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ABSTRACT

The emerging begomoviruses in the Sultanate of Oman, containing single-stranded circular DNA genome belongs to the family Geminiviridae are the phytopathogens transmitted by whitefly (*Bemisia tabaci* Genn.). Recently, Oman has been shown to be a sink of begomoviruses, resulted in significant yield losses in variety of Omani crops. The research on begomovirus has mainly involved the molecular characterization of the viruses, their phylogenetic analyses, infectivity's on host plants, DNA replication, transgenic resistance, promoter analysis and development of virus-based gene silencing vectors. This article mainly focused on the emerging begomovirus diseases in different crops, in the last 7 years in Oman and focused major future areas of begomovirus research that need more attention.

I. INTRODUCTION

Begomoviruses are either monopartite with a single genome (DNA-A) or bipartite (DNA-A and DNA-B) genome approximately 2.7kb in size, encapsidated in geminate particles (Fig.1). DNA-A encodes the proteins required for replication, transcription and encapsidation (Hanley-Bowdoin et al. 1999 and Rojas et al. 2005). And DNA-B encodes the proteins required for intra- and intercellular movement.

Begomoviruses (type species: Bean golden mosaic virus) are phytopathogens transmitted by whitefly, *Bemisia tabaci* Genn. belongs to the family Geminiviridae. Based on the genome organization, insect vector, and host range, the family Geminiviridae have been divided into four genera: Begomovirus, Mastrevirus, Curtovirus and Topocovirus (Khan and Akhtar 2014a, Brown et al. 2012). Different aspects of the Family Geminiviridae have been comprehensively reviewed earlier (Gutierrez 1999, Gutierrez 2000, Mansoor et al. 2003 and Jeske 2009). Begomoviruses are the largest group of the family Geminiviridae. They are major threat to large number of

dicotyledonous plants in tropical, sub-tropical and warm temperate regions (Nawaz-ul-Rehman et al. 2010).

The DNA-A and DNA-B components are arranged in two separate clusters of open reading frames (ORFs), separated by an intergenic region (common region, CR). The CR

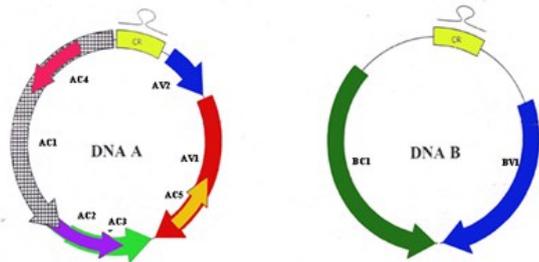


Fig.1. Typical Genome Organisation Of DNA-A and DNA-B of a bipartite Begomovirus

contains conserved sequences between both DNA components and it contains the origin of replication (Hanley-Bowdoin et al. 1999 and Rojas et al. 2005).

Based on complete nucleotide sequences of the DNA-A of bipartite and the complete single-component DNA of monopartite begomoviruses, the International Committee on the Taxonomy of Viruses (ICTV) has recommended a classification and scheme of nomenclature. In accordance with the ICTV species demarcation criterion for the genus Begomovirus is $\geq 91\%$ sequence identity for the complete DNA-A. The name of each virus include, the host plant, common symptoms and also reflect the year and location of collection (Fauquet et al. 2008, Fauquet et al. 2000). Viral infections trigger a series of defence responses in plants, manifested by specific degradation of the invading viral RNA into small fragments (siRNA), a response known as RNA-interference (RNAi). This defence response is conserved in many organisms and the components participating in this response share a high degree of homology. It is now believed that successful viral infection results only upon suppression of this defence response by specific viral proteins, known as RNAi suppressors. RNAi suppressor activities have been discovered in several begomoviral gene products (reviewed by Voinnet 2005). RNAi based resistance in transgenic tomato plants against Tomato yellow leaf curl virus-Oman (TYLCV-OM) along with its betasatellite were shown by Ammara et al. (2015).

