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# Comparative *in silico* Analysis of Coat Protein (CP) of *Tomato Leaf Curl Virus* (ToLCV) and *Tomato Yellow Leaf Curl Virus* (TYLCV) and their Molecular Docking with GroEL Protein of *Hamiltonella* an Endosymbiont of their Vector *Bemisia Tabaci*

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**Abstract**

Begomoviruses belonging to the family *Geminiviridae* are one of the devastating group of DNA viruses causing huge losses to agricultural crop production. Begomoviruses are characterized by the presence of monopartite or bipartite genome and genetic material being the single stranded circular DNA with overlapping open reading frames (ORFs). *Tomato leaf curl virus* (ToLCV) and *tomato yellow leaf curl virus* (TYLCV) are the major begomoviruses that infect tomato crop. These viruses are transmitted by whitefly, *Bemisia tabaci* in a circulative and persistent manner. The successful infection of these viruses on healthy plant mainly rely on the interaction between the viral proteins and whitefly proteins. Coat Protein (CP) of both the viruses are crucial for the successful transmission of viruses from infected plant to a healthy plant. During the process of transmission, CP interacts with the whitefly proteins in the digestive tract, midgut, haemolymph and salivary glands. The amino acid sequences of TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL are retrieved from NCBI database and subjected to pair wise alignment. The alignment results of TYLCV-CP and ToLCV-CP revealed that the proteins have very few differences. Homology modelling was carried out using SWISS-MODEL and the obtained models are subjected to validation on PDB sum web server. Ramachandran plot and Ramachandran plot statistics confirmed that the modelled structures are reliable. The modelled structures are used for protein-protein docking studies on H-dock online tool. Docking between TYLCV-CP and *Hamiltonella* GroEL and ToLCV-CP and *Hamiltonella* GroEL showed that the interaction between CP of TYLCV and *Hamiltonella* GroEL is stronger compared to the interaction of ToLCV-CP and *Hamiltonella* GroEL. Although, the number of amino acids of TYLCV-CP involved in interaction with *Hamiltonella* GroEL are lesser, the frequency at which amino acids of TYLCV-CP involved in interaction is higher than that of ToLCV-CP, indicating that CP of TYLCV interacts strongly with *Hamiltonella* GroEL in comparison with CP of ToLCV.

*Keywords* : Tomato leaf curl virus, Tomato yellow leaf curl virus, Hamiltonella GroEL

Begomovirus belongs to the family *Geminiviridae* and is the largest genus among viruses (Gutierrez, 1999). They majorly infect dicotyledonous crops causing huge crop losses in the tropical and sub-tropical region (Rana *et al*., 2012). The group of virus has led to the severe outbreak of many diseases such as cassava mosaic disease in Africa, cotton leaf curl disease in India, tomato leaf curl disease (ToLCD), tomato yellow leaf curl disease (TYLCD), yellow vein disease of okra, papaya leaf curl disease and mung bean yellow mosaic disease (Varma and Malathi, 2003). In addition to these crops,



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begomoviruses also infect chilly, beans, cucurbits, cabbage and potato (Inoue-Nagata *et al*., 2016; Kumar *et al*., 2011 and Leke *et al*., 2015). Begomoviruses either have a monopartite genome (DNA-A) or a bipartite genomes (DNA-A and DNA-B) with circular single stranded DNA (ssDNA) as the genetic material that encode the proteins that are required for replication, movement (intracellular and intercellular), transmission and pathogenesis (Hanley-Bowdoin *et al*., 2013). Bipartite begomoviruses possess two genomes, *i.e.,* ~2.7 kb of DNA-A and ~2.6 kb of DNA-B. Monopartite begomoviruses are characterized by the presence of only DNA-A component of ~2.7 kb. DNA-A and DNA-B components have partially overlapping open reading frames (ORFs) which are reported to be present in a bidirectional manner (Fontenelle *et al*., 2007 and Kheyr-Pour *et al*., 2000).

Sweet potato white fly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) transmits begomoviruses from infected plant to a healthy plant when it feeds on the phloem sap of the healthy plant. The vector, *B. tabaci* transmits begomoviruses in a persistent and circulative manner (Hogenhout *et al*., 2008). When *B. tabaci* feeds on the begomovirus infected plant, the insect ingests the begomoviral particles into the alimentary canal while ingesting the phloem sap. This is followed by subsequent movement of begomoviral particles into the filter chamber and midgut region. In the midgut region, begomovirus particles cross the gut membrane and enter into the haemolymph. Further, virion particles reach the salivary glands, pierce them and settle in salivary duct. Upon feeding on a healthy plant in the following feeding cycle, the acquired begomoviral particles are egested out into the healthy plant along with the saliva (Czosnek *et al*., 2002 and Ghanim *et al*., 2001).

