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REVIEW ARTICLE

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Ethylene Effect on Soybean Root Infection by Soybean Cyst Nematodes

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INTRODUCTION

Nematodes, specifically **cyst** nematodes, are the most damaging pest to US **soybean** production (Wrather and Koenning, 2006). With an increasing number of acres planted with **soybean** and new varieties being developed to geographically broaden profitable cultivation of **soybean** in the US and across the world, the continued study of this devastating pest is of the utmost importance. **Soybean cyst** nematodes (SCN) are obligate parasites that can alter **root** cell development to support its nutritional and reproductive needs (Williamson and Gleason, 2003; Davis et al., 2004). The localized commandeering of plant developmental processes **by** the nematode requires interactions with the host that involve changes in host gene expression. A number of **studies** have demonstrated that both **root** knot and **cyst** nematodes may alter the balance of plant hormones to achieve the cellular conditions needed for development of the feeding structure. In particular, auxin and **ethylene** may play important roles in the formation of the nematode feeding structure (Goverse et al., 2000; Wubben et al., 2001). Alteration in the localized balance of these two hormones would be expected to have a marked impact **on** gene expression, irrespective of any other factors that might also affect gene expression.

How the nematode brings about changes in plant hormone levels and developmentally regulated processes in the host is of great interest. The nematode oesophageal glands are a potential source for pathogenicity factors secreted from the nematode. The oesophageal glands have been successfully targeted for preparation of organ-specific cDNA libraries and many transcripts identified have the potential to be pathogenicity factors (Gao et al., 2003; Huang et al., 2003). Currently a few of the oesophageal gland proteins have a demonstrated potential to alter plant development when expressed in transgenic plants (Doyle and Lambert, 2003; Wang et al., 2005; Huang et al., 2006).

In addition to the characterization of pathogenicity factors of nematode origin, cataloguing changes in susceptible host gene expression in response to SCN **infection** will identify developmental and mechanistic processes associated with SCN colonization of **soybean roots** and distinguish host targets for controlling nematode pathogenicity of **soybean**. To achieve this objective, **soybean roots** were inoculated with SCN and after 8, 12, and 16 d small pieces of the **root** that had multiple swollen female nematodes protruding from the **root** were dissected out. Elimination of **root** material not directly associated with actively growing nematodes greatly enhances our ability to detect changes in gene expression associated with SCN **infection**. The RNA from these **root** pieces was hybridized to Affymetrix **soybean** GeneChips and statistical analysis of the microarray hybridization signals identified 1404 transcripts that increase >2-fold in SCN-colonized **root** pieces and 739 that decreased >2-fold in the same **root** pieces.

LYSOBACTER

The genus **Lysobacter** belongs to the family Xanthomonadaceae within the gamma proteobacteria and includes thirteen named species: Lysobacter enzymogenes, L. antibioticus, L. gummosus, L. brunescens, L. defluvii, L. niabensis, L. niastensis, L. daejeonensis, L. yangpyeongensis, L. koreensis, L. concretionis, L. spongiicola and L. capsici. Lysobacter spp. were originally grouped with myxobacteria because they shared the distinctive trait of gliding motility, but they uniquely display a number of traits that distinguish them from other taxonomically and ecologically related microbes including high genomic G+C content (typically ranging between the 65-72%) and the lack of flagella. The feature of gliding motility alone has piqued the interest of many, since the role of gliding bacteria in soil ecology is poorly understood. In addition, while a number of different mechanisms have been proposed for gliding motility among a wide range of bacterial species, the genetic mechanism in Lysobacter remains unknown. Members of the Lysobacter group have gained broad interest for production of extracellular enzymes. The group is also regarded as a rich source for production of novel antibiotics, such as β-lactams containing substituted side chains, macrocyclic lactams and macrocyclic peptide or depsipeptide antibiotics like the katanosins

HABITAT

Lysobacter spp. have been described as ubiquitous inhabitants of soil and water. Their presence has been largely ignored, since members often are minor components in sample screenings when using conventional isolation procedures. However, because of improved molecular methods of identification and better descriptions for the genus, their agricultural relevance is becoming increasingly evident especially as members of ecologically significant microbial communities associated with soil and plants. Recent evidence suggests that Lysobacter spp. may occupy a wide range of ecological niches beyond those associated with plants, including a broad range of 'extreme' environments. For example, 16S rDNA phylogenetic analyses show Lysobacter clades that include sequences obtained from hydrothermal vents, isolates from Mt. Pinatubo mud flows and upflow anaerobic blanket sludge reactors, and an iron-oxidizing, microaerophilic lithotroph.

BIOLOGICAL CONTROL

The potential of Lysobacter species as biological control agents for plant diseases has been recognized recently. Among L. enzymogenes strains, C3 is the most thoroughly characterized strain at both the molecular and biological levels. The ecological versatility of the strain is reflected by the range of diseases it is able to control, as well as the various plant hosts and plant parts it is capable of colonizing. For example, L. enzymogenes strain C3 (erroneously identified as Stenotrophomonas maltophilia) has been reported to control foliar diseases such as leaf spot of tall fescue caused by Bipolaris sorokiniana, bean rust caused by Uromyces appendiculatus and Fusarium head blight of wheat . L. enzymogenes strain C3 also has been reported to suppress soilborne diseases, such as brown patch in turfgrass caused by Rhizoctonia solani, the seedling disease Pythium damping-off of sugarbeet and summer patch disease of Kentucky bluegrass caused by the root-infecting Magnaporthe poae.

DISEASE SUPPRESSIVE SOILS

Lysobacter species have also been isolated from soils suppressive to Rhizoctonia solani. Clay soils with natural suppressiveness against Rhizoctonia contained higher numbers of antagonistic isolates of L. gummosus, L. antibioticus and/or L. capsici. Although the mechanism behind this phenomenon is not yet understood, it appeared that growing grass/clover increased the number of these Lysobacter species as well as the Rhizoctonia suppressiveness.

MECHANISMS OF ANTAGONISM

Originally characterized as a biological control agent for plant diseases, L. enzymogenes strain C3 is unique in that it expresses a wide range of mechanisms contributing to microbial antagonism and biological control that are not shared by all strains of the species. The strain produces numerous extracellular enzymes that contribute to biocontrol activity, including multiple forms of β-1,3-glucanases and chitinases. The strain also has been demonstrated to induce systemic resistance in certain plants, protecting them from pathogen infection. In addition, recent studies have indicated important roles for secondary metabolites with antibiotic activity and biosurfactant activity in fungal antagonism . Several of these traits are globally controlled by a regulator encoded by the clp gene. Mutations in clp are intriguing for two reasons. First, the mutant phenotype implies that a broad range of genes is involved in secreted antimicrobials associated with the clp regulon, many of which remain unidentified. The second is that mutations in clp result in significant loss of extracellular enzyme activities and antimicrobial activity displayed by L. enzymogenes strain C3. These activities normally are phenotypically overwhelming and often lead to masking of other phenotypes in standard assays, making mutation effects of non-related genes difficult or nearly impossible to evaluate. However, strains harboring clp gene mutations provide a means to separate clp-regulated phenotypes from others (such as that describe below), thus making their evaluation feasible.

LYSOBACTER GENETICS

L. enzymogenes strain C3 is a genetically tractable strain allowing for easy construction of gene knockouts, supporting its use as a model genetic system for unraveling the molecular basis of pathogenicity, as well as identifying mechanisms of microbial antagonism and biological control. Indeed, a number of derivative strains of L. enzymogenes strain C3 already have been constructed, including mutants affected in structural genes encoding enzyme activities, the regulatory clp gene and various combinations thereof.

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