한국현미경학회지 제39권 제2호 2009
Korean J. Microscopy 39(2), 73~80(2009)

종 설

A Survey of Plastid Crystals and Microtubules in Flowering Plants

InSun Kim*

Biology Department, College of Natural Sciences, Keimyung University, Daegu 704-701, Korea
(Received May 27, 2009; Accepted June 24, 2009)

꽃피는식물 색소체 내 결정구조와 미세소관의 발달양상 조사 연구

김 인 선*

계명대학교 자연과학대학 생물학과

ABSTRACT

The plastid inclusion has long been known to exist in leaves of numerous plant species, especially in those of flowering plants. Among the inclusions, crystalline bodies are the most frequently distinguished structures of the foliar plastids, however, microtubules and phytoferritins are also reported occasionally. The crystalline inclusions vary in shape, and are located either in the stroma or within intrathylakoidal spaces, whereas microtubules and phytoferritins are more uniform in shape and are formed in the stroma. In crystalline structures, the composing elements exhibit a lattice pattern and/or paralleled tubules that are either bounded by membranes or exist without membrane enclosing. Other types of inclusions have not been shown to be enclosed by any membranous structures. According to the current survey, the plastid inclusion, with the exception of phytoferritins, has been shown to exhibit a crystalline or tubular pattern, and has been reported in more than 56 species of various families. Their occurrence is not restricted to any photosynthetic pathway, but is found to be randomly distributed among C-3, C-4 and CAM species, without phylogenetic relationships.

The progress in plastid inclusion research reveals more information about the function and complexity, but the need for characterizing the 3-D structure of the crystalline inclusions also has been acknowledged in previous studies. A 3-D characterization would utilize tilting and tomography of serial sections with appropriate image processing that would provide valuable information on the sub-structures of the crystalline inclusions. In fact, recent studies performed on 3-D reconstruction of the plastid inclusions revealed important information about their comprising elements. In this article, the crystals and microtubules that have been reported in various types of plastids have been reviewed, with special consideration given to their possible sub-cellular function within the plastids.

Keywords : Crystals, Flowering plants, Microtubules, Plastid inclusions

The author would like to thank Dr. Tatsuo Arii of NIPS at NINS, Okazaki, Japan for providing the facilities, including the H-1250M HVEM, and for technical assistance during a collaborative study of the plastid crystalline inclusions in species of *Sedum* and *Salsola*.
* Correspondence should be addressed to Dr. InSun Kim, Biology Department, College of Natural Sciences, Keimyung University, Daegu 704-701, Korea. Ph.: (053) 580-5305, Fax: (053) 580-5305, E-mail: botany@kmu.ac.kr

INTRODUCTION

The common structural features of the plastid within two enveloping membranes are the stroma and internal membrane system. The stroma is the inner compartment of the aqueous matrix which not occupied by membranes where various soluble proteins and enzymes embedded (McDonald, 2003). Plastoglobuli, electron-dense spherical lipid bodies, are also common in most plastid stroma. The internal membrane system, well known as thylakoids in chloroplasts, are the flattened cisternae that contain enzymes and pigments required for photosynthesis, yet the membrane complexity may differ considerably by the plastid type. Five or six different types of plastid (Gunning & Steer, 1996), ranging from the simplest protoplast to well-organized chloroplasts, can be recognized by the tissue or by the developmental stage.

The proplastid is a precursor form having simple internal structure and has the capacity to develop into more complex types under certain developmental, physiological and/or environmental factors during growth (McDonald, 2003). Proplastids can develop into chloroplasts in photosynthetic tissues with illumination, while they turn to etioplasts without light in etiolated tissues. In the absence of photosynthesis, proplastids can acquire different functions. Because of the different roles that the plastid can have within the cell, this can dramatically change the internal structure of the plastids themselves. Examples of such transformed plastids include the chromoplast and amyloplast. The proplastid can be transformed into the chromoplast for pigmentation, and to the amyloplast for starch storage. Chromoplasts are frequently found in flower parts or fruits since they are responsible for colored pigmentation. Amyloplasts are usually found in grains, seeds or roots due to their storage function. Additionally, leucoplasts can be observed in non-green epidermal tissues with unknown function, although the frequency at which they are found is low.