Monopartite begomoviruses are mostly associated with one or more DNA beta satellite components (~1.4 kb in size). Two types of satellite DNAs (the alphasatellites and betasatellites) are known. The alphasatellites encode their own replication-associated protein and are believed to have originated from the nanoviruses. Whereas, on the other hand the betasatellites do not code for any replication-associated proteins and have a single ORF ($\beta C1$). The alpha- and betasatellites are helping in replication and often reduce the symptoms produced by the helper virus components (DNA-A and DNA-B) (Idris et al. 2011). Beta satellites are dependent on the DNA-A component for replication, encapsidation, and movement within plants (Bridson et al. 2006, Jose and Usha 2003 and Saunders et al. 2004).

Genetic resistance against plant viruses, if available in the germplasm, is considered to be the one of the most efficient ways to control viral infections. The genes conferring such resistance phenotypes can be transferred to cultivated varieties by breeding, often assisted by molecular markers. Against begomoviruses, very few resistance genes are known, the most important of them being the Ty series of genes available in wild tomato (*Solanum chilense*) against Tomato yellow leaf curl virus (TYLCV), a begomovirus infecting cultivated tomato, mainly in the Mediterranean countries. However, although the above gene and its alleles have been introgressed into commercial tomato cultivars for TYLCV resistance, convenient molecular tools for its widespread use are not yet available (Verlaan et al. 2011). Transgenic resistance against begomoviruses has been achieved in a number of plants using a variety of strategies. The strategies include expressing proteins of viral origin (CP, Rep and its derivatives and TrAP), expressing nonviral proteins having an anti-viral effect (toxic protein dianthin, antibodies raised against viral CP), DNA interference involving defective viral DNAs and RNAi against viral transcripts (reviewed by Vanderschuren et al. 2007). More recently, novel resistance approaches, such as expressing the GroEL chaperon protein of bacterial endosymbionts, which protects the begomoviral particle from degradation within the vector whiteflies, in the phloem tissue of tomato plants, have resulted in the viral particles getting trapped within the plants, thereby resulting in resistance (Akad et al. 2007). The emerging threat of the viruses belonging to the genus Begomovirus has been extensively addressed earlier by Varma and Malathi (2003). The extent of yield loss caused by some geminiviruses has been estimated by Dasgupta et al. (2003) to be as high as 100%. Up to 96% loss in yield has been reported by Bendi yellow vein mosaic virus (Pun and Doraiswamy 1999). In legumes, the yield losses have been estimated to be approximately \$300 million per year taking blackgram, mungbean and soybean together (Varma and Malathi 2003).

Oman has been a network for begomoviruses from diverse geographic origins (Khan et al. 2014b). With their proclivity to do recombination, a major mechanism for evolution of these viruses, and because Oman (and many other Arabian countries) is a major focal point for trade and travel by air and sea, the possibility of transmission is increasing (Khan et al. 2013a). The virus generates new, virulent strains through recombination. This region of the Middle East has extensive trade/travel links with the rest of the world, so the chances of this virus spreading are high. The substantial revenue losses and socio economic improvement warrants efforts to study and devise long-term strategies for management of the devastating viruses to provide sustainable and profitable outcome, without major inputs of insecticides. Whitefly transmitted leaf curl is one of the most devastating viral disease of cultivated crops like tomato, sweet pepper, chilli, squash, melon, cucumber and other important

vegetable crops in Oman (Khan et al. 2012b). Yield losses of these crops can vary from 0 – 100% depending on management practices (such as using shade houses, pesticides to avoid incidence of whitely vectors) which were recorded in Nizwa, Al-Batinah, Musandam, Bureimi, Salalah and Interior regions of Oman.

Within the last 7 years, a few number of begomoviruses have been investigated in Oman, encompassing many economically important root crops and vegetables. More recently, research in Oman are focusing on only molecular characterization of these viruses which just a preliminary step to develop a strategy to fight against these important plant viruses and subsequently their resistance. Hence, more work needs to be undertaken like, functions of viral proteins, the molecular interactions between begomoviruses and their hosts, natural and experimental, virus-derived transgenic resistance and associated satellites, to gain insights on the molecular cross-talk, which might throw light on newer and hitherto unexplored aspects of their biology and reveal novel approaches for their control and management. Considering the importance of begomoviruses to Oman agriculture, the salient research achievements related to begomoviruses, carried out in Oman in the last approximately 7 years, have been reviewed here and the possible directions in which future efforts could be channeled to manage these viral diseases more effectively have been pointed out.

