VIRAL DISEASES OF PITAYA AND OTHER CACTACEAE PLANTS

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ABSTRACT

Pitaya (*Hylocereus* spp.), also called dragon fruit, pitahaya or pitajaya, native to the forests of Latin America, and the West Indies, belongs to the family of Cactaceae. Among the cactus fruit crops, pitaya is classified as the climbing epiphytic species and produces edible fruits which have sweet pulps with numerous small black seeds on the trailing cladode stems. Due to the progress in breeding and cultivation techniques in Taiwan, pitaya is becoming an important fruit crop in the domestic and foreign markets. During a disease survey of pitaya in Taiwan, some plants were found with systemic mild mottling on the stems, and these were found to be infected by a potexvirus, *Cactus virus X* (CVX). In addition, another two potexviruses *Zygocactus virus X* (ZyVX) and Pitaya virus X (PiVX), were identified later in Taiwan. Because of the similar features of Cactaceae plants, there is high possibility that cactus-infecting viruses will infect pitaya just like CVX and ZyVX did. The objective of this article is to provide information of viral diseases of pitaya and other Cactaceae plants so as to help further study of pitaya-infecting viruses and propose the control strategy.

Keywords: pitaya, *Hylocereus*, Cactaceae, viral diseases

INTRODUCTION

Pitaya, also called dragon fruit, pitahaya or pitajaya, native to the forests of northern South America, Central America, Mexico, and the West Indies, belongs to the genus *Hylocereus* in the family of Cactaceae (Mizrahi et al. 1997; Le Bellec et al. 2006). Among the cactus fruit crops, pitaya is classified as the climbing epiphytic species (Mizrahi et al. 1997) and produces edible fruits which have sweet pulps with numerous small black seeds on the trailing cladode stems. According to the Britton and Rose classification (Britton and Rose 1963), the genus of *Hylocereus* contains 16 species of plants, five of these are planted as fruit trees including *H. purpusii*, *H. polyrhizus*, *H. costaricensis*, *H. undatus*, and *H. trigonus* (Le Bellec 2006). The pitaya industry is distributed mainly in Latin America, such as Mexico, Colombia, Costa Rica and Nicaragua, in Asia, such as Vietnam and Israel, and also in Australia (Le Bellec et al. 2006). In Taiwan, pitaya had been firstly introduced by Dutch colonists in 1600s, and pitaya cultivars with higher yield have been further introduced from South America and Vietnam in recent decades (Hsu 2004). Due to the progress in breeding and cultivation techniques in Taiwan, pitaya is becoming an important fruit crop in the domestic and foreign markets. Among the three major species cultivated in Taiwan, *H. undatus* plant produces oblong rosy-red fruit with white pulps, whereas the ovoid fruit of *H. costaricensis* and the oblong fruit of *H. polyrhizus* plants contain purple-red and purple-red pulps, respectively. The first two *Hylocereus* species are also the most widely cultivated pitaya species in the world (Le Bellec et al. 2006). Pitaya fruit is noticed with

high nutrients and antioxidants, for example, betalains including betanin, phyllocactin, and hylocerenin which only present in few families of plants (Stafford 1994; Stintzing et al. 2002; Wybraniec and Mizrahi 2002; Stintzing et al. 2005). Therefore, pitaya is the best source of betalains among the fruits in Taiwan.

Based on the record by Taiwan's Agriculture and Food Agency in 2012, the planting area and yield of pitaya in Taiwan were about 979 hectares and 23,550 tons, respectively. Compared to other fruit crops, there are not many pests and pathogens causing serious problems on pitaya, so the application of chemicals is only infrequent during the growth season. However, since the cultivation of pitaya in commercial plantations started in earnest, symptoms of soft rot, lesions and spots in stems and fruits which were caused by bacteria and fungi were observed (Valencia-Botin et al. 2013). During a disease survey of of pitaya in Taiwan, some plants were observed with systemic mild mottling on the stems, and these were found to be infected by a potexvirus, *Cactus virus X* (CVX) (Liou et al. 2001; Liou et al. 2004a, 2004b). In addition, another two potexviruses *Zygocactus virus X* (ZyVX) and Pitaya virus X (PiVX), were identified later in Taiwan (Mao 2008). Consequently, for a promising and important fruit crop as pitaya, study in diseases of pitaya is essential. Because of the similar features of Cactaceae plants, there is high possibility that cactus-infecting viruses will infect pitaya just like CVX and ZyVX did. For this reason, we collected the literatures of plant viruses which have been reported to infect cactus plants. The objective of this article is to provide information of viral diseases of pitaya and other Cactaceae plants so as to help further study of pitaya-infecting viruses and propose the control strategy.

