Metabolism and Biochemical Activities of Cytokinins

CHONG-MAW CHEN*

ABSTRACT

This paper reviews recent progress in the field of cytokinin research. It will deal primarily with:

a) the biosynthesis, interconversion and degradation of cytokinin;
b) enzymic regulaton of cytokinin metabolism;
c) cytokinin hormone receptors; and
d) the effect of cytokinin in protein synthesis and RNA metabolism.

INTRODUCTION

Cytokinins are a group of N^6-substituted adenines (Fig. 1) which function hormonally in the regulation of plant growth and development. These substances promote cell division and enlargement, and formation of shoots and flowers. They affect the metabolism of other macromolecules, modify DNA, RNA, protein biosynthesis or degradation in appropriate biological systems (Skoog and Armstrong, 1970; Kende, 1971; Fox, 1977; Guern and Peaud-Lenoel, 1981). Cytokinins also influence morphogenesis and transport of nutrients through the plant and enhance its resistance to both aging and adverse environments. In mammalian systems, one of the naturally occurring cytokinins, i^6Ade^2, exhibits immuno suppressive activity and inhibits the growth of leukemic cells *in vitro* and *in vivo* (Mittelman and Chheda, 1975). Moreover, this hypermodified ribonucleoside occurs in various tRNA (Hall, 1970) and is always adjacent to the 3′ side of those anticodons having A at the 3′ position (Skoog and Armstrong, 1970). This has suggested an involvement in the control of

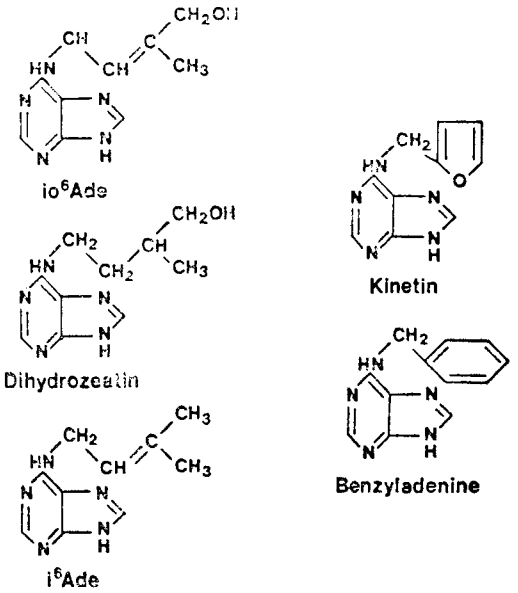

Fig. 1. Structures of some naturally occurring and synthetic cytokinins.

* Depart of Life Science and Biomedical Research Institute, University of Wisconsin-Parkside, Kenosha, Wisconsin 53141 USA

The review is dedicated to my former professor, Dr. Tuan-sheng Miu, on the occasion of his 80th birthday.

Abbreviations:
i^6Ade: N^6-(Δ^2-isopentenyl)adenine;
i^6Ado: N^6-(Δ^2-isopentenyl)adenine;
t-io^6Ade: *trans*-6-(4-hydroxy-3-methyl-2-butenyl amino)-purine;
t-io^6Ade: *trans*-6-(4-hydroxy-3-methyl-2-butenyl amino)-9-β-D-ribofuranosyl purine;
Δ^2-iPP: Δ^2-isopentenyl-pyrophosphate

protein biosynthesis (Hall, 1970) and has also stimulated speculation as to whether the presence of cytokinin in tRNA or the incorporation of cytokinins into tRNA is related to their mode of action in the regulation of growth (Fox and Chen, 1967; Chen and Hall, 1969).

Studies on the function of cytokinins within the plant and their interaction with other plant hormones are becoming an important part of the efforts of plant scientists, and these studies will have a decided impact on plant biochemistry and genetic engineering because these substances play a key role in plant cell division and differentiation.

