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REVIEW

The development of chloroplast structure during leaf ontogeny

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Abstract

Advances achieved during last fifteen years in the understanding the development of chloroplast ultrastructure during natural leaf ontogeny are summarized. Life span of a typical C_3 mesophyll cell chloroplast is outlined and placed into the scheme of cyclic plastid interrelationships. Possible modifications of this development by stresses, environmental factors or experimental treatments are also shown.

Additional key words: environmental effects; leaf life span; stresses.

Chloroplast development

"Chloroplast biogenesis is a fascinating area of plant biology", wrote Link (1991). The development of these photosynthetic organelles has been studied from structural, biochemical, genetic, and molecular points of view. The majority of higher plants' chloroplasts is localized in the cells of leaf chlorenchymas. Lawlor (1993) gives a very instructive semi-quantitative analysis of the photosynthetic apparatus in a "mean" higher plant leaf. During the life span or ontogeny of the leaves, plastids in the cells of various leaf tissues go through their specific developmental pathways (see Virgin and Egnéus 1983). From the point of view of photosynthesis studies, the transformation of proplastids under natural light/dark conditions into fully functional chloroplasts of leaf mesophyll cells, and senescence of these chloroplasts (their transformation into gerontoplasts) are the most important events of this development. This developmental sequence was characterized in detail by Whatley (1978) in the framework of her theory of cyclic plastid development (see Fig. 1). The leaves in which chloroplasts develop, emerge, expand, mature, turn themselves from importing into exporting organs, and finally age and fall (Woolhouse 1982). Rapid

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transformation of etioplasts in the cells of dark grown plants into chloroplasts after irradiation, although it serves frequently as a model of chloroplast development, differs in some extent from the above mentioned developmental pathway (see, *e.g.*, Leech 1984, 1986, Ougham and Davies 1990). In the present review, this "greening" will be left aside as far as it will be possible. Frequently, just the senescence (ageing)

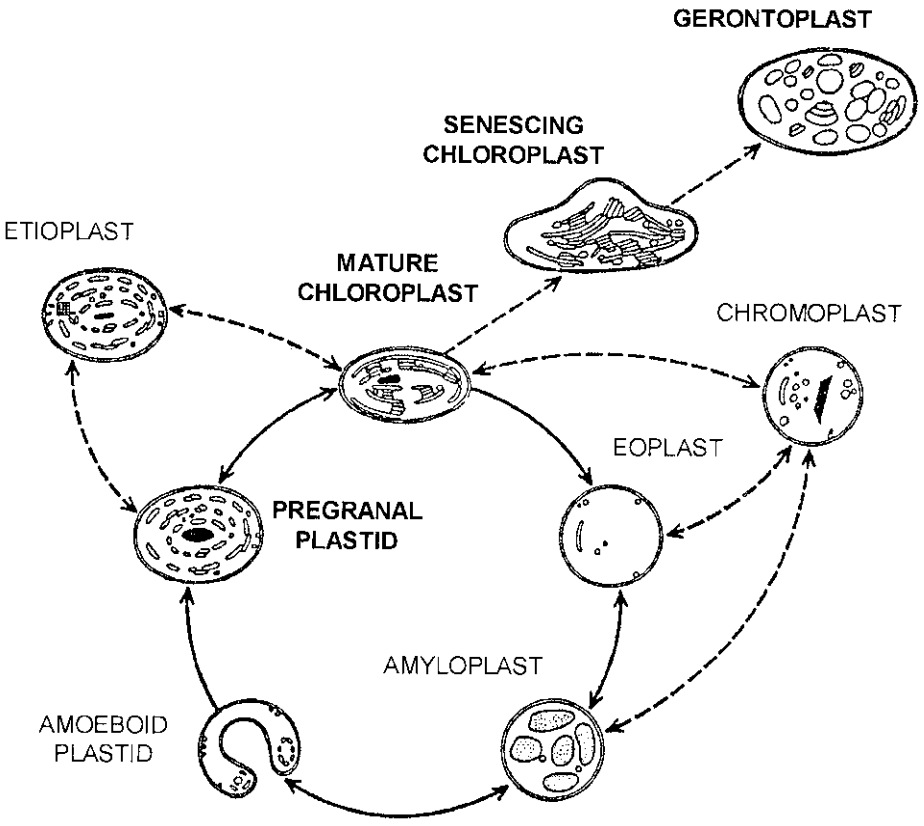

Fig. 1. Cyclic plastid development. Modified from Thomson and Whatley (1980). The part of plastid development which is dealt with in this review is emphasized.

of the leaves and the chloroplasts in them are studied in detail (see, *e.g.*, Matile 1992 and Hudák 1997 for reviews). Molecular biology of leaf senescence was reviewed recently by Buchanan-Wollaston (1997). Sitte (1977) formulated the concept of "gerontoplast", senescent plastid without functional DNA, not able of further transformations, and therefore the final stage of plastid developmental interrelationships. The gerontoplasts contain altered remnants of the system of photosynthetic membranes—thylakoids, and large part of their volume is occupied by lipoid vaste inclusions—plastoglobuli. However, the term "gerontoplast" has not been used frequently. The senescence of a leaf is commonly caused by shading of the

leaf on the plant and in the canopy but it may also be started by developmental changes taking place elsewhere in the plant (growth of younger leaves, formation of seeds) or by changing environmental factors, especially by shortening daylength in autumn. Nevertheless, leaf photosynthetic activity as well as the structure and composition of leaf chloroplasts develop gradually during the whole leaf ontogeny (see Čatský and Šesták 1997, Hudák 1997).

Thirteen years ago, in the monograph on changes in photosynthesis during leaf development (Šesták 1985), I attempted to summarize the knowledge of structural changes taking place in the chloroplasts during normal leaf development, from leaf emergence to its abscission, under diurnal light/dark cycle (Kutík 1985). In the present article, I shall review more recent literature relevant to this topic, beginning in most cases with papers dated in 1982. My attention has been concentrated on chloroplast ultrastructure, observed by electron microscopy and evaluated using stereological methods. This ultrastructural development of the chloroplasts has rarely been comprehensively treated. However, according to my opinion, gradual developmental changes of the chloroplast structure during leaf ontogeny must be taken into account in all photosynthetic studies. Moreover, during leaf development, structure/function relationships in the chloroplasts are manifested. Practical importance of such information for increasing photosynthetic productivity of various crop plants by plant breeding or growing is also obvious.

