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Immunity and starvation: new opportunities to elevate disease resistance in crops

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Plants use multiple mechanisms to defend themselves against invading microbes. Besides using their immune system to surveil and eliminate pathogens, plants actively block the pathogens' access to nutrients as an alternative way to prevent colonization. In this review, we focus on immunity and starvation as major obstacles for pathogens' adaptation. We summarize the key mechanisms employed by pathogens to modulate host immunity and to guarantee sugar uptake. In contrast to genes that deal with the immune system and show high levels of plasticity, pathogen genes involved in sugar acquisition are highly conserved, and may not have adapted to co-evolving interactions with the host. We propose a model to assess the durability of different control strategies based on the ability of pathogens to deal with host immunity or starvation. This analysis opens new opportunities to elevate disease resistance in crops by reducing the likelihood of pathogen adaptation.

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Introduction

Microbes that colonize plants require a full spectrum of nutrients to sustain growth. The key question is thus: Are all essential nutrients available in sufficient supplies, either as a pool or delivered by sufficient flux over time? Patrick [1] suggests that the flux may be insufficient. In that scenario, nutritional attainment of a microbe would depend on effective manipulation of the host cell.

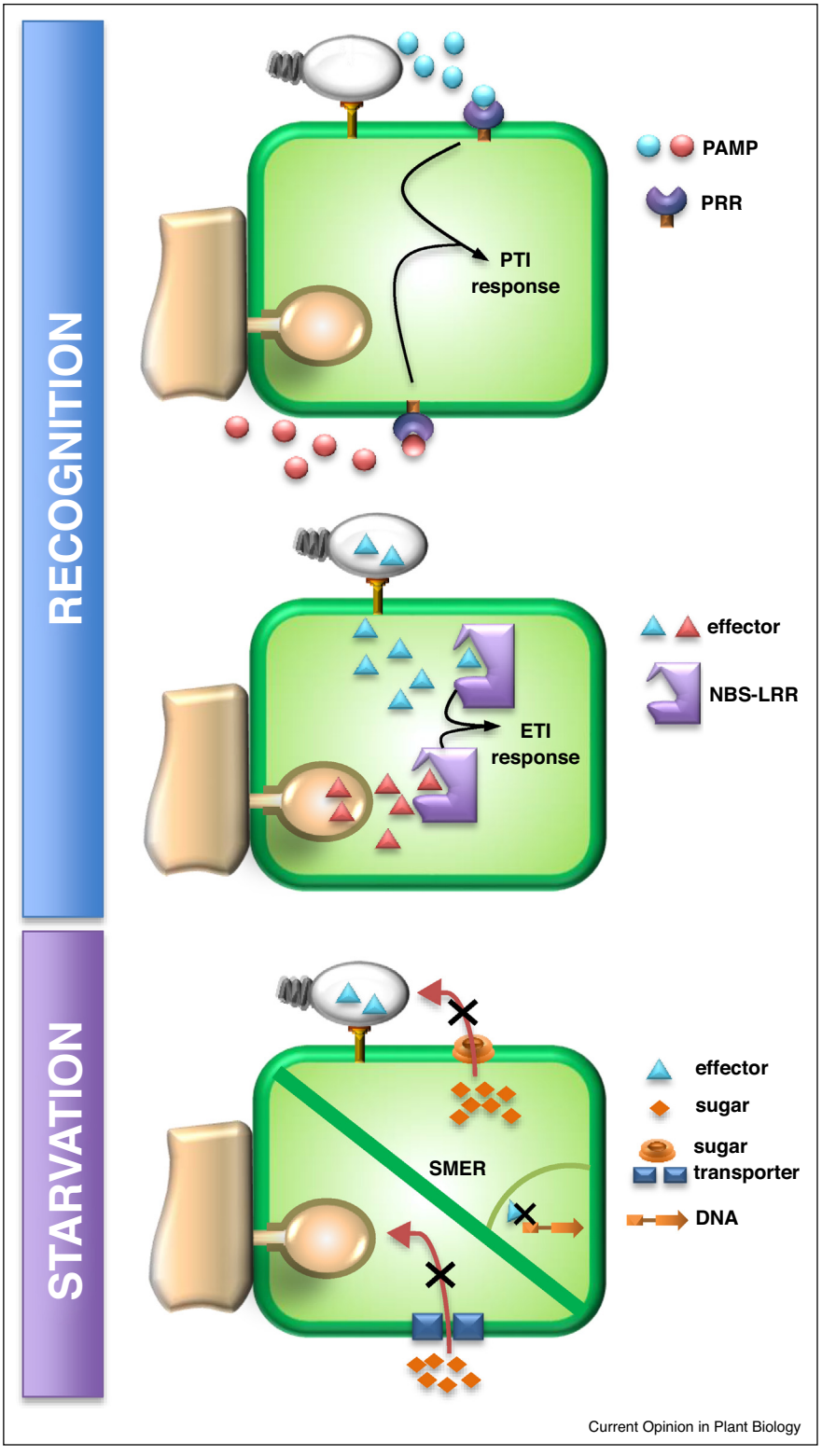
Nutrient deprivation and immunity represent ways in which the plant filters foes out of the system (Figure 1). During compatible interactions, pathogens activate major signaling cascades to exploit host nutrients but also to modulate defenses [2]. Sugars, amino acids, and minerals need to be extracted, processed, and incorporated in a coordinated fashion. Pathogens' importing machinery (*e.g.*, invertases, nutrient transporters, siderophores) articulates with corresponding host substrates to ensure a continuous supply. In parallel, pathogens need to overcome host defenses that perceive different pathogen determinants. The first layer of protection relies on the recognition of extracellular pathogen-associated molecular patterns (PAMPs) and the activation of PAMP-triggered immunity (PTI). A second layer called effector-triggered immunity (ETI) acts as a surveillance system to sense pathogen-derived proteins that target different subcellular compartments [2–4].