This paper attempts to discuss and review recent progress in the field of cytokinins, particularly in the areas of biosynthesis, interconversion and degradation of naturally occurring cytokinins, cytokinin-binding molecules, and the effect of cytokinin in protein synthesis and RNA metabolism.

BIOSYNTHESIS OF CYTOKININS

In order to understand the molecular basis of cytokinin action in plant cell division and differentiation, we need to know:

a) What are the origin of these substances?
b) How are they metabolized (interconversion and degradation)?

Studies of cytokinin biosynthesis were reported in the late 1960s. In a series of experiments, Hall and co-workers demonstrated that a cytokinin, i^6Ado, was synthesized by attachment of the Δ^2-isopentenyl side chain to preformed tRNA (Chen and Hall, 1969; Kline and Hall, 1969). Chen and Hall (1969) investigated the snythesis of tRNA-bound cytokinin in tobacco callus which required an exogenous supply of a cytokinin for optional growth. When radioactive mevalonate was added to the culture medium, it was incorporated into tRNA and was localized in i^6Ado. A crude enzyme preparation from tobacco callus catalyzed the formation of tRNA-bound i^6Ado, with mevalonic acid and permanganate-treated tRNA serving as substrates. The enzyme, Δ^2-isopentenyl pyrophosphate: tRNA Δ^2-isopentenyltransferase, that catalyzes this reaction has been partially purified from various organisms (Hall, 1970).

While cytokinin bases occur in tRNA of microorganisms, animals and plants, free cytokinins (low molecular weight) have mostly been found only in higher plants. Exceptions to this are some plant pathogens, parasites, and symptoms in an infected plant that can be mimicked by cytokinin treatment. There is no conclusive evidence that turnover of tRNA would represent a source of cytokinin adequate to maintain the cytokinin needs of a particular organism. Thus, the main questions to be answered were:

a) Is there a free cytokinin biosynthetic pathway?
b) If so, how are the free cytokinins biosynthesized in the plant tissues?

Indirect evidence supporting the free cytokinin pathway has been published (Chen and Echert, 1976; Burrow, 1978; Wang and Cove, 1981; Stuchbury *et al.*, 1979; Chen *et al.*, 1974). Direct evidence supporting *de novo* biosynthesis was provided by the recent discovery of cytokinin synthetase (Δ^2-isopentenyl pyrophosphate: 5′-AMP Δ^2-isopentenyltransferase) from cytokinin-autotrophic tobacco callus by Chen and Melitz (1979). This enzyme catalyzes the formation of cytokinins in the absence of RNA. The presence of this enzyme was also reported in *Dictyostelium discoideum* (Tava *et al.*, 1978). *Corynebacterium fasciens* (Murai, 1981) and other plants (Nishinari and Syono, 1980). Plant tissues might use both tRNA and tRNA-independent pathways under varying circumstances. A possible cytokinin biosynthetic pathway in higher plants are shown in Fig. 2.

Crown gall tumors induced by *Agrobac-*

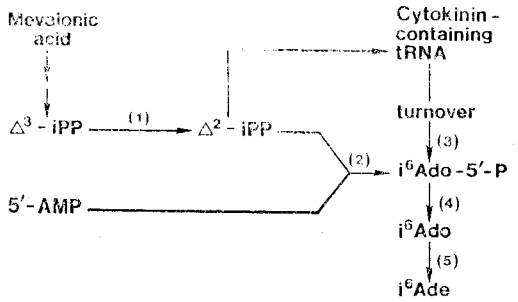

Fig. 2. Pathways of cytokinin biosynthesis in plant tissues. The numbers between compounds refer to the following enzymes or sequences of enzymes: (1) isopentenylpyrophosphate Δ^3-Δ^2-isomerase; (2) Δ^2-isopentenylpyrophosphate: AMP-Δ^2-isopentenyltransferase; (3) nucleases; (4) 5'-nucleotidase: (5) adenosine nucleosidase.

terium tumefaciens have been shown to have been shown to have elevated levels of endogenous cytokinins. i^6Ado, *t*-io^6Ade, *t*-io^6Ado and other cytokinin derivatives have been shown to be present in *Vinca rosea* crown gall tissue (Chen *et al.*, 1976; Miller, 1974; Paterson and Miller, 1977; Morris, 1977). The biosynthetic pathways of these cytokinins have not been studied. They are probably synthesized both by tRNA-independent and tRNA turnover pathways.