PLANT VIRUSES FOUND IN THE CACTACEAE PLANTS

The reported cactus-infecting viruses

The family Cactaceae comprises between 122 and 200 genera consisting of 1600 to 2000 species, and nearly all members have spiny and succulent stems, found especially in the semi-arid regions of Latin America (Mizrahi et al. 1997; Le Bellec et al. 2006). Since the study of Amelunxen on cactus virus, several viruses with elongated particles similar to *Potato virus X* (PVX) have been found in wild and cultivated cactus plants (Giri and Chessin 1975a). More than 40 species in the family Cactaceae have been reported to be infected by these elongated viruses (Koenig et al. 2004). Up to now, at least five different genera of plant viruses, including *Carlavirus*, *Carmovirus*, *Potexvirus*, *Tobamovirus* and *Tospovirus*, have been identified in Cactaceae plants.

In the late 1950s, several reports about cactus-infecting elongated viruses were published in German (Amelunxen 1955a, 1955b, 1958). Brandes and Bercks (1962) isolated a virus (B1 isolate) from *Zygocactus* sp. which was morphologically and serologically similar to Amelunxen's cactus virus, and they proposed the name *Cactus virus X* (CVX) for all elongated cactus viruses similar to PVX (Brandes and Bercks 1962). Plese and Milicic (1966) compared the host reactions of B1 isolate from *Zygocactus* sp. to a K11 isolate from *Schlumbergera bridgesii* and four isolates from *Opuntia* spp. in Yugoslavia, and all these so-called CVX isolates displayed different virulence in the tested plants (Plese and Milicic 1966). Milicic et al. (1966) found all CVX isolates were morphologically similar but serologically different, and described that the *Zygocactus* isolate B1 and the four isolates from *Opuntia* spp. were serologically closely related, whereas the *Schlumbergera* isolate K11 and another isolate CC10 from an *Opuntia* plant in the U.S.A. were found to be only distantly related serologically to other five CVX

isolates. Therefore, Milicic et al. raised a question whether these three CVX isolates, B1, K11 and CC10, should be considered as separate viruses (Milicic et al. 1966). This question has not been answered until the article of Koenig et al. who published the sequence information of B1, K11 and CC10 isolates in 2004. According to the results of sequence comparison, the B1 isolate from *Zygocactus* sp., the K11 isolate from *S. bridgesii,* and the CC10 isolate from *Opuntia* sp. should be regarded as distinct virus species of the genus *Potexvirus* for which the names *Zygocactus virus X* (ZyVX), *Schlumbergera virus X* (SchVX) and *Opuntia virus X* (OpVX) are proposed (Koenig et al. 2004). In the same year, the complete nucleotide sequence of CVX of a Hu strain was published by Liou et al. at National Taiwan University isolated from pitaya plants (*H. undatus*) with systemic mild mottling symptoms (Liou et al. 2004a).

In addition to the above mentioned potexviruses which possess a single-stranded positive-sense RNA genome encapsidated into flexuous filamentous particles, Casper and Brandes identified a virus from a symptomless Christmas cactus (*Zygocactus* X *Schlumbergera* hybrid) and named it Zygocactus virus (ZyV) which had different properties from CVX (Casper and Brandes 1969). Giri and Chessin reported another potexvirus isolated from Christmas cactus (Giri and Chessin 1972) and designated the virus as *Zygocactus virus X* (ZyVX) which differed from the B1 isolate and Casper's Zygocactus virus (ZyV) in host range test (Giri and Chessin, 1975a). This virus was found distantly related serologically to PVX and CVX but not related to ZyV (Giri and Chessin, 1975a). However, there is no further information or sequence about Giri's ZyVX or Casper's ZyV; the species status of these two potexviruses has not yet been determined. Therefore, there are four formal species of the genus *Potexvirus*, *Cactus virus X* (CVX), *Opuntia virus X* (OpVX), *Schlumbergera virus X* (SchVX) and *Zygocactus virus X* (ZyVX), reported to be cactus-infecting viruses so far.

