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Host-delivered-RNAi-mediated resistance in bananas against biotic stresses

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ABSTRACT

Both the biotic and abiotic stressors restrict the yield potential of many crops, including bananas. Bananas belong to the genus *Musa* and are the world's most popular and widely produced fruit for their nutritional and industrial importance. The demand for bananas is growing each day worldwide. However, different pest infestations are hampering the production of bananas, making it a matter of concern for global food security. Several biotechnological tools and applications including RNA interference (RNAi) have been employed to enhance the biotic stress resistance in plants. The capacity to silence targeted genes at transcriptional and post-transcriptional levels makes the RNAi technique a popular choice for gene knock-down and functional genomics studies in crops. Silencing of different suppressor molecule coding genes through RNAi helps crops to combat the detrimental effects of plant pathogens. The host-induced gene silencing (HIGS) technology, also known as the host-delivered RNAi (HD-RNAi), is nowadays gaining popularity due to its ability to target an array of pathogens, comprising bacteria, nematodes, fungi, viruses, and insects. This methodology is employed to manage disease pest outbreaks in a diverse range of crop species, including bananas. Besides HIGS, virus-induced and spray-induced gene silencing (VIGS and SIGS, respectively) are the potential approaches where RNAi technology is exploited to control plant-pathogenic diseases. The current review emphasizes the different kinds of diseases of bananas and the potential of HD-RNAi, a new-age and promising technology to build a barrier against significant crop and economic loss.

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1 Introduction

Biotic and abiotic stresses are the major threats to global food security due to their potential to cause severe yield loss in crops. Banana is a major fruit crop worldwide, covering over 136 subtropical and tropical countries, and it provides food security to over 500 million people (Pillay et al. 2012; FAOSTAT 2018; Jekayinoluwa et al. 2020a). India secures 1st position worldwide in terms of area and production of bananas (FAOSTAT 2018). Bananas and plantains are popular crops due to their year-round availability, high nutritious value, and economic importance. The yield of banana and plantains are drastically affected by numerous biotic and abiotic stressors. Biotic stressors like bacteria, nematodes, fungi, viruses, and insects can cause complete yield loss in banana cultivation. Most of the popular banana cultivars are propagated through vegetative propagation, restricting the chances of generation of genetic variation in the banana gene pool (Ghag and Ganapathi 2019). The most devastating diseases of bananas are fungal diseases like Sigatoka disease and *Fusarium* wilt, viral diseases like Banana Bunchy Top Disease (BBTD), and weevil infestation (Figure 1). The breeding approaches to develop disease resistance in bananas are very difficult due to the triploid genetics of bananas. Extensive use of inorganic pesticides, herbicides, and insecticides is impacting detrimental effects on the environment as well as living organisms.

Biotechnological approaches are the alternative to imposing pathogen resistance in bananas in a sustainable way. One such approach is the utilization of RNA interference to combat different biotic stresses. RNAi is not only used as a popular reverse genetic tool but also explored to confer resistance against disease pest infestation in crops due to its capability to alter gene expression for desired traits (Younis et al. 2014). The biological mechanism, RNAi employs dsRNA molecules to inhibit protein synthesis by sequence-specific targeting of complementary mRNA (Taning et al. 2021). The RNAi mechanism can be activated through the endogenous production of micro-RNA (mi-RNA) or the exogenous introduction of single-interfering RNA (siRNA). Dicer is an enzyme posing RNase-III-like activity, which cleaves the dsRNA for the formation of single-interfering RNA (siRNA) duplexes (19–24 bp). This siRNA duplex uses a single strand incorporated into the argonaute (AGO) protein complex, creating a RISC (RNA-induced silencing complex). The target mRNA is then degraded through cleavage or the translational suppression is seen as a result of the RISC binding to the target mRNA in a sequence-specific way (Figure 2).

