Viruses Infecting Papaya (*Carica papaya* L.): Etiology, Pathogenesis, and Molecular Biology

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ABSTRACT

During the last few decades, over 20 plant virus species capable of infecting papaya (*Carica papaya* L.) have emerged in tropical and subtropical regions. The extent and severity of disease symptoms vary widely from minor or unapparent to reduced tree vigor, yield, and impaired fruit quality. Existing data on molecular characteristics of viruses infecting papaya also vary; while phenotypic data are available for the majority, the genotype of many have not been characterized and partial or complete nucleotide sequences have not been determined. As a result, some virus species are classified in recognized taxa while others are tentatively assigned to genera or have not been sufficiently distinguished from viruses in recognized genera so as to form a new genus. This paper presents an overview of the virus species capable of infecting papaya, diseases they elicit, genetic structure and diversity, and factors contributing to their emergence where molecular data are available.

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INTRODUCTION

Papaya (*Carica papaya* L.) is a large fast growing arborescent herb cultivated for its climacteric, melon-like fruit. It is native to Central and South America and is widely distributed throughout many tropical and subtropical countries (Manshardt 1992). Papayas can usually be found in home gardens intermixed with other fruit trees or in the wild. More recently, organized commercial plantings have been established across various regions in attempts to satisfy growing local and international markets. In 1997, the Food and Agriculture Organization (FAO) estimated that papaya production accounted for 10% of the volume of the four major tropical fruits (including mangoes, pineapples, and avocados) produced worldwide. Since then papaya production has doubled. About 6.6 million metric tonnes were produced in 2005, with countries of Latin America and the Caribbean accounting for roughly 45% (FAO Statistics 2007). Brazil is the largest producer of papaya, harvesting

1.6 million metric tonnes in 2005. Nigeria followed producing 834,000 metric tonnes in the same year, India with 783,000, Mexico 710,000, Indonesia 647,000, and Ethiopia which produced 259,000 (FAO Statistics 2007).

This increase in demand for papaya, particularly in the Unites States and Europe, is claimed to have been triggered by the new trend in health consciousness. Papaya is rich in vitamin A, vitamin C, potassium, high in crude fiber, and carbohydrates but is low in protein, fats, and calories (Manshardt 1992; Reiger 2006). Apart from being widely produced and marketed as fresh fruit, as a preserve, and for juice, various parts of the fruit and plant have pharmaceutical, medicinal and industrial purposes. Unripe fruit is commonly used to dress wounds (Wimalawansa 1981; Starley *et al.* 1999; Hewitt *et al.* 2000) and to treat insect bites. The latex of green fruit contains proteinases of broad spectrum activity that are employed in the treatment of digestive disorders, in the manufacture of cosmetics, meat tenderizers, and in the clarification of beer (Madrigal *et al.* 1980). Green

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fruit is also consumed as salad in Asia (Sankat and Maharaj 1997) but is more commonly processed and used as a condiment and spice. The seeds of papaya are sometimes used as a substitute for pepper, in the treatment for intestinal worms, and for promoting abortions in some regions of the Caribbean and Polynesia (Morton 1987). Papaya bark has generally been regarded as having little value but it was recently shown that it is an efficient biosorbent of heavy metals and has potential in the treatment of wastewater (Saeed *et al*. 2006).

Papaya is an attractive cash crop because it is easy to grow from seed, mature fruits are produced 9 to 12 months after establishment in the field, fruit is produced continuously year round, and little maintenance of plants is required. However, the key to successful production of papaya lies in the countries' post-harvest and transport technology that keep the easily injured fruit in good condition for extended periods, as well as in the prevalence of abiotic and biotic diseases. As with many tropical and subtropical crops, papaya is host to various pests and pathogens. In 1990, Singh reported 4 insect and mite species as major pests of papaya; and a number of bacterial, fungal and viral pathogens also reduce plant vigor and affect the quality of papaya fruits (OECD 2003).

This review focuses on the etiology, pathology, and molecular biology of virus pathogens affecting papaya production over the past 50 years. The first attempt to describe papaya viruses was by Jensen in 1949 and since then a few reviews of some of the viruses have been published (Wan and Conover 1983; Gonsalves 1994; Zettler and Wan 1994; Fermin and Gonsalves 2003; Ventura *et al*. 2004). Viruses belonging to 9 taxonomic groups, 4 tentatively classified species, and 3 unassigned species are reported as etiological agents capable of infecting papaya. Virus-host interactions, climatic conditions, cultural management practices, vector populations, and whether the papaya fruit is destined for local or international markets contribute to the economical importance of the viral pathogen.

POTYVIRUSES

In 1949, Jensen reported that the first papaya disease attributed to a virus was recognized by Smith in Jamaica in 1929. In his accounts, Smith stated that the virus induced yellowing and mottling of leaves as well as a reduction in the terminal leaves to a pencil point. Smith purported that the primary reason for no large-scale papaya cultivation in Jamaica was due to this viral disease. Similarly in 1937, Stell recommended that commercial cultivation of papaya in Trinidad should not be undertaken due to the prevalence of a mosaic disease of papaya. Acuña and Zayas between 1940 and 1946, described a disease of papaya trees in Cuba referred to as Cotorro mosaic that caused severe distortion of the leaves, and the development of chlorotic and/or puckering patterns in the inter-veinal regions. Lesions were occasionally observed on fruits of these infected trees. In 1946, Adsuar also described a mosaic disease of papaya that was transmissible by mechanical inoculation, grafting, and by *Aphis spiraecola* in Puerto Rico (Jensen 1949). Similarly, Mueller described a mosaic disease of papaya in Venezuela in 1941. Given the symptomatology in all these instances, it appears that PRSV has been in the Caribbean and Venezuela since the early 1900s before the first description of the prototype virus in Hawaii. PRSV was first noted on Oahu Island, Hawaii in 1945. The virus has since been recognized in many tropical and subtropical areas including South America, Africa (Costa *et al*. 1969; Purcifull *et al*. 1984; Diallo *et al*. 2007), India (Khurana 1975), Mexico (Alvizo and Rojkind 1987), Australia (Thomas and Dodman 1993), Thailand, Taiwan, China, the Philippines (Gonsalves 1994), Japan (Maoka *et al*. 1995), and more recently, Iran (Pourrahim *et al*. 2003), Bangladesh (Jain 2004), and the French Polynesia and Cook Islands (Davis *et al*. 2005).

