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Opine, a Chemical Mediator Governing Physiology of the Plant-Pathogen, *Agrobacterium*, in Rhizosphere

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The genus *Agrobacterium* contains plant pathogens causing tumors on dicotyledonous plants in nature. Five species of *Agrobacterium* have been recognized: *A. radiobacter, A. tumefaciens, A. rhizogenes, A. rubi, and A. vitis* (Ophel and Kerr, 1990). These species are distinguished primarily by their phytopathogenicity and the types of eliciting tumors. *A. radiobacter* strains are avirulent. *A. tumefaciens* and *A. rhizogenes* cause crown gall and hairy root disease, respectively. *A. rubi* induces cane galls, and the genera *A. rubi* and *A. vitis* induce galls on grapevines. Crown galls and the pathogenic bacteria have been intensively studied since the first suggestion was made a century ago that the crown galls are caused by a microorganism (Toumey, 1900). In the early studies, the identification of *Agrobacterium* as a tumor-inducing organism prompted the efforts of many scientists to search for a corresponding microorganism that could cause animal tumor. However, such efforts turned out to be futile, and nowadays it is broadly accepted that such bacterium-causing tumorigenesis is the phenomenon found only in plant.

Analysis of the DNA content of various *Agrobacterium* strains showed that all pathogenic *A. tumefaciens* isolates contain a large plasmid which is absent in avirulent *Agrobacterium* strains (Watson et al., 1975). Virulence was lost upon curing of the plasmid, and was recovered when the plasmid was introduced by conjugation into an avirulent agrobacterial recipient (Moore et al., 1979). These extrachromosomal elements responsible for virulence were called Ti (tumor-inducing) plasmids. Other virulent elements also were found in *A. rhizogenes* which causes hairy root disease, and they were named Ri (root-inducing) plasmids (White and Nester, 1980). Tremendous amount of work has been accomplished to elucidate molecular basis of the Ti- or Ri-plasmid-causing plant transformation. It is well known that a part of a Ti or Ri plasmid, called T-DNA is transferred to plant and stably incorporated into the genome of plant. Expression of oncogenes encoded on the T-DNA results in neoplasis of infected plant cells (for reviews, Zambrisky, 1988; Ream, 1989).

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Novel Compounds, Opines Produced by Plant Tumors

An intriguing part of the *Agrobacterium*-mediate plant transformation is the presence of compounds called 'opines'. Without exception, the opine compounds have been found in all the *Agrobacterium*-elicited plant tumors. Animal oncologists speculated that such corresponding compounds may also be found in animal cancer tissues, and tried to isolate such diffusible compounds from animal cancer cells. However, such effort has not been successful, and nowadays, it is accepted that opine is a chemical marker typically produced only in plant cancer cells.

At the early stage of *Agrobacterium* study, researchers did not realize the scientific significance of the compounds. However, it has been emerging that the novel compounds produced by plant tumors exert various effects on physiology of the pathogenic agrobacterial strains. In this review, the biosynthetic and catabolic aspects of the opines, and recent advances in biochemical and molecular genetic studies of the opine-related genes and the gene products are summarized. Recent researches also are summarized that provide new scopes that the compounds do not just serve as food for the causative bacterium, but rather act as a chemical mediator affecting various effects on bacterial populations residing in rhizosphere.

The Opine Concept; Relationship between Plant Tumors and Causative *Agrobacterium*

The biological significance of opine has not been well appreciated until a French microbiologist, Tempé and col-

leagues (1979) suggested a hypothesis called 'the Opine Concept'. In the hypothesis, it was proposed that opines act as chemical mediators in the relationship between host plants and pathogenic agrobacteria, and that *Agrobacterium* engineers the host plant to produce opines which are specific substrates for the causative *Agrobacterium*. This hypothesis was based on the observation that a type of opine produced by a pathogenic agrobacterial strain can be utilized as sole carbon source by the causative bacterium. For instances, *Agrobacterium* strains that cause plant tumors producing an opine, nopaline, can utilize nopaline as sole caron source. Similarly, strains that cause plant tumors producing octopine can utilize the opine as sole carbon source.