II. BEGOMOVIRUS RESEARCH IN OMAN

Only the preliminary research work has been carried out, such as, sequence analysis, phylogeny and infectivity on the begomoviruses in Oman. Till date, begomoviruses have been reported from at 6 different groups of crop in Oman (Table.1). This review collates the research work performed in Oman, focusing on the above aspects. They are described in the alphabetical order of their major hosts below.

Table.1 Molecular studies of important begomoviruses in Oman

Name of the virus	Acronym	Strain found in Oman	Crop infected	Symptoms produced	Reference(s)
<i>East African cassava mosaic Zanzibar virus</i>	<i>EACMZV</i>	<i>EACMZV</i>	Cassava	symptoms typical of CMD	Khan et al. (2013a)
<i>Chili leaf curl virus</i>	<i>ChLCV</i>	<i>ChLCV-OM</i>	Tomato, Pepper	yellowing, leaf curling, stunting and shortening of internodes	Khan et al. (2013a)
<i>Cotton leaf curl Gezira virus</i>	<i>CLCuGV</i>	<i>CLCuGV</i>	Papaya	Leaves with severe curling, vein darkening, and vein thickening	Khan et al. (2012a)
<i>Okra leaf curl Oman virus</i>	<i>OLCOMV</i>	<i>OLCOMV</i>	Okra	Vein clearing, yellowing, reduced leaf lamina and fruit size	Akhtar et al. (2013b)
<i>Tomato leaf curl Sudan virus</i>	<i>ToLCSDV</i>	<i>ToLCSDV-OM</i>	Tomato	Vein clearing, stunting; infection at the seedling stage can make plants sterile	Khan et al. (2014c)
<i>Tomato leaf curl Al-Batinah virus</i>	ToLCABV	ToLCABV	Tomato	Vein clearing, stunting; infection at the seedling stage can make plants sterile	Khan et al. (2013b)
<i>Tomato leaf curl Barka virus</i>	ToLCBrV	ToLCBrV	Tomato	Vein clearing, stunting; infection at the seedling stage can make plants sterile	Khan et al. (2013b)
<i>Tomato leaf curl Oman virus</i>	<i>ToLCOMV</i>	<i>ToLCOMV</i>	Tomato	Vein clearing, stunting; infection at the seedling stage can make plants sterile	Idris et al. (2012)
<i>Tomato yellow leaf curl virus</i>	<i>TYLCV</i>	<i>TYLCV-OM</i>	Tomato	yellowing, leaf curling, stunting and shortening of internodes	Khan et al. (2008)
<i>Watermelon chlorotic stunt virus</i>	<i>WmCSV</i>	<i>WmCSV</i>	Squash	leaf curling, yellowing and stunting	Khan et al. (2012b)

2.1 CASSAVA

Oman is growing cassava on a small scale for the local consumption, unlike other Arabian countries. In Oman, wilayat A'Seeb, Muscat, cassava plants were identified with the symptoms Cassava Mosaic Disease. East African cassava mosaic Zanzibar virus (EACMZV), was isolated from symptomatic plants, which was previously occur only in Zanzibar and Kenya (Khan et al. 2013a).

2.2 CUCURBITS

Squash (*Cucurbita moschata*) collected from an experimental field in Oman was found to show the typical symptoms of begomoviruses such as yellowing, leaf curling and stunting. Watermelon chlorotic stunt virus (WmCSV) is a bipartite begomovirus infects and causes economic losses to plants of the family Cucurbitaceae, across the Middle East. From these symptomatic plant leaves, DNA was extracted, cloned and sequenced. It showed 97.6-99.9% nucleotide sequence identity with DNA-A and 93-98% identity with DNA-B component of WmCSV isolates (Khan et al. 2012c). Agro-inoculation of these clones in *Nicotiana benthamiana* showed the symptoms fifteen days post inoculation (Khan et al. 2012c). This was the first report of bipartite begomovirus identified in Oman showing the highest levels of sequence identity to a WmCSV isolate of Iran.