The plastid inclusion has long been known in leaves of numerous plant species, especially of flowering plants. The plastid inclusions are diverse in morphology, although most of the inclusions reported are shown to be crystals that have crystalline or tubular nature. The crystalline structures, as typical crystals, are the most frequent and distinguished type of the foliar plastids, but microtubules and phytoferritins are also reported occasionally. The crystals are located either in the stroma or within intrathylakoidal spaces with various structures in morphology, whereas the latter two are relatively uniform and occur in the stroma. In crystalline inclusions, the composing elements exhibit either a lattice and/or tubular pattern that are bounded by membranes or without membrane enclosing (Kim, 2006; Lee, 2007). Additionally, electron-opaque phytoferritin aggregates have been noted in row-like arrangements or paracrystalline clusters in the stroma. High amounts of the phytoferritin is present in the stroma of developing plastids, however, they were excluded from the current review because they play a role in forming iron reserves as an iron-binding protein complex during development or during senescence (Ryberg et al., 1993). The presence of crystals or tubular inclusions has drawn much attention in many species and their function within plastids or during photosynthesis has been speculated in numerous prior studies (see Kim, 2006; Lee, 2007). Therefore, the present study addresses only the aforementioned two types of plastid inclusions known to be involved either directly or indirectly with the thylakoid or photosynthesis. This article has mainly focused those of the flowering plants and discussed their possible sub-cellular function during photosynthesis.

CRYSTALS AND MICROTUBULES AS PLASTID INCLUSIONS

The inclusion structures were generally found to develop within proplastids, etioplasts, chloroplasts, or chromoplasts, but rarely within leucoplasts and amyloplasts. Among the type, chloroplasts are the one where the most inclusions are formed. According to the current survey, the plastid inclusion has been reported in more than 56 species of various families (Table 1). They are shown to be mostly crystals of crystalline structures, while microtubules are reported less frequently. Their occurrence is not restricted to any photosynthetic pathway, but is found to be randomly distributed among C-3, C-4 and CAM species without phylogenetic relationships. The stroma and the intrathylakoidal space of plastids are frequently known to contain crystalline or tubular inclusions. Since the first description of membrane bounded plastid inclusions in the hyperplastic or tumor tissues of the Solanaceae (Hohl, 1961), numerous studies reported the presence of plastid inclusions in the vegetative or reproductive tissues. They were also found in unhealthy tissues that had been infected by virus, while no differences were noted between virus-infected and healthy plants (Diaz-Ruiz, 1975; Esau, 1975). In other studies (Wrischer, 1970, 1973), causal relationship has been shown between the inclusion formation and stressful conditions of chilling or

Table 1. Plastid crystals and microtubules in various flowering plants

Family	Species	Location	Inclusion	Plastid	Reference
Acanthaceae	*Hypoestes sanguinolenta*	stroma	mt	chl	Vaughn & Wilson, 1981
Aizoaceae	*Carpobrotus edulis*	stroma	mt	chl	Salema & Brandao, 1978
	Lithops sp.	stroma	mt	chl	Santos & Salema, 1981
	Mesembryanthemum crystallinum	stroma	mt	chl	Salema & Brandao, 1978
Amaranthaceae	*Amaranthus patulus*	stroma	cr	chl	Suzuki, 1978
Amaryllidaceae	*Narcissus poeticus*	INT	cr	Chr	Kuhn, 1970
Araceae	*Orontium aquaticum*	stroma	cr	chl, chr	Casadoro et al., 1982
Arecaceae	*Chamaerops humilis*	stroma	cr	amy	Gailhofer & Thaler, 1974
	Cocos nucifera	stroma	cr	chl	Price et al., 1966 Gailhofer & Thaler, 1974
	Phoenix dactylifera	stroma	cr	amy, leu, pro	Gailhofer & Thaler, 1974
	Washingtonia robusta	stroma	cr	leu	Gailhofer & Thaler, 1974
Asteraceae	*Taraxacum officinale*	INT	cr	chl	Gailhofer et al., 1990
Balsaminaceae	*Impatiens noli-tangere*	stroma	mt	chr	Emter et al., 1990
Brassicaceae	*Brassica rapa*	stroma	cr	pro	Oross & Possingham, 1991
Cactaceae	*Echinomastus intertextus*	stroma	mt	pro	Rivera & Arnott, 1982
	Opuntia ficus-indica	stroma	mt	chl	Thomson & Journett, 1970
Chenopodiaceae	*Beta vulgaris*	stroma	cr	pro	Hoefer & Esau, 1975 Oross & Possingham, 1991
	Salicornia	stroma	cr	chl	Unpublished
	Salsola sp.	stroma	cr	chl	Kim et al., 2006
	Spinacia oleracea	INT	cr	chl	Esau, 1975 Miller et al., 1976 Rascio et al., 1985 Shojima et al., 1987
		stroma	cr	pro	Oross & Possingham, 1991
	Suaeda maritima	stroma	cr	chl	Kim, unpublished
Crassulaceae	*Aeonium domesticum*	stroma	cr	chl, pro	Knoth, 1982
	Kalanchoe sp.	stroma	mt	chl	Santos & Salema, 1981
	Kalanchoe fedtschenkoi	stroma	mt	chl	Santos & Salema, 1981
	Kalanchoe pinnata	stroma	cr	eti, chl	Lee & Thompson, 1973 Thompson et al., 1977
	Orostachys malacophyllus	stroma	cr	chl	Kim, unpublished
	Sedum sp.	stroma	mt	chl	Brandao & Salema, 1974
	Sedum rotundifolium	stroma	cr	chl, eti, pro	Kim, 1997 Kim, 2006 Kim et al., 2006
	Sedum spectabilis	stroma	mt	chl	Santos & Salema, 1981
	Sedum telephium	stroma	mt	chl, pro	Brandao & Salema, 1974 Santos & Salema, 1983
	Umbilicus rupestris	stroma	mt	chl	Santos & Salema, 1981
Cuscutaceae	*Cuscuta pentagona*	INT, stroma	mt	chl	Sherman et al., 1999 Lee, 2007
	Cuscuta japonica	INT	cr	chl	Lee et al., 2000 Lee, 2007a, b
	Cuscuta pedicellata	INT	cr	chl	Lyshede, 1989
Fabaceae	*Acasia cornigera*	stroma	mt	chl, chr, pro,	Rickson, 1975
	Phaseolus vulgaris	stroma	cr	chl, leu, pro	Newcomb, 1967 Wrischer, 1967 Larsson, 1973
	Vicia faba	stroma	cr	chl	Wrischer, 1973 Larsson, 1973 Shumway et al., 1967