During the movement of begomovirus in the whitefly vector, the viral particles interact with whitefly proteins facilitating the transport from the digestive tract to the haemolymph followed by movement from haemolymph to salivary glands. (Rana *et al*., 2016). Once the viral particles are in the salivary glands of whitefly, they are translocated into the salivary duct which are egested into the healthy plants when the whitefly feeds on them (Gray, 1996). Proteomics and transcriptomics studies have revealed the interaction of various whitefly proteins with the coat protein (CP) of the begomovirus. According to Briddon *et al*. (1990) and Noris *et al*. (1998), CP of the begomovirus is the only viral protein required for insect mediated transmission of the virus. Earlier studies by Noris *et al*. (1998) has shown that altering the amino acid sequence of the CP results in change in vector specificity and ability of the vector to transmit the virus.

Rana *et al*. (2016) have reported the role of *B. tabaci* midgut protein (MGP) in transmission of tomato leaf curl virus (ToLCV) by carrying out *in vitro* pull down assay, dot blot assay and yeast two hybrid assay using ToLCV-CP as bait. Some of the interactions between the virus and the whitefly reduces the spread of viral transmission. *B. tabaci* heat shock protein 70 (HSP70) interacts with CP of *tomato yellow leaf curl virus* (TYLCV) leading to the inhibition of virus transmission (Gotz *et al*., 2012). Saurav *et al*. (2019) have confirmed the interaction of *B. tabaci* thioredoxin-like protein (TLP) with the CP of ToLCV by carrying out *in vitro* pull down experiments and dot blot assays. However, the exact role of TLP to be involved in virus transmission or inhibition is yet to be investigated. Similarly, many of the whitefly proteins either promote begomoviral transmission or reduce the viral transmission such as peptidoglycan recognition protein (PGRP) (Wang *et al*., 2016), cyclophilin B (Kanakala & Ghanim, 2016), GroEL of the endosymbionts *Hamiltonella* and *Arseonophonus* (Morin *et al*., 1999; Rana *et al*., 2012), tumorous imaginal disc (TID) (Zhao *et al*., 2020) interact with the CP of begomoviruses. All these reports show that CP of the begomovirus is responsible for circulative and persistent transmission of the virus via its vector.

Considering the importance of the CP from the earlier studies, we have carried out *in silico* comparison of the CP of TYLCV and ToLCV. The amino acid sequences of the CP of both TYLCV

and ToLCV are collected, followed by homology modelling for the prediction of 3D structure of the protein. The predicted 3D structure of the protein was used for molecular docking with GroEL of the whitefly endosymbiont.

## Material and Methods

### Collection of Amino Acid Sequences of TYLCV-CP, ToLCV-CP and the *Hamiltonella* GroEL Proteins

The amino acid sequences of CP of both TYLCV and ToLCV are collected from NCBI (https://www.ncbi.nlm.nih.gov/). The CP of the TYLCV carrying the accession number AXR75906.1 was retrieved. Similarly, the CP of ToLCV carrying the accession number BAP27993.1 was also retrieved. The amino acid sequence of the Hamiltonella GroEL was also retrieved from NCBI database with the accession number AFQ62604.1.

### Pair Wise Alignment of TYLCV-CP and ToLCV-CP

The collected sequences are subjected to pair wise alignment using Needleman-Wunsch algorithm (https://www.ebi.ac.uk/Tools/psa/emboss_needle/).

### Homology Modelling of TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL Proteins

The retrieved amino acid sequences of TYLCV-CP and ToLCV-CP are used for the prediction of the three dimensional structure of the proteins on swiss-model (https://swissmodel.expasy.org/). CP of the geminivirus determined by electron cryo-microscopy with global model quality estimation (GMQE) score of 0.55 and identity *per cent* of 74.51 was used as the template for the prediction of 3D structure of ToLCV-CP. GMQE score ranges from 0 to 1 and higher the value better the reliability of the predicted structure. To predict the 3D structure of TYLCV-CP, near atomic resolution structure of a plant geminivirus determined by electron cryo-microscopy with the GMQE score of 0.54 and identity per cent of 81.46 was used as template. 3D structure of *Hamiltonella* GroEL was also predicted in a similar way using GroEL of *Xanthomonas oryzae pv. oryzae* as template, which have GMQE value of 0.83 and the identity per cent of 73.90. All the structures are saved in PDB format.