PRSV is the most damaging virus pathogen to papaya. Losses incurred by PRSV range from decreased acreage under production, reduction in employment, sporadic production, and significant decrease in fruits for local markets and losses in foreign exchange for countries involved in supplying the international market. Losses of up to 70% (Barbosa and Paguio 1982) and 100% (Dahal *et al*. 1979) have been reported in some regions. In Jamaica, production of papaya was down by 40% between 1994 and 1998, resulting in a loss of some US$ 11 million per annum (pers. comm. Jamaica Papaya Growers' Association). In Venezuela, PRSV was brought to national attention in 1993 when papaya orchards were decimated in the Lake Maracaibo basin and later incidents were observed in almost all orchards across the country (Vegas *et al*. 2004). Production of papaya virtually came to a halt in the 1950s in Hawaii due to the spread of PRSV in the major growing regions of Oahu island, Hawaii. This resulted in a relocation of the industry in the early 1960s to the Puna District on the Hawaii Island. However by 1992, PRSV was discovered in Puna which by then grew 95% of Hawaii's papaya and by 1994, PRSV was widespread in Puna (Gonsalves 1998). By 1988, Taiwan was no longer capable of exporting papaya to Hong Kong and Japan given the spread and destruction of most of the commercial plantings since 1978 (Wang *et al*. 1978; Yeh *et al*. 1988). The domestic supply of papaya is insufficient on Thailand where papaya is an important subsistence crop after rice in Northeastern territories (Prasartee *et al*. 1995).

The disease induced by PRSV causes stunting of papaya trees and drastically reduces the quality of fruits and yield (Purcifull *et al*. 1984). In initial stages of infection, plants develop mottle patterns on the leaves, followed by severe leaf distortion and reduction similar to damage caused by mites. Some strains such as those in Taiwan induce symptoms of wilting along with mosaic (Chang 1979). In later stages of infection, oily streaks develop on petioles and stems and the diagnostic water-soaked ringspot blemishes on fruits (Gonsalves 1994). Virus particles are generally detected in the cytoplasm and cell vacuoles of all parts of the host plant. Amorphous inclusion bodies (Martelli and Russo 1976) and pinwheel inclusions (Purcifull and Edwardson 1967) are generally found consisting of a 51 kD (de Meija *et al*. 1985) and 70 kD protein (Yeh and Gonsalves 1984), respectively. Trees of all ages are susceptible to PRSV and generally express symptoms 2-3 weeks following inoculation. Trees that become infected with the virus shortly after planting do not produce fruit. Symptom expression is highly influenced by environmental conditions and is more severe during periods of cool temperatures (Gonsalves 1994).

Two serologically indistinguishable biotypes of PRSV have been described. Type P is pathogenic to papaya while type W (previously designated as *Watermelon mosaic virus 1*) is pathogenic to cucurbits. Other hosts of PRSV belong to the family *Chenopodiacae*. PRSV induces local lesions on *Chenopodium quinoa* and *C. amaranticolor* (Purcifull *et al*. 1984). Recent work with recombinant severe and mild type P strains from Hawaii showed that mutations in the C-terminal portion of two virus proteins (P1 and HC-Pro) were critical in determining the hypersensitive response in *C. quinoa* and systemic infection in papaya (Chiang *et al*. 2007).

PRSV is sap transmissible and is vectored by 23 aphid species (Hemiptera, *Aphididae*) in a non-persistent manner (Purcifull *et al*. 1984). Depending on the number of winged aphids, a papaya orchard can become totally infected in 3-4 months after introduction of the virus. However, papaya is not a preferred host of aphids and acquisition and transmission of the virus occur during the brief superficial probing when aphids test the suitability of papaya as a feeding host. Studies with other potyviruses have shown that helper factors are required for transmission and retention of the virus on the aphid stylet. The current hypothesis is that the non-structural protein HC-Pro forms a bridge between the D-A-G motif on the N-terminus of the virus coat protein and a putative receptor in the aphid mouthparts (Pirone and Blanc 1996). It is widely accepted that PRSV is not seed-borne

(Purcifull *et al.* 1984). However, seed transmission was demonstrated in a study conducted in the Philippines in 1990. Two of 1355 seedlings (0.15%) from fruit of an infected tree were reported to develop symptoms of PRSV 6 weeks after emergence (Bayot *et al.* 1990). Presence of PRSV was subsequently confirmed by ELISA, aphid transmission and indicator host assays with *C. quinoa*. Further studies on seed transmissibility of PRSV have not been reported to date.

Spread of PRSV in the field is presumably accomplished from papaya to papaya, and cucurbit hosts play a minor role. Only one incident of field transmission from papaya to cucurbits has been documented in an experimental trial (Persley 1998 in Bateson *et al.* 2002). However, the list of cucurbits acting as hosts for PRSV type P is growing (Magdalita *et al.* 1990; Ferwerda-Licha and Pingel 2003; Noa-Carrazana *et al.* 2006; Chin *et al.* 2007a). Given the widespread distribution and their potential of serving as a reservoir of PRSV type P, cucurbit hosts most likely play a role in the epidemiology of PRSV and deserve more attention.

PRSV is a flexuous rod-shaped virus built with single coat protein subunits and measures approximately 760-800 nm in length and 12 nm in diameter. Much of the characterization of PRSV was done with the PRSV HA strain out of Hawaii. The strain has been completely sequenced (NC_001785, Yeh *et al.* 1992). PRSV is classified as a *Potyvirus* in the family *Potyviridae*. Its monopartite genomic positive sense RNA consists of 10,326 nucleotides with a 5′ genome-linked protein (VPg) and a 3′ poly (A) tract (Yeh *et al.* 1992). Like other potyviruses, the genetic organization is VPg - 5′ nontranslated region, 63 K P1, 52 K helper component (HC)-proteinase (HC-Pro), 46 K P3, 72 K cylindrical inclusion (CI), 6 K, 48 K nuclear inclusion a (NIa), 59 K nuclear inclusion b (NIb), 35 K coat protein (CP), 3′ noncoding region, and poly (A) tract. PRSV RNA codes for a single polypeptide species which is cleaved into functional proteins by the autocatalytic activity of virally encoded proteinases (Yeh and Gonsalves 1984). Studies with PRSV HA have postulated two cleavage sites for the N terminus of the CP; an upper site at positions 3,034 to 3,042 (Yeh *et al.* 1992) resulting in a functional polymerase protein (NIb, 517 aa) and the lower site some 20 aa downstream for an aphid transmissible coat protein (35 K). Based on work with other potyviruses, the roles of the functional proteins include: CP for RNA encapsidation; NIb, NIa, P1, HC-Pro, and CI for genome amplification; NIa, P1, HC-Pro for polyprotein processing; CP and CI for cell-to-cell movement; CP, HC-Pro and VPg for long distance movement; and HC-Pro and CP for aphid transmission (Riechmann *et al.* 1992; Shulka *et al.* 1994; Revers *et al.* 1999). More recently, HC-Pro has been implicated as a pathogenicity enhancer by disrupting host defense responses (Vance *et al.* 1995; Pruss *et al.* 1997; Shi *et al.* 1997). Both initiation and maintenance phases of RNA silencing can be targeted for suppression in somatic tissues (Anandalakshmi *et al.* 1998; Brigneti *et al.* 1998; Kasschau and Carrington 1998). In addition, P3 appears to be involved in virus replication and pathogenicity when associated with CI (Mandahar 1999; Urcuqui-Inchima *et al.* 2001).

