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Co-infection of tomato brown rugose fruit virus and cucumber mosaic virus in tomato in Iran

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Abstract

During surveys conducted in several greenhouses in northwestern and southwestern Iran in the fall of 2021-2022, viral symptoms such as leaf mosaic, leaf deformation, and shoestring were observed in several tomato plants. Reverse transcription polymerase chain reaction (RT-PCR) was performed using specific primers to detect the tomato brown rugose fruit virus (ToBRFV). A 458 base pair fragment corresponding to a part of the coat protein gene was amplified in all symptomatic samples. Sequence blast analysis and multiple alignment of the sequenced isolate with those of the isolates obtained from GenBank revealed 99.76% nucleotide sequence identity with existing GenBank isolates. Phylogenetic analysis grouped ToBRFV isolates into three clades, the Iranian isolate (Jol-F-2022) fell into clade II. The possibility of mixed infection in the samples with important viruses was investigated using universal orthotospovirus primers, pepper mild mottle virus (PMMoV), tomato mosaic virus (ToMV), and cucumber mosaic virus (CMV)-specific primers. In five samples, CMV-specific primers amplified a 657-base pair fragment of the envelope protein gene, whereas no fragment was amplified with general primers for the orthotospovirus genus and specific primers for PMMoV, ToMV. Nucleotide blast (BLASTn) analysis revealed a nucleotide sequence identity around 95.13-98.85 between the Iranian CMV isolate and the corresponding sequences in the GenBank. Phylogenetic analysis based on the nucleotide sequences of the coat protein gene grouped the CMV isolates into three major groups, the Iranian isolate grouped with the Indian CMV isolates in the subgroup IB. Biological studies were performed by mechanical inoculation of an infected sample on Nicotiana rustica. The inoculated plants showed severe mosaic symptoms at 15 days post inoculation (dpi), and infection by both viruses was confirmed through RT-PCR using specific primers. This study presents the first report of mixed infection of tomato plants with ToBRFV and CMV in Iran.

Keywords: Phylogentic analysis, Tomato, Emerging threat, Subgroup IB, Mixed infection.

آلودگی همزمان گوجه فرنگی با ویروس چروکیدگی قهوهای میوه گوجه فرنگی و ویروس موزائیک خیار در ایران

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چکیدہ

طی بررسیهای انجام شده در چندین گلخانه شمال غرب و جنوب غرب ایران در پاییز ۱۴۰۰–۱۴۰۱، علائم ویروسی از جمله موزاییک برگ، تغییر شکل و بدشکلی برگ و بند کفشی در چندین گیاه گوجه فرنگی مشاهده شد. واکنش زنجیرهای پلیمراز رونویسی معکوس (RT-PCR) با استفاده از آغازگرهای اختصاصی برای تشخیص ویروس چروکیدگی قهوهای میوه گوجه فرنگی (ToBRFV) انجام شد. یک قطعه ۴۵۸ جفت بازی مربوط به بخشی از ژن پروتئین پوششی در تمام نمونههای علائمدار تکثیر شد. تجزیه و تحلیل بلاست توالی و هم ترازی چندگانه جدایه توالی یابی شده با جدایههای بهدست آمده از بانک ژن، شباهت توالی نوکلئوتیدی ۹۹٬۷۶ درصد را با جدایههای بانک ژن نشان داد. آنالیز فیلوژنتیک جدایههای ToBRFV را در سه کلاد گروهبندی کرد، جدایه ایرانی (Jol-F-2022) در کلاد دو قرار گرفت. احتمال آلودگی مخلوط نمونهها با ویروسهای مهم با استفاده از آغازگرهای عمومی ارتوتوسپوویروسها (orthotospovirus)، و آغازگرهای اختصاصی ویروس پیسک خفیف فلفل (PMMoV)، ویروس موزائیک گوجهفرنگی (ToMV) و ویروس موزاییک خیار (CMV) مورد بررسی قرار گرفت. در پنج نمونه، آغازگرهای اختصاصی CMV یک قطعه ۶۵۷ جفت بازی از ژن پروتئین پوششی را تکثیر کردند، در حالی که هیچ قطعهای با آغازگرهای عمومی برای جنس ارتوتوسپوویروس و آغازگرهای اختصاصی برای PMMoV وToMV تکثیر نشد. تجزیه و تحلیل بلاست نوکلئوتیدی (BLASTn) شباهت توالی نوکلئوتیدی را در حدود ۹۵٬۱۳–۹۸٬۸۵ بین جدایه CMV ایرانی و توالیهای مربوطه در بانک ژن نشان داد. آنالیز فیلوژنتیک بر اساس توالیهای نوکلئوتیدی ژن پروتئین پوششی، جدایههای CMV را در سه گروه اصلی گروه بندی کرد، جدایه ایرانی با جدایههای CMV هندی در زیرگروه IB گروه بندی شد. مطالعات بیولوژیکی با تلقیح مکانیکی یک نمونه آلوده روی توتون (Nicotiana rustica) انجام شد. گیاهان تلقیح شده علائم موزائیک شدیدی را در ۱۵ روز پس از تلقیح (dpi) نشان دادند و آلودگی توسط هر دو ویروس از طریق RT-PCR با استفاده از آغازگرهای اختصاصی تایید شد. این مطالعه اولین گزارش از آلودگی مخلوط گیاهان گوجه فرنگی با ToBRFV و CMV در ایران را ارائه می دهد.