### Validation of Predicted Protein Structure

Based on the geometry, geometry and the solvent potential of the protein model, the SWISS-MODEL web server automatically calculates the Qualitative Model Energy Analysis (QMEAN) score. The SWISS-MODEL also provides the Z-score which are compared with the expected value for any structure. The 3D structure of the proteins generated by SWISS-MODEL was checked for the quality using PROCHECK. This is done by uploading the .pdb file format obtained from SWISS-MODEL to PDBsum webserver. This provides the Ramachandran plot as well as the Ramachandran plot statistics. Ramachandran plot is used to assess the quality of the modelled protein and the Ramachandran plot statistics shows the total number of amino acid residues present in favourable, allowed and disallowed regions.

### Molecular Docking

The molecular docking studies were carried out using an online tool, H-dock (Yan *et al*., 2020). The 3D structures generated by homology modelling on SWISS-MODEL were used for docking studies. TYLCV-CP was docked with *Hamiltonella* GroEL, similarly, ToLCV-CP was also docked with *Hamiltonella* GroEL. 10 different conformation were generated from docking tool and were ranked according to their binding energies.

## Results and Discussion

### Pair Wise Alignment of TYLCV-CP and ToLCV-CP

The amino acid sequences of TYLCV-CP and ToLCV-CP retrieved from NCBI were used for pair wise alignment using Needleman-Wunsch algorithm. The alignment date is represented in Fig. 1.

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MSKRPGDIIISTPVSKVRRRLNFDSPYSTRAAVPIVQGTNKRRSWTYRPM
|:|||.|||||.|.||||||||||:||..||.|||.:.| |.::||.|||
MAKRPADIIISIPASKVRRRLNFDNPYGARAVVPIARVT-KAKAWTNRPM

YRKPRIYRMYRSPDVPRGCEGPCKVQSYEQRDDIKHTGIVRCVS------
.||||:|||||||||||||||||||:|.|        .||||
NRKPRMYRMYRSPDVPRGCEGPCKVQSFESR--------ARCVSYWQSHV

---DVTRGSGITHRVGKRFCVKSIYFLGKVWMDENIKKQNHTNQVMFFLV
   |||||:|:||||||||||||:|.|||:|||||||.:||||.||||||
VLVDVTRGTGLTHRVGKRFCVKSVYVLGKIWMDENIKTKNHTNSVMFFLV

RDRRPYGSSPMDFGQVFNMFDNEPSTATVKNDLRDRFQVMRKFHATVIGG
|||||.| ||.|||:||||||||||||||..|||:||:||:||||.||
RDRRPTG-SPQDFGEVFNMFDNEPSTATVKNMHRDRYQVLRKWHATVTGG

PSGMKEQALVKRFFKINSHVTYNHQEAAKYENHTENALLLYMACTHASNP
....:|||||::|.::|::|.||.|||.||||||||||:||||||||||
TYASREQALVRKFVRVNNYVVYNQQEAGKYENHTENALMLYMACTHASNP