Development of chloroplast structure during life span of the leaves

During last fifteen years, broad material concerning chloroplast structure has been accumulated. In this time, distinguishing between cell and chloroplast ultrastructure and substructure (or supramolecular structure—see Kutík 1985), lost its sense. Various levels of biological, especially membrane structure, have became interconnected by emerging knowledge of protein (and other) macromolecules' biosynthesis, targeting, and functioning. The observation of three-dimensional structure of living chloroplasts by means of confocal scanning laser microscopy (van Spronsen *et al.* 1989) filled up traditional gap between light and electron microscopy of the chloroplasts. Wide application and improving of stereological methods in electron microscopic study of the chloroplasts (see, *e.g.*, Fagerberg 1983, 1984, Milashvili and Gamaleï 1985) has brought considerable advance in the evaluation of chloroplast structure and development. In the period mentioned, several important, more general insights into the chloroplast development emerged.

Whatley *et al.* (1982) studied, using the high voltage transmission electron microscopy, spatial establishment of chloroplast thylakoid system in French bean (*Phaseolus vulgaris*) primary leaves. Such works have remained rather rare. Silaeva (1994), on the basis of her studies of "thick" sections of sugar beet, maize, and wheat leaf chloroplasts, supposes "near-granal thylakoids" as a specific part of the thylakoid system, connecting grana with intergranal, non-appressed thylakoids. According to Albertsson (1995), the thylakoid membranes are divided into three main domains: the stroma lamellae (intergranal thylakoids), the grana margins, and the grana core

(thylakoid partitions). Linear electron transport occurs in the grana while the cyclic one is restricted to the intergranal thylakoids. The grana (core plus margins) represent about 80 % of all the thylakoid membranes, the stroma lamellae account for the remaining 20 %. However, this ratio, derived from the material of several plant species obtained by several authors, concerns probably mature chloroplasts only. Mustárdy (1996) recapitulated three-dimensional models of thylakoid arrangement in higher plant chloroplasts. According to him, the helically arranged granal system allows an efficient lateral separation of accumulation of protons in the grana from their utilization (*via* ATP-synthase) in the intergranal thylakoids. The multiple connections of granal and intergranal thylakoid membranes may also facilitate rapid diffusion of membrane components between both membrane regions. In fact, all the thylakoid lumina in a chloroplast form only one, immensely complicated compartment.

New evidence for cyclic plastid developmental interrelationships (see Whatley 1978) have emerged. The division of mature chloroplasts or chloroamyloplasts in the cells living more than one vegetation season, rejected by most of earlier authors (see, *e.g.*, Gamalcï and Kulikov 1978), was proved by Sagisaka (1993a,b, 1994a,b). So called "plastid initials" are formed in the cells of green cortex of various trees as well as in their leaf and flower bud cells during winter and early spring. The plastid initials, small vesicles with double envelope and almost without any internal structures, arise by budding of the chloroplasts or chloroamyloplasts. They are present in the cells contemporarily with well differentiated plastids—the occurrence of various plastid types in the same cell was also rejected earlier—and they develop into mature chloroplasts or chloroamyloplasts. Similar observations were already made by Miroslavov and Alekseeva (1990) in *Taxus* needles. During mesophyll cells´ life, their chloroplasts are at least partially renewed. In October-January, a part of the chloroplasts (senescent ones but with well organized system of thylakoids) divides. During winter and early spring (January-April), some couples of the chloroplasts merge and other chloroplasts are destroyed. These changes take place in the needles of current year as well as in those of older shoots. Also Endler *et al.* (1990) observed in the needles of *Pinus sylvestris* well differentiated chloroplasts and proplastids in the same cells.

Casadoro *et al.* (1984) closed their many years´ studies of "lightly stained" thylakoid membranes containing "dark", electron dense loculi with the conclusion that this type of stainability of the system of thylakoids is most probably connected with an early step of the chloroplast development in certain environments, *e.g.*, in aquatic plants. Its reason is probably not the presence of endogenous tannins or chloroplast catechol oxidase. Also Varkey and Nadakavukaren (1982) observed in basal, slowly developing parts of young *Coleus* leaves the mesophyll cell chloroplasts with light thylakoid membranes and dark loculi, connected with "dense-staining inclusion bodies" containing reserve proteins and lipids. In apical, faster developing parts of the same leaves, the chloroplast ultrastructure was of the current type.

In several laboratories chloroplast structural development has been traditionally studied. Mokronosov (1983) summarizes extensive structural and functional studies of leaf and plant photosynthesis made in his laboratory mainly on potato plants. He

presents many quantitative values concerning chloroplast development, *e.g.*, mean chloroplast number per cell, mean chloroplast volume, or mean number of chlorophyll (Chl) molecules per chloroplast. Differences between palisade and spongy parenchyma cells are stressed: palisade cells form the main leaf chlorenchyma that contains 65-70 % of all leaf chloroplasts. Laverycheva (1983) studied stereologically the ultrastructure of palisade and spongy cells' chloroplasts of three spring ephemeroid herb species and two herbaceous species with a season heterophylly. The leaves just finishing growth and these at the end of April or at the end of June (in heterophyllous species) were evaluated. Irrespective of the species, in mature ephemeroid leaves and in the spring generation of heterophyllous herb leaves the chloroplasts of "sun type" with small grana (see, *e.g.*, Lichtenthaler *et al.* 1984) are present. During ageing of ephemeroid leaves and in the summer generation of heterophyllous herb leaves "shade type" chloroplasts are formed: volume density of thylakoids increases from about 30 to 70 %, almost entirely by growth of the grana. There are no substantial differences between the chloroplasts in palisade and spongy parenchyma cells. Similar studies were performed also by Eliáš and Čiamporová (*1986*, *1987*). In forest hemi-ephemeroids, *Dentaria bulbifera* and *Symphytum tuberosum*, after "canopy closure" during spring, leaf mesophyll chloroplasts acquired the "low light" character (more developed system of thylakoids, larger grana, more of Chl *b*, less of starch, but surprisingly also less plastoglobuli) comparing with leaves before "canopy closure". In young, mature, and overwintering leaves of *Oxalis acetosella*, young ("high light"), mature ("low light"), and senescent chloroplasts were found by these authors.

