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Resistance to Papaya Ringspot Virus: *a Review*

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ABSTRACT

Papaya is known to be affected by many viruses, out of which the most important are PRSV; PRSV-P (Papaya exhibits yellowing, leaf distortion, and severe mosaic) and PRSV-W (PRSV-W causes mottling and distortion of leaves and fruit). The type that gave the virus its name is the Type P isolates (PRSV-P). The other type, Type W isolates (PRSV-W), does not infect papaya. Isolates of PRSV-W do infect cucurbits such as watermelon, cucumber, squash, etc., and were originally known as Watermelon Mosaic Virus. It has been documented as PRSV is transmitted by several species of aphids like Aphis nerii, Aphis gossypi, Aphis spiraecola, Myzus persiciae, Toxoptera aurantii, Aphis craccivora and Rhopalosipum maidis in a nonpersistant manner. Prevention through Quarantine and Geographical displacement is an important aspect of their management. IPM for various aphid species has been successfully achieved by using Bio-control agents like using fungi Lecanicillium lecanii, Beauveria bassiana or Isaria fumosorosea. Given pathogen derived resistance, the coat protein (CP) gene from a mutant mild strain of PRSV provided a high level of resistance to Hawaiian strain of PRSV has been reported. Transgenic papaya to prevent PRSV has been developed soon after the successful development of transgenic tobacco expressing CP genes of the Tobacco Mosaic Virus (TMV) showing resistance. However, the success and effectiveness of CP mediated PRSV resistance depend on the origin of PRSV isolates and their translatable and untranslatable constructs. The discovery of RNA interference (RNAi) mediated resistance in transgenic tobacco against potato virus Y has emergd as an important molecular tool for crop improvement and the study the function of gene and gene silencing mechanism using RNAi mediated resistance may be one of the important tools for managing the virus in case of papaya ringspot virus. Advances in our knowledge and adoption of various technologies like pathogen-derived resistance, replicase gene mediated resistance, cross-protection, post-transcriptional gene silencing method with a better understanding of the occurrence, symptoms of disease, transmission, vector of the virus and their genome structure will provide various researchers to study and develop proper strategies for the better management of the disease.

Keywords: *Papaya ringspot virus, PRSV-P, PRSV-W, resistance, watermelon mosaic virus, coat protein, transgenic papaya, tobacco mosaic virus, aphid.*

INTRODUCTION

Papaya is an important fruit in tropical and sub-tropical countries. It belongs to the family Caricaceae. It has originated in southern Mexico and Costa Rica It is also known as papaw and tree-melon [1]. Papaya can be grown very easily either directly from seeds or through raising seedlings and the plant generally grows up to 10 or 12 ft in height. Fruiting in the plant generally starts within 9-12 months after planting and the plant can continue to produce fruits for about 2-3 years. Sex expression in papaya is very complicated [1]. Hofmeyrreported nine different sex forms in papaya as female, male, elongated sterile, hermaphrodite, coenomonoecious, pentandria, coexistence of elongate andpentandria, pistillate and hermaphrodite and pistillate and staminate flowers on the same plant [2]. Fertile hermaphrodite types also have some pistillate flowers which may show male tendency in summer and female tendency in winter [1]. The fruits of female plants are spherical with thinner flesh and few seeds in the central cavity, whereas hermaphroditic fruits are pyriform, oval or cylindrical with a grooved surface and have thick flesh with more seeds that's why it has more demand in consumer [3]. Carica papayais a cultivated species found all over the world; however there are many wild Carica species such as Caricaca liflora, Carica pubescens, Carica quencifolia, etc. [4]. Papaya crop is raised over 136000 hain the world with a production of 6108 million tons. India comes in first place for papaya production with the production of 5.5 million tons annually and along with Brazil provides 57% of global papaya supply [5]. It is a rich source of vitamin A, and Band C. It is also very rich in Proteolytic enzyme like Papain, Chymopapain and Beta-carotene. These properties of Papaya are useful for the pharmaceutical and cosmetic industries as it may cure cancer, diabetic, dengue and heart diseases [6]. Papaya crop is fast growing herbaceous plants with

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palm-shaped leaves and axial flowers. It is polygamous with male, female and hermaphrodite plant [3].