The Opine Concept predicts that all plant tumors will contain one or more of these novel compounds. However, agrobacterial strains inducing plant tumors that seemingly did not contain nopaline or octopine were identified in the late 1970's (Sciaky et al., 1978). However, careful chemical analysis revealed that these so-called null-type tumors produced previously undescribed opines (Firmin and Fenwick, 1978). These included the mannityl opines, succinamopine, leucinopine as well as chrysopine family-opines recently identified (Chilton et al., 1995).

It is of striking that alfalfa nodules caused by *Rhizobium meliloti,* a species of *Rhizobiaceae,* to which *Agrobacterium* also belongs, also produce opine-like compounds, called rhizopines. These compounds are also catabolized specifically by the *Rhizobium*, and the genes for biosynthesis and catabolism of the opine-like compounds are encoded by the megaplasmid, Sym plasmid, in the bacterium (Murphy et al., 1987). It appears that the compounds are important in symbiosis between this bacterium and host plant.

The best way to assess the validity of the Opine Concept would be to perform ecological studies to examine whether an opine-utilizing agrobacterial strain is able to more selectively colonize a plant producing the opine than is a non-opine-utilizing bacteria. Guyon et al. (1993) determined the effect of the *Lotus* hairy root system, which was transformed to produce opines, on the changes in populations of opine-catabolic and opine-noncatabolic strains of *Agrobacterium*. They showed that growth of opine-utilizing bacteria was favored when bacteria were associated with transformed plants, but was not when associated with normal plants. It also has been reported that a *Pseudomonas fluorescens* strain which can utilize agropine and mannopine has a competitive growth advantage over an isogenic *P. fluorescens* strain which cannot utilize the opines in the rhizosphere of plants that produce those opines. However, in an environment lacking opines, there were no differences in the capabilities of the two *Pseudomonas* strains to colonize the root systems (Savka, 1993). More recently, Oger et al., (1997) also showed that in rhizosphere where opine-producing transgenic plants are planted, agrobacterial strain that can utilize the opine could outgrow over other non-opine-utilizing species. These experiments have apparently demonstrated the validity of the Opine Concept.

The Chemical Structures of Opines

Up to now, more than twenty opines have been identified. Figures 1 and 2 show the chemical structures of some representative opines, in which biochemistry and molecular genetics of biosynthesis and degradation have been intensively studied. Except for agrocinopine-family opines, all the opines are compounds in which a sugar molecule is reductively conjugated with an amino acid or its derivative. Opines generally contain one or two atoms of nitrogen, and hence can be utilized by causative agrobacterial strains as sole nitrogen source. Agrocinopine molecules do not contain a nitrogen atom but do contain a phosphate atom (Fig. 2).

T-DNA-Encoded Genes for the Biosynthesis of Opines by Plant Tumors

The genes for the biosynthesis of opines are encoded by T-DNA region of Ti- or Ri-plasmids. Generally, genes encod-