كلمات كليدى: آناليز فيلوژنتيك، گوجه فرنگى، تهديد نوظهور، زير گروه IB، آلودگى مخلوط

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Introduction

Tomato plants hold significant importance for farmers in Iran and worldwide, serving as a valuable source of nutrition and income. However, tomatoes are highly susceptible to viruses that cause substantial yield and quality losses in tomato cultivation. The rise in the number of viruses affecting tomatoes can be attributed to the globalization of agricultural trade and rapid climate change (Gautam *et al.* 2013; Menzel *et al.* 2019). Moreover, the global trade of agricultural products plays a pivotal role in facilitating the spread of plant viruses and spread of newly introduced viruses (Jones & Naidu 2019).

Among the viruses infecting tomato crops, tomato brown rugose fruit virus (ToBRFV) has gained significant attention due to its rapid global spread. ToBRFV belongs to the Tobamovirus genus within the Virgaviridae family. It is characterized by rod-shaped particles and a single-stranded, positive-sense RNA genome contains four open reading frames (ORFs) (Luria et al. 2017). In the infected plants, ToBRFV causes a range of symptoms, including mild to severe mosaic patterns on leaves, as well as the development of yellow or green spots, deformations, green grooves, and irregular brown spots on fruits that these symptoms significantly impact the marketable yield of tomatoes (Luria et al. 2017). Since its initial outbreak in tomato crops in Jordan (Salem et al. 2016), ToBRFV has rapidly spread and become a significant global threat to tomato production. Moreover, the infection of ToBRFV in pepper plants is also increasing. The swift transboundary movement of the virus across countries within just seven years of its initial report in Jordan can be attributed to the global trade of infected fruits and seeds, as well as its mechanical transmissibility. In 2021, ToBRFV was detected in greenhouse-grown tomato plants in Iran (Ghorbani et al. 2021; Esmaeilzadeh & Koolivand 2022), and later that year, it was also found to infect pepper plants in greenhouses (Esmaeilzadeh & Koolivand 2022).

In recent years, there have been reports of mixed infections involving ToBRFV with other viruses such as *tomato spotted wilt virus* (TSWV), *pepino mosaic virus* (PepMV), resulting in more severe symptoms and reduced yields compared to single infections (Luria *et al.* 2017; Klap *et al.* 2020). Mixed-infections with two or more plant viruses are common in nature or fields. During these mixed-infections, various types of interactions occur, which can be either synergistic or antagonistic in nature (Syller *et al.* 2012; Klap *et al.* 2020). The majority of studies have indicated that southern tomato virus (STV), a widely spread viral disease with high incidences in tomato plants, does not induce apparent symptoms in tomatoes when infecting them alone. However, when STV interacts with other viruses like PepMV, CMV, PhCMoV or ToMV, it may induce the severe symptoms. In the case of ToBRFV, synergistic interactions have been observed, resulting in more severe symptoms on tomato fruits (Luria et al. 2017). Furthermore, mixed infections provide opportunities for viral recombination between coinfecting viruses, leading to the emergence of new variants or species and new viral disease problems in the future (Lukman et al. 2019). Mixed infection of ToBRFV and TSWV, ToBRFV and pepper mild mottle virus (PMMoV) have previously been reported from Iran (Esmaeilzadeh & Koolivand 2023). However, specific studies on the interaction between ToBRFV and CMV in mixed infections are currently lacking in the available literature. The objective of the present study is to investigate the occurrence of mixed infections of ToBRFV with members of the Orthotospovirus genus, PMMoV, ToMV and CMV in tomato plants under natural greenhouse conditions. Understanding the effect of these mixed infections is crucial for comprehending the interactions between these viruses and their impact on tomato plant health. Additionally, it sheds light on the potential risks associated with the emergence of novel viral variants through recombination events.