VYATMKIRIYFYDSISN
||||:||||||||::|
VYATLKIRIYFYDSVTN
```

Fig. 1 : Pair wise alignment of amino acid sequences of TYLCV-CP and ToLCV-CP.
"|" indicates conserved residue; "-" indicates gap; "." Indicates mismatch; ":" indicates substitutions

**Homology Modelling**

3D structures of TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL were built using SWISS-MODEL. The GMQE score and QMEAN values of TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL are 0.74 and -2.66, 0.71 and -2.40 and 0.82 and -0.90, respectively. The GMQE score and QMEAN values of all the modelled structures indicate that the modelled structures are reliable and have good quality (Benkert *et al*., 2009).

**Structure Validation of Modelled Protein**

The predicted local similarity to target against the predicted 3D structure of TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL is represented in the Fig. 2A, 2B and 2C, respectively. The value of most of the residues is more than 0.6, indicating that the local quality estimates of the residues of the predicted models are good. According to the reports of Oduselu *et al*. (2019), the residues having the value of less than 0.6 are considered to be of poor quality. The modelled structures of TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL lie within the range of other protein structures in protein data bank (PDB) indicating the reliability of the predicted models (Fig. 2D, 2E and 2F).

Further validation was caried out by uploading the obtained models (.pdb) to PDbsum web server. Ramachandran plot (Fig. 3A, B, C) and Rama chandran plot statistics were obtained from the server. According to Ramachandran plot statistics, the model predicted for TYLCV-CP had 88.7 per cent in the most favoured regions, 10.8 per cent in the additional allowed regions, 0.5 per cent in the generously allowed region and 0 per cent in disallowed region (Fig. 3D). The model predicted for ToLCV-CP had 91.4 per cent of residues in the most favoured regions, 7.6 per cent in the additional allowed

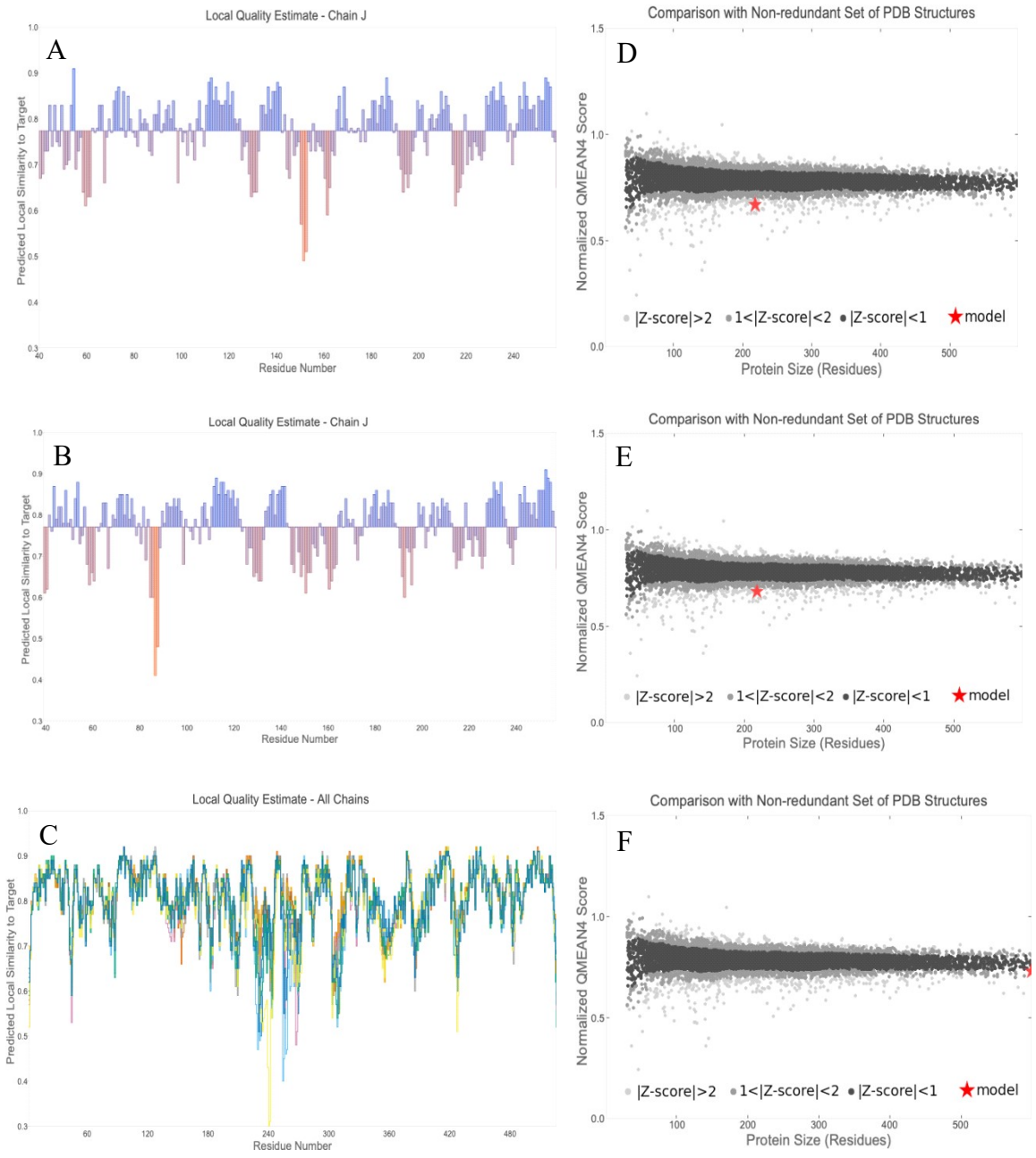
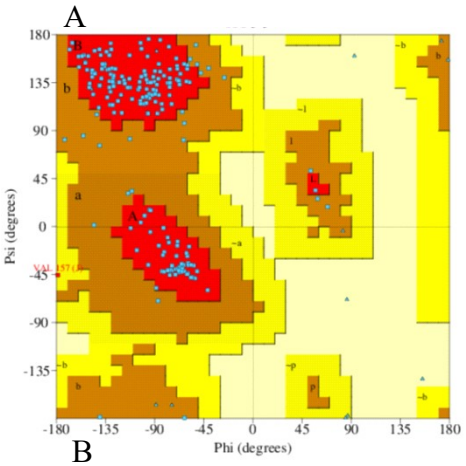



Fig. 2 : Structure validation of modelled TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL. A, B, C – local quality estimate of the residues of the predicted TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL; D, E, F - comparison of the predicted structures of TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL with nonredundant set of PDB structures

regions, 1 per cent in the generously allowed region and 0 per cent in disallowed region (Fig. 3E). For the model predicted for *Hamiltonella* GroEL, 91.2 per cent of residues in the most favoured regions, 6.6 percent in the additional allowed regions, 1.1 per cent in the generously allowed region and 1 per cent in disallowed region (Fig. 3F). These results validate that the predicted structures are good models (Oduselu *et al*., 2019).

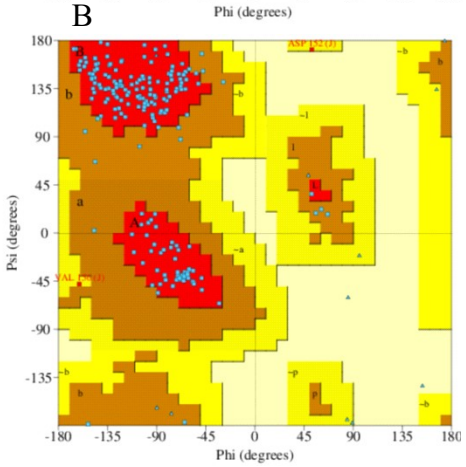