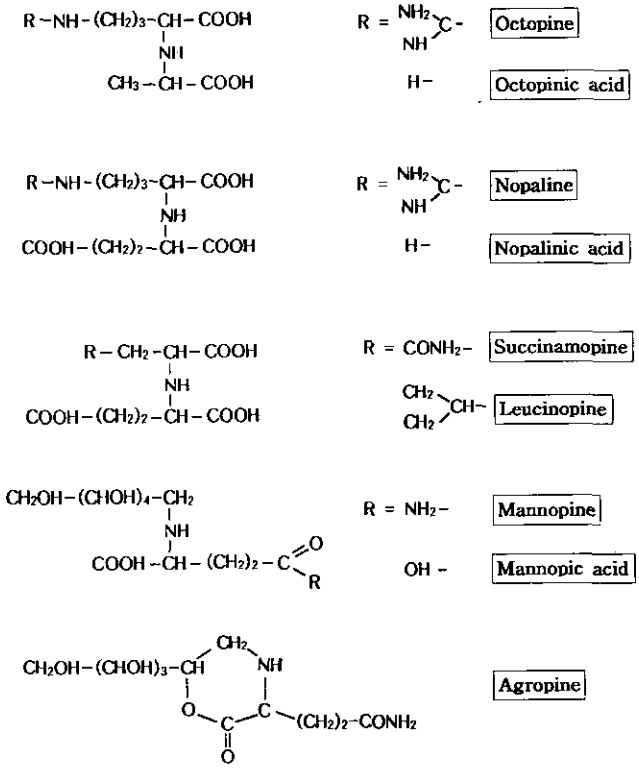

Fig. 1. Chemical structures of representative Opines.

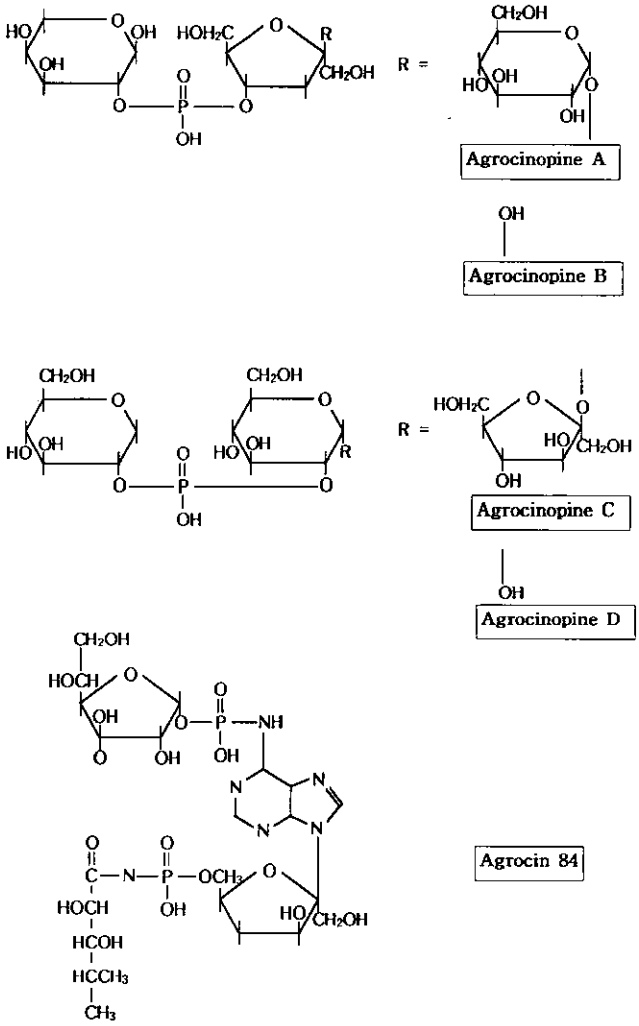

Fig. 2. Chemical structures of agrocinopines and agrocin 84.