Table 1. Continued.

Family	Species	Location	Inclusion	Plastid	Reference
Geraniaceae	*Pelargonium zonale*	stroma	cr	chl	Diaz-Ruiz, 1975
Gesneriaceae	*Saintpaulia ionantha*	INT	cr	pro	Finer & Smith, 1983
Lamiaceae	*Coleus* sp.	stroma	cr	pro	Varkey & Nadakavukaren, 1982
Liliaceae	*Asphodelus microcarpus*	stroma	cr	chl, leu	Gailhofer & Thaler, 1978
Magnoliaceae	*Liriodendron tulipifera*	stroma	mt	chl	Ljubesic, 1979
Poaceae	*Carex siderosticta*	stroma	cr	chl	Kim et al., 1992
	Echinochloa crus-galli	stroma	cr	pro	Vanderzee & Kennedy, 1982
	Hordeum vulgare	stroma	cr	chl, eti	Sprey, 1975
	Zea mays	stroma	cr	chl	Williams, 1974 Galatis & Apostolakos, 1991
Portulacaceae	*Portulaca pilosa* *P. oleraceae* *P. sclerodarpa*	stroma	mt	chl	Kim & Fisher, 1990
Ranunculaceae	*Ranunculus bulbosus*	stroma	cr	chl	Gailhofer, 1983
Salicaceae	*Salix* sp.	stroma	cr	chl	Vapaavuori et al., 1984
Saxifragaceae	*Chrysosplenium*	INT, stroma	mt	chl	Sitte, 1974
Solanaceae	*Capsicum annum*	stroma	mt	chl	Spurr & Harris, 1968
	Nicotiana sp.	stroma	cr	chl	Ames, 1972 Ames & Pivorun, 1974
	Nicotiana tabacum	stroma	cr	chl	Willison & Davey, 1976
Tropaeolaceae	*Tropaeolum majus*	stroma	mt	chr	Emter et al., 1990

Abbreviation: cr, crystal; INT, intrathylakoidal space; mt, microtubule; amy, amyloplast; chl, chloroplast; chr, chromoplast; eti, etioplast; leu, leucoplast; pro, proplastid

water deficit. Further, the presence of inclusions has been reported even in detached leaves (Wrischer, 1978) as well as in isolated protoplasts (Takebe et al., 1973). Surprisingly, leaves of parasitic species are also known to develop such inclusions (Lee, 2007). However, cases of the inclusion formation are recorded most frequently with environmental factors and developmental stages of the plants. Such cases known from various species are discussed In the followings.