## Docking of TYLCV-CP and ToLCV-CP with *Hamiltonella* GroEL

The validated models of TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL obtained from SWISS-MODEL



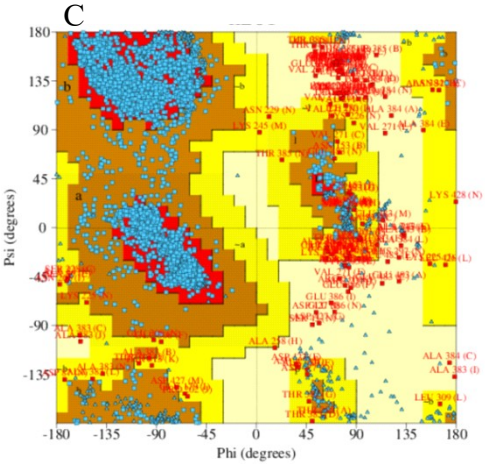

D

| | | No. of residues | %-tage |
|---|---|---|---|
| Most favoured regions | [A,B,L] | 173 | 88.7%* |
| Additional allowed regions | [a,b,l,p] | 21 | 10.8% |
| Generously allowed regions | [~a,~b,~l,~p] | 1 | 0.5% |
| Disallowed regions | [XX] | 0 | 0.0% |
| Non-glycine and non-proline residues | | 195 | 100.0% |
| End-residues (excl. Gly and Pro) | | 2 | |
| Glycine residues | | 12 | |
| Proline residues | | 10 | |
| Total number of residues | | 219 | |




E

| | | No. of residues | %-tage |
|---|---|---|---|
| Most favoured regions | [A,B,L] | 180 | 91.4% |
| Additional allowed regions | [a,b,l,p] | 15 | 7.6% |
| Generously allowed regions | [~a,~b,~l,~p] | 2 | 1.0% |
| Disallowed regions | [XX] | 0 | 0.0% |
| Non-glycine and non-proline residues | | 197 | 100.0% |
| End-residues (excl. Gly and Pro) | | 2 | |
| Glycine residues | | 11 | |
| Proline residues | | 9 | |
| Total number of residues | | 219 | |




F

| | | No. of residues | %-tage |
|---|---|---|---|
| Most favoured regions | [A,B,L] | 5925 | 91.2% |
| Additional allowed regions | [a,b,l,p] | 431 | 6.6% |
| Generously allowed regions | [~a,~b,~l,~p] | 73 | 1.1% |
| Disallowed regions | [XX] | 67 | 1.0%* |
| Non-glycine and non-proline residues | | 6496 | 100.0% |
| End-residues (excl. Gly and Pro) | | 28 | |
| Glycine residues | | 672 | |
| Proline residues | | 154 | |
| Total number of residues | | 7350 | |

Fig 3. Structure validation using Ramachandran plot and Ramachandran plot statistics.
A, B, C – Ramachandran plots of TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL; D, E, F – Ramachandran plot statistics of TYLCV-CP, ToLCV-CP and *Hamiltonella* GroEL

were used for docking. TYLCV-CP and ToLCV-CP were docked with *Hamiltonella* GroEL, separately, using an online tool, H-dock. The ToLCV-CP and TYLCV-CP docked with *Hamiltonella* GroEL are represented in the Fig. 4A and Fig. 4B. H-dock tool also lists the amino acid residues that are involved in protein-protein interaction. Table 1 and 2 lists out the amino acids involved during the interaction of

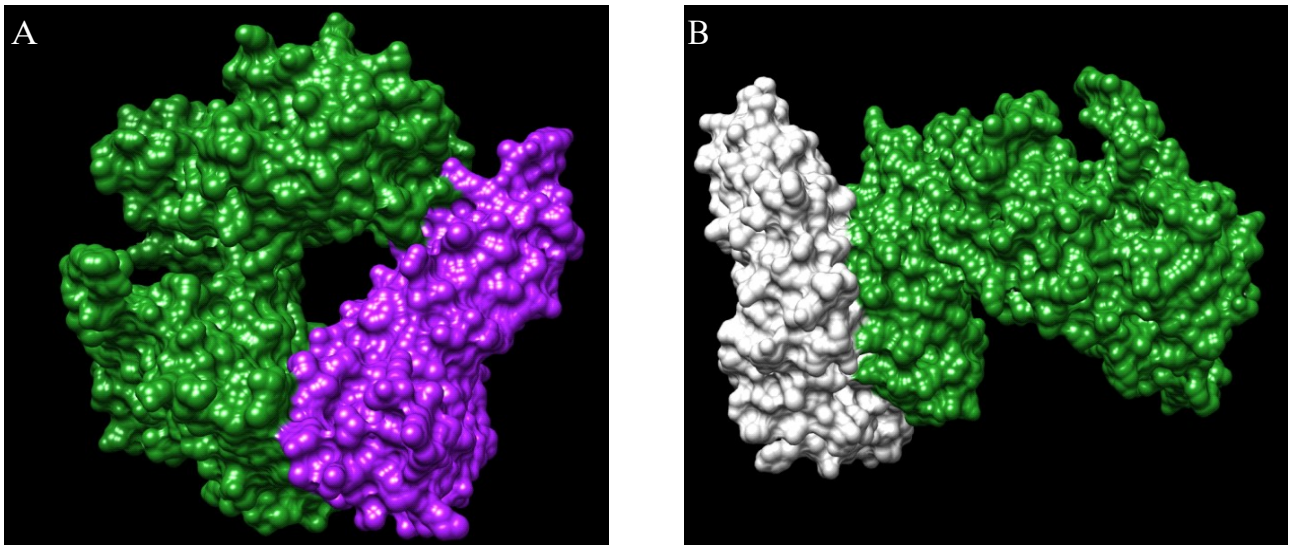



Fig. 4 : Docking of ToLCV-CP with *Hamiltonella* GroEL (A) and TYLCV-CP with *Hamiltonella* GroEL (B). Green colour structure - *Hamiltonella* GroEL; Purple colour structure – ToLCV-CP; grey colour structure – TYLCV-CP

TABLE 1

Amino acids involved in interaction between ToLCV-CP and *Hamiltonella* GroEL

| Amino acids of TYLCV-CP | Position of TYLCV-CP amino acids | *Hamiltonella* GroEL amino acids | Position of *Hamiltonella* GroEL amino acids |
|---|---|---|---|
| Pro | 63 | Asp | 283, 316, 361 |
| Asp | 64 | Lys | 286, 297, 311, 343, |
| Arg | 67, 142, 144, 182, 203 | Ala | 287, 293, 299, 356 |
| Gly | 68 | Gln | 290, 348, 351, 352 |