The great adaptation of this plant and worldwide acceptance of this fruit gives us a great scope for the papaya cultivation crop for local and export purposes. It is considered as one of the important cash crops in the tropical and subtropical countries. However, papaya ringspot virus [PRSV) is considered as one of the most important factors that hinders the production of this economically important fruit crop. Further the fruits of papaya are fragile and perishable in nature which limits large-scale exportation, and hence papaya lags behind bananas and pineapple in the world market.

Papaya ringspot disease in papaya is caused by the type 'P' strain of PRSV [7]. Typical symptoms of PRSV include mosaic, chlorotic and distorted leaves, stunted trees, drastically reduced fruit yield, small fruits anda clear-cut ringspot appearing on the fruit surface [7]. The disease incidence and the expression of symptoms are highly influenced by environmental conditions. Symptoms were found more pronounced during cooler months [8]. PRSV is sap transmissible and has been found that it is easily vectored by many species of aphids, including Myzus persicae, Aphis gossypii, A. craccivora, and A. maidis in a non-persistent manner [7]. Non-persistent manner mode of transmission means there is a short acquisition period followed by a short inoculation period and the insect rapidly loss infectivity [7], [9]. An entire papaya orchard could become completely infected with PRSV in three to four months [10]. The disease can cause yield loss of up to 70% [11].

The conventional breeding in C. papaya for PRSV is difficult because resistance for PRSV does not exist [12], [13]. Although there are some cultivars like Florida- 'Cariflora', Thailand- 'Thapra' [14] and 'Red Lady' that shows some tolerance to the disease, as these cultivars have poor horticultural properties such as sweetness, hardiness, shape, and shelf-life, hence these cultivars are not being cultivated for commercial purposes [15], [16]. The tolerant cultivar might also become infected with the PRSV but the plant shows very mild expression of the symptom and its effect on fruit size and quality is not hindered [10]. The various horticultural practices such as roguing, quarantine, bagging the transplanted seedling with a plastic bag, intercropping with corn or bajra or jowar and also using these crops as barrier crops are some important measures to minimize the disease incidence [17], [18]. And these practices are only effective in regions where disease pressure is low. Cross-protection is also another method where the plant is infected by a mild strain of virus using the approach involving the deliberate infection of a crop with a mild virus strain to prevent economic damage caused by the virulent strains (PRSV).But this method has some limitations, like it requires a large-scale inoculation program, there is a chance that mild strain may become virulent to some cultivar, and also there is yield loss due to infection [18], [19, [20]. In the case of genetically modified or transgenic cultivars such as 'UH Rainbow' or 'UH SunUp', that are commercially being cultivated in Hawaii but these genetically modified or transgenic cultivars are less popular and not favoured by consumer [21]. As we all are aware of the economic importance of papaya cultivation throughout the world and PRSV is a major threat for its cultivation, we have to look for a concrete solution to manage the disease. In this review, we had discussed the nature of virus, their vectors, the general symptoms and various strategies to manage the disease. There is still a requirement to expand our knowledge and comprehend various technologies like pathogen-derived resistance, Replicase gene-mediated resistance, cross-protection, post-transcriptional gene silencing method; vector control etc. that will allow us for the better management of the disease.In this review, the nature of the PRSV virus, its transmission, vector and management of the disease has been discussed. We will concentrate on understanding the various disease management strategies including vector control, pathogen-derived resistance, coat protein (CP) mediated resistance, RNAi mediated resistance, replicase gene mediated resistance, cross-protection and provided new opportunities and avenues for future research.

2 Papaya Ringspot Virus

2.1 Geographical Distribution: Type P isolates occur in most tropical and subtropical areas where papaya is grown [22] including the USA [23], [24], [25], South America, the Caribbean countries [26], India [27], Taiwan [13], Africa [28] and Okinawa [29]. Type W isolates have been reported in cucurbits in many areas, including the USA [30], Mexico [31], Caribbean countries [32], Australia [33], Germany [34], France [35], Italy [36], India [37], Middle eastern countries [38], [39], [40] and South America [41].