Valanne and Valanne (1984) followed, not quantitatively, the development of birch (*Betula pubescens*) leaf chloroplasts from bud opening to leaf maturity. In young chloroplasts, they observed light thylakoid membranes and dark loculi (see Casadoro *et al.* 1984). Aro *et al.* (1985) studied stereologically diurnal and seasonal changes in the chloroplast ultrastructure of *Deschampsia flexuosa* leaves and found changes corresponding to those summarized by Kutík (1985). According to Pihakaski (1988), in the leaves of the nordic evergreen *Diapensia laponnica* (always two youngest mature leaves on the shoot), the largest chloroplasts of the flattest shape are present in summer whereas in winter the chloroplasts are smaller and roundish. Volume density of starch inclusions peaks in June, in winter the chloroplasts do not contain starch. Largest grana from many thylakoids are formed in August and September when leaf photosynthetic rate is high. However, Nurmi (1985) found in the leaves of *Brassica, Sisymbrium*, and *Tanacetum* the maximal photosynthetic rate sooner, when the chloroplasts had many small, narrow grana of few thylakoids. According to Nurmi (1990), in ageing leaves of *Brassica rapa* ssp. *oleifera* (under high or low irradiance), density of photosystem 2 (PS2) particles decreases but dimensions and density of peripheral light-harvesting complex 2 (LHC2) increase, which is paralleled by growth of the grana. Ruuska *et al.* (1994) studied the development of photosynthetic apparatus including chloroplast ultrastructure during early ontogeny of birch leaves, whereas Pääkkönen *et al.* (1995) followed chloroplast development in senescing birch (*Betula pendula*) leaves. They observed no increase

in number or dimensions of plastoglobuli in the chloroplasts. Senescent birch chloroplasts are roundish and form extensions.

The chloroplasts of woody plants have been often studied during leaf overwintering. Wrischer *et al.* (1986) summarized their earlier results from many studies of this type. Modrušan and Wrischer (1987) studied stereologically the development of chloroplast ultrastructure in leaves of blackberry (*Rubus fruticosus*) together with pigment content and photosynthetic activity of leaves. In blackberry, there are two generations of leaves during a year: those developed in spring die in autumn whereas those grown during summer and autumn overlive winter and die during the spring of the next year. As concerns chloroplast ultrastructure, relatively small differences in volume density of granal and intergranal thylakoids during a year are surprising. Peripheral reticulum (more typical for chloroplasts of C_4 plants) is temporarily formed in blackberry chloroplasts during winter. Chloroplast development in overwintering leaves of cherry laurel (*Prunus laurocerasus*) is strongly accelerated by proximity of leaf nectaries which probably concentrate saccharides (Muraja *et al.* 1990). Only in the cells close to the nectaries, the chloroplasts developing in autumn complete their development in the same year whereas the chloroplasts in other parts of the leaves are fully developed in next spring. In the stroma of senescent cherry laurel chloroplasts, iron binding phytoferritin is accumulated.

Chloroplast overwintering has been studied also by other authors. Hudák and Salaj (1986) followed seasonal changes of chloroplast structure in mesophyll cells of the green parts of first year variegated leaves of *Aucuba japonica*. They observed chloroplasts with large starch inclusions (chloroamyloplasts) in April, senescent chloroplasts with many plastoglobuli in August, and typical chloroplasts with well developed system of thylakoids surprisingly in November and January. In cherry laurel Hudák and Salaj (1990) observed during spring chloroamyloplasts whereas in summer, chloroplasts with a well developed system of thylakoids were present. In autumn, diminishing of starch inclusions in the chloroplasts was apparent, and in winter senescent chloroplasts with dilated thylakoids and large plastoglobuli were seen. These chloroplasts were not grouped around cell nucleus as it is frequent during winter. Ruetze *et al.* (1987) followed chloroplast senescence in mesophyll cells of the needles of a rare conifer ("living fossil"), *Metasequoia glyptostroboides*. These needles fall every winter similarly as in European larch. During their autumnal yellowing, decrease of starch content, weak dilatation of intergranal thylakoids, reduction of the system of thylakoids, dilatation of granal thylakoids, increase in number (more or less not in the size) of the plastoglobuli, diminishing of the chloroplasts and acquiring of a roundish shape, and finally the destruction of the chloroplasts occur successively.

Rascio *et al.* (1985) and Polettini *et al.* (1986) studied the chloroplast development in leaves of spinach. In autumn, this development (as well as growth of the spinach plants) is slower than in summer, and prolamellar bodies, typical for plastids developing in dark, persist in the chloroplasts even in light. In both seasons, intrathylakoid crystals [consisting probably of the ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) protein] are present in the chloroplasts until leaf

maturity and full photosynthetic activity. The chloroetioplasts with persisting prolamellar bodies in young leaf parts and with light thylakoid membranes and dark loculi even in mature leaf parts were observed by Mariani Colombo *et al.* (1983a) in mesophyll cells of the leaves of sea vascular plant *Posidonia oceanica*. They also studied (1983b) mesophyll cell chloroplast development during leaf ontogeny in a fern, *Phyllitis scolopendrium*. The chloroplasts from base, middle part, and apex of the leaves were followed in six leaf ontogenetic stages, from folded to mature leaves. In ferns, the system of thylakoid membranes with Chl is formed even in dark similarly as in conifers sprouting in the dark. Prolamellar bodies are present in these chloroplasts in light as well as in the dark. Temporary formation of long grana is similar to that in mature chloroplasts of green algae. The authors stressed that *Pteridophyta* are a suitable subject for studies on leaf cells' growth and differentiation because their shoots have only one apical initial cell. Mariani *et al.* (1984) followed chloroplast differentiation in *Ephedra distachya*, a gymnosperm near to angiosperms. Also chloroplast development is intermediary here: in dark conditions, chloroetioplasts are formed in *Ephedra* cotyledon cells whereas in shoot apex cells typical chloroplasts differentiate. From the phylogenetic point of view, chloroplast development in *Cycadaceae* is also interesting (Medeghini Bonatti and Sabato 1984, Medeghini Bonatti and Baroni Fornasiero 1990, Morassi Bonzi *et al.* 1992). Characteristic ultrastructural features of leaf chloroplasts in these gymnosperms are various precursors of thylakoid membranes (prolamellar bodies in the light, membrane bound crystalline bodies in young chloroplasts) and giant grana (up to 180 thylakoids) in mature chloroplasts. The reasons for their occurrence are probably slow development of cycas leaves and their specific shade character.

Many recent studies of chloroplast development during leaf ontogeny have been made using several important crop plants. A detailed stereological study of the development of chloroplasts and other cell organelles in palisade parenchyma cells of expanding sunflower leaves was done by Fagerberg (1984). The leaves long 10 (phase 1), 45 (phase 2), and 150 (phase 3 - mature leaves) mm were compared. Volume density of the chloroplasts in the cells increases three times from phase 1 to 2, from 2 to 3 it is more or less constant. (During this period, volume density of cell nuclei decreases owing to cell volume growth whereas that of mitochondria is more or less constant from 1 to 2 and decreases strongly from 2 to 3.) In the mitochondria, surface to volume ratio of the system of their internal membranes does not change substantially during leaf growth whereas in the chloroplasts, surface to volume ratio of both granal and intergranal thylakoids increases steadily. Whereas Fagerberg (1984) studied in sunflower leaves chloroplast maturation only, Schmidt (1988) followed, on the contrary, chloroplast senescence and gerontoplast formation in bean (*Vicia faba*) leaf mesophyll cells. When yellowing bean leaves lose 95 % of their Chl, the chloroplasts turn to the gerontoplasts having only several non-appressed thylakoids and many plastoglobuli containing carotenoids. These gerontoplasts aggregate with mitochondria and cell nuclei. Gerontoplast thylakoid membranes contain many LHCs and have a fairly high photochemical activity. The whole chloroplast ultrastructural development, in pea leaves, was recorded by Somersalo and Aro (1987). Dimensions of grana and their relative area on chloroplast sections