The sites of cytokinin biosynthesis in plants are not limited to root site (Kende and Sitton, 1967) is also located in the shoot (Chen and Petschow, 1978) as demonstrated by cytokinin biosynthesis in cultured rootless tobacco plants.

METABOLISM OF CYTOKININS

Cytokinins, naturally occurring or synthetic, are metabolized *in vivo* and cell-free systems to a series of compounds. A metabolic pathway for the naturally occurring cytokinin, i^6Ade, is shown in Fig. 3. The interconversion and degradation of i^6Ade are catalyzed by enzymes isolated from several plant sources (Chen *et al.*, 1975; Chen and Eckert, 1977; Chen and Eckert, 1978; Chen and Kristopeit, 1981; Chen, 1981; Chen *et al.*, 1982; Laloue *et al.*, 1977; Summons *et al.*, 1981; Horgan *et al.*, 1981). These reactions are of interest because of their possible significance in the control of the physiological activities of cytokinins either by the interconversion of cytokinin base to its nucleotide through cytokinin nucleoside, or by destroying the "active form" of cytokinin. Although the cytokinin base is a more active cytokinin than its corresponding riboside or ribotide in various bioassay systems (Hecht *et al.*, 1975) it is still

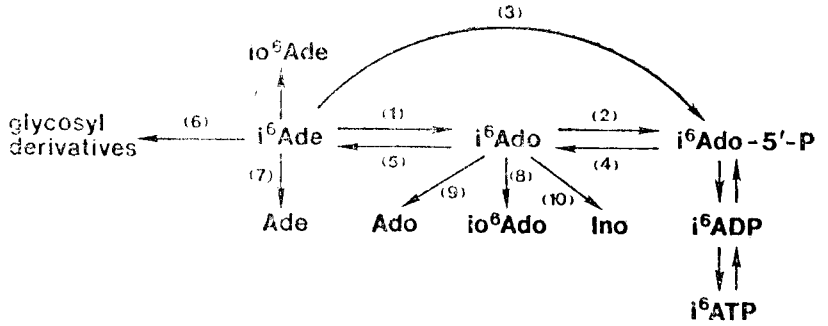

Fig. 3. Enzymes of cytokinin interconversion and degration in plant tissues. The enzymes which catalyze these reactions are: (1) adenosine phosphorylase; (2) adenosine kinase; (3) adenine phosphoribosyltransferase; (4) 5'-nucleotidases; (5) adenosine nucleosidase; (6) cytokinin glycosyltransferases; (7 and 8) enzyme unknown; (9) cytokinin oxidase; (10) adenosine deaminase. Reactions (1) to (8) are cytokinin interconversion, (9) and (10) are cytokinin degradation.

not clear if a cytokinin base serves as an "active form" of cytokinin. Because, a cytokinin base supplied to plant tissues is readily converted to other forms of cytokinins such as cytokinin riboside or ribotide.

While the question of whether cytokinin base *per se* serves as the "active form" of cytokinin remains to be resolved, cytokinin-binding protein studies (Fox, 1977; Erion and Fox, 1981; Moore, 1979; Sussman and Kende, 1981; Chen *et al.*, 1980) suggest that cytokinin base may be one of the active forms cytokinin. Thus, the enzymic regulation of cytokinin interconversion and degradation may be important for providing an adequate level of "active cytokinin" in plant cells.