Since the early reports on PRSV HA, complete sequences of type P isolates from Taiwan (X97251, Wang and Yeh 1997), Thailand (AY162218), India (EF017707, Parameswani *et al.* 2007), China (EF183499), and Mexico (AY 231130, Noa-Carrazana *et al.* 2007) have been elucidated. Comparative analysis of the polyprotein of biotypes from Hawaii (S46722 type P), Taiwan (X97251 type P and AY 027810 type W), Thailand (AY162218 type P and AY 010722 type W) and Mexico (AY231130 type P) gave two clades (Noa-Carrazana *et al.* 2007). One cluster included the type P isolates from Hawaii and Mexico and the second cluster contained the Asian isolates. The most conserved proteins were CI, NIb and HC-Pro while the most variable proteins were P1, P3, 6 K and CP. Three biotype specific aa differences were observed in P1 and NIa proteins. While type P isolates have a proline residue in position 200 in the P1 protein, type W isolates have a serine residue. The other two differences were noted in positions 2,309 and 2,487 in the NIa protein. Lysine and aspartic acid were detected at position 2,309 in type P and type W isolates, respectively. Isoleucine and valine were detected at position 2,487 in type P and type W isolates, respectively.

Researchers in many regions such as Australia (Bateson *et al.* 1994), Brazil (Lima *et al.* 2002), Hawaii (Wang and Yeh 1992), India (Jain *et al.* 2004), Mexico (Silva-Rosales *et al.* 2000; Noa-Carrazana *et al.* 2006), Thailand, Vietnam, the Philippines (Bateson *et al.* 2002), Jamaica, and Venezuela (Chin *et al.* 2007b) have examined the molecular characteristics of PRSV type P through sequence analysis of the *cp* gene of isolates differing in geographical origin within the country. In general, patterns between geographic origin and diversity are evident based on the country of origin rather than the locations within the country from which the isolates were collected. However, the converse is true; in that variation between isolates within a country have been observed in India, Mexico, Jamaica, and Venezuela. Type P isolates from India, on the other hand, were reported to be divergent up to 11%. In their analysis, Jain *et al.* (2004) concluded that the population consisted of a mixed population with defined sub-populations which were the result of movement and mixing of isolates. The diversity was attributed to the wide range of cropping systems and cultivation practices of farmers across the geographical regions of India and not to the geographical origin of the isolates across the country (Jain *et al.* 1998). Recent analysis of isolates from Mexico suggests clear patterns between sequence variability and the location from which the isolates were collected in the country (Noa-Carrazana *et al.* 2006). Greater diversity between isolates was observed with PRSV isolates from regions of higher economic development. Increased exchange of genetic resources and movement of plant materials were associated with the degree of variation. Similarly, patterns of isolate diversity, time of collection, and origin of isolates within the country were found in Venezuela (Chin *et al.* 2007b). These patterns are presumably being driven by introductions, geographical isolation and disease management strategies. Analysis of virus populations of Venezuelan isolates collected in 1993 and later in 2004 revealed greater diversity among populations collected in 2004. In general, isolates originating close to the borders of the neighboring highland Andean states were more closely related. However, isolates from Zulia, Mérida and Trujillo, from these same regions but separated by geographical (high peaks between Mérida and Trujillo and arid zones surrounding Mérida) and agricultural barriers (huge extensions of plantain plantations in Zulia) were less related. Analysis of type P isolates from Jamaica in 1990 and in 1999 showed that the latter isolates were very similar but diverged up to 8% from the isolate collected during the earlier epidemic in 1990 (Chin *et al.* 2007b).

Comparative analysis of *cp* gene sequences of isolates from differing geographical locations indicate variation up to 15.9% and clustering of the isolates according to geographic origin (Bateson *et al.* 1994; Wang *et al.* 1994). That is, the isolates from the Caribbean cluster with those of the United States and Australia; Asian isolates group together and although the Indian isolates are within the latter group, they appear to share a closer relationship with each other. Isolates from Sri Lanka group separately. The Caribbean isolates share similarities of 92.5 to 95.9% with isolates from the United States and Australia but lower similarities of 84.9 to 89.8% with those from Asia. Differences with PRSV isolates as with potyviruses in general (Riechmann *et al.* 1992; Silva-Rosales *et al.* 2002; Jain *et al.* 2004) are scattered throughout the *cp* sequences, but most polymorphisms are located within the 5′-proximal quarter of the gene and the identity increases towards the 3′ end. Moreover, not all nt substitutions lead to aa substitutions.

Mutation, in addition to movement of PRSV, appears to be significant in the molecular evolution of PRSV. Strong

evidence supports the hypothesis that type P isolates arose through mutation from type W isolates. Sequence analysis of the *cp* genes of type P and W populations in Australia showed tight clustering of the isolates and high nt identity of 98% (Bateson *et al*. 1994). Similar observations were noted in analyses of biotypes from Thailand where type P isolates diverged from a common branch within a diverse background of type W isolates, Vietnam (Bateson *et al*. 2002), Brazil (Lima *et al*. 2002), and India (Jain *et al*. 1998). However, the type P and type W isolates from these countries are not as closely related (93 to 96.6%) as those reported from Australia. Recent *in silico* recombination analyses with complete sequences of PRSV genomes from Hawaii, Mexico, Taiwan, and Thailand, provide evidence of putative recombination regions in the P1 protein (Noa-Carrazana *et al*. 2007). Sites of recombination were also observed in 6 cistrons (HC-Pro, P3, CI, NIa, NIb, CP, except 6 K) and the 2 untranslated regions but more consistent results were obtained with P1. Recombination has been shown to contribute to sequence diversity in potyviruses (Garcia-Arenal *et al*. 2001) and may be linked to host adaptation (Valli *et al*. 2007). Evidence of interspecific recombination was observed in comparative analysis of the P1 of *Watermelon mosaic virus* (WMV), *Soybean mosaic virus* (SMV), and *Bean common mosaic virus* (BCMNV). The N terminal half of WMV P1 showed no relation to that of SMV but was 85% identical to BCMV (Desbiez and Lecoq 2004). Similarly analysis of the P1 of the NL-3K strain of *Bean common mosaic virus* (BCMNV) from the United States (Idaho) suggests that the strain is a recombinant between the NL-3 D (Drifjhout) strain and the Russian strain RU1 (Larsen *et al*. 2005). Since PRSV types P and W share cucurbit hosts, it is conceivable that recombination, in addition to mutation, is involved in the derivation of type P from type W. No field data on recombination in PRSV are available.

