

Fitness cost, priming, and induced systemic resistance

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Plants have evolved numerous mechanisms to defend themselves against microbial pathogens. Some of these defense mechanisms are constitutive, such as the physical barriers of the cell wall, while others are induced. Induced defense mechanisms can be divided into two categories. The first is systemic acquired resistance (SAR). SAR develops locally and systemically in response to broad-spectrum resistance after initial attack by pathogen. This phenomenon rapidly enhances the defense response of the host plant a response such as the hypersensitive response, HR. SAR induce a set of pathogenesis-related (PR) protein genes. The production of PR-proteins is mediated via a process dependent on salicylic acid (SA). However, as shown in the example of chemical inducer, benzo(1,2,3)thiadiazole-7-carbothioic acid S-methyl ester (BTH), application of BTH on the wheat grown in the field resulted in reduction of yield. Compared to constitutive resistance, induced resistance has the disadvantage of leaving plants unprotected until resistance is expressed. Therefore, the advantage of this resistance demands an explanation. One possible explanation is "allocation fitness cost". In the ecological point of view, fitness costs can result from the allocation of limited resources of plants to resistance. These resources then can not be used for growth or reproduction or allocation costs. If resistant plants reproduce less effectively than sensitive plants when there is no pathogen attack, then the disadvantages of any temporal delay in inducing resistance may be outweighed by the benefit of not incurring these resistance related costs when resistance is unnecessary.

The second category of induced resistance is induced systemic resistance (ISR). The process of active resistance in ISR is dependent on the host plant's physical or chemical barriers, which are activated by biotic agents (inducing agent) such as plant growth-promoting rhizobacteria (PGPR). ISR develops systemically without visible HR in response to colonization of plant roots by PGPR. ISR has been considered a sound means to control pathogens including soilborne or foliar fungi, bacteria, virus, and even insect. Intriguingly, PGPR elicited ISR coupling to plant growth promotion in many cases. If PGPR elicited ISR also require allocation fitness cost, the elicitation of both ISR and promotion of plant growth at the same time can not be easy to be explained.

Regarding this point, recent results reported that plants just prime defense mechanisms and its direct responses against pathogens following elicitation of ISR/SAR and HR resulting that plants do not need to consume their resource constitutively. In general, some of the compounds normally associated with ISR are expressed in noninfected tissue in response to an initial infection site. Other biochemical changes during elicitation of ISR become obvious only in response to an additional infection and only in plant parts where an effective resistance is required. This result has been described as priming and also called as conditioning, potentiation, or sensitization. The effects of priming can be induced by chemical inducers such as BTH. Responses such as phytoalexin synthesis or cell wall lignification then occur more rapidly and more strongly than during the primary infection. ISR mediated priming on the defense genes of Arabidopsis was reported by transcriptome analysis after challenge of bacterial speck pathogen. However, a single common determinant of both plant growth promotion and ISR was not reported until 2003.

In 2003, volatile organic compounds (VOCs) emitted from two *Bacillus* spp. were discovered to be primary determinants of both plant growth promotion and elicitation of ISR in Arabidopsis. Ryu et al. (2003) demonstrated significant growth promotion of Arabidopsis by *B. subtilis* strain GB03 and *B. amyloliquefaciens* strain IN937a. Among the VOCs from strain GB03, 2,3-butanediol was the major compound that elicited plant growth promotion and ISR against *Erwinia carotovora* subsp. *carotovora*. Collectively, PGPR seems to prime plant to be resistant against plant pathogens. However, the molecular mechanisms underlying priming and its relationship with allocation fitness cost in the overall plant resistance still remain to be investigated.