| Tyr | 116 | Ile | 294, 301, 305, 342 |
| Gln | 179 | Gly | 298, 306 |
| Val | 180 | Val | 300 |
| Met | 181 | Ser | 302, 340, 344, 358 |
| Lys | 183, 202, 206 | Met | 307 |
| Phe | 184, 204, 205 | Glu | 308, 315, 338, 347,355 |
| His | 185, 210 | Thr | 313, 341, 357 |
| Ala | 186 | Arg | 345, 353, 362 |
| Thr | 187 | Leu | 365 |
| Leu | 200 | | |
| Ile | 207 | | |
| Asn | 208 | | |
| Ser | 209 | | |
| Glu | 226 | | |

TABLE 2

Amino acids involved in interaction between TYLCV-CP and *Hamiltonella* GroEL

| ToLCV-CP amino acids | Position of ToLCV-CP amino acids | *Hamiltonella* GroEL amino acids | Position of *Hamiltonella* GroEL amino acids |
|---|---|---|---|
| Pro | 63 | Asp | 283, 316, 361 |
| Asp | 64 | Lys | 286, 297, 311, 343 |
| Arg | 67, 203 | Ala | 287, 293, 299 |
| Gly | 68 | Gln | 290, 348, 351, 352 |
| Tyr | 116 | Ile | 294, 301, 305, 342, |
| Gln | 179 | Gly | 298, 306 |
| Val | 180 | Val | 300 |
| Met | 181 | Ser | 302, 340, 344, 358 |
| Lys | 183 | Met | 307 |
| Phe | 184 | Glu | 308, 315, 338 |
| His | 185 | Thr | 313, 341, 357 |
| Ala | 186 | Arg | 345, 353, 362 |
| Thr | 187 | Glu | 347, 355 |
| Leu | 200 | Ala | 356 |
| Phe | 204, 205 | Leu | 365 |
| Ile | 207 | | |
| Asn | 208 | | |
| Ser | 209 | | |
| His | 210 | | |
| Glu | 226 | | |

ToLCV-CP with *Hamiltonella* GroEL and TYLCV-CP with *Hamiltonella* GroEL, respectively. The interaction between TYLCV-CP protein and *Hamiltonella* GroEL is stronger in comparison with the interaction between ToLCV-CP and *Hamiltonella* GroEL. The number of amino acids of TYLCV-CP that are involved in interaction with *Hamiltonella* GroEL are more than that of ToLCV-CP. Earlier reports by Czosnek *et al*. (2017) supports our results that TYLCV-CP interacts with GroEL of *Hamiltonella*.

This study shows that there are similarities among the CP of TYLCV and ToLCV as shown by Needleman-Wunsch based pair wise alignment. Though there are similarities, the interaction of TYLCV-CP and ToLCV-CP with *Hamiltonella* GroEL studied by protein-protein docking shows differences in the way they interact with GroEL protein. GroEL proteins of many other whitefly endosymbionts such as, *Rickettsia* and *Arsenophonus* are reported to interact poorly with TYLCV-CP (Gottlieb *et al*., 2010). This ability of the begomoviruses, especially TYLCV-CP, to interact with various proteins of whitefly and its endosymbionts has made it one of the devastating disease on tomato leading to huge crop loss.

Molecular docking studies can be used to study the protein-ligand as well as protein-protein interactions. These studies can be performed to know how many/ what are the amino acids that are involved in interaction. Also, docking studies reveals how strongly the two molecules are interacting with each other. Further, docking studies can be exploited to know what are the whitefly proteins interacting with CP of

other group of viruses. This help us to understand the pathway that virus follows within a whitefly and will probably be helpful in understanding to prevent plant viral infection, leading to improved crop yield.