Some workers pointed out that one difficulty in working with the cactus viruses has been the lack of external symptoms in the virus-infected cactus plants (Bercks 1971). However, a strain of CVX was identified to infect California barrel cactus plants (*Ferrocactus acanthodes*) in a cactus forest in San Bernardino County, California in 1974. The virus-infected plants showed distorted areoles, malformed spines, necrosis and systemic mottle (Attathom et al. 1978). In Taiwan, a strain of CVX infected Indian fig opuntia (*Oputina ficus-indica*) and resulted in poor growth and inconspicuous chlorotic mottling (Chen and Tzeng, 1996). Recently, single and mixed infection of CVX, OpVX, SchVX and ZyVX in three different cactus plants, *Opuntia tuna*, *Hylocereus undatus* and *Schlumbergera truncate*, showing chlorotic spots and mosaic symptoms were reported in Brazil (Duarte et al. 2008). Consequently, the outcome of virus-infected cactus plant depends on the combination of plant and virus as well as the environment.

Until now, there are four cactus-infecting tobamoviruses described which have rod-shaped particles containing a single-stranded positive-sense RNA genome (Sammons and Chessin 1961; Giri and Chessin 1975b; Min et al. 2006; Kim et al. 2012). *Sammons's Opuntia virus* (SOV) was the first reported tobamovirus isolated from *Opuntia engelmannii* in Arizona in the United States (Sammons and Chessin 1961). Although the amino acid composition of the capsid protein (CP) of SOV has been reported (Gibbs 1977), no nucleotide sequence of this virus is available so far. A severe strain of *Tobacco mosaic virus* (TMV) was found and isolated from the Beavertail cactus (*Opuntia basilaris*) grown in the wild of Arizona (Giri and Chessin 1975b). The antiserum prepared against the purified virus showed a positive reaction with TMV common strain.

However, the result of indicator plant assay indicated this virus is a new strain of TMV, and is tentatively named the Beavertail Cactus strain of TMV (Giri and Chessin 1975b). In 2001, *Cactus mild mottle virus* (CMMoV), a cactus-infecting tobamovirus, was isolated from diseased moon cactus (*Gymnocalycium mihanovichii*) which was grafted onto *Hylocereus trigonus* in Korea (Min et al. 2006). The CMMoV-infected cactus showed very mild mosaic and its rootstock revealed ring-type mottling along the stem. Western blot analysis showed that the virus was unrelated to SOV (Min et al. 2006). The complete genome sequence of CMMoV was determined and phylogenetic analysis of the viral replicases and MP indicated that CMMoV is closely related to cucurbit-infecting tobamoviruses, while the CMMoV CP is more closely related to brassica- and solanaceous infecting tobamoviruses (Min et al. 2009). Recently another new tobamovirus, *Rattail cactus necrosis-associated virus* (RCNaV), was identified in rattail cactus (*Aporocactus flagelliformis*) plants showing necrosis symptoms and the complete genome sequenced was determined (Kim et al. 2012). Phylogenetic analysis suggests that RCNaV could be clustered in a new subgroup, cactaceae-infecting tobamoviruses, with CMMoV (Kim et al. 2012).

Another cactus-infecting virus with flexuous filamentous particles is *Cactus virus 2* (CV-2) which was first reported by Brandes and Wetter (1959), belongs to the genus *Carlavirus* and is grouped into aphid-borne carlaviruses (Adams et al. 2004). However, no further information or sequence about CV-2 has been reported.

The first and only isometric virus isolated from the family Cactaceae is *Saguaro cactus virus* (SgCV) which belongs to the genus *Carmovirus* and is the first virus to be found in saguaro cactus (*Carnegiea gigantea*) in Arizona (Milbrath and Nelson 1972). According to a cactus virus survey, 52 (40%) out of 131 sampled saguaros were infected with SgCV. It was suggested that the cactus is a latent carrier of SgCV therefore the widespread virus has not been noticed for a long time (Milbrath and Nelson 1972).