Other early reports in the 1970s document a virus species from Puerto Rico that shares some biological characteristics that are very similar to those of PRSV. Papaya trees infected with the virus, named Papaw isabela mosaic virus, exhibited typical PRSV symptoms that included yellow mottling, some mild leaf distortion, and oily spots on the stem. However, the occurrence of diagnostic ringspot blemishes on fruits was not mentioned. Infection of 5 cucurbit genera, *Cucumis*, *Luffa*, *Citrullus*, *Lagenaria* and *Melothria*, was demonstrated. Neither mechanical nor seed transmission in papaya was documented but rather transmission by the nematode, *Trichodorus christiei* (Adsuar 1972). Until now, serological or molecular evidence supporting the biological data and classification of this virus as a *Potyvirus* has not been provided.

Another virus of papaya that is tentatively classified as a *Potyvirus* is the *Papaya leaf distortion mosaic virus* (PLDMV). PLDMV was first identified on the island of Okinawa, Japan, in 1954. Given the mosaic symptoms on foliage, ringspot blemishes on fruits, and the detection of flexuous virus particles, the virus was initially considered PRSV (Yonaha 1976; Kawano and Yonaha 1992). However, it was not found serologically related to PRSV and was subsequently named after the papaya host and the leaf symptoms (Kawano and Yonaha 1992). Later between 1990 and 1995, three strains of PLDMV were described based on differing symptomatology on papaya field trees in Japan; leaf distortion mosaic (PLDMV-P (LDM), mosaic (PLDMV-P (M), and yellow mosaic (PLDMV-P (YM) (Maoka and Hataya 2005). PLDMV is transmitted by aphids in a non-persistent manner (Maoka *et al*. 1995; Maoka and Hataya 2005). Low (33%) rates of transmission were observed with the green peach aphid *Myzus persicae* and PLDMV-P 56. Higher rates between 78 and 100% were obtained with the same species and the 3 strains, PLDMV-P (LDM), PLDMV-P (M), and PLDMV-P (YM) (Maoka and Hataya 2005).

Molecular characterization of the *cp* sequences of PLDMV-P 56 was conducted in the late 1990s. Comparative sequence analysis of these *cp* sequences and PRSV type P indicated aa identity of up 57% (Maoka *et al*. 1996);

thus corroborating the initial finding that the two viruses are serologically unrelated. The complete genome of PLDMV-P (LDM) (AB088221) and *cp* sequences of the two other type P, PLDMV-P (M) and PLDMV-P (YM) have been reported (AB092814 and AB092815, respectively). *cp* sequences (AB092816) of a cucurbit biotype PLDMV-C (T) have also been determined. PLDMV-C (T) is capable of infecting *Cucumis melo*, *Cucurbita moschata*, *Lagenaria siceraria*, and *Nicotiana benthamiana* but unable to infect papaya and is serologically indistinguishable from PLDMV-P (Maoka and Hataya 2005).

The RNA genome of PLDMV-P(LDM) consists of 10,153 nts and is the fourth largest reported genome of the *Potyvirus* genus, after *Sweet potato feathery mottle virus*, *Onion yellow dwarf virus* and PRSV. The genome codes for a single large ORF of 3,269 aa. Highly conserved aa motifs reported for potyviruses are present in PLDMV with some substitutions. Namely, (1) H_{388}-X_8-D_{397}-X_{32}-G_{429}-X-S_{431}-G_{432} involved in proteinase activity in P1, (2) in HC-Pro, the zinc finger metal binding motif C-X_8-C-X_{13}-C-X_4-C, and C-C-C-V-T, K-I-T-C, P-T-K implicated in long distance movement and aphid transmission, respectively, (3) G_{1423}-X-X-G_{1426}-X-G_{1428}-K-S-T_{1431} motif of a nucleotide phosphate binding site involving helicase activity (4) S-G-X_3-T-X_3-N-T-X_{30}-G-D-D found in NIb and characteristic of positive sense stranded viral RNA dependent RNA polymerases, and (5) D-A-G motif in the N-terminus of the CP that contributes to aphid transmissibility. The PLDMV polyprotein shares 44 to 50% identity with that of other potyviruses. The *cp* sequences of the type P isolates were 95 to 98% identical but share lower identities of 88 to 89% with the cucurbit biotype (Maoka and Hataya 2005). In addition to Japan, outbreaks of PLDMV-P have been reported in Saipan in the Northern Mariana Islands (Kiritani and Su 1999) and Taiwan (Chen *et al*. 2000). PLDMV-P from Taiwan shares 95% identity with the virus from Japan.

Recently, the *Moroccan watermelon mosaic virus* (MWMV), a tentative member of the genus *Potyvirus* and etiological agent of severe epidemics in cucurbit crops in Africa and the Mediterranean basin (van der Meer and Garnett 1987; Quiot-Douine *et al*. 1990; Roggero *et al*. 1998; Lecoq *et al*. 2001), was detected in papaya orchards of the Democratic Republic of Congo (Arocha *et al*. 2007). Infected trees exhibited foliar and fruit symptoms typical of PRSV. Unlike PRSV-infections however, tumor-like growths were observed within the trunk of these trees. In the initial stages of infection the internal tissues of the trunk were pink and over time the tissues turned brown or black and fibrous. Samples from the infected trees were found positive for potyvirus in enzyme linked immunosorbent (ELISA) assays but they were negative in similar tests for the detection of PRSV. Amplicons of the expected size (1639 bp) were obtained in reverse transcriptase polymerase chain reaction (RT-PCR) with primers designed to part of the NIb gene, the entire *cp* and 3′ nontranslated region of MWMV (AF305545, Lecoq *et al*. 2001). The amplicons were sequenced (EF211959) and share 84% nt and 93% aa identity with MWMV (Arocha *et al*. 2007).

Occurrences of *Zucchini yellow mosaic virus* (ZYMV) along with PRSV and the rickettsias responsible for papaya bunchy top disease were recently reported in Puerto Rico. Field samples collected from papaya trees showing signs of bunchy top and viral infection were tested for the pathogen of bunchy top and for PRSV and ZYMV in ELISA. Of the 43 samples analyzed, most were positive for bunchy top while 34% were positive for PRSV and 53% for ZYMV (Fewerda-Licha 2002). ZYMV is a common devastating virus of cucurbits that is transmitted by several aphid species in a non-persistent manner (Lisa and Lecoq 1984). The ZYMV strain from papaya has not yet been characterized.

RHABDOVIRUSES

Three putative rhabdoviruses are described as pathogens of papaya in tropical and subtropical regions; *Papaya apical*

necrosis virus, *Papaya droopy necrosis virus*, and *Lettuce necrotic yellows virus*. Of these, only two are purported to induce apical necrosis and plant death in papaya.