## References


Benkert, P., Kunzli, M. and Schwede, T., 2009, QMEAN server for protein model quality estimation. *Nucleic Acids Res.*, **37** : 510 - 514.

Briddon, R. W., Pinner, M. S., Stanley, J. and Markham, P. G., 1990, Geminivirus coat protein gene replacement alters insect specificity. *Virol.*, **177** (1) : 85 - 94.

Czosnek, H., Ghanim, M. and Ghanim, M., 2002, The circulative pathway of begomoviruses in the whitefly vector *Bemisia tabaci* - Insights from studies with *Tomato yellow leaf curl virus*. *Ann. Applied Biol.*, **140** (3) : 215 - 231.

Fontenelle, M. R., Luz, D. F., Gomes, A. P. S., Florentino, L. H., Zerbini, F. M. and Fontes, E. P. B., 2007, Functional analysis of the naturally recombinant DNA-A of the bipartite begomovirus *tomato chlorotic mottle virus. Virus Res.*, **126** (1 - 2) : 262 - 267.

Ghanim, M., Rosell, R. C., Campbell, L. R., Czosnek, H., Brown, J. K. and Ullman, D. E., 2001, Digestive, salivary and reproductive organs of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) B type. *J. Morphol.*, **248** (1) : 22 - 40.

Gotz, M., Popovski, S., Kollenberg, M., Gorovits, R., Brown, J. K., Cicero, J. M., Czosnek, H., Winter, S. and Ghanim, M., 2012, Implication of *Bemisia tabaci* Heat Shock Protein 70 in Begomovirus-Whitefly Interactions. *J. Virol.*, **86** (24) : 13241 - 13252.

Gottlieb, Y., Zchori-Fein, E., Mozes-Daube, N., Kontsedalov, S., Skaljac, M., Brumin, M., Sobol, I., Czosnek, H., Vavre, F., Fleury, F. and Ghanim, M., 2010, The Transmission efficiency of *tomato yellow leaf curl virus* by the whitefly *Bemisia tabaci* is correlated with the presence of a specific symbiotic bacterium species. *J. Virol.*, **84** (18) : 9310 - 9317.

Gray, S. M., 1996, Plant virus proteins involved in natural vector transmission. *Trends Microbiol.*, **4** (7) : 259 - 264.

Gutierrez, C., 1999, Geminivirus DNA replication. *Cell. Mol. Life Sci.*, **56** (3-4) : 313 - 329.

Hanley-Bowdoin, L., Bejarano, E. R., Robertson, D. and Mansoor, S., 2013, Geminiviruses: Masters at redirecting and reprogramming plant processes. *Nat. Rev. Microbiol,*, **11** (11) : 777 - 788.

Hogenhout, S. A., Ammar, E. D., Whitfield, A. E. and Redinbaugh, M. G., 2008, Insect vector interactions with persistently transmitted viruses. *Ann. Rev. Phytopathol.*, **46** (1) : 327 - 359.

Inoue-Nagata, A. K., Lima, M. F. and Gilbertson, R. L., 2016, A review of geminivirus diseases in vegetables and other crops in Brazil: Current status and approaches for management. *Hortic. Bras.*, **34** (1) : 8 - 18.

Kanakala, S. and Ghanim, M., 2016, Implication of the whitefly *Bemisia tabaci* Cyclophilin B protein in the transmission of *tomato yellow leaf curl virus*. *Front. Plant Sci.*, 7.