2.3 OKRA

In symptomatic plants of okra from Barka, Al-Batinah region of Oman, a begomovirus and associated beta and alpha-satellites were identified. Okra leaf curl disease (OLCD) is caused by begomovirus-satellite complexes. After sequence analysis, they showed to be a new begomovirus and very similar to Cotton leaf curl Gezira virus (CLCuGeV). With CLCuGeV isolate it showed <85% nts sequence identity and named as Okra leaf curl Oman virus (OLCOMV) (Khan et al. 2013b). Further analysis revealed that the OLCOMV is a recombination of CLCuGeV isolates with Tomato yellow leaf curl virus-Oman (TYLCV-OM). An unique alpha- and a betasatellite were also identified in the same plant sample. However, although the betasatellite showed to be of African origin and the alphasatellite showed to be a South Asian origin. New naturally occurring recombinant begomovirus variants (total five; >96% shared nt identity) were reported in tomato plants from Gezira, Sudan, and found to be isolates of the ToLCSDV Shambat strain (Mohammed et. al. 2014). This is the first report of a satellite DNA complex from okra in Oman (Khan et al. 2013b).

2.4 PAPAYA

The severely infected leaf curl diseases Papaya were collected in the Quriyat region of Oman. Papaya is one of the important fruit crop grown in Oman with the production of 20 tonnes per year. Total nucleic acids extracted from symptomatic leaves, cloned and sequenced. Sequence analysis showed the Pap-2 isolate have 83.3 to 95.1% sequence identity to CLCuGeV sequences. According to ICTV, the virus identified in Oman is a variant of CLCuGeV. CLCuGeV is a begomovirus of African origin which is

different from the Middle East and Asia origin begomoviruses (Khan et al. 2012a).

The recombination of CLCuGeV with Tomato yellow leaf curl virus isolate from Iran (Pierre et al. 2010), the association of CLCuGeV with cotton in Pakistan (Muhammad et al. 2011) and hollyhock in Jordan (GU945265) revealed, this virus has migrated into the Middle East and Asia from Africa. The identified CLCuGeV in Oman shows the widespread presence of this virus species (Khan et al. 2012a).

2.5 PEPPER

A virus, Chili leaf curl virus (ChLCV) and associated betasatellites were found associated with tomato and pepper diseases in vegetable grown areas of Oman which is previously only identified in the Indian subcontinent. Total 19 full-length begomovirus and 8 betasatellite clones were sequenced. Pepper is grown in Oman in a large scale for local consumption. Sequence analysis to sequences available in the databases showed the highest levels of nucleotide sequence identity (88.0-91.1%) to isolates of the "Pakistan" strain of ChLCV (ChLCV-PK), suggesting a new strain (ChLCV-OM). The betasatellite sequences showed high levels of identity to a previously identified Oman isolate tomato leaf curl betasatellite (ToLCB). ChLCV-OM is first identified in *Capsicum* in Oman (Khan et al. 2013c). Agroinoculation studies showed the symptoms induced by the virus in the presence of the betasatellite was enhanced.

2.6 TOMATO

Symptomatic leaves were collected, total nucleic acids were extracted, full length viral genome were cloned and sequenced. During the winter season, tomato is cultivated in a large scale in Al-Batinah region in Oman. Sequence analysis showed that the virus from Oman was closely related to TYLCV-IR at 91% nt identity which is a monopartite begomoviral species from Iran. Oman isolate has been designated TYLCV-OM and is considered an isolate of TYLCV-IR. The sequence analysis of satellite DNA showed that it shared 88.5% similarity with DNA beta molecules from Pakistan and this is the first report of a satDNA beta associated with the TYLCV species. The TYLCV-Om and associated alfa and beta satellite reported, thus represent a begomovirus-complex at the Asian-Middle East (Khan et al. 2008). This alphasatellite shared 90% nucleotide identity to an unusual DNA-2-type *Ageratum* yellow vein Singapore alphasatellite (AYVSGA). ToLCOMV was found to have a recombinant of TYLCV-OM and Papaya leaf curl virus from the Indian subcontinent.