HD-RNAi and HIGS exploit the RNAi mechanism for the production of dsRNA that targets pathogenesis-related genes. At the time of a pathogen attack, the dsRNA moves inside the pathogen cell and is converted into siRNAs (Bharat et al. 2021). The siRNAs are taken up by pathogens during infection, and they activate the RNAi machinery and suppress the target gene transcription in pathogens (Bharat et al. 2021). The pathogenesis-related genes and suppressor molecules are taken as the target genes for designing HD-RNAi constructs (Artificial Pre-miRNA, hairpin RNA, sense or antisense RNA) that are introduced into the host plant. At the time of pathogen infection, the HD-RNAi

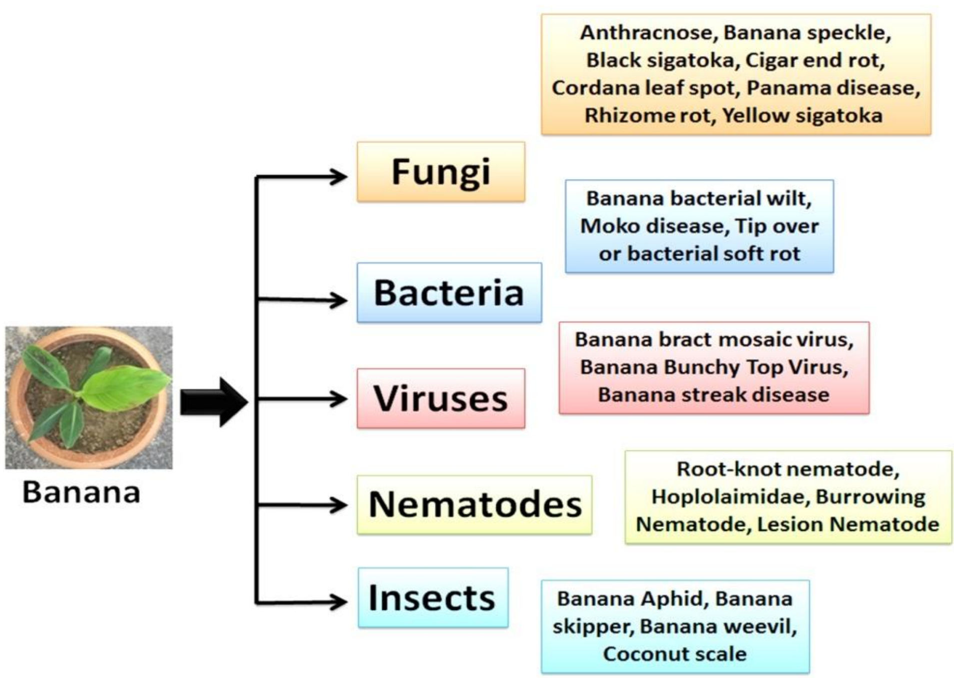

Figure 1 The most devastating biotic stressors of banana crops

constructs are converted to small RNAs by Dicer-like nucleases (DCLs) in the host cell, and one strand of the small RNA is incorporated with AGO to form the RISC complex. In the next step, the mRNA of the target gene interacts with the RISC complex by complementary binding and gets disintegrated, resulting in pathogenesis inhibition (Figure 3). The HD-RNAi approach has been employed against numerous pathogens, including fungi, viruses, bacteria, nematodes, and herbivorous insects to protect crops from yield loss. HD-RNAi technology is gaining popularity day by day for providing disease pest resistance to the banana.

