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Harnessing inherent immune defenses of crops for sustainable pest management

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A Viewpoint on the Frontiers in Science Lead Article
Enabling sustainable crop protection with induced resistance in plants

Key points

- Sustainable crop protection practices are crucial to meet the United Nations Food and Agriculture Organization's (FAO) projection of needing 50% more agricultural output by 2050, ensuring the growing population's needs for food, feed, fiber, and fuel are met while preserving the environment for future generations.
- Strategies that exploit the inherent ability of plants to control diseases and simultaneously reduce reliance on pesticides, including those that leverage resistance genes, induced resistance (IR) mechanisms, and mutant alleles at susceptibility genes loci, will be major contributors to integrated pest management (IPM) approaches for controlling plant diseases.
- Education and outreach to farmers and consumers addressing long-term benefits of IPM strategies are critical to the success of IPM in crop protection, particularly with the relevant legislation and sufficient funding.

Introduction

Agriculture is an important part of human evolution. Besides aiding humans in meeting their nutritional and energy needs, agriculture is also a major contributor to the gross domestic product (GDP) and economic development of a large part of the world. Almost 80% of the world's farms are small holdings that contribute to one-third of global agricultural output. The United Nations Food and Agriculture Organization (FAO) estimates that 50% more agricultural productivity will be needed by 2050 to support the food, feed, fiber, and fuel requirements of the growing world population (1). Given the context of climate change, environmental pollution, ecological degradation, and constraints on natural resources, sustainable practices are vital for meeting future agricultural demands while simultaneously protecting our environment.

Resistance genes and cultivars

Diseases and invasive pests contribute to an average 40% decrease in global agricultural production at a combined cost of US$290 billion to the global economy (1). In the case of bread wheat (*Triticum aestivum*)—a major source of protein and calories consumed by humans—nearly 21% of yield is lost annually to diseases, with leaf rust and Fusarium head blight being the most damaging diseases economically (2). Practices that limit agricultural loss to diseases and insect infestations by exploiting the inherent ability of plants to control pests and simultaneously reduce reliance on pesticides are critical for sustainable agriculture. Over the past three decades, plant resistance (*R*) genes, most of which encode intracellular immune receptors that are directly or indirectly associated with perceiving pathogen-derived effectors, have been successfully utilized to develop plant varieties with full or partial resistance to individual diseases, which in some cases is accompanied by a hypersensitive response. In the case of bread wheat, over 190 exotic *R* genes have been introduced from elite varieties, with resistance conferred against stem rust by *Sr2* from emmer wheat (*T. turgidum*), *Sr25* from tall wheatgrass (*Thinopyrum obtusiflorum*), and *Sr31* from rye (*Secale cereale*) being notable successes (3). While the identification and characterization of *R* genes and their implementation have facilitated the development and deployment of disease-resistant crops, the ensuing process takes several years and can be accompanied by linkage drag; the crop is often rapidly overcome by the pathogen, especially when resistance is due to deployment of a single *R* gene. Furthermore, while effective against biotrophic pathogens that obtain nutrients from live cells/tissues, *R* gene-conferred resistance is not as prevalent against necrotrophic pathogens that have a lifestyle that involves killing host cells for nutrients.

Crop vaccination to limit diseases

In their *Frontiers in Science* lead article, Flors et al. (4) discuss the value of sustainable crop protection by way of another strategy, induced resistance (IR), which is naturally utilized by plants to limit disease. IR, which is systemically activated in plants in response to a localized prior infection [a phenomenon termed "systemic acquired resistance" (SAR)] or by exposure of roots to plant growth-promoting microbes (a phenomenon termed “induced systemic resistance”), involves “memory” of a prior infection/exposure. This memory is associated with defense priming that conditions the plant, conveying upon it the ability to rapidly turn on full-blown defenses in response to a subsequent infection. Crop vaccination (CV), which includes IR and natural products that can activate plant defenses to confer broad-spectrum resistance, is a preventive (not curative) strategy that can be valuable, especially in cases where genetic resistance is not available. Considering its multigenic nature, resistance conferred by CV is less likely to break down. While CV will not eliminate the use of pesticides, if used as a complementary approach it can reduce agriculture’s dependence on pesticides. Considering the development of new agricultural policies and initiatives to reduce the use of pesticides across the globe, this review by Flors et al. (4) is timely and informative. It summarizes the milestones in IR research, overviews the epigenetic underpinnings of defense priming associated with IR, and discusses opportunities that IR offers for sustainable agriculture as well as the factors that limit the adoption of IR. Further, they offer some solutions to address the bottlenecks hindering the adoption of IR for crop protection.