increase during leaf ontogeny. The largest starch inclusions are present in just mature leaves whereas the largest plastoglobuli appear in the oldest leaves where the starch inclusions are negligible. In the oldest, yellow leaves, the chloroplasts become shrunken. Nii *et al.* (1988) followed, not quantitatively, the senescence of chloroplasts in palisade parenchyma cells of peach leaves. In fully green leaves (in September), moderately senescent chloroplasts with slightly dilated thylakoids and large plastoglobuli are present. With a decrease of leaf Chl content during autumn, chloroplast senescence progresses. Fluorescence microscopy shows that chloroplast DNA is degraded during leaf senescence, and disappears completely at leaf death (in late November). In a stereological and biochemical study of chloroplast development during soybean leaf ontogeny, Xu *et al.* (1993) recorded relatively large amounts of starch even in young chloroplasts. Maximum of its volume density was simultaneous with maximal volume density of thylakoids whereas plastoglobuli occurred in the chloroplasts beginning from their maturity. During chloroplast senescence, Hill reaction activity, content of Chls, and photosynthetic rate of the leaves decreased successively.

We studied (Kutík *et al.* 1984, 1988, Kutík 1988) stereologically the development of mesophyll cells' chloroplasts during ontogeny of "primary" (first after cotyledons) and "secondary" (first trifoliate) leaves of *Phaseolus vulgaris* (Fig. 2). In intact plants, volume density of the system of thylakoids (granal and intergranal thylakoids are not distinguished here) increases in very young "primary" leaves, decreases during growth of chloroplast dimensions (the chloroplasts in mature leaves are the largest), and then increases again and attains its main maximum (followed by a final decrease) in the third quarter of leaf ontogeny. First maximum of starch inclusions occurs when the leaves attain their final size, before the maximum of thylakoids, the second maximum occurs in senescent chloroplasts at the end of leaf ontogeny. Large starch inclusions in the chloroplasts of mature French bean leaves may be the reason of the sharp maximum of photosynthetic activities of the chloroplasts isolated from these leaves because envelopes of the chloroplasts break and so the access of synthetic electron donors and acceptors to their thylakoid membranes increases. Volume density of the plastoglobuli increases during leaf ontogeny, most quickly in its last quarter. In "secondary" bean leaves, the development of chloroplasts is more or less similar to that in "primary" leaves. A more complex shape of their blades complicates the comparison. In decapitated bean plants, the ontogeny of "primary" leaves is prolonged considerably, probably owing to an accumulation of cytokinins formed in intact root systems. The growth of plastoglobuli in chloroplasts is slowed down whereas strong accumulation of starch in them is the reason for shift of their maximum size into the senescent phase of leaf ontogeny. All these studies were accomplished on palisade parenchyma cells' chloroplasts. However, there are no substantial differences between the chloroplast ultrastructure in palisade and spongy cells of leaf mesophyll of the same age (Kutík 1989). In mesophyll cells of French bean cotyledons, the development of chloroamyloplasts into gerontoplasts is prolonged by plant decapitation over cotyledons (Wilhelmová *et al.* 1997).

Monocotyledonous crops wheat, barley, maize, and rice are frequent subjects of the studies on chloroplast development. In these plants with long narrow leaves,

plastid structure in successive leaf blade segments is usually studied instead of studying corresponding parts of the leaves of different ages.

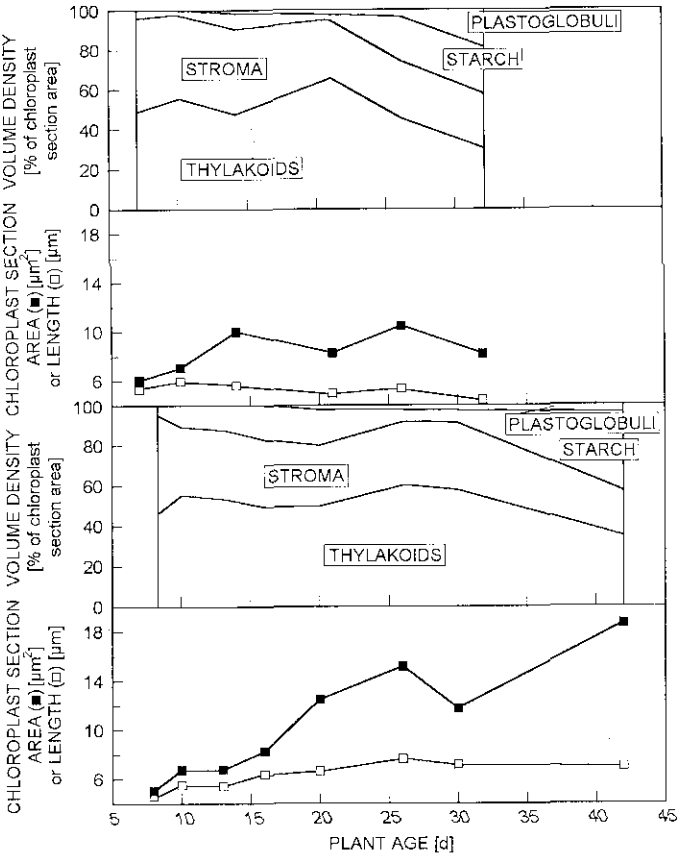

Fig. 2. Chloroplast development in palisade parenchyma cells of „primary" leaves of intact (*top*) and decapitated (*bottom*) plants of *Phaseolus vulgaris* L. From Kutík (1997).