Kheyr-Pour, A., Bananej, K., Dafalla, G. A., Caciagli, P., Noris, E., Ahoonmanesh, A., Lecoq, H. and Gronenborn, B., 2000, *Watermelon chlorotic stunt virus* from the Sudan and Iran: Sequence comparisons and identification of a whitefly-transmission determinant. *Phytopathol.*, **90** (6) : 629 - 635.

Kumar, Y., Hallan, V. and Zaidi, A. A., 2011, *Chilli leaf curl Palampur virus* is a distinct begomo virus species associated with a betasatellite: C*hilli leaf curl Palampur begomovirus*. *Plant Pathol.*, **60** (6) : 1040 - 1047.

Leke, W. N., Mignouna, D. B., Brown, J. K. and Kvarnheden, A., 2015, Begomovirus disease complex: Emerging threat to vegetable production systems of West and Central Africa. *Agriculture & Food Security*, **4** (1) : 1.

Morin, S., Ghanim, M., Zeidan, M., Czosnek, H., Verbeek, M. and Van Den Heuvel, J. F. J. M., 1999, A GroEL homologue from endosymbiotic bacteria of the

whitefly *Bemisia tabaci* is implicated in the circulative transmission of *tomato yellow leaf curl virus*. *Virol.*, **256** (1) : 75 - 84.

Noris, E., Vaira, A. M., Caciagli, P., Masenga, V., Gronenborn, B. and Accotto, G. P., 1998, Amino acids in the capsid protein of *tomato yellow leaf curl virus* that are crucial for systemic infection, particle formation and insect transmission. *J. Virol.*, **72** (12) : 10050 - 10057.

Oduselu, G. O., Ajani, O. O., Ajamma, Y. U., Brors, B. and Adebiyi, E., 2019, Homology modelling and molecular docking studies of selected substituted benzo [*d*] imidazol-1-yl) methyl) benzimidamide scaffolds on *Plasmodium falciparum* adenylosuccinate lyase receptor. *Bioinform. Biol. Insights*, **13**.

Rana, V. S., Popli, S., Saurav, G. K., Raina, H. S., Chaubey, R., Ramamurthy, V. V. and Rajagopal, R., 2016, A *Bemisia tabaci* midgut protein interacts with begomoviruses and plays a role in virus transmission. *Cellular Microbiol.*, **18** (5) : 663 - 678.

Rana, V. S., Singh, S. T., Priya, N. G., Kumar, J. and Rajagopal, R., 2012, *Arsenophonus* GroEL Interacts with CLCuV and is localized in midgut and salivary gland of whitefly *B. Tabaci*. *PLoS ONE*, **7** (8) : e42168.

Saurav, G. K., Rana, V. S., Popli, S., Daimei, G. and Rajagopal, R., 2019, A thioredoxin-like protein of *Bemisia tabaci* interacts with coat protein of begomoviruses. *Virus Genes*, **55** (3) : 356 - 367.

Varma, A. and Malathi, V. G., 2003, Emerging geminivirus problems: A serious threat to crop production. *Ann. Applied Biol.*, **142** (2) : 145 - 164.

Wang, Z. Z., Shi, M., Huang, Y. C., Wang, X. W., Stanley, D. and Chen, X. X., 2016, A peptidogly can recognition protein acts in whitefly (*Bemisia tabaci*) immunity and involves in Begomovirus acquisition. *Sci. Rep.*, **6** (1) : 37806.

Yan, Y., Tao, H., He, J. and Huang, S. Y., 2020, The HDOCK server for integrated protein - protein docking. *Nat. Protoc.*, **15** (5) : 1829 - 1852.

Zhao, J., Guo, T., Lei, T., Zhu, J.C., Wang, F., Wang, X.W. and Liu, S. S., 2020, Proteomic analyses of whitefly-begomovirus interactions reveal the inhibitory role of tumorous imaginal discs in viral retention. *Front. Immunol.*, **11** : 1596.