ing enzymes for the synthesis of opines are localized next to the right T-DNA border. Since the transfer of T-DNA to a plant cell starts at the right border, the opine synthesis genes are the first T-DNA genes to be transferred to plant cells (Dessaux et al., 1992). The genes for the synthesis of octopine, nopaline, and mannityl opines have been extensively studied. Octopine and nopaline are synthesized in one step by octopine synthase and nopaline synthase, respectively (Goldmann et al., 1969; Kemp et al., 1979). Octopine synthase reductively conjugates pyruvic acid with arginine, lysine, histidine, and ornithine to produce octopine, lysopine, histopine, and octopinic acid, respectively. Nopaline synthase reductively conjugates 2-ketoglutaric acid with arginine or ornithine to produce nopaline and nopalinic acid respectively (Depicker et al., 1982). The genes for the biosynthesis of mannityl opines have been studied by Salomon et al. (1984) and Ellis et al. (1984). In contrast to the cases of octopine and nopaline, members of mannityl opines, mannopine (MOP) and mannopinic acid (MOA), are synthesized in two steps. The enzyme encoded by the *mas2'* gene is believed to condense glucose and glutamine or glutamic acid to yield deoxyfructosyl glutamine (dFru-Gln) that is commonly called santhopine (SOP) and deoxyfructosyl glutamic acid (dFru-Glu), respectively. These resulting compounds are reduced to MOP and MOA by an oxidoreductase encoded by the second gene *mas1'*. The third enzyme encoded by *mas0* (or *ags*) lactonizes MOP to agropine (AGR). Agropinic acid (AGA) is generated non-enzymatically from MOP or AGR by spontaneous rearrangement (Tate et al., 1982).

Opine Catabolism

Opines synthesized by plant tumors are utilizable by *Agrobacterium* as growth substrates. The genes responsible for the transport and the degradation of opines are generally encoded by Ti or Ri plasmids, but outside of the T-DNA region. The biochemical pathways for catabolisms of octopine and nopaline by *Agrobacterium* have been well established. Octopine catabolism is inducible by octopine, octopinic acid, and lysopine (Montoya et al., 1977; Klapwijk et al., 1976). Nopaline catabolism is inducible by nopaline (Klapwijk et al., 1976). Octopine also is utilizable by nopaline-type strains, but only after pregrowth with nopaline or even after preinduction with octopine (Firmin and Fenwick, 1978). The region for octopine catabolism (*occ*) is located within 12-kb segment between the *tra* and *moc* (mannityl opine catabolism) regions in octopine-type Ti plasmid (de Greve et al., 1981). The region for nopaline catabolism (*noc*) is present in a 14-kb segment to the right of the T-region of the nopaline-type Ti plasmid pTiC58 (Holster et al., 1980; Schardle and Kado, 1983). The degradation of octopine and nopaline each is mediated by three enzymes. Octopine, octopinic acid, and lysopine are degraded by a membrane-associated octopine oxidase to arginine and pyruvate, respectively (Montoya et al., 1977; Klapwick et al., 1976; Jubier, 1972). Nopaline is degraded by nopaline oxidase to arginine and α-ketoglutarate (Schindler et al., 1989). The second enzyme, arginase, degrades arginine to ornithine with the release of ammonia (Dessaux et al., 1986). Ornithine is converted to proline by an unusual enzyme, ornithine cyclodeaminase (OCDase) (Dessaux et al., 1986; Sans et al., 1987; Schindler et al., 1989). Nopaline-type Ti plasmids encode the nopaline oxidase, arginase, and OCDase. However, octopine-type Ti plasmids encode only octopine oxidase and OCDase. In octopine-type stains, arginase is not encoded by the Ti plasmid. Instead, arginine appears to be converted to ornithine by an arginase encoded elsewhere in the bacterial genome (Dessaux et al., 1986). The octopine and nopaline oxidases are