Wellburn *et al.* (1982) studied quantitatively the plastid ultrastructure in segments taken from meristematic base to the apex of the first leaf of 7-d-old barley (*Hordeum vulgare*) plants cultivated under fairly low irradiance. They observed, in accordance with Whatley (1977), successively the eoplasts, amyloplasts, amoeboid plastids, and pregranal and mature chloroplasts: all these types of plastids contained prolamellar bodies. In the eoplast-amyloplast zone, many mitochondria and high level of ATP and 3-phosphoglyceric acid were recorded. In the zone of amoeboid plastids and immature chloroplasts, starch degradation and synthesis of components of the photosynthetic apparatus (Chls and carotenoids) and decrease in contents of ATP and 3-phosphoglycerate were apparent. The synthesis of material for building thylakoid membranes continued in mature chloroplasts. Martinoia *et al.* (1983) followed the chloroplast senescence in mesophyll cells of first leaf of barley, either in natural

conditions or after dark induction. In both variants, chloroplast number per cell decreases considerably less than contents of Chl, RuBPCO, and other proteins. Hence during the senescence of the barley leaves (except its end), chloroplasts as whole organelles were not destroyed but they diminished and lose their Chl and proteins. However, Ono *et al.* (1995) observed in senescing first leaves of wheat (*Triticum aestivum*, from attaining their final size to full yellowing) a decrease of chloroplast number per mesophyll cell (of about 20 %) together with chloroplast diminishing. Both processes are slow at beginning and quick at the end of leaf's life. Also Yamasaki *et al.* (1996) found in *Chenopodium album* leaves of decreasing insertion (*i.e.*, of increasing age) loss of whole chloroplasts in mesophyll cells. Chloroplasts in senescing leaves served as a source of nitrogen for the synthesis of Chl and proteins in higher inserted, younger leaves.

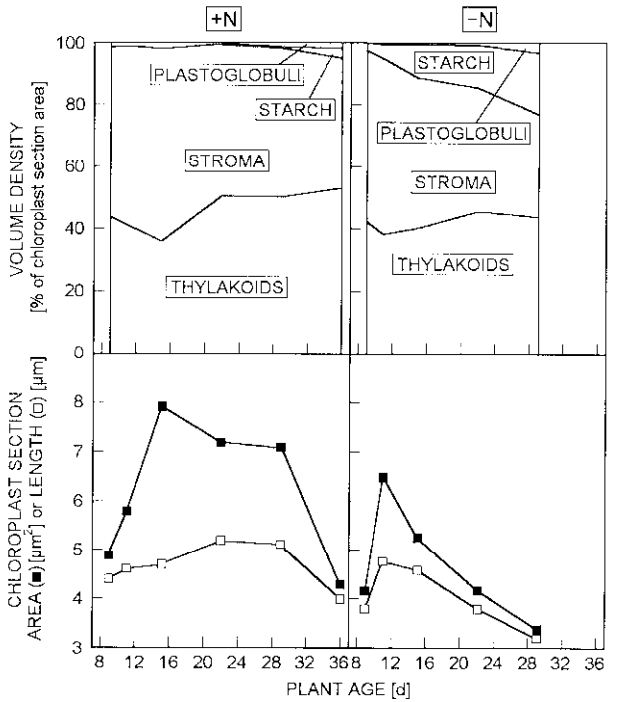

Fig. 3. Chloroplast development in mesophyll cells from the middle third of second leaf of *Triticum aestivum* L. plants developing normally (+N) or under nitrogen deficiency (-N). From Kutík (1997).

In developing wheat (*T. aestivum*) leaf mesophyll chloroplasts, microtubule-like structures were observed (Kutík 1992). Similar cytoskeletal structures were recorded in chloroplasts of green algae and higher plants also by other authors (*e.g.*, Lawrence and Possingham 1984) but the homology with cytoplasmic microtubuli is not clear (Artus *et al.* 1990). Microtubuli-like structures may play a role in orientation of thylakoids during chloroplast development. We studied stereologically chloroplast

ultrastructural development during ontogeny of the second leaf of wheat under nitrogen deficiency (Kutík *et al.* 1993, see Fig. 3). The development of chloroplast ultrastructure and dimensions of mesophyll cells in control wheat plants are similar to those described for chloroplasts of "primary" leaf mesophyll cells of French bean (Kutík *et al.* 1984, 1988, Kutík 1988). However, volume density of starch inclusions in the chloroplasts is very small in control wheat plants.

Wang and Hu (1988) studied mesophyll cell chloroplast ultrastructure, content of Chls, and photosynthetic rate in leaves of maize (*Zea mays*) differing in both their position on the plant and their age. The measurements were several times repeated during ontogeny of maize plants. The content of Chls as well as the photosynthetic rate were in close positive linear correlations with the number of chloroplast thylakoids per granum. In the leaf under maize ear, there was the most developed system of granal and intergranal thylakoids and the largest grana. This leaf had in its maturity also the maximal content of Chls ($a + b$) per unit of leaf area and the largest photosynthetic rate as compared with other leaves on a plant.

In mesophyll cells of third leaf of two new, photosynthetically contrast genotypes of maize and in their hybrids we studied (Kutík and Kočová 1996) stereologically the development of chloroplast ultrastructure and Hill reaction activity. Middle thirds of blade of young, mature, and aged leaves (13, 27, and 41 d after sowing of maize caryopses) were compared. Volume densities of granal and intergranal thylakoids were evaluated separately. In mature and aged leaves, volume density of the thylakoids was larger than in young leaves. In the genotype more efficient in Hill reaction activity, larger volume density of the thylakoids as well as larger volume density ratio of granal/intergranal thylakoids were found when compared with the less efficient genotype. Starch is almost absent in these chloroplasts during the whole leaf development, and plastoglobuli accumulate in the chloroplasts of aged leaves. Volume density of peripheral reticulum, the membrane system typical for C_4 chloroplasts that is not directly connected with primary photosynthetic reactions, is more or less constant during the leaf ontogeny. Shape of the chloroplasts changes during leaf ontogeny from a relatively flat to a more round one.

Chloroplast development in rice (*Oryza sativa*) has also been frequently studied. Hashimoto *et al.* (1989) followed senescence of the photosynthetic apparatus in seedlings of rice, comparing mature and senescent third leaf and mature sixth leaf. They recorded desorientation of thylakoids, decrease in number of starch inclusions, increase in number and size of plastoglobuli, formation of large, shade type grana (from 20 to 30 thylakoids), and, finally, decrease in number and size of the chloroplasts. Kura-Hotta *et al.* (1990) analysed natural senescence of mesophyll cells in rice leaves. They concluded that the decrease in Hill reaction activity during leaf senescence was done mainly by the decrease in chloroplast number per cell and in chloroplast dimensions. In rice plants influenced by nitrogen nutrition, Chonan *et al.* (1991) followed chloroplast development only in the leaves after finishing their growth (day 0). Under normal nitrogen supply, the large starch inclusions present at day 0 disappeared at day 15 when the system of thylakoids was more developed. Decrease in the thylakoids and diminishing of the chloroplasts occurred at the day 34.

In a study on terpene production in *Mentha piperita,* Maffei and Codignola (1990) evaluated quantitatively the chloroplast-microbody-mitochondrium complexes during leaf development. The highest granal/intergranal thylakoid ratio was in the leaves having about one half of their final length, but the most thylakoids per granum (up to 45) were in mature leaves. The number of plastoglobuli per chloroplast section did not increase substantially during leaf senescence but their volume density increased almost one hundred times.