Fusarium head blight, which is caused by several fungal species in the genus *Fusarium*, is a damaging disease of wheat and other small grain cereals that affects grain yield and quality (5). In 2003, a major outbreak in the Southeastern United States resulted in a total loss of wheat amounting to US$13.6 million (5). Similar outbreaks and losses because of this disease have occurred in other wheat-growing areas of the world. Despite global efforts over the past 20 years to combat Fusarium head blight in wheat, no *R* gene for this disease has been identified in bread wheat and related species. Current control efforts combine planting partially resistant varieties along with crop rotation, seed treatments, and fungicide application. However, the efficacy of fungicides is inconsistent and only provides disease suppression. Furthermore, the window for applying fungicides is limited by the short infection window of 1 week around anthesis and the warm and humid weather that is conducive to infection. Fusarium head blight is a prime example of a disease that CV strategies can help control. Resistance in wheat against Fusarium head blight is enhanced by application of SAR-inducing activity purified from *Arabidopsis thaliana* leaves (6), application of SAR-signaling metabolite salicylic acid or its synthetic analog benzothiadiazole, and by increasing the expression of *NPR1*, which encodes a salicylic acid receptor and is a key regulator of SAR (7).

Targeting susceptibility genes for crop protection

Another promising strategy that aims to provide new genetic sources for durable resistance is targeting the knockdown of susceptibility (*S*) genes in plants (8–10). Pathogens leverage plant *S* genes to facilitate infection. The *Mildew Locus O* (*MLO*) is a well-characterized *S* gene associated with susceptibility to powdery mildew infection by *Blumeria graminis* f. sp. *tritici*. Recessive *mlo* alleles in barley, which result in a reduction in *MLO* activity, confer resistance against a broad spectrum of powdery mildew strains by preventing fungal penetration of host cells. Additionally, *mlo*-based resistance has similarly been noted in several other plant species, including wheat (8, 10). *XA13* in rice is another well-studied *S* gene. The expression of *XA13* in rice, which encodes a sugar transporter, is targeted by *Xanthomonas oryzae* pv *oryzae*, the causal agent of bacterial blight, and *xa13* mutant alleles confer resistance to bacterial blight in rice. Similarly, several candidate *S* genes have been reported in wheat that, when knocked down, confer disease resistance (10). Besides facilitating pathogen (pre)penetration (e.g., *MLO*), *S* genes can be involved in other stages of infection, including providing plant-derived cues that signal transcriptional reprogramming of the pathogen, host factors required for translocation of pathogen-derived effectors, factors that facilitate feeding/nutrient acquisition and sustenance of the pathogen, and factors that suppress plant defenses (8–10). *DMR6* in tomato, which is involved in hydroxylating salicylic acid, and *EDR1* in Arabidopsis and wheat, which encodes a MAP kinase, are examples of *S* genes that suppress immune mechanisms (8, 10). The knockdown/knockout of *S* genes provides an effective way to enhance broad-spectrum resistance using targeted gene editing or genetic variants like those available from Targeting Induced Local Lesions IN Genomes (TILLING) populations. These mutant *S* alleles provide the additional advantage of not being genetically modified, thus facilitating consumer acceptability. Many of these *S* genes are conserved among plants. However, the application of mutant alleles at *S* loci for breeding resistance has been limited due to potential pleiotropy. The availability of genome-editing technology offers the potential to develop novel disease-resistance-conferring *S* alleles without pleiotropic effects.

Integrated pest management

The cornerstone of sustainable agriculture should be based on the principles of managing pathogens and pests (not eradicating them) while simultaneously considering pathogen evolution. It should include an integrated approach, such as integrated pest management (IPM), that merges preventive and curative measures that comprise a combination of planting resistant and tolerant plant varieties, cultural practices that include crop rotation, cultivar mixing and/or intercropping, crop vaccination, and biological control, with chemical control as a last option. Education and outreach efforts that are mindful of the long-term benefits of sustainable practices for the farmer, the consumer, and the environment are critical for the successful acceptance of IPM. These approaches must be complemented by legislation that supports IPM as well as sufficient funding that allows for the development and testing of IPM strategies. Such support is essential to ensuring that innovations contributing to sustainable agriculture are available also to small and poor farming communities: they will continue to play an important role in feeding the world.

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Author contributions

JS: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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