2.2 PRSV: The etiology of PRSV disease was first reported during the 1937 Oahu in Taiwan [42]. Since it is only Potyvirus of family Potyviridaeand it is transmitted in non-persistent manner by several species of aphids. It has 94.5% protein and 5.5% nucleic acid by weight. The positive sense ssRNAgenome has10324 nucleotides. PRSV each flexuous rod-shaped, non- enveloped virus whose genome is 800-900 mm long and 12nm in diameter. Like other Potyviruses, PRSV encodes a single large protein consisting of 3,344 amino acids. And this large protein is further cleaved into smaller proteins (Fig. 1) i.eP1, HC-Pro, P3, Cl, 6K, Vpg, Nla-Pro, Nlb and CP with various functions (Table I). These different functional proteins are made by a cascade of site-specific cleavage events performed by three virus encoded proteases viz., P1, Hc- Pro, and Nla [43].The phylogenetic study about the virus revealed that it has been originated in Asiamost likely in India more than 2000 years ago, and slowly-slowly it was introduced to China, Australia and America. From the introduction of Papaya in India (500 years ago), the virus evolutes and switched from cucurbits [44].

Figure 1. *Cleaved Protein of PSRV*

Table I: Functions of different Proteins of PRS

Proteins	Size (M_r)	Functions	Reference
P1	63K	Proteinase Cell-to-cell movement	[45]
HC-Pro	52K	Vector transmission Proteinase Suppressor of RNA silencing Cell-to-cell movement	[46], [47], [48]
P3	46K	Unknown, but possible role in replication	[49]
6K1	6K	Unknown, but possible roles in: RNA replication Regulation; inhibition of NIa nuclear translocation Replication	[49]
CI	72K	Genome replication (RNA helicase) Membrane attachment Nucleic acid stimulated ATPase activity Cell-to-cell movement	[50], [51]
6K2	6K	Same as 6K1	[49]
NIa-VPg	21K	Genome replication (Primer for initiation of RNA synthesis)	[45]
NIa-Pro	27K	Major Proteinase	[45]
Nib	59K	Genome replication (RNA-dependent RNA polymerase, RdRp)	[49]
CP	35K	RNA encapsidation Vector transmission Pathogenicity Cell-to-cell movement	[45]

3 Variability in PRSV

There has been a tremendous increase in the number of Potyvirus that have been isolated recently and these viruses are co-evolving with their host from a very long time. The various information about the diversity of PRSV will be very helpful to find an effective way to manage the disease [52]. There are two major types of PRSV which are almost indistinguishable and have very little genetic differences hence it is considered to be of the same virus species. They are designated as Type P and Type W. Type P is able to infect papaya as well as many cucurbits while Type W is unable to infect papaya but infects watermelon and known as Watermelon mosaic virus 1 [53]. The diversity at amino acid and nucleic acid levels was highest among Asian isolates [54]. The CP and HC pro genes collected from India showed highest diversity of PRSV nucleotides [55]. Both PRSV types are known be present in the countries like Taiwan, Africa, India, Italy, Germany, France etc. However, PRSV–P is more confined in the Middle East Africa, south and Central America where as PSRV-W in Caribbean, Mexico, Italy, Germany and Australia [22]. In India, PRSV-P was first reported from North India in 1960 and it was reported in South India in 1995 [55]. Within a span of 5 to 6 years, PRSV had spread throughout South India [56].

4 Symptomology

The diseases caused by Potyvirus are easily recognized by their distinctive symptoms in plants infected with the virus. As the name suggests there is a ringed spot formed on the fruits of infected plants [24]. Plants showstypical viral symptoms of mosaic and chlorosis of leaves, followed by stunted growth. The plant lossesvigor produces poor distorted fruit with ringed spot which render the fruit unmarketable (Fig. 2). Distorted leaves and water soak lesions on the petiole and upper part attack of stem phyto make it to like mites [7], [10]. It shows the symptoms of leaf curling, rolling, puckering, resetting or crowding of leaves due to shortening of nodes and internodes, stunting of plants, leathery and brittle older leaves, blistering of internodes area and swelling of the veins PRSV has been reported by several investigators across worldwide wherever papaya is grown (Fig. 2) [57].