Chloroplasts may also be present in mesophyll cells of flower petals. Vainstein and Sharon (1993) studied their differentiation in petunia and carnation flowers whereas Smith *et al.* (1992) followed their senescence (as a part of flower petal senescence) in flowers of *Dianthus caryophyllus.* As a curiosity let me mention the work by Voskoboinikov and Kamnev (1989) on plastid (pheoplast) senescence in the sea brown alga *Sargassum pallidum,* the thallus of which resembles a higher plant body. In contrast to senescence of a higher plant leaf, even in senescing fyloids of *Sargassum* the plastids multiplicate and contain many ribosomes. The amount of their photosynthetic membranes per cubic micrometer of plastid stroma increases steadily up to the abscission of phyloids.

Environmental or experimental modifications of chloroplast development

The development of chloroplast structure during leaf ontogeny is always influenced by environment. Its most important factors are quality and quantity of irradiation and its diurnal changes, temperature, water potential, mineral nutrition (including carbon dioxide concentration), and quantity and mutual relationships of natural growth regulators. The development of chloroplasts is, of course, strongly modified in plants with C_4 (or, in a lesser extent, CAM) photosynthesis. Among experimental modifiers of chloroplast development, plant decapitation, growth regulators or herbicides, or intermittent irradiation are used most often. The development of chloroplasts has been frequently studied in various nuclear or plastid mutants including also genetically manipulated plants. Environmental factors affecting chloroplasts were recently reviewed by Mostowska (1997): high irradiance, ultraviolet radiation, air pollutants, herbicides, heavy metals, and water stress induce oxidative stress and production of active oxygen species in chloroplasts. From the ultrastructural point of view, accelerated chloroplast senescence (swelling of thylakoids, accumulation of plastoglobuli and eventually of starch) occurs rather uniformly under these circumstances.

Some examples of environmental modifications of chloroplast development (not those concerning differences between mature chloroplasts under various conditions only) will be briefly reviewed here. Differences in chloroplast ultrastructure at various positions of chlorenchyma cells on the area of mature leaf blade are expected, but their extent has not been proved yet. On the contrary, developmental gradients in the chloroplast ultrastructure along growing leaf blades of grass type have been used as examples of chloroplast development (see, *e.g.*, Virgin and Egnéus 1983, Leech 1984, Link 1991).

Control of plastid development (in the sequences containing the chloroplast stage) as a part of plant photomorphogenesis was summarized by Virgin and Egnéus (1983). Schopfer and Apel (1983) described the photoregulation of chloroplast development in context of intracellular photomorphogenesis. Here, diurnal changes in chloroplast ultrastructure connected with changing irradiance must be mentioned because they interfere with developmental changes in the ultrastructure. Differences in dimensions of starch inclusions (minimum in early morning, maximum in early evening) are the most prominent. Absolute surface area of granal and intergranal thylakoids is at night approximately double than during a day because of a rise of chloroplast volume but arrangement or relative dimensions of the grana are not changed during the diurnal cycle (Fagerberg 1983, Aro *et al.* 1985). According to Semenova (1989), dimensions of intramembrane particles in thylakoid membranes change during diurnal cycle in pea and potato leaves. For example, the LHC2 particles are the largest in morning and evening and the smallest in afternoon and the second half of night. In the CAM plant *Sedum telephium*, tubular protein inclusions accumulate in leaf chloroplasts during a day and disappear during a night when these proteins participate in CAM photosynthesis (Santos and Salema 1984). Diurnal regulation of photosynthetic carbon metabolism in C_3 plants was recently reviewed by Geiger and Servaites (1994).

Chloroplast ultrastructural development is considerably modified when intermittent irradiation (*e.g.*, one minute light/one minute darkness) is applied on plants instead of constant irradiation of the same overall duration per day. Thylakoid grana are reduced and irregularly oriented, starch inclusions are much smaller, plastoglobuli are prominent (Naylor and Giles 1982, Maróti and Takács 1983, Takács and Maróti 1984). Under flashing irradiation, plastids develop more or less as etioplasts (Naylor and Giles 1982).

Differences between chloroplasts developing under high or low irradiance ("high light" or "low light", chloroplasts, respectively—see, *e.g.*, Lichtenthaler *et al.* 1984, Nurmi 1990, Makovetskiĭ and Manzhulin 1990) are as follows: "high light" chloroplasts contain more numerous but smaller grana, more starch, and lesser plastoglobuli compared with "low light" ones. High irradiance stimulates chloroplast senescence in older leaves, especially growth of plastoglobuli (Nilsen *et al.* 1988). Under "light stress", lipid-protein particles may be formed instead of plastoglobuli (Ghosh *et al.* 1994). Under supplemental far-red irradiation (5 min at the end of day), tobacco chloroplasts develop with more numerous but smaller grana whereas under red supplemental irradiation, they contain more of larger starch inclusions and less of soluble saccharides in comparison with control without supplemental irradiation (Kasperbauer and Hamilton 1984). In developing leaves of the short-day plant *Perilla ocymoides*, slowly growing and slowly dividing chloroplasts with dark thylakoid loculi and light thylakoid membranes are formed under continuous irradiation whereas under short-day conditions, the chloroplasts of "current" type are present. These differences are connected with different contents of auxins in the leaves (Danilova and Kashina 1995).

Environmental temperature is the second major factor also of the chloroplast development during leaf ontogeny. Huner (1988) reviewed adaptations of chloroplast

thylakoid membranes to low temperatures. Chemical composition of these membranes is very stable, neither increase in membrane fluidity nor changes of protein/lipid ratio occur during plant cold adaptation. Interaction of phosphatidylglycerol with the main pigment-protein complex of thylakoid membranes, LHC2, is probably changed and electron transport in PS1 is enhanced. In rye under cold hardening temperatures, there are thicker cytoplasmic layers in leaf mesophyll cells and more frequent smaller grana in the chloroplasts as compared with normal temperature (Huner *et al.* 1984), *i.e.*, cell and chloroplast development seems to be slowed down. In overwintering cereals, PS1 functions almost exclusively in their chloroplasts and cyclic photophosphorylation occurs, even under snow cover. Lipid/protein ratio is increased in intergranal and "end" granal thylakoid membranes under these conditions (Klimov 1987). Modrušan and Wrischer (1987) observed in *Rubus fruticosus* leaf chloroplasts a temporary formation of peripheral reticulum during winter. Morré *et al.* (1991) induced the same process in discs from leaves of various plant species by lowering temperature to 4-18 °C.

Santarius and Weis (1988) overviewed influences of heat stress on chloroplast thylakoid membranes. Long-term adaptation to heat is achieved by lowering thylakoid membrane fluidity, and as short-term adaptation, migration of PS2 core and inner LHC from grana to intergranal thylakoids occur. Under heat (35-45 °C), the grana disintegrate. Total dissociation of PS2 complexes results in irreversible damage of the chloroplasts. PS1 is much more stable under heat conditions (as well as under cold ones) than PS2.