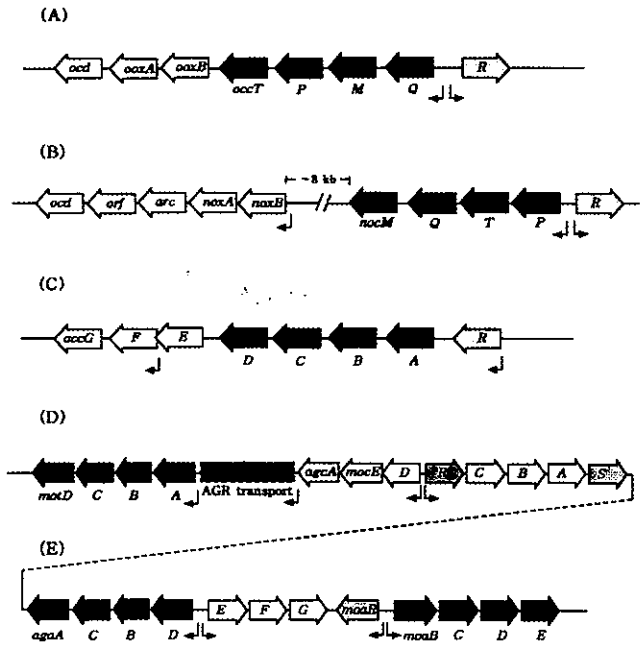

Fig. 3. Structures of genes for catabolism of opines.
(A) The octopine catabolic region in the octopine-type Ti plasmids pTi15955 and pTiR10. (B) The nopaline catabolic region in the nopaline-type Ti plasmid pTiC58. (C) The agrocinopine catabolic region in the nopaline-type Ti plasmid pTiC58. (D) The mannopine and agropine catabolic region in the octopine-/mannityl opine-type Ti plasmid pTi15955. DNA nucleotide sequences of the genes responsible for the AGR transport have not yet been completely determined. (E) The mannopinic acid and agropinic acid catabolic region in the octopine-/mannityl opine-type Ti plasmid pTi15955. The open arrows indicate the genes encoding for the enzymatic degradation of the opines, and the solid arrows indicate the genes encoding for the transport of the opines. The shadowed arrows indicate the genes responsible for the regulation of the operons. Position and direction of promotors are indicated below the gene maps.

heterodimers composed of 50- and 44-kDa subunits, respectively. It is of interest that *Agrobacterium* and *Rhizobium* are the only gram-negative bacteria which degrade arginine by arginase, and among the few that have OCDase (Stalon et al., 1987).

The genes responsible for octopine degradation and arginine catabolism are organized as an operon (Fig. 3A) (Wang et al., 1992). Habeeb et al. (1991) showed that the expression of the regulatory gene *occR* and the structural gene cluster *occQ, occM, occP, occJ, ooxB, ooxA*, and *ocd* are controlled by divergently oriented promoters. The LysR-type regulatory protein encoded by *occR* appears to have dual functions. OccR regulates the expression of its own gene negatively either in the presence of or in the absence of octopine, and it also positively regulates the expression of the *occ* genes and the *ocd* gene in the presence of octopine (Wang et al., 1992). Similarly, the transcriptional activator NocR (Fig. 3B) activates transcription of the *noc* operon in response to nopaline (von Lintig et al., 1991).

The utilization of agrocinopine A and B (Ryder et al., 1984) conferred by the nopaline-type Ti plasmid pTiC58 also has been studied. The genes for these opines (the *occ* genes) are encoded in the 8 o'clock region of the plasmid (Hayman and Farrand, 1990). The DNA sequences of the *acc* genes have been completely determined (Kim and Farrand, 1998). The operon is composed of eight genes: *accR, A, B, C, D, E, F,* and *G* (Fig. 3C). A product encoded by *accR* is similar to the FucR-family of transcriptional repressors at the deduced amino acid sequence level. The genes *accABCD* encode for transport genes for the opines. The genes *accF* and *accG* showed homology to UgpQ of *E. coli*, which is a phosphodiesterase, and to inositol monophosphatase from various eucaryotes, respectively.