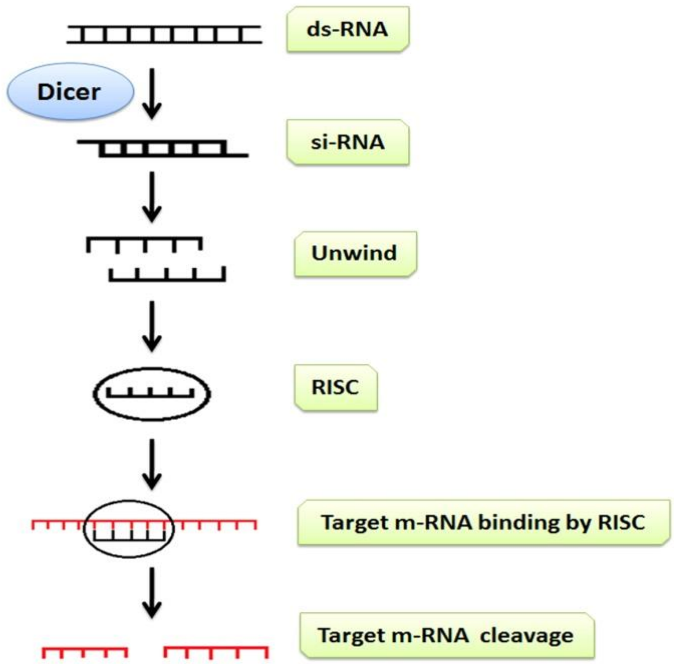

Figure 2 A simple conceptual representation of RNAi mechanism in plants

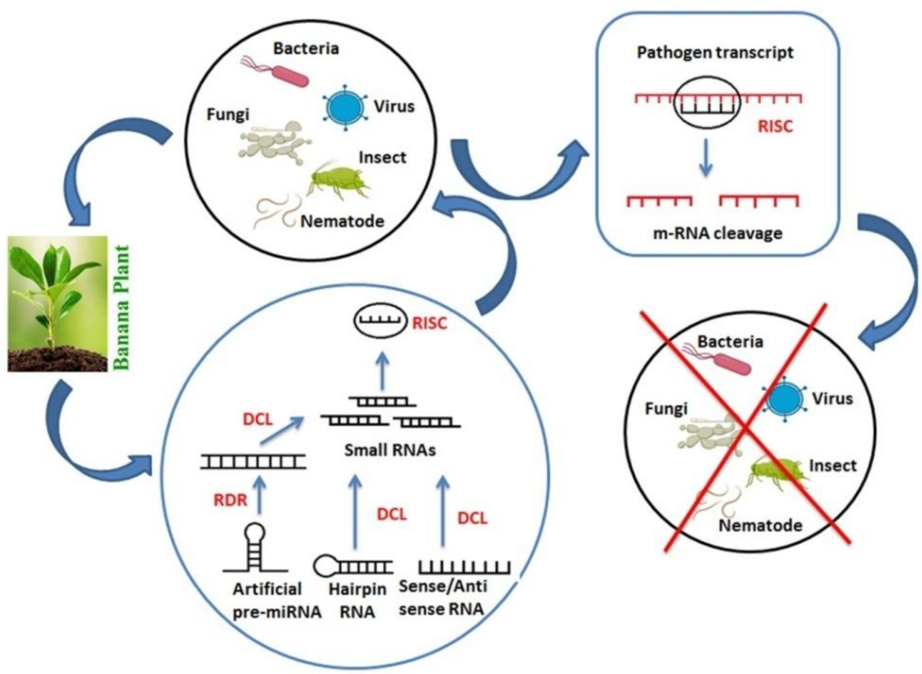

Figure 3 A pictorial representation of the HD-RNAi-mediated defense in banana plants against biotic stressors.

Table 1 List of major pathogens in banana crop and the method of RNAi implemented for their control

Pathogens	Resistance strategies employed	Reference
Mycosphaerella fijiensis	ds-RNA	Mumbanza et al. (2013)
Pseudocercospora fijiensis	RNAi	Thomas et al. (2021)
	ds-RNA	Mumbanza et al. (2013)
	ds-RNA	Fei et al. (2016)
Fusarium oxysporum	HIGS	Duo et al. (2020)
	HIGS	Ghag et al. (2015)
	HIGS	Ghag et al. (2014)
	RNAi	Elayabalan et al. (2013)
Banana Bunchy Top Virus	RNAi	Krishna et al. (2011)
	RNAi	Shekhawat et al. (2012)
Pentalonia nigronervosa	RNAi	Jekayinoluwa et al. (2020a)
Cosmopolites sordidus	ds-RNA	Mwaka et al. (2021)
Meloidogyne incognita	hd-RNAi	Kakrana et al. (2017)

2 HD-RNAi mediated resistance in banana

Banana is highly susceptible to disease-pest infestation (Table 1). Biotitic stressors like fungi, bacteria, viruses, insects, and nematodes cause huge yield loss in banana cultivation. HD-RNAi has the potential to combat biotic stressors.

