and Biogenesis of Mitochondria and Chloroplasts, eds. N. K. Boardman, A. W. Linnane, R. M. Smillie, North Holland Publishing Co., Amsterdam—London, 453—465.
Butler R. D., 1967. J. Exp. Bot. 18: 535—543.
Chichester C. D., Nakayama T. O. M., 1965, [in]: Chemistry and Biochemistry of Plant Pigments, ed. T. W. Goodwin, Academic Press, London and New York, 439—457.
Chrastil J., 1956. Cs. Biologie 5: 337—343.
Dodge J. D., 1970. Ann. Bot. 34: 817—824.
Ferguson C. H. R., Simon E. W., 1973. J. Exp. Bot. 24: 307—316.
Fiske C. H., Subbarow Y., 1925. J. Biol. Chem. 66: 375—400.
Fletcher R. A., Osborne D. J., 1965. Nature 207: 1176—1177.
Freedland R. O., 1952. Plant Physiol. 27: 685—690.
Gej B., 1966. Acta Soc. Bot. Pol. 35: 209—224.
Goodwin T. W., 1958. Biochem. J. 68: 503—511.

Griffiths W. T., Threlfall D. R., Goodwin T. W., 1968. Eur. J. Biochem. 5: 124—132.
Gyldenholm A. O., Whatley F. R., 1968. New Phytol. 67: 461—468.
Hardwick K., Wood M., Woolhouse H. W., 1968. New Phytol. 67: 79—86.
Harnischfeger G., 1973. J. Exp. Bot. 24: 1236—1243.
Harnischfeger G., 1974 a. Z. Pflanzenphysiol. 71: 301—312.
Harnischfeger G., 1974b. J. Exp. Bot. 25: 269—276.
Hernandez-Gil R., Schaedle M., 1973. Plant Physiol. 51: 245—249.
Ikeda T., Ueda R., 1964. Bot. Mag. 77: 336—341.
Jeffrey R. N., Griffith R. B., 1947. Plant Physiol. 22: 34—41.
Jewiss O. R., Woledge J., 1967. Ann. Bot: 31: 661—671.
Kisaki T., Hirabayashi S., Yano N., 1973. Plant Cell Physiol. 14: 505—514.
Larson P. R., Gordon J. C., 1969. Am. J. Bot. 56: 1058—1066.
Leech M. R., Rumsby M. G., Thomson W. W., 1973. Plant Physiol: 52: 240—245.
Lichtenthaler H. K., Park R. B., 1963. Nature 198: 1070—1072.
Lichtenthaler H. K., Sprey B., 1966. Z. Naturforsch. 21b: 690—697.
Lichtenthaler H. K., 1969. Z. Naturforsch. 24 b: 1461—1466.
Ljubešić N., 1968. Protoplasma 66: 369—379.
Lyttleton J. W., Ts'o P. O. P., 1958. Arch. Biochem. Biophys. 73: 120—126.
Młodzianowski F., Kwintkiewicz M., 1973. Protoplasma 76: 211—226.
Młodzianowski F., Ponitka A., 1973. Z. Pflanzenphysiol. 69: 13—25.
Młodzianowski F., 1974. Rozprawa habilitacyjna, Uniwersytet im. A. Mickiewicza, Poznań.
Mothes K., 1960. Naturwissenchaften 47: 337—351.
Park R. B., Pon N. G., 1963. J. Mol. Biol. 6: 105—114.
Park R. B., Sane P. V., 1971. Ann. Rev. Plant Physiol. 22: 395—430.
Pohl P.., Glasl H., Wagner H., 1970. J. Chromatog. 49: 488—492.
Remy R., 1971. FEBS Letters 13: 313—317.
Richardson S. D., 1957. Acta Bot. Neerl. 6: 445—457.
Roughan P. G., Batt R. D., 1968. Anal. Biochem. 22: 74—88.
Sane P. V., Goodchild D. J., Park R. B., 1970. Biochim. Biophys. Acta 216: 162—178.
Šesták Z., Čatský J., 1962. Biol. Plant. 4: 131—140.
Šesták Z., 1963. Photochem. Photobiol. 2: 101—110.
Šesták Z., Čatský J., 1967 [in]: Le chloroplaste croissance et vieillissement, ed. C. Sironval, Masson et Cie, Paris, 213—262.
Šesták Z., 1968—1969. Carnegie Institution Year Book 68, 572—573.
Shaw M., Battacharya P. K., Quick W. A., 1965. Can. J. Bot. 43: 739—746.
Singh B. N., Lal K. N., 1935. Ann. Bot. 49: 291—307.
Smillie R. M., 1962. Plant Physiol. 37: 716—721.
Tendille C., Gervais C., 1963. Ann. Physiol. Vég. 5: 193—201.
Thorne G. N., 1963. Ann. Bot. 27: 155—174.
Wada Y., 1968. Bot. Mag. Tokyo, 81: 25—32.
Wellburn A. R., Hemming F. W., 1966. [in]: Biochemistry of Chloroplasts, ed. T. W. Goodwin, Academic Press, London and New York, t. 1, 173—180.
Whitfield D. M., Rowan K. S., 1974. Phytochemistry 13: 77—83.
Wintermans J. F. G. M., 1960. Biochim. Biophys. Acta 44: 49—54.
Wintermans J. F. G. M., 1971. Biochim. Biophys. Acta 248: 530—535.
Wollgiehn R., 1967. Symp. Soc. Exp. Biol. XXI "Aspects of the Biology of Ageing", Cambridge University Press, 231—246.
Wolf F. T., 1956. Am. J. Bot. 43: 714—718.

Woolhouse H. W., 1967. Symp. Soc. Exp. Biol. XXI "Aspects of the Biology of Ageing", Cambridge University Press, 179—214.
Zurzycki J., 1955. Acta Soc. Bot. Pol. 24: 27—63.

*Author's address*
*Dr. Danuta Wolińska*
*Institute of Biology,*
*M. Curie-Skłodowska University*
*Akademicka 19; 20-033 Lublin, Poland*

## *Funkcjonalne i strukturalne zmiany w chloroplastach starzejących się liści tytoniu*

Streszczenie

Zbadano współzależność między strukturą i funkcją chloroplastów starzejących się liści tytoniu. Na podstawie obserwacji struktury chloroplastów w mikroskopie elektronowym potwierdzono wyniki innych autorów o wcześniejszej degradacji lamell stromy w porównaniu z granami. Wykazano, że procesowi temu towarzyszą zmiany w zawartości galaktolipidów (przede wszystkim MGDG) oraz wcześniejszy rozpad białka lamellarnego związanego z Fotosystemem I. Konsekwencją tego jest spadek aktywności fotosyntetycznej liści oraz wcześniejszy zanik aktywności Fotosystemu I.