The genes for catabolism of mannityl opines also have been intensively studied biochemically and molecular-genetically. The study has been carried out mostly on the genes encoded by the octopine-/mannityl opine-type Ti plasmid pTi15955. The genes for mannopine (MOP) and its lactonized derivative agropine (AGR) are clustered to form operons, and the genes for mannopinic acid (MOA) and agropinic acid (AGA) are also linked in the same plasmid, forming operons located just next to those for MOP and AGR (Fig. 3D and 3E). Genetic study and DNA sequence analysis indicate that three genes are directly involved in the metabolism of MOP. MOP, which is either taken up by the MOP-specific transport genes or delactonized from AGR by MOP cyclase encoded by *agcA* (Hong et al., 1993; Hong et al., 1994), is oxidized by the *mocC* product, MOP oxidoreductase in the expense of NAD^+ as a cofactor (Kim et al., 1996). The product, deoxyfructosyl glutamine (dfg, also commonly called santhopine; SOP) is further degraded by the products encoded by *mocD* and *mocE* (Kim and Farrand, 1996), the functions of which have not yet been clearly elucidated biochemically. It is of interest that MocD from pTi15955 is a homolog of Mas2, the anabolic conjugase encoded by *mas2'* in the T-DNA of the same plasmid, and that MocE and MocC are closely related to the amino half and the carboxyl half, respectively, of Mas1 (MOP reductase), that is the second enzyme for MOP biosynthesis (Kim and Farrand, 1996). Furthermore, *agcA* on pTi15955, encoding for catabolic MOP cyclase, shows homology with the anabolic MOP cyclase, the *ags* gene, located in the T-region of the same plasmid (Hong et al., 1977). These findings suggest a functional and evolutionary relatedness between catabolic genes and anabolic genes for the metabolism of MOP and AGR. The catabolic operon also contains two additional genes, *mocA* and *mocB*, which showed strong homology in the deduced amino acid level with glu-

cose-6-phosphate dehydrogenase and 6-phosphogluconate dehydratase, respectively. These two enzymes are involved in the key steps in the Entner-Doudoroff pathway, that is known to be the main sugar-degrading pathway in *Agrobacterium* spp.. The genes *mocA* and *mocB* are not essential for growth of *Agrobacterium*, indicating that these two genes are present redundantly and probably provide the bacterium with a better efficiency in utilizing sugar moieties split from mannityl opines. The gene *mocR* encodes for a repressor that negatively-regulates *moc* genes (Jung et al., 1999). The operon also encodes gene, *mocS*, that showed homology with *mocR* in the deduced amino acid sequences. Recent study showed that MocR represses the expression of *mocC* and *mocD*, and the repression was relieved upon the addition of AGR (Jung et al., 1999). The role of *mocS* in the regulation of the mannityl opine regulation remains to be elucidated. Recently, the operons responsible for the utilization of MOA and AGA are studied (Sangbon et al., 1999). The operons are mapped right next to the operons for MOP and AGR utilization (Fig. 3E). Genetic study suggested that the products of two genes, *moaF* and *moaG*, are involved in the delactonization of AGA to MOA. MOA is further splitted into mannose and glutamate by deconjugase encoded by *moaE*.

The operons associated with utilization of each opine also encodes for transport systems specific for each of opines (Fig. 3). Commonly, these transport operons encodes for ABC-type transport systems. Among these, it is of interest that the transport system for agrocinopines also confers transport of an antibiotic agrocin 84 (Fig. 2) (Ellis and Murphy, 1981). The antimicrobial activity of this compound will be further discussed below.

Recent studies showed that the megaplasmid called pAtC58 present in nopaline-type strain C58 encodes genes for degradation of a chrysopine-type opine, santhopine (Vaudequin-Dransart et al., 1998) (Fig. 1). As stated above, this compound can be enzymatically produced from MOP by oxidation reaction. Therefore, when *mocC*, the gene encoding the MOP oxidoreductase from *moc* operon, is introduced into a Ti plasmid-cured strain, the resulting strain can grow using MOP as sole carbon and nitrogen sources. Molecular genetic study suggested that two genes for the enzymatic degradation, and, as are the cases of other opines, genes showing strong homologies with ABC-type transport system are involved in the utilization of the opine (unpublished results). This is the first discovery showing that whole functions necessary for utilization of an opine are encoded on avirulent plasmid that lacks T-DNA region - hence lacks oncogenes and opine-synthesis genes - in *Agrobacterium*. This finding may suggest that the genes for opine-utilization evolved on Ti plasmid before did the genes for biosynthesis of the opine, and that those catabolic genes located in the megaplasmid may be a proto-form of the catabolic genes in Ti plasmid.