2.1 Resistance to fungi

Resistance against fungal pathogens can be achieved via RNAi technology. Among the diseases caused by fungi, Sigatoka disease, Panama wilt, and anthracnose are the main threat to banana cultivation. The production quality and quantity of bananas are severely affected due to fungal infection. Rasthali a banana cultivar susceptible to *Fusarium* wilt, showed resistance against the *Foc* Race 1 infection when *Fusarium transcription factor* 1 (*ftf1)* of the fungal race was targeted through HIGS (Ghag et al. 2014). By targeting the *ERG6* (*C*-24 sterol methyltransferase), and *ERG11* "(cytochrome P450 lanosterol *C*-14α-demethylase) genes of *Foc* TR4 through HD-RNAi approach, resistance against the fungal strain has been developed (Duo et al. 2020). RNAi-mediated silencing of polyketide synthase genes like *PKS8-2* and *PKS10-2* conserved genes of *Pseudocercospora fijiensis* showed a reduction of pathogenicity in bananas (Thomas et al. 2021). Targeting four genes, such as, *Gene A, Gene B, Gene C,* and *Gene D* of *Fusarium oxysporum* f. sp. cubense (FOC) through the HD-RNAi approach, developed resistance against the soil-borne fungal infection in bananas (Fei et al. 2016).

2.2 Resistance to bacteria

The harmful interactions between pathogenic bacteria and plants lead to disease development by using virulence factors and effector molecules (Ronald and Joe 2018). Bacterial diseases like Banana *Xanthomonas* wilt (causative organism: *X. campestris* pv. *musacearum*, moko and bugtok (causative organism: *Ralstonia solanacearum*), and bacterial head rot (causative organism: *Erwinia spp.*) are the most devastating diseases resulting in huge yield loss in banana cultivation (Blomme et al. 2017). Genetic engineering and genome editing are the most important tools of modern biotechnology to impose resistance against bacterial diseases in numerous crop species, including bananas. Targeting the pathogenesis-related genes or expressing the *R* (Resistance) genes, antimicrobial genes, and defense-related genes in the host plant lead to combating pathogenesis (Mohandas and Ravishankar 2016). Transgenic plants bearing the *plant ferredoxin-like protein* (*Pflp*) and *hypersensitive response assisting protein* genes (*Hrap*) of chili showed resistance against numerous plant-pathogenic bacteria, such as *Xanthomonas spp, Pseudomonas, Erwinia,* and *Ralstonia* (Tripathi et al. 2017). Transgenic bananas of the cultivar 'Sukali Ndiizi' (AAB) and 'Nakinyika' (AAA) having *Hrap* or *Pflp* gene insertion, showed resistance to *Xanthomonas* wilt disease without compromising the architecture or yield of banana plants (Tripathi et al. 2010; Namukwaya et al. 2012; Tripathi et al. 2014a). Transgenic banana-bearing pattern recognition receptor (PRR) XA21 from rice exhibited improved response to *Xanthomona campestris pv. Musacearum* in greenhouse conditions (Tripathi et al. 2014b). In rice, the knockdown of *OsSSI2* through RNAi enhanced the resistance against *X. oryzae* attacks (Jiang et al. 2009). The utilization of siRNA to silence oncogenesin *Arabidopsis*, *Nicotiana*, and *Lycopersicum* conferred resistance against *Agrobacterium tumefaciens* (Escobar et al, 2001). RNAi mechanism can be used to target bacterial pathogens by designing dsRNA to suppress the virulence factors and the effector molecules of bacteria. HIGS can be employed to achieve bacterial disease resistance in bananas through genetic engineering.

2.3 Resistance to viruses

In HIGS, host plants are engineered to incorporate an inverted repeat sequence of a gene of interest inside the plant genome. At the time of pathogen attacks, the inverted repeat sequence will be converted to ds-RNA first and subsequently to s-RNA, leading towards the activation of RNAi machinery. The success story of applying RNAi mechanism to provide plant viral disease resistance has been enlisted in numerous cases of papaya ring spot virus, mung bean yellow mosaic virus, cucumber mosaic virus, cassava mosaic virus, and soybean mosaic virus (Jekayinoluwa et al. 2020b). Among the plant pathogenic viruses of bananas, the Banana Bunchy Top Virus (BBTV), Banana Streak Virus (BSV), and Banana Bract Mosaic Virus (BBrMV) are the main constrain for the cultivation and production of bananas. BBTV is a multipartite virus with six genomic components. By designing RNAi construct against the BBTV DNA-*R* gene, BBTD resistance has been developed in transgenic Grand Nain banana (Elayabalan et al. 2013; Elayabalan et al. 2017). Genetically engineered bananas with ihp-RNA construct targeting DNA-R (replication initiation gene) component showed improved resistance against BBTV (Shekhawat et al. 2012). The utilization HD-RNAi, targeting the *replicase* gene of BBrMV, protected from Banana Bract Mosaic Virus (Rs et al. 2021).