Besides positive-sense RNA viruses, two species of the genus *Tospovirus* with negative-sense RNA genomes, *Impatiens necrotic spot virus* (INSV) and *Tomato spotted wilt virus* (TSWV), have been reported in cactus plants (Hausbeck and Gildow 1991; Blockley and Mumford 2001). During a survey of greenhouse ornamentals in Pennsylvania, TSWV was detected in samples of the Thanksgiving cactus (*Schlumbergera truncata*) which were symptomless or showed mild symptoms of sunken chlorotic lesions, dark green spots, chlorosis, necrosis, and distortion (Hausbeck and Gildow 1991). The possible role of *S. truncata* as a reservoir for TSWV should be considered when developing the disease management strategies. In the United Kingdom, prickly pear cactus (*Opuntia microdasys* var. *albata*) with necrotic spots or lesions was proved to be infected by INSV (Blockley and Mumford 2001).

According to the above literatures, there are four potexviruses (CVX, OpVX, SchVX and ZyVX), four tobamoviruses (SOV, TMV, CMMoV and RCNaV), one carlavirus (SV-2), one carmovirus (SgCV), and two tospoviruses (TSWV and INSV) have been reported to infect cactus plants. Both potexviruses and tobamoviruses had much more information than the other three virus groups. Interestingly, most of the cactus-infecting viruses are only sap transmitted without vector except for thrips-transmited TSWV and INSV, and potentially aphid-transmitted SV-2. Among these cactus-infecting viruses, CVX is the most frequently reported and widely spread. However, the importance of other viruses may be observed when more virus surveys of the cactus plants are conducted as in Brazil (Duarte et al. 2008).

Viruses identified in pitaya (*Hylocereus* spp.)

Pitaya (*Hylocereus* spp.) is a popular fruit crop in Taiwan, and is becoming an important exporting agricultural product. *H. undatus* is the first pitaya species commercially cultivated in Taiwan, but the planting areas of other species such as *H. costaricensis* and *H. polyrhizus* as well as the new hybrid cultivars increase rapidly. Pitaya is mainly propagated by cutting, so if mother plant is infected with viruses, disease can be spread easily. Therefore, viral diseases of pitaya are becoming important issues. The genus *Potexvirus* is the only viral genus reported to infect pitaya (*H. undatus*) so far, including four virus species of *Cactus virus X* (CVX) (Liou et al. 2001; Lioa et al. 2003; Liou et al. 2004a, 2004b; Lu, 2007), *Zygocactus virus X* (ZyVX) (Mao, 2008), Pitaya virus X (PiVX) (Mao, 2008) and *Schlumbergera virus X* (SchVX) (Duarte et al. 2008). SchVX was only detected in pitaya plants which was mix infected with ZyVX according to a field survey in Brazil (Duarte et al. 2008). The rest of pitaya-infecting viruses were studied by the researchers in Taiwan. The first published pitaya-infecting virus is CVX by Liou et al. in 2001. The three pitaya isolates of CVX reported in Taiwan are CVX-Hu, first isolated in the Kawnshi area (Liou et al. 2001; Liou et al. 2004b), CVX-EL1 from Ilan (Lioa et al. 2003), and CVX-NTU from the experimental farm at Nation Taiwan University (Lu 2007). The antisera against CVX-EL1 and CVX-Hu had been produced (Lioa et al. 2003; Liou et al. 2004b), and used in virus survey which revealed high frequency of CVX infection on pitaya (Lioa et al. 2003; Lu 2007). The complete nucleotide sequence of CVX-Hu strain was first published by Liou et al. derived from pitaya with systemic mild mottling symptoms (Liou et al. 2004a) and the complete sequence of CVX-NTU was also determined (Lu 2007).