Papaya apical necrosis virus (PANV) was first reported in Venezuela in 1981 (Lastra and Quintero 1981). The virus has since been recorded in other regions in Venezuela (Marys *et al.* 2000), Cuba (Mejías *et al.* 1987), Mexico (Noé-Becerra *et al.* 1999), Brazil (Kitajima *et al.* 1991) and in some parts of Africa (Taylor 2004). Infections with PANV are characterized by initial yellowing of the plant followed by wilting of younger leaves and necrosis of the plant apex. Bacilliform viral particles (80-84 × 210-230 nm) are mainly found in parenchyma cells of the plant phloem. PANV is transmitted by the leafhopper, *Empoasca papayae*, but mechanical transmission has not been demonstrated (Lastra and Quintero 1981). Although the incidence of PANV is low, outbreaks of PANV have limited the production of papaya in some regions, such as the state of Zulia in Venezuela, during the late 1970's (Zettler and Wan 1994).

A similar rhabdovirus was reported in Florida in 1981 (Wan and Conover 1981). The virus, currently known as *Papaya droopy necrosis virus* (PDNV), is still found in Florida (Wan and Conover 1983; Zettler and Wan 1994). Both PDNV and PANV share common features in particle morphology and the apical necrosis and plant death symptoms induced on papaya, but progress of the disease induced by both viruses differs. Plants infected with PANV initially show yellowing and wilting of the leaves followed by necrosis of the apical parts of the plants whereas plants infected with PNDV exhibit drooping and curvature of the leaves and shortened petioles. As the disease advances, there is the development of a bunchy appearance of the plant crown; leaves eventually abscise, the stem tip becomes necrotic and the plant dies. Like PANV, PDNV is not mechanically transmissible. However, no natural vector for PDNV has been identified.

It should be noted that in a recent review on rhabdoviruses, PANV was referred to as an unassigned member of the genus (Jackson *et al.* 2005) but PNDV was not mentioned. Moreover, another rhabdovirus that can be transmitted to papaya seedlings by the aphid *Hyperomyzus* is *Lettuce necrotic yellows virus* (LNYV, Francki *et al.* 1989). Infection with LNYV is latent since no visible symptoms are observed following inoculation (Harding and Teakle 1993). In addition, rhabdovirus-like particles were found in samples collected from Distrito Federal, Venezuela, during a survey of the major papaya growing regions of Venezuela in 1997 (Marys *et al.* 2000). The virus was not characterized further.

POTEXVIRUSES

Papaya is host to the *Potexvirus*, *Papaya mosaic virus* (PapMV) of the family *Flexiviridae*. The virus was initially reported in Florida in the 1960s (Conover 1962) and later in Venezuela, Sri Lanka (Rajapakse and Herath 1981), India (Bhaskar 1983), Peru, Bolivia (Brunt *et al.* 1996) and Mexico (Noa-Carrazana and Silva-Rosales 2001). Recently, mixed infections with both PapMV and PRSV were reported in Mexico (Noa-Carrazana *et al.* 2006). Synonyms of PapMV include *Babaco yellow mosaic virus*, *Boussingaultia mosaic virus* (Phillips *et al.* 1985), and *Papaw mild mosaic virus*. *Argentine plantago virus* (Gracia *et al.* 1983; Milne 1988) and *Plantago severe mottle virus* (Rowhani and Peterson 1980; Gracia *et al.* 1983; Milne 1988) are reported strains. In addition to papaya, PapMV can infect members of 5 plant families; namely, *Amaranthaceae*, *Basellaceae*, *Chenopodiaceae*, *Leguminosae-Caesalpinioideae* and *Scrophulariaceae*. Recently, a *Potexvirus* related to PapMV was isolated from moss rose (*Potulaca grandiflora*, *Portulacaceae*), a succulent ornamental, in Italy (Ciaffo and Turina 2004).

Infection with PapMV causes mosaic discolorations on foliage and stunting of papaya trees. However, in co-infections with PRSV, trees exhibit apical necrosis, leaf distortions, mottling, and mosaic (Noa-Carrazana *et al.* 2006). Flexuous virus particles (530 nm) can be found in all parts of the infected plant. Cellular inclusion bodies composed of virus particles have also been observed in cells (Purcifull *et al.* 1966; Zettler *et al.* 1968). The virus is transmitted in nature by mechanical contact but no invertebrate vector is known. Seed transmission has not been reported.

Molecular characterization of PapMV was conducted early in the 1980s with an isolate presumably from Asia. PapMV is a single stranded positive sense RNA virus of 6,656 nt. The RNA has a methylguanosine cap at the 5′ end while the 3′ has a poly (A) tail (AbouHaidar and Bancroft 1978; AbouHaidar 1988). The complete genome of the virus was reported in 1989 (D13957, Sit *et al.* 1989). Like other potexviruses, PapMV encodes 5 ORFs (Sit *et al.* 1989). Based on work with other potexviruses, the first ORF encodes the replicase, the next 3 overlapping ORFs (referred to as the triple gene block, TGB) encode proteins required for cell to cell movement along with the CP (Santa Cruz *et al.* 1998; Verchot-Lubicz 2005), and the final ORF encodes the CP (Santa Cruz *et al.* 1998). ORF 1 is translated from the genomic PapMV RNA while the overlapping ORFs and the CP are translated from 2 separate subgenomic RNAs (AbouHaidar and Gellatly 1999). Studies with *Potato virus X* demonstrated the role of one of the TGB proteins (TGBp1) as a pathogenicity enhancer. TGBp1 acts as a suppressor of RNA silencing by regulating the accumulation of 25 nt siRNA (short interfering RNA) which is the signaling factor in systemic silencing (Voinnet *et al.* 2000). In comparative analysis of *cp* sequences, the early PapMV isolates (D00240, D13957, Sit *et al.* 1989) are 98.4% identical to an isolate recently reported from China (EF183500, Shen Tang, Lu Niu, and Zhou 2006 unpublished). The early isolates however share lower identities of 72.7 to 73.8% with three isolates from Mexico (AY017186, AY017187, AY017188, Noa-Carrazana *et al.* 2001). The Mexican isolates were collected from papaya (AY017186) and pumpkin (AY017187, AY017188) and are 91.1% identical.