2.4 Resistance to insects and nematodes

Numerous major diseases of bananas are transmitted through insect vectors. The most destructive insects that cause severe yield loss to bananas are banana aphids, banana skippers, banana weevils, and coconut scales. Thus, the transmission of disease can be manipulated by either interfering with the aphid-pathogen interaction or controlling the aphid population. RNAi-mediated targeting of *RR-1* genes in *Pentalonia nigronervosa* and DNA-N of BBTV can open up a potential path to control the spreading of BBTV through banana aphids. RNAi-mediated silencing of *snf7*, *rps13*, and *mad1* genes of banana weevil (*Cosmopolites sordidus*) were successful in controlling the insect population (Mwaka et al. 2021). Application of RNAi technology by designing dsRNA against the acetylcholinesterase (AChE) gene of banana aphids, showed a significant reduction in the aphid population (Jekayinoluwa et al. 2021). RNAi-mediated suppression of the *ubiquitin E2* gene caused 100% mortality in banana weevils (Ocimati et al. 2014).

The most devastating plant-pathogenic nematodes of bananas are *Pratylenchus goodeyi*, *Radopholus similis*, *Helicotylenchus multicinctus, Meloidogyne incognita, and Pratylenchus coffeae*. The expressions of plant cystatins and peptides are seen to develop resistance against *Radopholus similis* and *Helicotylenchus multicinctus* (Atkinson et al. 2004; Tripathi et al. 2015). Bt endotoxin genes and lectins have the potential for suppressing *Meloidogyne* species (Yu et al. 2015). RNA interference-based defenses are being developed against *Meloidogyne* species (Papolu et al. 2013), *Pratylenchus* species (Tan et al. 2013), and *R. similis* (Li et al. 2015). Further, siRNA or hairpin RNA construct containing genetically engineered banana plants can be utilized as a potential weapon against banana insects and nematode infestations.

3 Conclusion and Future prospects

RNAi has the potential to control disease pest infestation sustainably. HIGS or HD-RNAi approach has revolutionized the way of developing pathogen resistance. Identification of target gene sequence through genomics or transcriptomics analysis is a prerequisite for designing of HD-RNAi construct. To avoid ectopic expression, tissue-specific promoters can be added while designing the construct. Targeting the intronic regions that are poorly conserved across species for HIGS, can minimize the off-target effect. The advances in the field of biological science have made it possible to utilize the HD-RNAi approach to pave the path toward precision agriculture. The production quality and quantity of bananas can be maintained properly by exploiting the HD-RNAi approach.

Production problems, particularly disease-pest infestation, represent a threat to global food security. The uncontrollable and extensive use of synthetic pesticides is the most preferred method for protecting crops from pathogens. Some of these substances have been in use for about a decade and impose hazardous effects on the environment as well as living beings. Consequently, it is necessary to develop advanced technologies that are more eco-friendly and sustainable. A unique and powerful strategy called RNA interference (RNAi) is gaining popularity nowadays as a way to combat disease-pest infestations in many commercially significant crops. Natural RNAi pathways have an impact on antiviral defense, cross-kingdom communication between species, and gene regulation in plants. Meanwhile, numerous labs have been successful in taking advantage of the RNAi mechanism to generate significant changes for promoting plant disease resistance by manipulating the components involved in RNAi-mediated gene silencing. Against various disease-pest infestation, transgenic and non-transgenic plant-based RNAi methods have shown promising results, and significant opportunities to pave the pathway toward new horizons. Despite a few drawbacks, numerous studies have demonstrated that the use of RNAi to enhance disease resistance in plants, is anticipated to be the most effective and significant strategy moving forward. The designing and generation of exogenous dsRNA targeting the pathogenesis-related gene is an essential tool for employing RNAi strategy against pathogens. The review concentrated on focusing on the utilization of RNAi technology for combating the most destructive pathogens of bananas to secure the yield potential. By targeting the intronic regions and using tissue-specific promoters, the off-target effect and ectopic expression due to the RNAi strategy can be overcome. The root-specific promoter can be used while designing the HD-RNAi construct targeting root pathogens, *Fusarium* in bananas to avoid the expression of that construct in other plant parts. When it comes to controlling pests and pathogens, RNAi technology will be incredibly effective for not only bananas but also all types of crops.

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