Chloroplast ultrastructural development is also strongly influenced by plant mineral nutrition (for review, see Repka 1986). Probably the most striking phenomenon is accumulation of starch (formation of large starch inclusions) during chloroplast development under deficiency of nitrogen (Selga *et al.* 1983, Saux *et al.* 1987, Chonan *et al.* 1991, Kutík *et al.* 1993, 1995): plants are underdeveloped, sinks for photosynthates are weak, and starch accumulates in chloroplasts. Leaf and chloroplast senescence are accelerated under these circumstances which is reflected, *e.g.*, by enhanced growth of plastoglobuli in chloroplast stroma. However, Laza *et al.* (1993) did not observe an increase in dimensions of starch inclusions under nitrogen deficiency in rice leaves. They found smaller chloroplasts with a less developed system of thylakoids, and smaller grana. Kutík *et al.* (1995) observed an extensive starch accumulation in sugar beet leaf chloroplasts only when nitrogen deficiency was combined with increased carbon dioxide concentration in air. According to Terashima and Evans (1988), the part of leaf nitrogen allocated in spinach leaves to the chloroplast thylakoids is independent of irradiance and nitrogen supply. Feller and Fischer (1994) reviewed nitrogen metabolism in senescing leaves. According to them, demolition of chloroplasts occurs early whereas mitochondria remain active longer and supply energy for nitrogen remobilisation (from chloroplasts mainly). An attention has been devoted to effects of iron nutrition on chloroplast development, including ultrastructural changes (cf. Pushnik *et al.* 1984, Brecht 1990). 80 to 90 % of overall plant iron is contained in chloroplasts as a part of phytoferritin, iron sulphur proteins, and various heme proteins. Electron dense particles of phytoferritin (a protein binding excess iron ions) form, especially under stress, clusters in

chloroplast stroma. Iron functions as an enzyme cofactor at several steps of Chl biosynthesis, and has a complex and integrating role in chloroplast development and activities. Under iron deficiency, when plant chlorosis may be seen macroscopically, a decrease in number and dimensions of chloroplast grana, and a dilatation of granal thylakoids are observed. Disorganization of chloroplast thylakoid system brought about by iron deficiency may be reverted by additional iron supply (Platt-Aloia *et al.* 1983).

According to Maksymiec *et al.* (1995), excess copper ions induce senescence-like changes in mesophyll cells' chloroplasts of *Phaseolus coccineus* "primary" leaves only after application on the plants with mature "primary" leaves. Accelerated ageing of Norway spruce needles and the chloroplasts in mesophyll cells of them under industrial air pollution was confirmed quantitatively by Wulff *et al.* (1996).

Increasing carbon dioxide concentration in Earth's atmosphere is a new important condition of photosynthesis. First studies of influences of experimentally elevated carbon dioxide concentration in the air on chloroplast ultrastructure and its development have appeared (*e.g.*, Vu *et al.* 1989, Kutík *et al.* 1995, Robertson and Leech 1995). Chloroplast ultrastructure is not strikingly influenced by doubling of recent natural CO_2 concentration. Interestingly, a decrease of chloroplast starch inclusions is seen under such conditions (Robertson and Leech 1995, Kutík *et al.* 1995) as well as a decrease in volume density of thylakoids (Kutík *et al.* 1995).

The processes of chloroplast ultrastructural development are influenced by mutual relationships of phytohormones' concentrations in leaf cells. Cytokinins slow down leaf and chloroplast senescence (Thomas 1982). However, this effect depends on actual leaf and chloroplast age, and on time of cytokinin application (Bassi and Orsenigo 1982, Caers and Vendrig 1986). The ageing of chloroplasts formed during cytokinin treatment is accelerated whereas the ageing of mature chloroplasts is delayed. In young *Pinus ponderosa* cotyledons, thylakoid development, and Chl and protein accumulation in the chloroplasts are hampered by cytokinins because they induce meristemization of cotyledon cells (Mazari and Camm 1993). The cytokinin benzyladenine can revert inhibition of chloroplast development from etioplasts induced in maize by heat stress (Caers *et al.* 1985). Cytokinin effects on chloroplasts were reviewed recently (Nyitrai 1997). The effects similar to those induced by exogeneous cytokinins may be induced in leaf chloroplasts by plant decapitation (see, *e.g.*, Greening *et al.* 1982, Kutík *et al.* 1984). "*Rejuvenation*" *of the chloroplasts in* leaves or cotyledons under detached top of a plant is apparently due to accumulation of root cytokinins in the leaves of decapitated plants. Auxins probably act in photoperiodic regulation of chloroplast ultrastructure (Danilova and Kashina 1995).

Many substances used as herbicides induce accelerated chloroplast senescence, which was demonstrated, *e.g.*, by Hudák and Dekánková (1989) in *Sinapis alba*, or by Maffei and Codignola (1990) in *M. piperita*. The herbicide amitrole (2-amino-1,2,4-triazole) induces formation of unusual long grana from tightly appressed thylakoids which are later transformed into aggregates composed from spherical particles lacking PS1 and PS2 activity (Wrischer *et al.* 1992, Agnolucci *et al.* 1996). Growth retardant chlorcholinchloride induces chloroplast senescence in young green leaves of wheat (Ignat'ev and Kalimulina 1990) whereas in greening etiolated wheat

seedlings, it acts (probably as a structural analog of acetylcholin) synergistically with red radiation in promoting formation of PS2 reaction centres and etioplast/chloroplast transformation (Vasilenko *et al.* 1991).

In the last decade, chloroplast development has often been studied from the viewpoint of molecular biology (cf. reviews by Leech 1986, Akoyunoglou and Argyroudi-Akoyunoglou 1986, Taylor *et al.* 1987, Mullet 1988, Link 1988, Rajasekhar 1991, Smart 1994, Barkan *et al.* 1995, Mayfield *et al.* 1995, *etc.*, and chapters in Pessarakli 1997). Chloroplast ultrastructural development is usually not in the centre of attention there. However, several examples of relationship between this development and control of realization of nuclear and plastid genetic information related to it can be cited here.

During expansion of sugar beet leaves, the chloroplasts in their mesophyll cells divide two or three times, mean diameter of them increases from 1.5 to 4.9 μm, and mean number of DNA copies per chloroplast decreases from 104 to 29. Similar results were obtained for other crop plants (Tymms *et al.* 1983). Distribution of plastid nucleoids in developing chloroplasts in the leaves of oats is given mainly by the pattern of grana formation in the chloroplasts (Hashimoto and Possingham 1989). Thylakoid membranes participate probably also in chloroplast proteosynthesis. According to Filippovich *et al.* (1985, 1994), compartments of the grana (in pea leaf chloroplasts) are formed from cyclic structures on "primary" thylakoids, consisting of mRNA fibrils and polyribosomes. Jagendorf and Michaels (1990) distinguish chloroplast ribosomes (or polysomes) distributed freely in chloroplast stroma, and those bound on the thylakoid membranes as two functionally different ribosome types.

