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Susceptibility of rice to the blast fungus, Magnaporthe grisea

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Summary

The interaction between rice and the blast fungus Magnaporthe grisea is the focus of extensive studies on rice disease resistance and fungal infection mechanisms. Here, we review the characteristics of susceptible rice blast infections in terms of physiology, cytology and both host and pathogen transcriptional responses. The success of the infection and the type of disease symptoms strongly depend on environmental and developmental cues. After its penetration into a host cell, the fungus differentiates invasive hyphae that fill up the plant cell lumen and are in direct contact with the membrane of the infected cell. The infected plant cell is alive, displaying considerable vesicle accumulation near the fungus, which is consistent with the establishment of a biotrophic phase at this stage of the infection. Colonization of host tissues by the fungus occurs through the perforation of cell walls from adjacent cells, likely using plasmodesmata as breaking points, or through hyphal growth in the apoplasm. After a few days of biotrophic growth within rice tissues, the fungus switches to a necrotrophic-like phase associated with the onset of sporulation, leading to visible lesions. Genome-wide transcriptomic studies have shown that classical plant defence responses are triggered during a susceptible infection, although the kinetics and amplitude of these responses are slower and lower than in resistant interactions. Infected rice cells are submitted to an intense transcriptional reprogramming, where responses to hormones such as auxins, abscissic acid and jasmonates are likely involved. Consistent with the extensive plant-fungal exchanges during the biotrophic phase, many rice genes expressed during infection encode plasma membrane proteins. At the onset of lesion formation

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Abbreviations: ABA, abscissic acid; dpi, day post-inoculation; EST, expressed sequence tag; EIHM, extra-invasive hyphal membrane; GO, gene ontology; IH, invasive hyphae; JA, jasmonic acid

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(5 days after the start of infection), *M. grisea* is actively reprogramming its transcription towards active DNA, RNA and protein syntheses to sustain its rapid growth in infected tissues. A striking characteristic of *M. grisea* genes expressed at this stage of the infection is the over-representation of genes encoding secreted proteins, mainly of unknown function. However, some of these secreted proteins are enzymes involved in cell wall, protein and lipid degradation, suggesting that the fungus is starting to degrade host polymers and cell walls or is remodelling its own cell wall. The next challenge will be to decipher the role of these induced plant and fungal genes in the susceptible interaction.

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Introduction

Rice is a staple crop of economic importance in many countries and it is estimated that its production (600 million tons in 2000) will have to increase by 40% in 2030. This increase will have to face less land and water for rice cultures as well as fewer fertilizers and chemicals. According to the FAO, diseases, insects and weeds are responsible for vield losses of up to 25% in rice. One of the most serious and widespread diseases of rice is blast caused by the ascomycete fungus Magnaporthe grisea. In Japan, blast causes annual yield losses corresponding to 275,000 tons of rice (25% of production) and requires the extensive use of fungicides (1.8 million euros in 2000). Fungicides, resistant cultivars, agronomical practices and biotechnological methods have been developed and used to control this important disease. Rice resistance to blast is widespread and controlled by a large number of independent major resistance genes. However, most of these resistances are broken down after a few years of intensive agricultural use (Correa-Victoria et al., 2004). The mechanisms involved in resistance of rice to blast are still poorly understood, hampering their use in breeding or biotechnology. Over the years, the rice/M. grisea pathosystem has become a model for the study of plant-microbe interactions as both genome sequences are available and molecular genetics tools are available and routinely used. This model system is so far the only interaction between a monocot plant and a fungus for which such molecular and genomic tools are available. M. grisea is considered as a hemibiotrophic fungus (Talbot, 2003) with a significant biotrophic phase at the early stages of infection (Kankanala et al., 2007). A better understanding of the mechanisms involved in M. grisea infection and responsible for damage to the host plant may provide new methods to control this disease. In this review, we give a brief overview of our current knowledge on disease susceptibility to rice blast, with an emphasis on novel cellular and molecular information on the infection process.

Overview of rice susceptibility to blast

M. grisea can infect all aerial rice tissues, including leaves (Figure 1), stem and panicles (neck blast disease). Interestingly, rice mutants that are affected in disease susceptibility in leaves are also affected in the susceptibility of panicles to neck blast (J.B. Morel, unpublished). This suggests that studying leaf blast may provide important elements to improve resistance to neck blast disease, which is the major cause of yield loss caused by M. grisea. M. grisea is also able to infect rice roots and xylem vessels using developmental processes typical of root-infecting fungi (Sesma and Osbourn, 2004). However, the importance of this type of infection in field epidemics remains unclear. Susceptibility to blast is dependent on several developmental and environmental cues. It usually decreases with plant (adult resistance) and leaf age (Figure 1A). Susceptibility of rice to M. grisea is dramatically increased by excess nitrogen fertilizers, as observed as early as 1941 by Ito and Sakamoto (cited in Suzuki (1965); Figure 1B). Although the mechanisms underlying the variations in susceptibility of rice to blast are unknown, this phenomenon shows that susceptibility strongly depends on plant developmental stage and physiological status. Furthermore, susceptible blast symptoms display an astonishing diversity in shape and type when considering lesions induced by the fungus (Figure 1C). Typically, ellipsoidal lesions corresponding to the region colonized by the fungus appear on infected leaves 5-7 days post-inoculation (dpi). Their aspect varies from fully susceptible light green spreading lesions to partially susceptible dark green lesions with a brown margin that corresponds to a local induced resistance. This observation is particularly important since the presence of such green/brown lesions is characteristic of symptoms observed on rice cultivars with

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