Contrary results of the inclusion formation are recorded with water deficit in *Spinacia* (Esau, 1975) and with well-watered leaves in *Salix* (Vapaavuore et al., 1984). In *Salix*, the number of inclusions decreased with water stress and further resulted in complete absence in severely stressed plants. Another factor that probably affects the inclusion formation during growth is the developmental stages of the plastid. In matured chloroplasts of *Spinacia* (Miller et al., 1976; Shojima, 1987) and *Salix* (Vapaavuori et al., 1982), intrathylakoidal crystalline inclusions that are bounded by membranes have been well-documented, while they are found in still developing plastids of other species. In fully differentiated chloroplasts of *Coleus, Saintpaulia* and *Spinacia*, they are usually not found or observed rarely (Varkey & Nadakavukaren, 1982; Finer & Smith, 1983; Racio et al., 1983). In CAM-performing *Sedum*, non membrane-bounded inclusions have been well demonstrated in proplastids, etioplasts and developing chloroplasts, but complete disappearance was noted within mature chloroplasts (Kim, 2006; Kim et al., 2006). Development of the crystalline inclusions occurred not only in autotrophic plants, as stated above, seedlings of the parasitic *Cuscuta* species has also shown to accumulate in the plastids (Lee, 2007a, b). Membrane bound amorphous proteinaceous inclusions are found in many plastids and are suggested to contain precursors for thylakoid membrane growth (Ames & Pivorun, 1974) as suggested for those in parasitic seedlings (Lee, 2007).

The inclusions are usually bounded by membranes when they are formed in the epidermal cells, but both cases of membrane bounded or non-membrane bounded inclusions have been found in the mesophyll cells. Epidermal plastids are usually small, but the inclusions occupy relatively a large volume of the plastid compared to those occur in other cell types (Kim, unpublished). Crystalline inclusions in epidermal plastids occur either in the stroma or in the thylakoid lumen (Hoefert & Esau, 1975; Platt-Aloia & Thomson, 1979; Mikulska et al., 1981; Lyshede, 1989; Lee, 1997).

Fully differentiated leucoplasts can be found with chloroplasts in the same epidermal cells of the shoot, but inclusions, when formed, occur almost entirely within chloroplasts. In the root, however, leucoplasts are known to develop inclusion bodies within stroma (Gailhofer & Thaler, 1978). For these epidermal plastid inclusions, a storage function has been suggested (Hoefert & Esau, 1975).

In the past, a collection of plastid crystalline structures have been once called stromacenter, since they may contain different proteins in the form of fibrous or whorl-like clusters in the stroma (Lee & Thompson, 1973; Gailhofer & Thaler, 1978; Thompson et al., 1977; Ryberg et al., 1993). As in the epidermal plastid inclusion, similar enzyme storage function for the CAM pathway has been hypothesized, since it was discovered in CAM-performing *Kalanchoe* species (Lee & Thompson, 1973; Thompson et al., 1977). The same type of inclusions might have comprised of proteins (Hoefert & Esau, 1975). was revealed in another CAM-performing *Sedum*, where accumulation and disappearance noticed diurnally (Santos & Salema, 1983). It has been believed that their formation is not the result of water deficit stress, since they appeared regardless of the plant water conditions in CAM-performing plants (Santos & Salema, 1984; Kim, 2006). In CAM species, the most accepted view for the presence of such inclusion in developing stages is the storage of enzymes that are necessary for the operation of CAM in mature leaves. Unlike the storage role of the inclusions in CAM plants, quite different role has been proposed for certain C-3 species. In C-3 *Avena* leaf plastids, the crystal is shown to be an enzyme that activates the vacuole components when the cells are damaged (Nisius, 1988). In a study of *Aeonium* plastids, Knoth (1982) concluded that the crystals consist of protein, since the incubation of deosmicated ultrathin sections with pepsin results in a digestion of the crystalline structures.

The plastid tubular structures, except peripheral reticulum, that are similar to the cytoplasmic microtubules frequently observed in the stroma (Vaughn & Wilson, 1981; Rivera & Arnott, 1982; Kim & Fisher, 1990; Kim, unpublished). They have been found in developing and/or transforming plastids of flowering plants (Lawence & Possingham, 1984). As in cytoplasmic microtubules, the plastid microtubules have a cylindrical shape and their length varies from a few nanometers to up to one millimeter (Dustin, 1984; Dey & Harborne, 1997). However, ca. 10 ~ 13 nm in diameter, a rather smaller dimension relative to the cytoplasmic microtubules has been assessed for the plastid microtubules (Artus et al., 1990; Kim, unpublished). When they formed within stroma, they often occur as an aggregates consisting of several to dozens of microtubules around the periphery of prolamellar bodies in etioplasts (Artus et al., 1990) or in chloroplasts (Salema & Brandao, 1978; Santos & Salema, 1982; Kim & Fisher, 1990). In C-4 *Portulaca* species, the plastid microtubules appear close to developing or matured thylakoids (Kim & Fisher, 1990). In another C-4 *Salsola* leaves, several isolated microtubules are rarely detected along with the crystal in the stroma (Kim, unpublished). When they occur, the microtubules form in the peripheral area, while the crystal develops within thylakoidal boundary.

