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Review

Engineered plant virus resistance

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ABSTRACT

Virus diseases are among the key limiting factors that cause significant yield loss and continuously threaten crop production. Resistant cultivars coupled with pesticide application are commonly used to circumvent these threats. One of the limitations of the reliance on resistant cultivars is the inevitable breakdown of resistance due to the multitude of variable virus populations. Similarly, chemical applications to control virus transmitting insect vectors are costly to the farmers, cause adverse health and environmental consequences, and often result in the emergence of resistant vector strains. Thus, exploiting strategies that provide durable and broad-spectrum resistance over diverse environments are of paramount importance.

The development of plant gene transfer systems has allowed for the introgression of alien genes into plant genomes for novel disease control strategies, thus providing a mechanism for broadening the genetic resources available to plant breeders. Genetic engineering offers various options for introducing transgenic virus resistance into crop plants to provide a wide range of resistance to viral pathogens. This review examines the current strategies of developing virus resistant transgenic plants.

Contents

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1. Introduction

Plants are under constant stress from both biotic and abiotic factors that affect their physiology and productivity. Biotic pressures from different groups of plant pathogens, which include fungi, oomycetes, bacteria, nematodes, insects, viruses and parasitic plants cause serious crop yield loss. Because of their highly diverse presence in the environment, plant pathogens are irrefutably the most serious threat to worldwide food security.

Viruses are ubiquitous in the environment. As of 2012, the International Committee on Taxonomy of Viruses (ICTV) reported 2619 virus species (ICTV Master Species List, 2012 v2) [1]. This number continues to grow as new species are routinely identified. Disease caused by the large virus population in the ecosystem is undoubtedly one of the most limiting factors in crop production. Despite the absence of exact figures, damage from virus diseases is widely accepted to significantly cause worldwide economic yield losses [2]. Damages range from stunted growth, reduced vigor, decreased market esthetic values of the products and/or total yield loss. Unfortunately, no antiviral chemical is available to protect plants from virus diseases. Additionally, viruses have a very efficient system of dissemination through vector transmission by insects, arthropods, fungi and nematodes. Having no specific control techniques, farmers rely solely or by combining traditional cultural management practices such as field sanitation, crop rotation, planting of trap plants, spraying for vector [3], rouging and manual removal of infected plants upon detection of disease symptoms. Certified virus-free seeds or planting materials have also been used to prevent infection [4,5] but they do not guarantee that plants will remain uninfected in the field. These complexities in the management practices to control viruses limit the eradication of the disease and incur additional costs to the farmers.

2. Virus resistance

Resistance mechanisms in the host plant is governed by an incompatible gene for gene interaction involving the resistance (*R*) gene product from the host and the corresponding Avr gene product from the pathogen [6,7]. Plants respond to an intruding pathogen either by their constitutive or pre-formed defenses [8] or via host resistance induction [9–11]. Pre-formed defenses include the cuticle or thick waxy surfaces, cell walls, antimicrobial compounds and enzyme inhibitors that block the entry of pathogens or prevent vectors from transmitting viruses. Induced resistance is the ability of plant cells to activate and increase their level of resistance to infection after perceiving or being stimulated by intruding pathogens [9].

In early years, two major categories of disease resistance were recognized as non-host resistance and host resistance [12]. Non-host resistance occurs when all genotypes within a plant species show resistance or fail to be infected by a particular virus, which can be due to the host lacking susceptibility factors required by a particular virus [13,14]. Another manifestation of non-host resistance is the plant's capability of recognizing common pathogen (or microbe)-associated molecular patterns (PAMPs or MAMPs). MAMPs/PAMPs are essential molecules present in a specific form in pathogens, but they are foreign to plants. They serve as defense elicitors detected by pattern recognition receptors (PRRs) located in the plasma membrane of plants. Such type of non-specific immune system, known as innate immunity, maintains an inborn immunity of each cell and generates systemic signals emanating from the infection sites [15]. The innate immunity system is believed to be of common evolutionary origin in the defense systems of pathogens in higher eukaryotes [16,17]. While MAMPs/PAMPs and corresponding PRRs are yet to be fully recognized in plant virus infections, the terms are often used in animal virology. For example, the replicating intermediate dsRNA of +RNA viruses is recognized as a PAMP triggering interferon induced virus resistance [18].

Conversely, host resistance is evident when the genetic polymorphism for susceptibility is observed in plant species. This category of resistance is called specific resistance or cultivar resistance. Systemic acquired resistance (SAR) has been depicted as a third category based on the studies involving tobacco mosaic virus (TMV) [19,20]. SAR involves a spread of resistance resulting in a diminishing susceptibility to secondary pathogen invasion of distal tissues. It is usually manifested by the formation of necrotic lesions either as a form of hypersensitive response (HR) or as a disease symptom [20].

Resistance is often differentiated in accordance with the mode of interaction between the host and the pathogen. One of the most common mechanisms of resistance is dominant resistance conferred by an incompatible interaction between the host resistance (*R*) gene and the pathogen avirulence (*avr*) gene. A majority of the *R* genes identified encode proteins containing nucleotide binding sites and leucine-rich repeats, and elicit a HR in response to the presence of a pathogen [14,21]. Often conferred by dominant alleles, this active resistance to virus invasion is manifested by cell death or necrosis at the infection court preventing the spread of infection [22]. Due to the high mutation rate of RNA viruses the interaction between the host resistance factors and virus avirulance receptors is frequently suppressed often making dominant resistance less durable [23].

In contrast to dominant resistance, recessive resistance is thought to be more durable as the recessive mutations render a host nonpermissive to viral infection due to the absence of specific host factors that are required for a virus to complete its infection cycle [23,24]. This loss of susceptibility does not require any activity in plants thus is sometimes called passive resistance [25,26]. This resistance is considered more durable because the virus can defeat the host resistance only if they can adapt to the missing factors [23].

Resistance mechanisms may also vary according to the stage of viral infection cycle in the host plants. In the early stage of viral infection, some cultivars resist the accumulation of virus particles that are significant to effect infection. As a result, no virion can be detected in the *Potato Leaf Roll Virus* (PLRV) resistant cultivars following virus challenge [27]. This resistance to virus accumulation precludes upward movement and root infection as reported earlier for *Soil-borne Cereal Mosaic Virus* (SBCMV) [28].

Different forms of resistance to virus movement have been observed in different potato cultivars. Some of these include impaired movement of PLRV from sieve elements to the phloem bundles [29] or restricted movement of PLRV within leaves or from leaves to petioles [30] and induction of phloem necrosis [31]. Due to the suppression of virus accumulation in the phloem, a low concentration of virus is present in the leaf that contributes to the reduced acquisition of virus by insect vectors. Consequently, this results in resistance for plant to plant transmission or secondary spread of infection within a field [32].

3. Search for resistance

Most economically important crops such as potato, tomato, rice, wheat, corn and cassava are susceptible to viruses. Plant viruses manifest a wide variety of pathogenicity that requires individual management strategies. The use of a resistant cultivar remains the best and cheapest option in managing virus diseases. A desirable cultivar is characterized to have resistance against either two or more types of pathogen species or the majority of races of the same pathogen species, also called broad spectrum resistance (BSR) [33]. Similarly, the resistance should remain effective for at least

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