Physiological Roles of Opines in Plant-*Agrobacterium* Interactions

As mentioned above, opines released from transformed plant cells can be utilized as carbon and energy sources by agrobacteria. Probably due to the strong influence of the Opine Concept, insight to the biological significance of opines have rather been mainly limited to the role as a food for the pathogen. However, several lines of recent researches have broaden the scope on physiological roles of the compounds, and recent discoveries have suggested that opine plays additional roles of interest in the colonization of the bacteria and in the propagation of the virulence factors.

Enhancement of virulence. Exogenous opines enhance the acetosyringone-dependent induction of Ti plasmid-encoded *vir* genes 2- to 10-fold (Veluthambi et al., 1989). Even though opine is not directly involved in the virulence of the bacterium, this result indicates that opine produced by already infected plant cells can enhance the virulence of subsequently infecting *Agrobacterium*.

Inducer for conjugal transfer of Ti plasmid via the auto-induction mechanism. It has well been documented that certain opines also function as signals by inducing conjugal transfer of Ti plasmids. Since Kerr and his colleagues (1977) showed that the frequency of Ti plasmid conjugal transfer increases dramatically when the donor cells are grown in a medium containing certain opines, intensive studies for the opine-induced Ti plasmid conjugation have been carried out mainly using octopine-type strains pTi-15955 and pTiR10 and a nopaline-type strain pTiC58 as model systems. In the case of the octopine-type Ti plasmids, both opine catabolism and the conjugal transfer of Ti plasmids are co-regulated and octopine is an inducer for the expression of genes in the two systems. The LysR-type regulator OccR is responsible for the regulation of the expression of these two systems. The protein has a dual function; it represses the expression of its own gene and positively regulates the expression of Tra and Occ functions (Habeeb et al., 1991). In the case of nopaline-type Ti plasmids, agrocinopines A and B are inducer for conjugal transfer, which coordinatively regulate agrocinopine catabolism and conjugal transfer via the repressor AccR. In both types of plasmids, the expression of the *tra* genes is regulated directly by an activator encoded by *traR*, which can be expressed in the presence of the conjugal opines. TraR is closely related to LuxR, which is an activator responsible for the positive-regulation of transcription of the *lux* operon in *Vibrio fischeri* (Piper et al., 1993). For the activation of *tra* genes, TraR also requires a co-inducer called *Agrobacterium* auto-

inducer (AAI), that is an *N*-(3-oxooctanoyl)-L-homoserine lactone (for review, Fuqua et al., 1994; Hwang, 1999). Therefore, the *tra* functions are regulated by autoinduction (also called quorum-sensing) mechanism, and the initiation of the regulation is exerted by conjugal opines. Our recent study showed that in several mannityl opine-type isolates but not in the classical mannityl opine-type strains R10 or 15955, the expression of autoinducer molecules and conjugal transfer events are induced by the MOP (unpublished results), indicating that MOP also is a conjugal opine for these strains.

Opines as chemoattractant. As in the cases of most motile bacteria, the chemotaxis phenomenon is found also in *Agrobacterium*. *Agrobacterium* strains are attracted to exudates released from root cells (Hawes and Smith, 1989) and to phenolic compounds (Parke et al., 1987; Shaw et al., 1988). These observation suggest that the chemotactic behavior is important in the early settlement of the bacteria in the infecting site. Supporting this idea, mutant lacking chemotactic functions failed to cause tumorigenesis in plant inoculation assays (Hawes and Smith, 1898). Recently, Kim and Farrand (1998) showed that *Agrobacterium* strains are chemoattractive to opines. A nopaline-type strain C58 is chemoattracted to nopaline and agrocinopine A and B, and a octopine-/mannityl opine type strain is attracted to octopine, but not to mannityl opines. The functions for the chemotaxis are encoded by the cognate Ti plasmids. These observation suggest that opines are important for the recruitment of the bacteria in infected sites of plants, and hence help colonization of the bacteria in the rhizosphere.