During a survey of CVX in pitaya, a sample reacted positively to CVX antiserum, and produced a 150-bp nonspecific fragment without the expected CVX cDNA fragments (Lu 2007). Based on our studies, this fragment was derived from *Zygocactus virus X* (ZyVX), and a virus isolate was obtained, characterized, and named as ZyVX-P39 (Mao et al. 2007; Mao 2008). The complete sequence of ZyVX-P39 was determined and compared to other potexviruses (Mao 2008). This is the first report of ZyVX in pitaya and also the first record of ZyVX in Taiwan (Mao et al. 2007).

Another pitaya sample which was also collected from the same CVX survey produced a 300-bp unexpected RT-PCR product besides the CVX cDNA fragment (Lu 2007). The sequencing results indicated that this cDNA fragment was not derived from CVX or ZyVX, but it had high sequence identity with many potexviruses (Lu, 2007). Subsequently, the unknown potexvirus was isolated, characterized, and the complete sequence of the P37 isolate was determined and analyzed (Mao 2008; Li 2010). According to the species demarcating criteria of the genus *Potexvirus*, P37 isolate should be a new pitaya-infecting potexvirus and thus designated as Pitaya virus X (PiVX) (Mao 2008). The results of phylogenetic analyses on full-length genome of ZVX-P39, PiVX-P37 and other published potexviruses demonstrated that all Cactaceae-infecting potexviruses belong to the same cluster (Mao 2008; Li 2010).

In addition, a multiplex RT-PCR method was developed for field survey of CVX, PiVX and ZVX in pitaya plants in Taiwan (Mao 2008). However, the total RNA extraction from mucilaginous pitaya plants is difficult and time-consuming. To solve this problem, a rapid detection method, named magnetic nanoparticle-capture RT-PCR (MNC RT-PCR), was developed recently (Kuo 2015). Moreover, the antiserum against the CP of PiVX was generated for subsequent studies and field survey (Li 2010). To further study the properties of PiVX-P37, the full-length cDNA clone with a 35S promoter was constructed

and its biological activity was proved by inoculating plasmid DNA to *Chenopodium amaranticolor* and *C. quinoa* plants (Li 2010).

Although symptoms of pitaya caused by potexviruses have been described (Liou et al. 2001; Lioa et al. 2003; Li 2010), it is impossible to differentiate the virus species only by external symptoms; especially mixed infection appears very frequently (Figure 1). Moreover, the influence of virus infection on the growth of pitaya plants as well as the yield and quality of pitaya fruits is still unknown. This is question the most frequently asked by growers and need to be answered in the future.

Figure 1. Symptoms of pitaya (*Hylocereus undatus*) plants caused by potexviruses under natural field conditions. Pitaya infected by *Cactus virus X* (CVX) alone (left); pitaya mix-infected by CVX and *Zygocactus virus X* (ZyVX) (middle); pitaya mix-infected by CVX and Pitaya virus X (PiVX) (right).

CONCLUSION

Pitaya is mainly propagated by cutting, so if mother plant is infected with viruses, disease can be spread easily. Therefore, viral diseases of pitaya are becoming main issues. Even though pitaya is an important tropical fruit crop in many countries and the high virus incidence on pitaya plants, there are few studies on pitaya-infecting viruses. Because plants in the family Cactaceae have similar features, it is very likely that cactus-infecting viruses will infect pitaya. Most of the cactus-infecting viruses are only sap and grafting transmitted, so virus-free propagation materials are essential for controlling viral diseases. Since pitaya is becoming an important fruit crop in Taiwan,

the establishment of virus indexing system is strongly recommended. Both multiplex RT-PCR and MNC RT-PCR developed by our research team are convenient and rapid methods to detect individual potexviruses in pitaya and other cactus plants. These rapid and accurate detection methods can be used for field survey as well as the certification program of virus-free seedlings to control the viral diseases of pitaya.

REFERENCES

Adams, M.J., J.F., Antoniw, M. Bar-Joseph, A.A. Brunt, T. Candresse, G.D. Foster, G.P. Martelli, R.G. Milne, S.K. Zavriev, and C.M. Fauquet. 2004. The new plant virus family Flexiviridae and assessment of molecular criteria for species demarcation. Arch. Virol. 149:1045-1060.