To facilitate the analysis, we will dissect the complexity of host-pathogen interaction in two components: nutrient acquisition and immune modulation. Although both may share signaling networks, the evolution of each component might be independent. This review describes how plants restrict sugar mobilization into the apoplast to control microbial establishment. We also summarize the key mechanisms employed by plant pathogens to suppress local response and induce sugar leakage from the host. Although pathogens appear to rely on immune modulation to overcome plant resistance, sugar starvation represents a new opportunity to reduce overall pathogen adaptability and to elevate disease resistance in crops.

Sweet inside: apoplastic sugar restriction as a host tactic

Many pathogens live extracellularly (apoplast) or at least go through a phase in which they grow in the apoplast. It is thus conceivable that, besides activating the immune system, a simple way for the host to control microbial density is by limiting access to nutrients. For instance, plants have to transport sugars between cells and appear to use either symplastic or apoplastic transport mechanisms for loading the phloem [4]. Apoplastic mechanisms involve the secretion of sucrose by the phloem parenchyma via SWEET transporters, and subsequent uptake by the sieve element companion cell complex via SUTs [5], thereby releasing sugars at least transiently into the apoplast. However, this release is at the interface of a few cells deep inside the phloem, a mechanism that may have evolved to restrict the availability of sugars across the whole apoplastic space surrounding the epidermal and mesophyll cells. Symplastic (*i.e.*, cell-to-cell) transport via plasmodesmata would avoid transfer into the apoplast. Nevertheless, complete elimination of sugars from the

Figure 1



Major defense mechanisms used by plants to stop pathogens. Host defenses that rely on pathogen recognition are divided into PAMP-triggered immunity (PTI) and effector-triggered immunity (ETI). Host mechanisms that prevent or reduce nutrient leaking also lead to starvation-mediated resistance (SMER). Unicellular and filamentous infections are represented in each host cell. Circles represent PAMPs and triangles represent effectors derived from bacteria type III secretion apparatus (blue) or fungal haustoria (red). Legends are described on the right side of each mechanism.

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