Fig. 2: Symptoms of PRSV on Fruits and leaves of papaya

5 Transmission

These are numerous species of aphids that are transmitting the virus in a non-persistent manner to papaya and cucurbits. The host range of the virus also includes Chenopodium quinoa and Chenopodium amaranticolor. The transmission of PRSV through seeds has also been reported but it is not a significant way for the virus transmission [6]. Recently Momordica charatia, a climber-type plant of Cucurbitaceae family has been reported as the reservoir for PRSV–P in Jamaica [58]. The plant exhibits the typical viral symptoms of vein clearing, mottling and rosetting. Similar to other Potyvirus PRSV is transmitted by various species of aphids (mainly Myzus persicae and Aphis gossypii), a typical stylet born in a non- persistent manner. The acquisition and transmission period of the virion particles is very brief and CP and HC-pro protein encoded by virus is required for this process [59].

6 Vector

Aphids are the predominant means by which PRSV is transmitted. PRSV is a non-persistent virus, meaning it does not enter beyond the feeding mouthparts of the aphid and does not circulate or multiply within its insect host. Non-persistent viruses are transmitted quickly and easily between plants. Many species of aphid can transmit PRSV, particularly the Peach Aphid and Melon Aphid.Aphids belong to the family Aphididae of Order Hemiptera. The aphids are soft-bodied insects with two short and broad antennae, pair of compound eyes, long thin jointed legs and a tail like protrusion called Cauda also by their rectal apertures [60], [61]. They are sap-sucking insects and have special sucking tube-type mouth parts called stylet, which is enclosed by rostrum, a sheath formed from the modification of mandibles and maxillae. Aphids are among the most destructive insect pest on a wide variety of crops being grown all over the world. The insect in addition to sucking sap and thus weakening the plant it also serves as vectors of many plant diseases. Aphids secrete honeydew which allows various fungi like Capnodium, etc, to grow and cause sooty moulds. Honeydew also reduces the effectiveness of fungicides [62]. Myzus persicae (green peach aphid) has been reported to transmit more than 110 viruses. Cotton aphid (Aphis gossypi) is a vector of viruses in plant like papaya, peanut, sugarcane [63]. About 5000 species of aphids have been described and of these, around 450 species are plant pathogen that damages the crop either by sap sucking and transmitting viral diseases [64]. Because of the high reproducing capacity, they have a high biological fitness and successful organism on an basis of ecological point of view.

PRSV is transmitted by several species of aphids like Aphis nerii, Aphis gossypi, Aphis spiraecola, Myzus persicae, Toxoptera aurantii, Aphis craccivora and Rhopalosipum maidis in a nonpersistant manner [65], [66], [67]. This type of transmission is regarded as a short acquisition access period of a few seconds to minutes, lacking any distinct latent period with a brief inoculation period [68].