CYTOKININ-BINDING MOIETIES

Studies of the regulatory action of animal steroid hormones have revealed specific receptor proteins present in higher concentrations in the target tissues. Specific membrane receptor sites have also been identified for polypeptide hormones. The presence of receptors for the plant hormones cytokinins has also been reported. Studies of *in vitro* binding of cytokinins (Fox, 1977; Erion and Fox, 1981; Moore, 1978; Sussman and Kende, 1981; Chen *et al.*, 1980) indicate that there may be specific "receptor molecules" involved in the cytokinin action.

High affinity sites for cytokinins that appeared to have some of the properties expected for hormone receptors have been shown to occur in various plant cells (Erion and Fox, 1981; Moore, 1979; Sussman and Kende, 1981; Chen *et al.*, 1980; Roussell and Fox, 1979). Low affinity sites for cytokinins were also observed in much higher frequency. The reported binding affinity (Kd values) for cytokinins ranged from 4×10^{-5} M to 1×10^{-6} M (Erion and Fox, 1981; Moore, 1979; Sussman and Kende, 1981; Chen *et al.*, 1980; Roussell and Fox, 1979) depending upon the source of tissues.

Affinity chromatography has been employed in the isolation of cytokinin-binding molecules. Chen *et al.* (1980) reported an improved method for the isolation of cytokinin-binding proteins for tobacco callus by means of a cytokinin-affinity chromatography having a spacer arm. The spacer arm extends an immobilized cytokinin molecule away from the backbone of the matrix, resulting in a significant increase in the binding of cytokinin-binding molecule isolation.

Recently, a photoaffinity labeling technique has been widely employed in studying ligand-receptor interactions. This has been a powerful technique for animal hormone receptors (Chowdhry and Westheimer, 1979). The existence of azido-substituted cytokinins makes the technique of photoaffinity labeling accessible to plant biochemists working in the cytokinin field. Improvements in the synthetic methods of these reagents, a better knowledge of their properties and synthesis of new reagents may eventually help this technique to reach its full efficiency.

The question of how many cytokinin binding proteins exist in the cells, and what is their biological function remains to be answered. It is possible that a unique receptor exists which accounts for the biological role of cytokinins at a specific growth active site. However, the current evidence suggests that multiple cytokinin receptors may occur in higher plants acting as transducers for the numerous and diverse activities of this group of plant hormones.

CYTOKININ-STIMULATED PROTEIN SYNTHESIS

The effects of plant hormones on protein synthesis has been the subject of a number of investigations (Guern and Peaud-Lenoel, 1981). At present, there is no known mechanism on

protein synthesis.

Kulaeva *et al.* (1981) demonstrated that the polyribosomal preparations isolated from benzyladenine-treated pumpkin cotyledons were twice as active in protein synthesis *in vitro* as those isolated from the untreated ones. However, various growth regulators, including the cytokinins, had no effect in protein synthesis when added directly to the incubation mixture of the cell-free system.

Fosket and Tepfer (1978) proposed that shift from mono- to polyribosomes at a post-transcriptional level was modulated by cytokinin. In suspension cultures of soybean cells, the hormone-stimulated cell division was preceded by an enhanced polyribosome formation. Fosket *et al.* (1981) isolated a cytokinin-induced protein from cultured soybean cells. This protein had molecular mass of 55,000 daltons, and had approximately the molecular mass of the subunits of tubulin, the principle structure components of the microtubules which are necessary components for mitosis. These results imply that stimulation of cell division by cytokinin may be modulated by tubulins. In contrast to the results of Fosket and Tepfer (1978); Szweykowska *et al.* (1981) reported that the higher capacity of the ribosomal preparation after the cytokinin treatment of protonema of the mass *Ceratodon purpureus* was not due to an increased formation of polyribosomes, but rather to their increased activity. In the mass protonema, an enhancement of [^{14}C]-leucine incorporation into proteins was found as soon as 15 min after treatment with a cytokinin, i^{6}Ade. A pulse-chase experiment showed that the enhanced incorporation of [^{14}C]-leucine was accompanied by an enhanced decline of the precursor pool in the i^{6}Ade-treated protonema. The level of protease activity did not change during the several hours of the cytokinin treatment, so the enhanced precusor incorporation could not be a consequence of a decrease in the protein breakdown.