Begomoviruses are major threat for tomato crops in Oman. Out of 15 clones, the sequence analysis, seven were shown to be Tomato yellow leaf curl virus strain Oman (TYLCV-OM); three, Chili leaf curl virus strain Oman (ChLCV-OM); and one, Tomato leaf curl Oman virus (ToLCOMV). Four sequences showed to be a new species and named as Tomato leaf curl Al-Batinah virus (ToLCABV). ToLCABV shown to be a recombinant of ChLCV-OM and ToLCOMV (Khan et al. 2014b). Agro-inoculation studies showed, ToLCABV interacted in planta with ToLCB (Khan et al. 2013c).

Agroinoculation studies with different possible combinations of ToLCOMV, TYLCV-OM, ToLCB and AYVSGA showed attenuation of begomovirus-betasatellite symptoms by the unusual class of alphasatellites, which suggest that some DNA-2 alphasatellites encode a pathogenicity determinant that may modulate begomovirus-betasatellite infection by reducing betasatellite DNA accumulation. (Idris et al. 2011)

III. CONCLUSION AND FUTURE PROSPECTS

Still there is a urgent need to explore the diversity of begomoviruses occurring in Oman, to identify the predominant virus(es) infecting economically important edible and medicinal plants, their molecular characterization. Till date, only few number of begomoviruses have been reported from Oman (Table.1). The prevalence of these viruses probably in part due to its warm tropical climate supporting the year-round survival of the whitefly vector and different types of crop cultivation. Begomoviruses cause serious diseases in many crop plants, which is undoubtedly a primary reason for the strong research interest they have generated. An interesting aspect of Oman begomoviruses is their overlapping host range (for example, Cotton leaf curl Gezira virus (CLCGV) was found associated with Papaya). One of the major factors responsible for this overlapping host range could be the polyphagous nature of the vector whitefly and the mixed cropping systems prevalent in the country. An expected consequence of this scenario would be recombination and one would assume that there would be many more reports of such recombination events between begomoviruses than what has actually been reported, once bioinformatic tools for their detection are widely applied by the researchers. This also requires extra vigilance on the part of researchers to anticipate and deal with synergistic effects of multiple infections and/or recombinations, resulting in the emergence of unexpectedly virulent forms of begomoviruses, as experienced in the case of cassava begomoviruses in the African continent in the last decade (Khan et al. 2013a).

One recent example is the characterization of a new resistance trait in pepper against the two begomoviruses, Pepper golden mosaic virus and Pepper huasteco yellow vein virus in Mexico (Garcia-Neria and Rivera-Bustamante 2011). Since RNAi suppression by the begomoviruses is likely to play a major role in such synergisms, it necessitates a careful look into the mechanisms of RNAi suppression by begomoviruses prevalent in Oman. Recently the emergence of more a number of betasatellites and alphasatellites associated with begomoviruses in Oman is also remarkable (Khan et al. 2013c). The interdependence of the satellites and their helper begomoviruses is thus an area of tremendous importance for investigation and promises to be both scientifically fascinating as well as amply rewarding by opening up new methods of disease control, a challenge for begomoviral diseases in Oman. The strategies to combat begomoviruses infections in various crop plants are enlarging. The reports of success in controlling begomoviruses with virus-derived and other transgenes are encouraging. Well-characterized resistance genes are of immense importance in controlling begomoviruses.

However, as mentioned earlier, only a few such genes have been characterized to a level where they can be used for breeding begomovirus resistance and can be used to introgress into popular crop varieties. Hence, more work needs to be done to search for natural begomovirus-resistant wild varieties of crop plants, against begomoviruses, and, when found, to characterize the resistance traits.

The interaction of begomoviruses with the vector whiteflies, a pivotal step in the begomoviruses spread in the fields, also needs to be carefully looked at. These, as well as the exciting developments on plant-virus interactions, promise many more avenues of begomovirus control opening up in the near future. Due to begomoviral infections in the Sultanate of Oman, these need to be immediately deployed to assure crop protection against the huge economic losses incurred.