The microtubules found within plastid stroma do not fit the commonly known functional types of the cytoplasm ones. The cytoplasmic microtubules are known to be involved in controlling of cell expansion and division, and control of cell wall structure (Dey & Harborne, 1997). The microtubules, however, rather appear close to the role in response to environmental factors that probably correlated to the control of the biotic stress response or the control of the low temperature response as suggested (Nick, 2000). Another role in the reorganization of membrane components in developing plastids has been postulated, although their composition and function are still not known (Ryberg et al., 1993). In a study of microtubule structures in wheat plastids, Artus et al. (1990) reported that they are probably not composed of tubulin as in the cytoplasmic microtubules, since the structures are insensitive to microtubule inhibitors. Since succulent species more likely form microtubules within plastids as seen in Table 1, there might be a positive link between the plastid microtubule formation and the C-4 or CAM photosynthesis. Extensive ultrastructural and biochemical studies are needed for a better understanding of the microtubules formed in the plastids.

FUTURE RESEARCH

The progress in plastid inclusion research at the ultrastructural level and immunocytochemistry has given us important information about their function and complexity during photosynthesis. Genetic and molecular work with the improved techniques will definitely make us move forward when looking for correlations between plastid ultrastructure and the presence and function of inclusions during plastid development and differentiation (Ryberg et al., 1993). Among the inclusions, microtubules have been investigated the least due to difficulties of detecting them within stroma. With this and other reasons, the nature of plastid microtu-

bules has yet to be examined either at molecular or cytochemical level. The need for developing experimental techniques for purification and identification of their sub-structures has been noted recently and until then the plastid microtubules remains to be resolved.

Another field that gives more information in depth would be the 3-D reconstruction of the plastid inclusions. The need for characterizing the 3-D structure of crystalline bodies from the serial sections is apparent and has been pointed out in previous studies. In addition to transmission electron microscopy (TEM), applications of high voltage electron microscopy (HVEM), accompanied by appropriate image processing techniques, have made possible great improvements in the analysis of 3-D subcellular structures or cellular phenomena, since up to several micron thick sections can be examined by HVEM. Recent studies of *Sedum* leaves investigated three dimensional crystalline structures through the use of HVEM accompanied by tilting and tomography of serial sections, diffraction analysis, and image processing (Kim, 2006; Kim et al., 2006; Kim, 2008). From these studies, the periodicity of tubular elements, having ca. 10～12 nm in the epidermal plastids and ca. 16～18 nm in the mesophyll plastids, were assessed. Furthermore, development pattern of those inclusions has been examined from the thick serial sections and peculiar mode of formation pattern has been revealed in *Sedum* species (Kim, unpublished). Therefore, applications of TEM or HVEM following with appropriate techniques would allow for total 3-D reconstruction, which is necessary for enhanced resolution of the internal sub-structures. Such enhancements in resolution would further provide for a more in-depth analysis of the plastid inclusions. With this in mind, the author should include more studies dealt with plastid inclusions of other flowering plants before drawing any immature conclusions.

REFERENCES

Ames IH: The fine structure of genetic tumor cells. Amer J Bot 59 : 341-345, 1972.

Ames IH, Pivorun JP: A cytochemical investigation of a chloroplast inclusion. Amer J Bot 61 : 794-797, 1974.

Artus NN, Ryberg M, Sundqvist C: Plastid microtubule structures in wheat are insensitive to microtubule inhibitors. Physiol Plant 79 : 641-648, 1990.

Brandao I, Salema R: Microtubules in chloroplasts of a higher plant (*Sedum* sp.). J Submicr Cytol 6 : 381-390, 1974.

Brinkley W: Microtubules: a brief historical perspective. J Struct Biol 118 : 84-86, 1997.

Casadoro G, Rascio N, Pagiusco M, Ravagnan N: Flowers of *Orontium aquaticum* L.: membrane rearrangement in chloroplast-chromoplast interconversions. J Ultrastruct Res 81 : 202-208, 1982.