GEMINIVIRUSES

Several begomoviruses of the family *Geminiviridae* are associated with papaya in China, India, Pakistan, Taiwan, Jamaica and some countries in Central America. The begomoviruses associated with papaya are distinct species and most consist of a monopartite genome organization unlike most begomoviruses which have a bipartitie genome. The single stranded genome occurs as a covalently closed circular DNA molecule of approximately 2.5-3.0 kb that is housed in a geminate isometric icosahedral capsid (18 × 20 nm) constructed with 27-30 kD protein subunits (Howarth and Goodman 1982; Lazarowitz 1992; Zhang *et al.* 2001). All genes encoding proteins for replication, transcription, encapsidation and movement are on the single DNA component of the monopartite begomoviruses or the two DNA components of the bipartitie begomoviruses (Lazarowitz 1992). A region of about 200 bp, the intergenic region (IR) which is analogous to the common region (CR) in bipartite begomoviruses, has conserved motifs critical for virus genome replication and transcription (Argüello-Astorga *et al.* 1994). Recently three categories of novel satellite-like ssDNA molecules (DNA-1, DNAβ and defective interfering DNA) have been found associated with the DNA of some monopartite begomoviruses. These satellite molecules generally consist of a circular DNA molecule of about half the size (1.3 kb) of its associated viral DNA component. DNAβ, and not DNA-1, appears to influence symptom expression and viral replication but both require the helper virus for transmission and movement in the host plant (Briddon *et al.* 2004).

Two monopartite begomoviruses, *Papaya leaf curl China virus* (PaLCuCNV, AJ558122) and *Papaya leaf curl Guangdong virus* (PaLCuGDV, AJ558123), are associated with papaya leaf curl disease in the south of China. Infected papaya plants show downward leaf curling and vein thick-

ening but more severely affected plants develop twisted petioles and exhibit stunting. Invariably, infected trees produce distorted fruits; resulting in farmers abandoning diseased orchards. DNA sequence analysis indicates that PaLCuCNV and PaLCuGDV are only 73.4% similar and are more similar to several begomoviruses from the region including *Ageratum yellow vein China virus* (AYVCNV-[Hn2], AJ495813) and *Ageratum yellow vein virus* (AYVV, X74516) (Wang *et al*. 2004). PaLCuCNV was also recently isolated from a common roadside weed *Corchoropsis timentosa* in the Guangxi province of China. *C. timentosa* showed leaf curling, vein thickening and yellow vein symptoms. The presence of the virus in a common weed is likely to facilitate increased transmission of PaLCuCNV throughout Southern China (Huang and Zhou 2006a).

A similar papaya leaf curl disease has been known for more than 60 years in India (Saxena *et al*. 1997). However, between 1993 and 1996, there was an increase in the incidence of the disease. The causal agent was transmitted between papaya plants by the whitefly *Bemisia tabaci* and this suggested the possible occurrence of a begomovirus (Saxena *et al*. 1998). Symptoms of the Indian begomovirus on papaya are similar to those observed with the two begomoviruses in China. In addition to downward leaf curling, vein thickening and clearing symptoms, the leaves of affected plants are also rubbery and fragile and the petioles are distorted. Fruits from infected plants are reduced in number and never develop to full maturity, often falling from trees (Saxena *et al*. 1997). The causal agent of papaya leaf curl disease in India was identified as *Papaya leaf curl virus* (PaLCuV). The complete nucleotide sequence of PaLCuV (Y15934) suggests a monopartite begomovirus genome organization. PaLCuV was also detected in cotton in the Faisalabad region of Pakistan. Infected cotton plants developed leaf curling, vein swelling, vein darkening and leaf enations (Mansoor *et al*. 2003). The two papaya begomoviruses from China, PaLCuCNV and PaLCuGDV, were distinct from and only 67 to 68% similar to PaLCuV (Wang *et al*. 2004). PaLCuV is more similar (88 to 86%) to several begomoviruses from the surrounding region including *Tomato leaf curl New Delhi virus* isolate ToLCNDV-CTM (DQ629102), several isolates of *Chili leaf curl Pakistan virus* (DQ116877 DQ116878, DQ114477), and *Pepper leaf curl Bangladesh virus* (AF314531). This suggests a common evolutionary origin of some of the viruses on the Indian subcontinent. The close nucleotide similarity between PaLCuV and ToLCNDV might explain the isolation of the *cp* of ToLCNDV (EF194275) from papaya plants from Lucknow, India. ToLCNDV has a surprisingly broad host range and has caused severe economic losses to several crops on the Indian subcontinent. It is capable of infecting tomato (Padidam *et al*. 1995), potato (Usharani *et al*. 2004), chili pepper (Khan *et al*. 2006), and sponge gourd (*Luffa cylindrical*, Sohrab *et al*. 2003) in India, tomato, chili pepper (Shih *et al*. 2003; Hussain *et al*. 2004) and watermelon (Mansoor *et al*. 2000) in Pakistan, and tomato in Bangladesh (Maruthi *et al*. 2005).

There are also preliminary reports of geminiviruses associated with papaya in Taiwan and Jamaica. Infected papaya plants from Taiwan exhibit identical symptoms as PaLCuV-infected plants in India and the virus was presumed to be an isolate of PaLCuV. Amplicons were obtained in PCR analysis, using primers designed from the sequence of PaLCuV, and DNA extracted from infected plants in Taiwan. But partial nucleotide sequences of the *cp* gene (774 nt) of the Taiwan isolate (AY183472) were shown to be only 80% similar to PaLCuV. This suggested that the Indian and Taiwanese papaya viruses are likely to represent distinct begomovirus species (Chang *et al*. 2003; Mayo and Pringle 1998). Further analysis of the *cp* gene of the Taiwan virus indicated that it is highly conserved (85 to 97%) among several viruses from China including *Malvastrum leaf curl virus* (MLCV, AJ971253), PaLCuCNV, and PaLCuGDV. MLCV was isolated from papaya plants, showing leaf curl symptoms, from Guangxi Province China in

2005 (Wu and Zhou 2006). MLCV was first isolated from the common weed *Malvastrum coromandelianum* that was collected from the same region in China. Predominant symptoms on these plants included leaf curling and vein thickening. The satellite DNA component DNAβ about half the size of the DNA of MLCV was also found associated with infected *M. coromandelianum* (Huang and Zhou 2006b).

The partial DNA-A sequence of a presumed bipartite begomovirus was isolated from papaya plants with yellow mosaic symptoms in Jamaica (Roye *et al*. 2003). Nucleotide sequence analysis of 1300 nts which represented the 5′ portion of the replication associated protein, the *cp* and the entire CR of the Jamaican papaya virus suggested the presence of a distinct begomovirus. The Jamaican papaya virus is most similar to several previously reported begomoviruses from the region including *Jatropha mosaic virus* (JMV, AF324410), *Wissadula golden mosaic virus* (WGMV, U69280) both weed-infecting begomoviruses from Jamaica and *Tobacco leaf rugose virus* (AJ488768) from Cuba (Roye *et al*. 1997; Roye *et al*. 2006). DNA hybridization and PCR using degenerate primers detected the papaya virus in the eastern parish of St. Thomas and the central parishes of St. Catherine and Clarendon in Jamaica (Rojas *et al*. 1993; Roye *et al*. 2003). Attempts at amplifying a DNA-B component were unsuccessful but analysis of the genome organization of the partial DNA-A suggested a bipartite genome organization. Simultaneous occurrences of the virus and PRSV were also found in trees exhibiting symptoms typical of PRSV infection. Currently the papaya begomovirus does not seem to be a threat to papaya production in Jamaica.