REFERENCES

- [I] Akad F, Eybishtz A, Edelbaum D, Gorovits R, Dar-Issa O, Iraki Czosnek H (2007) Making a friend from a foe: expressing a *Grc* gene from whitefly *Bemisia tabaci* in the phloem of tomato *pla*. confers resistance to tomato yellow leaf curl virus. *Arch. Virol.* 1: 1323–1339.
- [II] Akhtar JK, Sohail A (2014a) Plant Virus–Host Interaction, Molecular Approaches and Viral Evolution, Engineering crops for resistance to geminiviruses. 291–323.
- [III] Ammara UE, Mansoor S, Saeed M, Amin J, Briddon RW, Al-Sadi AM (2015) RNA interference-based resistance in transgenic tomato plants against Tomato yellow leaf curl virus-Oman (TYLCV-OM) and its associated betasatellite. *Virol J.* 12(1):38.
- [IV] Briddon RW, Stanley J (2006) Subviral agents associated with plant single-stranded DNA viruses. *Virology* 344:198-210.
- [V] Brown JK, Fauquet C, Briddon RW, Zerbini FM, Moriones Navas-Castillo J (2012) Family Geminiviridae. In: King AMQ, Ada AJ, Carstens EB, Lekfowitz EJ (eds) *Virus taxonomy. ninth report the international committee on taxonomy of viruses.* Elsevier Academic Press, San Diego. pp 351–373.
- [VI] Fauquet CM, Briddon RW, Brown JK, Moriones E, Stanley J, Zerbini M, Zhou X (2008). *Geminivirus strain demarcation and nomenclature.* *Archives of Virology.* 153:783–821.
- [VII] Dasgupta I, Malathi VG, Mukherjee SK (2003) *Gene engineering for virus resistance.* *Curr. Sci.* 84 341–354.
- [VIII] Fauquet CM, Bisaro DM, Briddon RW, Brown J, Harrison L Rybicki EP, Stenger DC, Fauquet CM, Maxwell DP, Gronenborn Stanley J (2000) Revised proposal for naming geminiviruses. *Arch Virol.* 145 1743–1761.
- [IX] Garcia-Neria MA, Rivera-Bustamante RF (2011) Characterization of geminivirus resistance in an accession of *Capsicum chinense* Jacq. *Mol. Plant Microbe Interactions* 24 172–182.
- [X] Gutierrez C (1999) *Geminivirus DNA replication.* *Cell Mol. L Sci.* 56 313–329.
- [XI] Gutierrez C (2000) *Geminiviruses and the plant cell cycle.* *Mol. Biol.* 43 763–772.