Dey PM, Brownleader MD, Harborne JB: The plant cell and its molecular components, In: Dey PM, Harborne JB, ed, Plant Biochemistry, pp. 1-48, Academic Press, 1997.

Diaz-Ruiz JR: A Highly ordered protein from *Pelargonium*: structure and cellular localization. J Utrastruct Res 53 : 227-234, 1975.

Dodge JD, Lawes GB: Plastid ultrastructure in some parasitic and semi-parasitic plants. Cytobilogie 9 : 1-9, 1974.

Dustin P: Microtubules. Springer-Verlag, Berlin, pp. 94-126, 1984.

Emter O, Falk H, Sitte P: Specific carotenoids and proteins as prerequisites for chromoplast tubule formation. Protoplasma 157 : 128-135, 1990.

Esau K: Crystalline inclusion in thylakoids of spinach chloroplasts. J Utrastruct Res 53 : 235-243, 1975.

Finer JJ, Smith RH: Structure and development of plastids in epidermal cells of African violet (*Saintpaulia ionantha* Wendl.) in culture. Ann Bot 51 : 691-695, 1983.

Gailhofer M: Die Feinstruktur der Plastideneinschlsse von *Ranunculus bulbosus*. Phyton 23 : 197-210, 1983.

Gailhofer M, Kferbck T, Thaler I: Cytochemische Undersuchungen an Einschlssen in Plastiden der Bltter von *Taraxacum officinale.* Phyton 30 : 173-185, 1990.

Gailhofer M, Thaler I: Eiweibkristalle in den Plastiden der Keimpflanzen einiger Palmen. Phyton 15 : 251-258, 1974.

Gailhofer M, Thaler I: “Stromazentrum” in Leukoplasten der Epidermis von *Asphodelus microcarpus.* Phyton 19 : 97-102, 1978.

Galatis B, Apostolakos P: Microtubule organization and morphogenesis of stomata in caffeine-affected seedlings of *Zea mays.* Protoplasma 165 : 11-26, 1991.

Gunning BES, Steer MW: Plant Cell Biology: Structure and Function. Jones and Bartlett Publishers, Boston, pp. 1-60, 1996.

Hoefert LL, Esau K: Plastid inclusion in epidermal cells of *Beta.* Am J Bot 62 : 36-40, 1975.

Hohl HR: Plastids and tumorigenesis. Am J Bot 48 : 528, 1961.

Kim IS: Chloroplast microtubules in young leaves of *Sedum rotundifolium*. J Plant Biol 40 : 115-119, 1997.

Kim IS: Changes in the plastid ultrastructure during *Sedum rotundifolium* leaf development. J Plant Biol 49 : 376-383, 2006.

Kim IS, Fisher DG: Structure aspects of the leaves of seven species of *Portulaca* growing in Hawaii. Can J Bot 68 : 1803-1811, 1990.

Kim IS, Pak JH, Seo SB, Song SD: Foliar ultrastructure of Korean *Orostachys* species. Korean J Electron Microscopy 25 : 457-463, 1995.

Kim IS, Pak JH, Seo SB, Song SD: Ultrastructure of leaves in C_4 *Cyperus iria* and C_3 *Carex siderosticta*. J Plant Biol 42 : 213-221, 1999.

Kim IS, Park SC, Han SS, Kim ES: Three-dimensional analysis of the mesophyll plastids using ultra high voltage electron micro-

scopy. Korean J Electron Microscopy 36 : 217-226, 2006.

Knoth R: Protein crystalloids in ribosome-deficient plastids of *Aeonium domesticum* cv. *variegatum* (Crassulaceae). Planta 156 : 528-535, 1982.

Kuhn H: Chemismus, Struktur und Entstehung der Carotinkristllchen in der Nebenkrone von *Narcissus poeticus* L. var. 'La Riante'. J Ultrastruct Res 33 : 332-355, 1970.

Larsson C, Collin C, Albertsson P: The fine structure of chloroplast stroma crystal. J Ultrastruct Res 45 : 50-58, 1973.

Laudi G, Medeghini Bonatti P, Fricano G: Ultrastructure of plastids of parasitic higher plants. V. Influence of light on *Cuscuta* plastids. Isr J Bot 23 : 145-150, 1974.

Lawrence ME, Possingham JV: Observations of microtubule structures within spinach plastids. Biol Cell 53 : 77-82, 1984.

Lee KB: Structure and development of the upper haustorium in the parasitic flowering plant *Cuscuta japonica* (Convolvulaceae). Amer J Bot 94 : 737-745, 2007.

Lee KB: Ultrastructure and development of seedling of the parasitic weed *Cuscuta japonica*. J Plant Biol 50 : 213-219, 2007a.