Other begomoviruses in the GenBank database that can infect papaya include, *Papaya golden mosaic virus* (DQ318928) from Yucatan in Mexico, *Lindernia anagallis yellow vein virus* (DQ022658) in China and *Melon chlorotic leaf curl virus*, MCLCuV-[CR] (AY064391) in Costa Rica. MCLCuV-[GT] (AF325497) is also associated with muskmelon (*Cucumis melo*) in Guatemala and induces foliar chlorosis, leaf curling and reduced fruit set (Brown *et al*. 2001).

TOSPOVIRUSES

So far, the only reported tospovirus capable of infecting and causing symptoms in papaya is *Tomato spotted wilt virus* (TSWV; general description in Kormelink 2005). TSWV was first described in Hawaii in the mid 1980s by Gonsalves and Trujillo (1986), following an earlier report of a disease infecting papaya orchards in 1962 in Kauai. In their report, Gonsalves and Trujillo (1986) described the mechanical transmission of TSWV from lettuce to papaya seedlings. In similar greenhouse investigations, Harding and Teakle (1993) inoculated papaya seedlings with leaf sap extracts from TSWV-infected tomato in Australia. Two to three weeks after inoculation, plants exhibited irregular, necrotic lesions and chlorotic mottling on challenged leaves and after another 2 weeks similar symptoms also developed on the older, un-inoculated leaves. Although isometric TSWV particles were recovered from symptomatic papaya plants, the virus titer was low. Eventually, the apical parts of the plants became necrotic, and 7 to 9 weeks later the plants died. Additional evidence for TSWV-infection of papaya has been described in Brazil. Local reactions accompanied with systemic movement of virus through the plants were observed following experimental inoculations (Rezende and Costa 1987). In papaya orchards, the TSWV disease is characterized by spotting, chlorosis and necrosis of the leaves at the apex of the plant. As infection progresses, water-soaked lesions appear on petioles and stems. Surviving plants produce deformed and unmarketable fruits and plant death is not unusual (Gonsalves and Trujillo 1986). Similar disease symptoms have been described in Australia. In 1993, Harding and Teakle reported on the development of water soaked lesions as well as stunting of TSWV-infected plants in Australian fields. A recent update on the host range of TSWV confirms the initial findings that papaya is host to

TSWV (Parrella *et al.* 2003). TSWV was first discovered on tomatoes in 1919 and is now known to infect over 900 different plants of 70 botanical families. The virus is hosted by common weed species and is vectored by the well known thrips, *Frankliniella occidentalis*, in a circulative, propagative manner (Bautista *et al.* 1995). Molecular data on the virus from papaya are not available.

NEPOVIRUSES

Tobacco ringspot virus (TRSV), a *Nepovirus* of the family *Comoviridae* (Stace-Smith 1985), was shown to be the causal agent of terminal necrosis in experimental inoculations of papaya conducted by McLean and Olson in 1962 and later by Lambe in 1963 in back inoculations from orchard affected plants to healthy papaya seedlings. Biological evidence of TRSV was also provided in simultaneous experiments involving leaf sap inoculations from infected papaya plants to cucumber and cowpea seedlings (Lambe 1963). Yellow stippling developed on cucumber leaves and necrotic spots on cowpea leaves. Later in 1993, transmission and subsequent infection with TRSV from *Gladiolus* sp. to papaya were demonstrated (Harding and Teakle 1993). In these experiments, 74% (25 out 34) of the challenged plants showed ringspot blemishes on the old uninoculated leaves 3-4 weeks after inoculation. The leaves later became necrotic and plants exhibited severe stunting and bending. Field plants infected with TRSV quickly develop wilting symptoms 7 days after exposure to the virus followed by apical necrosis of the terminal growing point. By day 8, necrosis of the terminal leaves and tissues at the base of female blossoms was evident. Root symptoms typically occurred during the advanced stages of the disease and included discoloration, and eventually, rotting. Although TRSV is a cosmopolitan virus (Smith 2004), sporadic infections of papaya have solely been reported in Australia, the United States, and Nigeria (Lana 1980).

ILARVIRUSES

Experimental infection of papaya with *Tobacco streak virus* (TSV, general description in Scott 2001) was described in 1993. This is the only virus belonging to the *Ilarvirus* group that is reported to infect and cause symptoms on papaya plants. Harding and Teakle (1993) mechanically inoculated 15 papaya seedlings with sap from TSV-infected *Gomphocarpus physocarpus*. Three papaya plants displayed mild mottling on newly emerged leaves 3 weeks following inoculation. However, indicator *Nicotiana tabacum* plants that were back-inoculated from symptomatic and ELISA-positive TSV-infected papaya plants did not develop symptoms.

TOBRAVIRUSES

There is only one report on tobraviruses capable of infecting papaya under experimental conditions. Rezende and Costa, in 1987, demonstrated infection of greenhouse papaya plants with the tobraviruses *Pepper ringspot virus* (PepRSV, described in Robinson and Harrison 1989) and *Tobacco rattle virus* (TRV, described in Robinson 2003). Local infections were obtained following mechanical inoculations with either virus. Systemic infection was not observed.

CUCUMOVIRUSES

Evidence of local infection of papaya with *Cucumber mosaic virus* or CMV (Palukaitis and García-Arenal 2003) was documented on two occasions; in the 1950s and later in 1987. Adsuar in 1956 showed that papaya plants are susceptible to mechanical infection with CMV. In 1987, Rezende and Costa reported that papaya plants mechanically challenged with CMV developed local lesions on inoculated leaves.

UNASSIGNED VIRUSES

Three unassigned virus species capable of infecting papaya in South America have been reported in recent years. For two of the viruses, *Papaya lethal yellowing virus* (PLYV) and *Papaya meleira virus* (PMeV), complete molecular data are not yet available. The third virus, *Papaya mild yellow leaf virus* (PMYLV), appears to possess unique structural, biological, and molecular features. Some molecular data have been determined. However, the virus has not been sufficiently distinguished from viruses in recognized genera so as to form a new genus.