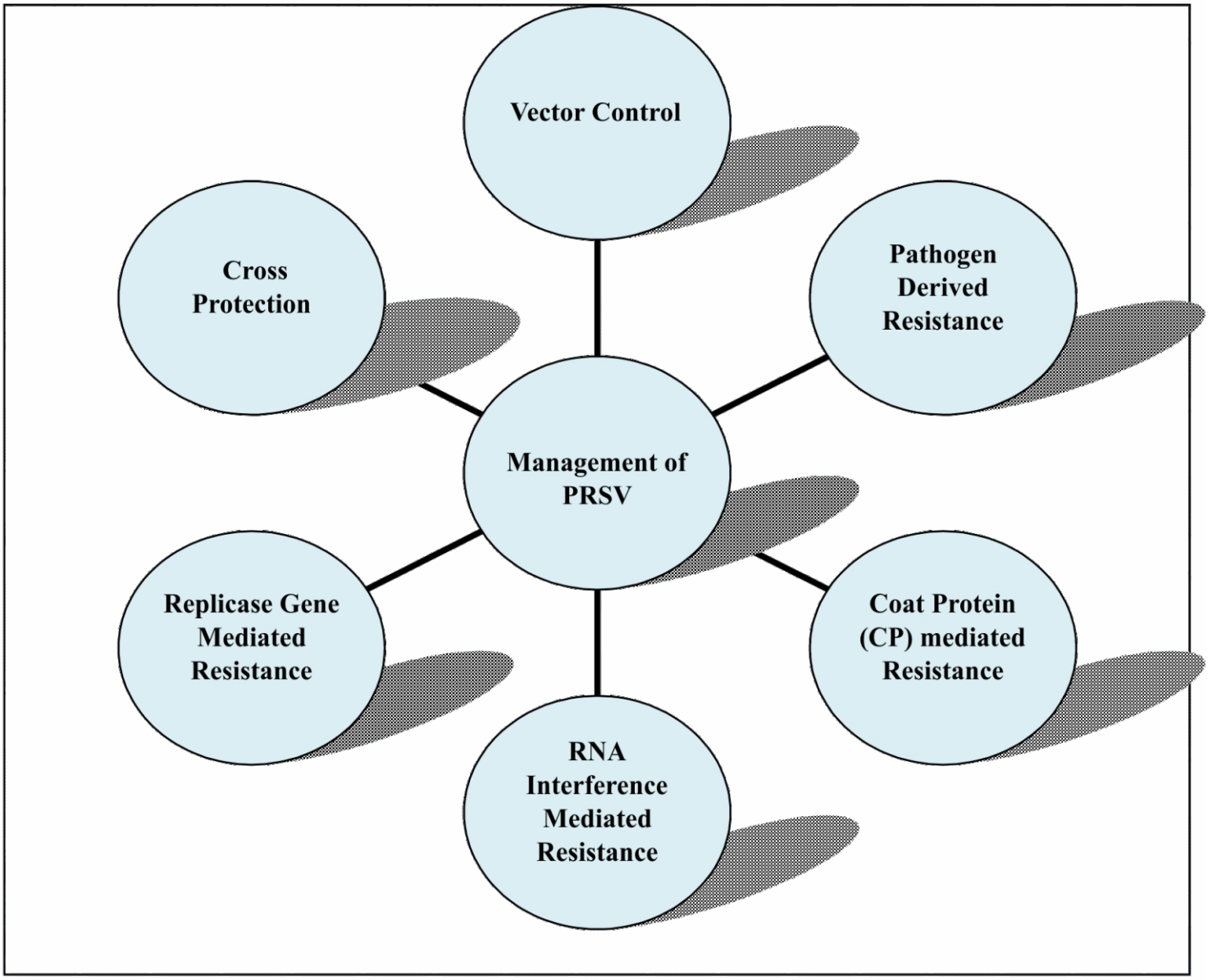

Fig. 3: Management options of PRSV

7 Management:

7.1 Vector Control: The management of vector to prevent the transmission of virus from an infected host to healthy host is one of the important strategies to manage viral diseases. But due to high fecundity rate of aphids, its management is quite difficult. High dose of fertilizer increases the foliar growth of of crops thus attracting the aphids hence a balanced dose of fertilizer should be preferred [69]. Aphids can be controlled by the application of systemic insecticides, but some aphid species have shown resistance against them like organophosphate, carbamate, pyrethroidsetc, so an integrated approach should be followed [70]. IPM for various aphid species has been successfully achieved by using Bio-control agents like using Fungi Lecanicillium lecanii, Beauveria bassiana or Isaria fumosorosea [71]. The fungi of order Entomopthorales are very effective to control aphids [72]. Aphids have been also effectively controlled by the release of natural enemies like lady beetles and parasitoid wasps. Nettings are also being used to prevent the insect vectors from being infested to healthy fields thus managing the spread of virus [73]. The netting is quite costly and less economical; however, it is being utilized in the country like Taiwan [74]. Prevention through Quarantine and Geographical displacement is also being practiced in Hawaii, Philippines, and Brazil [10], [73].

7.2 Pathogen Derived Resistance: A new approach for controlling PRSV: The concept of pathogen-derived resistance was developed around 1980s has opened a new approach for controlling PRSV [75]. In this approach, a transgenic plant is developed that contains a gene from pathogen that causes detrimental effects to the same or related pathogens. The host possesses a pathogen trait that is inappropriately expressed in the host plant that disrupts the parasitic relationship and thus provides resistance to host plant. The most commonly used pathogen-derived resistance is Coat Protein Mediated Protection (CPMP) against many plant viral diseases [76]. The resistance offered by this method ranges from nil to immunity and is based on the transformation of viral coat protein gene. A Hawaiian papaya cultivar Sunset with coat protein (CP) gene from a mutant mild strain of PRSV provided a high level of resistance to Hawaiian strain of PRSV [77], [78]. Various clones of coat protein gene-expressed resistant transforms (55-1) were characterized and evaluated under greenhouse condition

to test the pathogen-derived resistance against the virulent Hawaiin PRSV isolates. The experiment significantly showed resistance against Hawaiin PRSV isolates [79].