- [XII] Hanley-Bowdoin L, Settlage SB, Orozco BM, Nagar S, Robertson D (1999) Geminiviruses: Models for plant DNA replication, transcription and cell cycle regulation *Crit. Rev. Plant Sci* 18: 71-106.
- [XIII] Idris AM, Shahid MS, Briddon RW, Khan AJ, Zhu JK, Brown JK (2011). An unusual alpha satellite associated with monopartite begomoviruses attenuates symptoms and reduces beta satellite accumulation. *J Gen Virol* 706-17.
- [XIV] Jeske H (2009) Geminiviruses. *Curr. Top. Microbiol Immunol* 331:185–226.
- [XV] Jose J, Usha R (2003) Bendi yellow vein mosaic disease in India is caused by association of a DNA β satellite with a begomovirus. *Virology* 305: 310-317.
- [XVI] Khan AJ, Akhtar S, A.Al-Shihi A, Al-Hinai FM (2012a) Identification of Cotton leaf curl Gezira virus in Papaya in Oman. *Disease Notes* 96(11) 1704.
- [XVII] Khan AJ, Akhtar S, Al-Matrushy AM, Fauquet CM, Briddon RW (2013a) Introduction of East African cassava mosaic Zanzibar virus to Oman harks back to "Zanzibar, the capital of Oman" *Virus Genes* 46(1):195-8.
- [XVIII] Khan AJ, Akhtar S, Briddon RW, Um-Ammara, Al-Matrooshi A, Mansoor S (2012b) Complete Nucleotide Sequence of Watermelon Chlorotic Stunt Virus Originating from Oman *Viruses* 4: 1169-1181.
- [XIX] Khan AJ, Idris AM, Al-Saady NA, Al-Mahruki MS, Al-Subhi AM, Brown JK (2008) A divergent isolate of Tomato yellow leaf curl virus from Oman with an associated DNA beta satellite: an evolutionary link between Asian and the Middle Eastern virus-satellite complexes *Virus Genes* 36(1):169-76.
- [XX] Khan AJ, Mansoor S, Briddon RW (2014b) Oman: a case for a sink of begomoviruses of geographically diverse origins. *Trends Plant Sci* 19(2):67-70.
- [XXI] Khan AJ, Akhtar S, Singh AK, Al-Shehi AA, Al-Matrushy AM, Ammara U, Briddon RW (2013b) Recent evolution of a novel begomovirus causing tomato leaf curl disease in the Al-Batinah region of Oman. *Arch Virol* 159(3):445-55.
- [XXII] Khan AJ, Akhtar S, Al-Zaidi AM, Singh AK, Briddon RW. (2013c) Genetic diversity and distribution of a distinct strain of Chili leaf curl virus and associated beta satellite infecting tomato and pepper in Oman *Virus Res* 177(1):87-97.
- [XXIII] Mansoor S, Briddon RW, Zafar Y, Stanley J (2003) Geminivirus disease complexes: an emerging threat. *Trends Plant Sci.* 8 128-134.
- [XXIV] Mohammed A Al-Saleh, Ibrahim M Al-Shahwan, Judith K Brown, Ali M Idris (2014c) Molecular characterization of a naturally occurring intraspecific recombinant begomovirus with close relatives widespread in southern Arabia. *Virology* 11: 103.
- [XXV] Muhammad N, Tahir IA, Briddon RW, Shahid M (2011) The Merging of Two Dynasties—Identification of an African Cotton Leaf Curl Disease-Associated Begomovirus with Cotton in Pakistan. *PLoS One* 6(5): e20366.
- [XXVI] Nawaz-ul-Rehman MS, Nawaz-ul-Rehman, Nahid N, Mansoor S, Briddon RW, Fauquet CM (2010) Post-transcriptional gene silencing suppressor activity of two non-pathogenic alpha satellites associated with a begomovirus. *Virology* 405: 2, 300–308.
- [XVII] Pierre L, Darren PM, Gordon H, Philippe L, Alistair JAG, Sandra M, Francisco L, Adérito M, Jean-Michel L, Arvind V, Jahangir H (2010) The Spread of Tomato Yellow Leaf Curl Virus from the Middle East to the World. *PLoS Pathog* 6:e1001164.
- [XXVIII] Pun KB, Doraiswamy S (1999) Effect of age of okra plants susceptibility to Okra yellow vein mosaic virus. *Indian J Virol* 15 57–58
- [XXIX] Rojas MR, Hagen C, Lucas WJ, Gilbertson R L (2005) Exploiting chinks in the plant's armor: Evolution and emergence of geminiviruses. *Ann. Rev. Phytopath* 43:361-94.
- [XXX] Saunders K, Norman A, Gucciardo S, Stanley J (2004) The DNA β -satellite component associated with ageratum yellow vein disease encodes an essential pathogenicity protein (β C1) *Virology* 324:37-47.
- [XXXI] Stanley J (2003) Revision of taxonomic criteria for species demarcation in the family Geminiviridae, and an updated list of begomovirus species. *Arch. Virol* 148 405–421.
- [XXXII] Vanderschuren H, Stupak M, Futterer J, Gruissem W, Zhang P (2007) Engineering resistance towards geminiviruses – review and perspectives. *Plant Biotech J* 5 207–220.
- [XXXIII] Varma A, Malathi VG (2003) Emerging geminivirus problems: A serious threat to crop production. *Ann Appl Biol* 142: 145-164.
- [XXXIV] Verlaan MG, Szinay D, Hutton SF, de Jong H, Kromelink R, Visser RGF, Scott JW, Bai Y (2011) Chromosomal rearrangements between tomato and *Solanum chilense* hamper mapping and breeding of the TYLCV resistance gene Ty-1. *Plant J* 68 1093–1103.
- [XXXV] Voinnet O (2005) Induction and suppression of RNA silencing: Insights from viral infections. *Nat Rev Genet* 6 206–221.