Papaya lethal yellowing virus (PLYV), the etiological agent of lethal yellow disease of papaya, was reported in Brazil in the early 1980s. Sporadic occurrence of the disease is generally typical in Brazil but incidence of up to 40% has been documented (Loreto *et al.* 1983). Co-infections of PLYV and PRSV have been reported in Venezuela (Marys *et al.* 2000). Symptoms of infection caused by PLYV start with yellowing of young leaves on the plant's crown and later progresses to severe curling deformation and senescence of leaves, small chlorotic blemishes on fruits, and eventually death. *Vasconcellea cauliflora*, which is also a member of the *Caricaceae* family, is susceptible to mechanical inoculations with PLYV (Amaral *et al.* 2006). PLYV is readily transmitted on the surface of seeds isolated from infected fruits (Camarco *et al.* 1998) but virus has not been detected within the embryos of seeds (Saraiva *et al.* 2006). PLYV can also persist in the soil and this allows for infections of plants early in the growing season (Camarco *et al.* 1998). Transmission by contaminated hands was recently shown (Saraiva *et al.* 2006). So far, PLYV has only been characterized in Brazil. The virus consists of isometric particles 30 nm in diameter with a single stranded RNA molecule and a capsid protein ca 35 kDa. Initial evidence based on particle morphology, genetic composition, CP size, and sequence homology to *Tomato bushy stunt virus* (TBSV), proposed the classification of PLYV as a member of the Tombusvirus group (Silva *et al.* 1997). However, subsequent data suggest that the species belongs to the *Sobemovirus* group of plant viruses, family *Sobemoviridae* (Silva 2001 in Amaral *et al.* 2006).

Another economically important virus only reported in Brazil is *Papaya meleira virus* (PMeV). PeMV is the causal agent of sticky disease in papaya. The virus was first reported in the 1980s (Nakagawa *et al.* 1987; Correa *et al.* 1988 in Maciel-Zambolim *et al.* 2003) and since then research has been focused on the elucidation of the biological features of this novel virus. Molecular evidence is still lacking to definitively assign PMeV to a plant virus group.

First symptoms of the PMeV disease appear on the margins of young leaves which turn necrotic and curl. Necrosis has been attributed to the exudation of translucent and low viscous latex that is not characteristic of the latex produced by healthy plants. This exudation of latex is later observed on fruits which eventually display a "honeyed" appearance. It is from this feature that the name of the disease was derived (i.e., meleira). Discolored pale-green rings can also appear on the surface of fruits. The latter symptoms together with the exuded latex render fruits unmarketable. Based on indicator host range studies, PMeV appears to be limited to the plant host papaya. More than 47 plants were challenged with preparations of PMeV. However, plants of one genus other than *Carica* were infected. Double stranded RNA was recovered from papaya and *Brachiara decumbens* (a synomyn of *Uroloa decumbens*, a common signal grass) but no symptoms developed. Apart from mechanical transmission, PMeV appears to be transmitted by latex in nature (Maciel-Zambolim *et al.* 2003; Pessini-Rodrigues 2006). The natural vector has not been determined. However, PMeV can be transmitted by two genera of whiteflies, *Bemisia tabaci* and *Trialeurodes variabilis*, under controlled conditions (Culik and Martins 2004; Pessini-Rodrigues 2006).

The third unassigned virus species infecting papaya is

Papaya mild yellow leaf virus (PMYLV). PMYLV is the only reported supercoiled filamentous virus infecting dicotyledoneous plants (Marys *et al.* 1995). PMYLV disease is characterized by foliar symptoms of mild inter-veinal yellowing of young and adult leaves without a reduction in leaf area and stunting of the plant. The virus is apparently ubiquitous in Venezuelan papaya orchards since the mid 1990s and shares some similarity to members of the *Tenuivirus* group.

The main biological, structural, and serological features of PMYLV available so far include: (1) the host range seems to be restricted to species belonging to the families *Caricaceae* (*C. papaya*) and *Cucurbitaceae* (*Cucumis sativus*, *C. metuliferus*, *C. melo*, *Cucurbita maxima* and *C. pepo*). While mild interveinal yellowing is evident 20 to 25 days following mechanical inoculation of papaya, cucurbits mainly exhibit symptoms of mild mottling within 15 days, (2) virus particles aggregate often as crystalline arrays only in xylem tissue (3) viral preparations contain filamentous particles, made up of a single 39 kD protein component, are 400 to 700 nm long and 3 nm wide and the nucleic acid is composed of a single stranded RNA molecule, and (4) purified virus or extracts from infected leaves only react to homologous antibodies and do not react with antibodies raised against five different Tenuiviruses (Marys *et al.* 1995). Given the many disparities with Tenuiviruses, it was concluded that PMYLV probably represents a member of a new virus group.

CONCLUDING REMARKS

Since the identification of the first virus infecting papaya in the early 1900s, a number of other species belonging to few genera have been described. These viruses can be grouped into four general categories based on their history with the crop, whether they cause disease of economic importance, and the existing biological and genotypic characterization. PRSV belongs to the first category. It has a long history with papaya production, is the most widespread destructive virus infecting papaya and subsequently the most characterized virus. PRSV is the subject of numerous studies on disease management strategies including cross protection (Yeh and Gonsalves 1984; Yeh *et al.* 1988; Tennant *et al.* 1994), conventional breeding of tolerant and resistant cultivars (Conover *et al.* 1986; Prasartsee *et al.* 1995; Magdalita *et al.* 1996, 1997, 1998; Story 2002; Gonsalves *et al.* 2005; Drew *et al.* 2006a, 2006b), and more recently genetic engineering (Gonsalves 1998, 2002; Lines *et al.* 2002; Bau *et al.* 2003; Fermin *et al.* 2004; Davis and Ying 2004; Tennant *et al.* 2005; Umi *et al.* 2005). PapMV and PLDMV belong in a second category. Like PRSV, PapMV and PLDMV have a long history with papaya production and data on some genotypes are available. In addition, PapMV has been the subject of studies on the requirements for virion assembly (Tremblay *et al.* 2007) and as an expression vector for the development of animal virus vaccines (Raja and AbouHaidar 2006). Unlike PRSV, PapMV and PLDV are not as widespread and can be considered of local significance.

Although viruses in the third category are classified in recognized genera, they are known as etiological agents of important diseases in other major crops and ornamentals. These viruses were recently detected for the first time in papaya between 1980s and 2000s during experimental inoculations of indicator host plants conducted for the determination of etiological agents of various diseases. Apart from geminiviruses of papaya, the species isolated from papaya have not been further studied and molecular data are not available. They are, in general, of little significance to papaya production and include members of the genera *Tospovirus*, *Nepovirus*, *Ilarvirus*, *Tobravirus*, and *Cucumovirus*. Other recently described viruses can be grouped in a fourth category. These virus species are attracting increasing attention and hold economic potential. Phenotypic and genotypic characterization is ongoing and classification is tenuous. PLYV and PMeV are in this category. Of note, many of the viruses affecting papaya fall in the latter two categories. They have received little attention and hence molecular evidence is lacking to describe them thoroughly. Much still needs to be learnt about the viruses infecting papaya. A complete catalogue will not be available until partial or complete virus sequences of nucleic acids isolated from infected papaya plants are reported or a more thorough epidemiological analysis is performed.

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