7.3 Coat Protein (CP) Mediated Resistance: Transgenic papaya to prevent PRSV has been developed soon after the successful development of transgenic tobacco expressing CP genes of the Tobacco Mosaic Virus (TMV) showing resistance [76]. CP gene resistance to PRSV containing the neomycin phosphotransferase II (nptII) gene was employed to develop transgenic papaya using gene transfer system of immature zygotic embryos with a plasmid construction and was the first result that demonstrated CP mediated resistance in Papaya against [80]. The method of CP mediated resistance in papaya against PRSV is being employed globally. CP gene from Taiwaan strain of PRSV was used to make transgenic papaya by constructing a Ti binary vector using pBGCP through Agrobacterium showed resistance against virulent PRSV [81], [82]. Gonsalves used gene gun technology for transferring the CP genes to develop PRSV resistant papaya [10]. Similar findings were observed by Tennant, Bau,Magdalita etc. thus showing CP mediated resistance as an important tool for the management of PRSV [52], [83], [84]. However, the success and effectiveness of CP mediated PRSV resistance depend on the origin of PRSV isolates and their translatable and untranslatable constructs (Table II).

Table II: Effectiveness of CP mediated PRSV resistance on the basis of their translatable and untranslatable constructs

Types of CP	Method of Transfer of CP	Construct	Transgenic expression	References
Translatable cp	Biolistics	uidA leader + CaMV35S promoter + PRSV Bridgeman Downs cp gene from Q/S start with stop codon in the middle of sequence	p not detected in ELISA and low levels of cp detection in northern analysis	[85]
		CaMV35S + CMV leader + PRSV Bahia cp gene from Q/S start	low to high levels cp detected in ELISA	[86]
		CMV leader + 16 aa CMV cp + PRSV HA 5-1 cp gene from Q/S start	Low to high levels cp detected in ELISA and cp RNA detected by northern analysis	[86], [87]
		CaMV35S + CMV leader + PRSV Caymanascp from Q/S start	cp RNA detected in northern analysis	[86]
		uidA leader + CaMV35S promoter + PRSV YK cp gene from Q/S start	cp transcript detected in northern analysis	[83], [88]
		CaMV35S + uidA leader + PRSV Ratchaburi province cp	cp detected in western analysis	[89], [90]
	Agrobacterium	uidA leader + CaMV35S promoter + PRSV HIK cp gene from Q/S start	cp is not detected in northern analysis	[91]
		CaMV35S + CMV leader + PRSV EV and VE from Q/S start	cp RNA is not detected ELISA and low level cp detected in northern analysis	[92]
	Biolistics	CaMV35S + CMV leader + PRSV Caymanas untranslatable cp	cp RNA detected in northern analysis	[92]
		CaMV35S + CMV leader + PRSV Caymanas untranslatable cp	cp RNA detected in northern analysis	[92]

Unranslatablecp	**Agrobacterium**	uidA leader + CaMV35S promoter + PRSV HIK cp gene from Q/S start in **antisense**	cp is not detected in northern analysis	[91]
		uidA leader + CaMV35S promoter + PRSV HIK cp gene from Q/S start with **frame shift mutation**	cp is not detected in northern analysis	[91]
		uidA leader + CaMV35S promoter + PRSV HIK cp gene from Q/S start with **3 in frame stop**	cp is not detected in northern analysis	[91]