CYTOKININ CONTROL OF RNA SYNTHESIS

Cytokinins are well known to stimulate total RNA synthesis in various plant tissue (Skoog and Armstrong, 1970; Kende, 1971). However, the question of how the RNA synthesis are stimulated by the cytokinins is still unknown.

Rovchoudhury *et al.* (1965) reported that kinetin stimulated RNA synthesis in nuclei isolated from coconut milk. A similar effect of kinetin on nuclei from tobacco and soybean callus as well as from pea seedlings was observed by Matthysse and Abrahams (1970); Rick *et al.* (1970) reported that treatment of soybean cotyledons with benzyladenine resulted in the appearance of two new leucyl-tRNA species which otherwise were found only in senescing cotyledons. Trewavas (1970) however, found that benzyladenine stimulated both RNA synthesis and RNA breakdown, thus increasing the rate of RNA turnover but not the level of RNA.

Kinetin stimulated the precusor incorporation into poly(A)$^{-}$RNA, was reported by Szweykowska *et al.* (1981), but there was no difference in the incorporation into the poly(A)$^{+}$RNA, a fraction thought to constitute at least a major part of mRNA. They concluded that cytokinin may increase in polyribosome/monoribosome ratio, and is not a reflection of a hormone-induced increase in the rate of mRNA synthesis. Kulaeva (1981) demonstrated that cytokinin promoted the activities of not only RNA-polymerase I, but RNA-polymerase II as well. Consequently, cytokinin-activated specific RNA synthesis may in turn stimulate specific protein synthesis.

The direct incorporation of exogenous cyto-

kinin into tRNA (Fox and Chen, 1967) and rRNA (Murai *et al.*, 1978) of various plant tissues has been shown, but the biological significance of the cytokinin incorporation into RNA is not clear.

CONCLUSION

The biosynthesis, interconversion and degradation of cytokinins have been extensively studied, but the question of whether the free cytokinin bases, their derivatives or some specific cytokinin-receptor complex are the primary active molecules remains to be answered.

To understand the mechanism of cytokinin action in inducing cell division and differentiation, the isolation and purification of their receptor molecule(s) as well as study of the interaction of the hormone with its presumed binding site(s) should be indispensable. Although cytokinin bining proteins have been isolated from various plant tissues, the presence of the binding protein with regard to the hormone action in higher plants is still not clear.

The effect of cytokinins on protein and RNA synthesis has been reported, but the following questions remain to be answered:

1. What is the mechanism of cytokinin stimulation of various RNA synthesis in plant cells?
2. If RNA polymerases syntheses are activated by the hormone, how are these enzymes induced by the presence of cytokinins?
3. Assuming that cytokinins participate in regulation of protein synthesis at pos-transcriptional level, then is this effect due to the primary action of cytokinin at the transcriptional level?

Although there are some reports about cytokinin transport in plant cells (Lampugnani *et al.*, 1981), the mechanism of the hormonal transport in plant is still obscure.

In sum, the mechanism of cytokinin action is still an unsolved puzzle. It is hoped that this mini review will help in gathering the relevant pieces of this puzzle which must be put into their proper places when the whole picture is assembled.

ACKNOWLEDGEMENTS

Part of the author's personal research referred to in this review has been supported by the National Science Foundation grant PCM 76-82158 and PCM 79-03832, and by the National Institute of Health Grant GM 22543.

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細胞分裂素的代謝和生化活性

陳 正 茂
美國威斯康辛大學生命科學及生物醫學研究所

摘 要

本文爲有關細胞分裂素研究方面最新進展的評論，其基本內涵爲：

a. 細胞分裂素的生合成、相互轉變和破壞。
b. 在細胞分裂素代謝上酶的調節。
c. 細胞分裂素的受器。
d. 細胞分裂對蛋白合成和 RNA 代謝之影響。