Lee KB: Ultrastructure of crystalline inclusion in the thylakoids of dodder (*Cuscuta japonica*) plastids. J Plant Biol 50 : 325-330, 2007b.

Lee RE, Thompson A: The stromacentre of plastids of *Kalancho Pinnata* Persoon. J Ultrastruct Res 42 : 451-456, 1973.

Ljubesic N: Chromoplasts in the petals of *Liriodendron tulipifera* L. Z Pflanzenphysiol 91 : 49-52, 1979.

Lyshede OB: Electron microscopy of the filiform seedling axis of *Cuscuta pedicellata*. Bot Gaz 150 : 230-238, 1989.

McDonald MS: Photobiology of Higher Plants. John Wiley & Sons Ltd., San Fransisco, pp. 33-73, 149-198, 2003.

Mikulska E, Damsz B, Zolnierowicz H: Structural and functional polymorphism of plastids in leaves of *Clivia miniata* Rgl. I. Ontogenesis of plastids in epidermis and guard cells. Acta Soc Bot Pol 50 : 381-389, 1981.

Miller KR, Bloodgood RA, Staehelin LAL: Crystals within thylakoids: a structural analysis. J Ultrastruct Res 54 : 29-36, 1976.

Newcomb EH: Fine structure of protein-storing plastids in bean root tips. J Cell Biol 33 : 143-163, 1967.

Newcomb W: Plastid structure and development. In: Dennis DT, Turpin DH, Lefebvre DD, Layzell DB, eds, Plant Metabolism, pp. 255-259, Longman, Harlow, 1997.

Nick P: Plant Microtubules: Potential for Biotechnology. Springer, Berlin, pp.1-50, 83-136, 2000.

Nisius A: The stromacentre in *Avena* plastids: An aggregation of β-glucosidase responsible for the activation of oat-leaf saponins. Planta 173 : 474-481, 1988.

Oross JW, Possingham JV: Tubular structures in developing plastids of three dicotyledonous species. Can J Bot 69 : 136-139, 1991.

Pettifrew, WT, Vaughn KC: Physiological, structural, and immunological characterization of leaf and chloroplast development in cotton. Protoplasma 202 : 23-37, 1998.

Platt-Aloia KA, Thomson WW: Membrane bound inclusions in epidermal plastids of developing sesame leaves and cotyledons. New Pytol 83 : 793-799, 1979.

Price WC, Martinez AP, Warmke HE: Crystalline inclusions in chloroplasts of the coconut palm. J Ultrastruct Res 14 : 618-621, 1966.

Rascio N, Colombo PM, Vicca FD, Chitano P: Intrathylakoidal crystal appearance during the vital cycle of spinach chloroplasts. Protoplasma 126 : 153-157, 1985.

Rickson FR: The ultrastructure of *Acasia cornigera* L. Beltian body tissue. Amer J Bot 62 : 913-922, 1975.

Rivera ER, Arnott HJ: Tubular structure in the plastids of *Echinomastus intertextus* Brit. & Rose. New Phytol 90 : 551-561, 1982.

Ryberg H, Ryberg M, Sundqvist C: Plastid ultrastructure and development. In: Sundqvist, C Ryberg M. eds, Pigment-Protein Complexes in Plastids: synthesis and Assembly, pp. 25-62, Academic Press, San Diego, 1993.

Salema R, Brandao I: Development of microtubules in chloroplasts of two halophytes forced to follow Crassulacean acid metabolism. J Ultrastruct Res 62 : 132-136, 1978.

Santos I, Salema R: Chloroplast microtubules in some CAM-plants. Bol Soc Brot Ser (2) 53 : 1115-1122, 1981.

Santos I, Salema R: Stereological study of the variation of the chloroplast tubules and volume in the CAM plant *Sedum telephium.* Z Pflanzenphysiol Bd 113 : 29-37, 1983.

Sherman TD, Pettigrew WT, Vaughn KC: Structural and immunological characterization of the *Cuscuta pentagona* L. chloroplast. Plant Cell Physiol 40 : 592-603, 1999.

Shojima S, Nishizawa NK, Mori S: Do intrathylakoidal inclusions really contain RUBPCase? Protoplasma 140 : 187-189, 1987.

Shumway LK, Weier TE, Stocking CR: Crystalline structures in *Vicia faba* chloroplasts. Planta 76 : 182-189, 1967.

Sitte P: Plastid metamorphosis and chromoplasts in *Chrysosplenium*. Z Pflanzenphysiol 73 : 243-265, 1974.