Amelunxen, F. 1955a. Beobachtungen uber die Entwicklung der Eiweissspindeln bei Cactaceen. Protoplasma 45:164-172.

Amelunxen, F. 1955b. Uber die St rukturanalyse der Eiweissspindeln der Cactaceae. Protoplasma 45:228-240.

Amelunxen, F. 1958. Die Virus-Eiweibspindeln der. Kakteen. Darstellung, elektronenmikroskoskopische und biochemische Analyse dcs Virus. Protoplasma 49:140-178.

Attathom, S., L.G. Weathers, and D.J. Gumpf. 1978. Identification and characterization of a potexvirus from California barrel cactus. Phytopathology 68:14011406.

Bercks, R. 1971. *Cactus virus* X. CMI/AAB Descriptions of Plant Viruses No. 58. Kew Surrey, UK.

Blockley, A.L. and R.A. Mumford. 2001. Identification and isolation of *Impatiens necrotic spot virus* from prickly pear cactus (*Opuntia microdasys*). Plant Path. 50:805.

Brandes, J. and R. Bercks. 1962. Untersuchungen zur Identifizierung und Klassifizierung des Kakteen-X-Virus (*Cactus virus X*). Phytopath. Z. 46:291-300.

Brandes, J. and C. Wetter. 1959. Classification of elongated plant viruses on the basis of particle morphology. Virology 8:99-115.

Britton N.L. and J.N. Rose. 1963. *The Cactaceae: descriptions and illustrations of plants of the cactus family*, Vol. I and II, pp. 183–195. Dover Publications, Inc., New York, USA.

Casper, R. and J. Brandes. 1969. A new cactus virus. J. General Virol. 5:155-156.

Chen, M.J. and D.D.S Tzeng. 1996. Identification of Cactus X potexvirus in Taiwan and localization of its existence and multiplication in infected cells. Plant Path. Bull. 5:63-67.

Duarte, L.M.L., M.A.V. Alexandre, E.B. Rivas, R. Harakava, S.R. Galleti, and M.M. Barradas. 2008. Potexvirus diversity in cactaceae from São Paulo state in Brazil. J. Plant Path. 90:545-551.

Gibbs, A.J. 1977. Tobamovirus group. CMI/AAB *Descriptions of Plant Viruses* No. 184. Kew Surrey, UK.

Giri, L. and M. Chessin. 1972. Characterization of a virus isolated from Zygocactus. Phytopathology 62:1103 (Abstract).

Giri, L. and M. Chessin. 1975a. Zygocactus virus X. Phytopathologische Zeitschrift 83:40-48.

Giri, L. and M. Chessin. 1975b. A severe strain of Tobacco mosaic virus from cactus. Phytopathology 65:824-825.

Hausbeck, M.K. and F.E. Gildow. 1991. Report of *Tomato spotted wilt virus* on Thanksgiving cactus. Plant Dis. 75:215.

Hsu, W.T. 2004. Investigations on culture, growth habits and phenology in pitaya (*Hylocereus* spp.). M.S. thesis. National Taiwan Univ. (In Chineses).

Kim, N.R., J.S. Hong, Y.S Song, B.N. Chung, J.W. Park, and K.H. Ryu. 2012. The complete genome sequence of a member of a new species of tobamovirus (rattail cactus necrosis-associated virus) isolated from *Aporcactus flagelliformis*. Arch. Virol. 157:185-187.

Koenig, R., C.W.A. Pleij, S. Loss, W. Burgermeister, H. Aust, and J. Schiemann. 2004. Molecular characterisation of potexviruses isolated from three different genera in the family Cactaceae. Arch. Virol. 149:903-914.

Kuo, T.Y. 2015. Rapid detection method and magnetic nanoparticle therapy for pitaya-infecting potexviruses. Thesis of Master Program for Plant Medicine, National Taiwan Univ. (In Chinese).

Le Bellec, F., F. Vaillant, and E. Imbert. 2006. Pitahaya (*Hylocereus* spp.): a new fruit crop, a market with a future. Fruits 61:237-250.

Li, Y.S. 2010. Characterization, infectious clone construction and antiserum preparation of Pitaya virus X. M.S. thesis. National Taiwan Univ.