Protection of the host plant. Opines may help to protect host plants bearing the tumor against herbivore insects or competition from other plants. Sauerwein and Wink (1993) showed that mannopine and mikimopine were toxic to larvae of *Manduca sexta*, and that mikimopine retarded the germination of *Lepidium sarivum* seeds. These observations suggest that *Agrobacterium*-plant interactions may be of a symbiotic rather than pathogenic nature. That is, in the interaction between host plant and *Agrobacterium*, plant provides the bacterium with carbon and energy source and *Agrobacterium* protects host by inhibiting growth of invading parasites. However, very recently a few research groups claimed that above experiment cannot readily be reproducible (personal communication with Dr. S. K. Farrand, Univ. of Illinois, U.S.A.). An answer for this controversy remains to be awaited for more conclusive data.

Antiagrobacterial activity. The anti-agrobacterial antibiotic, agrocin 84, produced by *A. radiobacter* strain K84 inhibits the growth of certain isolates of *A. tumefaciens* and *A. rhizogenes*. The sensitivity is due to the ability of agrobacterial strain to take up the antibiotic. The functions associated with the susceptibility was well studied for the nopaline-type strains C58. As induced with agrocinopine, agrocin 84 can be taken up by the agrocinopine-transport functions encoded by the cognate Ti plasmid pTiC58 (Hayman and Farrand. 1988). As shown in Fig. 2, agrocin 84 is a chemical analogue of agrocinopines. It is speculated that the antibiotic-producing agrobacterial strain, that is an a-virulent strain, ensures the colonization in rhizosphere by displacing the already settled agrobacterial strains. This interesting phenomenon suggests that the nature of *Agrobacterium* in rhizosphere is quite complicated, providing a elegant model for the study of the plant-microbe interactions.

Recently, we showed that growth of certain mutants from octopine-/mannityl opine-type strain 15955, that has a null mutation in *mocC*, the MOP oxidoreductase gene, and contains a functional mannityl opine transport functions, is inhibited by mannopine and also by agropine less severely though (unpublished results). This observation allowed us to speculate that the presence of the opines in the rhizosphere ensures the propagation of wild-type clones by depleting spontaneous mutants deficient of the essential gene for the utilization of those opines. It also is possible that those opines may mimic the action of agrocin 84 in nature. If this hypothesis is to be valid, we could find natural isolates which can take up but cannot metabolize the opines. At the moment, it is not of certain that any such agrobacterial strains exist in nature. In the future, test of various isolates from a rhizosphere can provide chance to test this hypothesis.

Concluding Remarks

It has been almost a century since *Agrobacterium* was identified as a pathogen causing plant tumorigenesis. This bacterium attracted enormous interest due to its delicate pathogenic mechanism, existence of opine, and also agronomic importance. Furthermore, various genetic tools readily applicable to the bacterium also have made the molecular genetic study of the bacterium even more active. To the best of my knowledge, the interaction between this bacterium and host is still the only known case in which the interkingdom-genome-transfer event occurs. This amazing phenomenon ironically has rendered biologists less interested in other interesting features of this bacterium. Last decade, the study on tumorigenesis has been quite slowed down. In contrast, studies on the molecular genetic and physiological studies on opines has ceaselessly carried out for several decades. New types of opines are still discovered, and new roles of the compounds in microbe-plant interactions are being emerged. It is expected that the plant-microbe interaction mediated by these compounds will allow us to broaden our knowledge on the interkingdom

interaction, and will provide us with valuable information to understand and overcome bacterial pathogenesis and to develop useful artificial host-microbe interactions.

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