7.4 RNA Interference Mediated Resistance: Waterhouse and his worker first time discovered RNA interference (RNAi) mediated resistance in transgenic tobacco against Potato virus Y. This has emerged as an important molecular tool for crop improvement and study the function of gene [93]. It has been proved effective defense mechanism against both animate and inanimate causes of plants and thus allows us to produce clean and healthy crop in increasingly unfavorable environmental conditions. The idea beind this technology is to suppress certain gene or genes for developing disease resistance. In PRSV, it has a single open-frame RNA that is translated into a large polyprotein from where the final protein product is made [94]. It has been found that RNAi mediated resistance is highly effective when it is attacked by virus similar to transgene. The difference between different geographical isolates makes the use of RNAi mediated resistance using transgene difficult due to its failure in providing resistance because of the silencing of suppressing protein of viral origin [89]. However, in papaya this problem was overcome by the silencing suppressor protein HcPro through an RNA-silencing mechanism. This helper component proteinase has been proven highly effective as a suppressor of RNA silencing.Mangrauthia and his coworker in the year 2008 found that HcPro would be an important tool for the development of PRSV resistant papaya [95]. RNAi mediated defense mechanism shows a specific mechanism of posttranscriptional gene silencing (PTGS) and hence it is also referred as homology dependency resistance. PTGS is the phenomena of accumulation of 21–25 nucleotides small-interfering RNAs, the sequence-specific degradation of target mRNAs, followed by methylationof target gene sequences [96], [97]. Tennant and coworkerfound thattechnologies of transgenic papaya resistance against PRSV are sequence homology dependent and mediated by RNA via PTGS [98]. They observed that an untranslatable CP gene was able to provide resistance to the homologous strain of the virusisolate of PRSV by PTGS. In addition to this, the silencing suppressor was one of the important components for the suppression of PRSVtransgenic resistance [88]. Ruanjanand coworkerreported thattransgenic papaya showed resistant to PRSV by suppressingposttranscriptional gene silencing (PTGS) [89].

7.5 Other Methods:

7.5.1 Replicase Gene-Mediated Resistance: this is a protein-based resistance mechanism that involves the mutation in the primary structure of protein encoded by the transgene thus providing resistance. Replicase gene varies among different genera; the introduction of the replicase gene was first demonstrated in tobacco conferring resistance against tobacco mosaic virus [99]. Replicase gene with mutation is able to provide resistance against many viruses [100]. The transgenic papaya containing replicase gene provides resistant against PRSV was reported by Chen andWeireported that transgenic papaya withmutated replicase genes (RP) showed high resistance to PRSV [81].

7.5.2 Cross Protection: Cross protection is a method of providing resistance by infecting the host with mild strain of virus against the effects of infection by a more virulent related strain. This practice has long been known and has been used to control citrus tristeza, tobacco mosaic, and zucchini yellow mosaic viruses [8], [101], [102], [103]. The important factor in this method is the availability of mild strain that effectively control the target virus.Shyi-Dong Yeh in a greenhouse experiment proved that two mild strains, designated PRSV HA 5-1 and PRSV HA 6-1, provided resistance against PRSV in papaya [8], [94], [104]. Currently, the mild strain is very little used, mainly because it does not provide consistent economic returns to the farmers. The failure of the mild strain of PRSV to completely protect against PRSV is due to differences between the mild strain and the wild-type virus, as shown by greenhouse experiments [52]. Cross protection has not been widely accepted among farmers for several reasons: (a) the adverse effects of the mild strain, (b) cross protection requires extra cultural management and care, and (c) the reluctance of farmers to infect their trees with a virus [10].

8 Conclusions and Future Perspective

Papaya ringspot is one of the important diseases of Papaya. A better understanding of the occurrence, symptoms of disease, transmission, vector of the virus and their genome structure will provide various researchers to study and develop proper strategies for the management of the disease. Many researchers have been made and showed that using of transgenic papaya, which may contain coat protein gene is an effective method for managing the disease. Further gene silencing mechanism using RNAi mediated resistance may be one of the important tools for managing the virus. Advances in our knowledge and adoption of various technologies like pathogen-derived resistance, replicase gene mediated resistance, cross-protection, post-transcriptional gene silencing method; vector control etc. will allow us for the better management of the disease.

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Nishar Akhtar: Data collection, designing of the figures, and preparation of the manuscript.

ShahinaPerween: Manuscript preparation, English editing, and contribution to the breeding aspects of the content

Abdul Majid Ansari: Concept and designing of the research, contribution of the data collection and gathering technical information of the research, and overall supervision of the research as well as preparation of the manuscript and finalization.

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