Liao, J.Y., C.A. Chang, C.R. Yan, and T.C. Deng. 2003. Detection and incidence of Cactus virus X on pitaya in Taiwan. Plant Path. Bull. 12:225-234. (In Chinese).

Liou, M.R., Y.R. Chen, and R.F. Liou. 2004a. Complete nucleotide sequence and genome organization of a *Cactus virus X* strain from *Hylocereus undatus* (Cactaceae). Arch. Virol. 149:1037-1043.

Liou, M.R., C.L. Hong, and R.F. Liou. 2004b. Charaterization of a *Cactus virus X* infecting *Hylocereus undatus* and its detection by DAS-ELISA. Plant Path. Bull. 13:27-34. (In Chinese).

Liou, M.R., C.L. Hong, and R.F. Liou. 2001. First Report of *Cactus virus X* on *Hylocereus undatus* (Cactaceae) in Taiwan. Plant Dis. 85:229.

Lu, Y.C. 2007. Characterization of a new *Cactus virus X* isolate from pitaya and the construction of its infectious cDNA clone. M.S. thesis. National Taiwan Univ. (In Chinese).

Mao, C.H. 2008. Molecular characterization and detection of new *Zygocactus virus X* and *Pitaya virus X* from pitaya. M.S. thesis. National Taiwan Univ. (In Chinese).

Mao, C.H., Y.C. Lu, and Y.C. Chang. 2007. Characterization of a new *Zygocactus virus X* isolate from pitaya and its field survey. Plant Path. Bull. 17:97-98. (Abstract) (In Chinese).

Milbrath, G.M. and M.R. Nelson. 1972. Isolation and characterization of a virus from saguaro cactus. Phytopathology 62:739-742.

Milicic, D., N. Plese, R. Bercks, J. Brandes, R. Casper, and M. Chessin. 1966. Vergleichende serologische und elektronenmikroskopische Untersuchungen an Isolaten des Kakteen-X-Virus. Phytopath. Z. 55:211-217.

Min, B.E., B.N. Chung, M.J. Kim, J.H. Ha, B.Y. Lee, and K.H. Ryu. 2006. *Cactus mild mottle virus* is a new cactus-infecting tobamovirus. Arch. Virol. 151:13-21.

Min, B.E., Y.S. Song, and K.H. Ryu. 2009. Complete sequence and genome structure of *Cactus mild mottle virus*. Arch. Virol. 154:1371-1374.

Mizrahi, Y., A. Nerd, and P.S. Nobel. 1997. Cacti as crops. Hort. Rev. 18:291-319.

Nelson, M.R. and J.H. Tremaine. 1975. Physiochemical and serological properties of a virus from saguaro cactus. Virology 65: 309-319.

Plese, N. and D. Milicic. 1966. Vergleichende Untersuchungen an Isolaten des Kakteen-X-Virus mit Testpflanzen. Phytopath. Z. 55:197-210.

Sammons, I.M. and M.Chessin. 1961. Cactus virus in the United States. Nature 191:517-518.

Stafford, H.A. 1994. Anthocyanins and betalains: evolution of the mutually exclusive pathways. Plant Sci. 101:91-98.

Stintzing, F.C., K.M. Herbach, M.R. Mosshammer, R. Carle, W.G. Yi, S. Sellappan, C.C. Akoh, R. Bunch, P. and Felker. 2005. Color, betalain pattern, and antioxidant properties of cactus pear (*Opuntia* spp.) clones. J. Agri. Food Chem. 53:442-451.

Stintzing, F.C., A. Schieber, and R. Carle. 2002. Betacyanins in fruits from red-purple pitaya, *Hylocereus polyrhizus* (Weber) Britton & Rose. Food Chem. 77:101-106.

Valencia-Botin, A.J., H. Kokubu, and Y.D. Ortiz-Hernandez. 2013. A brief overview on pitahaya (Hylocereus spp.) diseases. Aust. Plant Path. 42:437–440.

Wybraniec, S., and Mizrahi, Y. 2002. Fruit flesh betacyanin pigments in hylocereus cacti. J. Agr. Food Chem. 50:6086-6089.