Thylakoid lipids probably play a more active role in the development and maintaining of chloroplast ultrastructure than it was supposed earlier. Substantial decrease in the amount of polyunsaturated fatty acids (in the leaves of an *Arabidopsis thaliana* mutant) is connected with smaller dimensions of the chloroplasts, their higher number per cell, and lesser development of the system of thylakoids (as compared with *Arabidopsis* wild plants, McCourt *et al.* 1987). In the *Arabidopsis* mutant "de-etiolated", leaf and plastid development are uncoupled: in darkness, seedling morphology is normal (not etiolated) but plastids in the leaves develop as etioplasts (Cabrera y Poch *et al.* 1993). In the tobacco mutant "aurea" (deficient in Chl *b*), both chloroplast ultrastructural development and leaf development are retarded as compared with tobacco wild plants (Šiffel *et al.* 1993).

Lohman *et al.* (1994) studied mRNAs from naturally senescing *Arabidopsis* leaves (without studying leaf ultrastructure), in which the beginning of senescence is given by their age. No one of "senescence-down-regulated-genes" codes here for the Chl *a/b* binding proteins or the RuBPCO small subunit. Schulz *et al.* (1993) proved the presence of ubiquitin conjugates with chloroplast proteins in thylakoid membranes of senescing chloroplasts. They suppose a participation of this widespread polypeptide in the turnover of chloroplast proteins. During artificially accelerated leaf senescence in non-yellowing ("stay green") soybean nuclear mutants, leaf chloroplast ultrastructure does not change whereas in normal soybean plants, the chloroplasts in the yellowing leaves senesce rapidly (Guiamét and Giannibelli 1994). Normal

chloroplast development is needed for normal development of palisade parenchyma cells in tomato leaves (Keddie *et al.* 1996).

The development of "dimorphic" chloroplasts in plants with C_4 photosynthesis, especially in maize, has often been studied (cf. review by Rüffer-Turner *et al.* 1984). Wrischer (1989), studying cytochemically PS1 and PS2 activities, described a stepwise differentiation of originally similar mesophyll (M) and bundle sheath (BS) cells' chloroplasts from base to tip of leaf blade in maize. According to Wang *et al.* (1993), in very young leaves of a C_4 dicotyledonous plant, amaranth, the genes for large and small subunit of RuBPCO are expressed in both M and BS chloroplasts. After sink to source transition of leaf tissues (from apex to base of a leaf), RuBPCO occurs in chloroplasts of the BS cells only. Nishioka *et al.* (1993) studied suppression of granal development in BS chloroplasts of NADP-ME C_4 plants maize and *Portulaca grandiflora* (a dicot). They deduce that if these chloroplasts have well developed grana, C_4 acid decarboxylation in them is inhibited by competition for $NADP^+$, reduced by PS2 in the grana to $NADPH + H^+$. According to them, in the NADP-ME C_4 grasses the bundle sheaths are probably derived from procambium, the mesophyll from ground meristem. In the C_4 dicot *Atriplex rosea*, the BS and M cells originate from neighbouring cell layers of the ground meristem. They also do not differ ultrastructurally from each other in young leaves (Liu and Dengler 1994). Roth *et al.* (1996) described the "bundle sheath defective 2" maize mutant having strongly disturbed development of ultrastructure and photosynthesis specific enzymatic activities in BS cells' chloroplasts. They suppose that the development of BS cells and chloroplasts is more sensitive to general defects in photosynthesis as compared with the development of M cells.

Conclusions

The development of chloroplast structure in a mesophyll cell of a C_3 plant during natural leaf development (under diurnal light/dark cycle) may be outlined as follows. After leaf unfolding, the chloroplasts have a system of thylakoid membranes consisting usually from several, more or less parallel layers of unstacked thylakoids bearing small grana (from a few thylakoids). Stroma of these young chloroplasts includes numerous plastid ribosomes, some small plastoglobuli, some starch inclusions, and several electron transparent regions—plastid nucleoids with DNA. Before the end of expansion of leaf blade area, the starch inclusions reach usually the largest dimensions. The system of thylakoids is usually most developed (high number of large grana from many thylakoids interconnected by many intergranal or unstacked thylakoids) in mature leaves, just after the end of leaf blade area expansion. In the third quarter of leaf ontogeny, particularly large grana (from many thylakoids) are usually formed. The chloroplasts so acquire a "shade character". At that period of leaf development, plastid ribosomes become less numerous and plastoglobuli considerably larger than in young chloroplasts. In the last quarter of leaf ontogeny, chloroplasts senesce. Loss of parallel arrangement of the thylakoids, dilatation and destruction of intergranal and (later) granal thylakoids, "vacuolation"

of the chloroplast stroma, and growth in size and/or number of the plastoglobuli are apparent in the senescent chloroplasts. Chloroplast volume decreases and chloroplast shape changes from lens-like to roundish. Such senescent chloroplasts which lack plastid DNA and are unable of further transformations, were named gerontoplasts (Sitte 1977).

The senescence of the chloroplasts may be accelerated, *e.g.*, by environmental pollution or other unfavourable factors (Mostowska 1997), or slowed down (or even reverted), *e.g.*, by plant decapitation (Kutík *et al.* 1984). In sempervirents, chloroplast life span takes several years. There, the described development is more or less repeated in each vegetation season. During leaf overwintering, temporary formation of peripheral reticulum in the chloroplasts of C_3 plants may occur (Modrušan and Wrischer 1987, Morré *et al.* 1991). In the needles of some conifers, division and merging of mature chloroplasts were proved from autumn to spring (Endler *et al.* 1990, Miroslavov and Alekseeva 1990). This is contradictory to the older idea that after leaf maturity, the same "generation" of the chloroplasts persists up to leaf senescence (Gamaleï and Kulikov 1978) but it is in full agreement with the theory of plastid cyclic interrelationships of Whatley (1978). This theory has also been supported by observations of inequal plastid divisions (giving mature plastid and proplastid) in the cells of green bark of many tree species during spring and in other systems, *e.g.*, in plant explants (Sagisaka 1993b, 1994a).

The understanding of chloroplast ultrastructural development during natural leaf ontogeny proceeds together with the advancement in ecological, physiological, molecular, and other studies of the photosynthetic apparatus. In the respective papers, many new pieces of knowledge on this complicated process are scattered.

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