Sprey B: Membranassoziierte Tubuli Wahrend der Chloroplastengenese von *Hordeum vulgare* L. Protoplasma 84 : 197-203, 1975.

Sprey B: Intrathylakoid occurrence of ribulose 1,5-diphosphate carboxylase in spinach chloroplasts. Z Pflanzenphysiol 78 : 85-89, 1976.

Spurr AR, Harris WM: Ultrastructure of chloroplasts and chromoplasts in *Capsicum annum*I. Thylakoid membrane changes during fruit ripening. Amer J Bot 55 : 1210-1224, 1968.

Suzuki S: Crystalline inclusion in epidermal and vascular plastids of the mature *Amaranthus* leaf. J Electron Microsc 27 : 141-143, 1978.

Thompson A, Vogel J, Lee RE: Carbon dioxide uptake in relation to a plastid inclusion body in the succulent *Kalancho pinnata* Persoon. J Exp Bot 28 : 1037-1041, 1977.

Thomson WW, Journett RD: Observations on bodies in subsidiary cells of *Opuntia* sp. J Ultrastruct Res 31 : 439-443, 1970.

Vanderzee D, Kennedy RA: Plastid development in seedlings of

Echinochloa crus-galli var. *oryzicola* under anoxic germination conditions. Planta 155 : 1-7, 1982.

Vapaavuori EM, Korpilahti E, Nurmi AH: Photosynthetic rate in willow leaves during water stress and changes in the chloroplast ultrastructure with special reference to crystal inclusions. J Exp Bot 35 : 306-321, 1984.

Varkey PJ, Nadakavukaren MJ: Influence of leaf differentiation on the developmental pathway of *Coleus* chloroplasts. New Phytol 92 : 273-278, 1982.

Vaughn KC, Coyle PC, Wilson KG: Modifications of plastid ultrastructure in an efficient yellow mutant of spinach. Photosynthetica 15 : 201-204, 1981.

Vaughn KC, Wilson KG: Improved visualization of plastid fine structure: plastid microtubules. Protoplasma 108 : 21-27, 1981.

Williams E: Fine structure of vascular and epidermal plastids of the mature maize leaf. Protoplasma 79 : 395-400, 1974.

Willison JHM, Davey MR: Fraction 1 protein crystals in chloroplasts of isolated tobacco leaf protoplasts: a thin-section and freeze-etch morphological study. J Ultrastruct Res 55 : 303-311, 1976.

Wrischer M: Kristalloide im Plastidenstroma I. Elektronenmikroskopisch-cytochemische untersuchungen. Planta 75 : 309-318, 1967.

Wrischer M: Protein crystalloids in the stroma of bean plastids. Protoplasma 77 : 141-150, 1973.

＜국문초록＞

다양한 색소체 내에 형성되는 결정체와 미세소관의 분포 및 발달양상을 식물이 수행하는 광합성 양식과 연계하여 꽃피는식물 종들에서 밝혀진 결과에 의하면, 색소체 결정체는 대개 격자 구조를 이루며 기질 또는 티라코이드 내에 형성되나, 미세소관은 비교적 규칙적인 형태로 기질에만 발달한다고 알려져 있다. 격자구조는 막으로 둘러싸이거나 막과는 무관하게 발달하며, 계통학적인 유연관계를 형성하지 않고 C-3 또는 C-4 또는 CAM 광합성을 수행하는 26개의 식물과, 약 56종에서 독립적으로 나타난다는 사실이 조사되었다. 색소체 결정체 및 미세소관 형성에 대한 지속적인 연구는 이들의 구조와 기능에 대하여 새로운 정보를 제공하나, 결정체에 대한 3차원적 입체구조 연구와 미세소관에 대한 분자생물학적인 실험법들이 요구되고 있는 실정이다. 특히, HVEM 고압전자현미경 및 tomography에 의한 연속절편 연구는 결정체의 3-D 입체구조 구현이 가능하여 심도 있는 구조정보를 제공하는 것으로 알려져 있다. 극히 일부의 식물에서만 보고되어 있는 색소체 내 미세소관에 대한 연구에 관해서는 먼저 색소체 기질에서 이들의 형성 시점을 알아내어 기질에서의 식별 및 분리 연구 등이 가능하게 돼야 함이 강조되고 있다. 본 논문에서는 꽃피는식물 종들의 여러 색소체 유형에서 보고된 결정체와 미세소관을 조사하여 색소체 내에서 이들의 기능을 광합성과 연계하여 종합적으로 논의하였다.