Material and methods

Sampling

In order to monitor the outbreaks of ToBRFV in various greenhouses across Iran following its worldwide emergence and recent report in the country, surveys were conducted during the growing seasons (September 2021 to February 2022). Tomato plants exhibiting viral symptoms, including mosaic and blistering on leaves, were sampled from multiple greenhouses located in the Southwest and Northwest regions of Iran including East Azerbaijan (Julfa), West Azerbaijan (Khoy), Zanjan and Hormozgan. In addition to ToBRFV-like symptoms, the collected samples showed symptoms such as shoestring and leaf deformation which are indicative of several different tomato viruses, suggesting the possibility of mixed infections. To investigate the presence of ToBRFV and other common tomato viruses, such as members of the Orthotospovirus genus, PMMoV, ToMV and CMV a total of 10 tomato samples were selected for further testing.



PCR amplification and sequencing

Total RNA was extracted from 100 mg of fresh leaf tissue using the RNX Plus Kit (SinaClon, Iran). The extracted RNA was then used to synthesize first-strand cDNA using the Easy cDNA Synthesis Kit (Parstous, Iran) with random hexamer primers according to the manufacturer's instructions. To detect the presence of ToBRFV, a polymerase chain reaction (PCR) was performed with specific primers TBRFV-F-5722 (5'-CACAATCGCAACTCCATCGC-3') and TBRFV-R-6179 (5'-CAGAGGACCATTGT AAACCGG-3') (Panno et al. 2019) corresponding to a part of the coat protein gene. The PCR amplification was carried out with a cycling condition of 95 °C for 5 min, followed by 40 cycles of 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 30 s, with a final extension at 72 °C for 10 min. Furthermore, the possibility of mixed infection with other viruses was investigated using the universal gl3637-F primer (5'-CCTTTAACAGT(A/T/G)GAAACAT-3') and gl4435c-R (5'-CAT(A/T/G)GC(A/G) CAAG A(A/G)TG(A/G)TA(A/G)ACAGA-3') (Chu et al. 2001) targeting the L segment (RdRp) of orthotospoviruses with the cycling condition of 94 °C for 2 min followed by 35 cycles of 94 °C for 30 s, 50 °C for 30 s and 72 °C for 1 min with 72 °C for 10 min of final extension. For PMMoV, the primers used were targeting the coat protein gene, PMMoVdF258 (5'-GTAAGAGAAATGATAATAAGGGTTTG-3') and PMMoVdR (5'- CGTTCGCAAATACACGTCAC -3') (Zhou et al. 2021) with a cyclic condition of 95 °C for 5 min followed by 35 cycles of 95 °C for 30 s of denaturation, 52 °C for 30 s of annealing, 72 °C for 1 min with final extension of 72 °C for 10 min. The presence of ToMV was investigated using primer pairs ToMVFor (5'-CTCCATCGTTCACACTCGTTACT-3') and ToMVRev (5'-GATCTGTCAAAGTCTGAGAAACTT-3') (Jacobia et al. 1998) with initial denaturation at 94 °C for 5 min, 40 cycles of 94 °C for 30s, 62 °C for 45s, and 72 °C for 1 min, and a final elongation at 72 °C for 5 min as well as the CMV coat protein gene-specific primers CMVCPF (5'-CGGATCCATGGACAAATCTGAATCAACC-3') CMVCPR (5'-GGCGGCCGCTCA and GACTGGGAGCACCCCAG-3') under the following conditions: 94°C at 2 min; 35 cycles of 94°C at 30 s, 52°C at 30 s and 72°C at 45 s with 72 °C for 10 min of final extension were used to test the presence of PMMoV from the symptomatic tomato samples. PCR

products were analyzed by agarose gel electrophoresis, visualized with SYBR Safe staining (SinaClon, Iran), and sent for Sanger sequencing (Sinuhe Biotech Company, Iran).

Phylogenetic and Recombination analysis

The obtained sequences from this study were subjected to BLASTn analysis to compare them with available sequences in GenBank. The complete CP sequences of other ToBRFV isolates and other CMV were downloaded from the National Center for Biotechnology Information (NCBI) database (Tables 1 and 2). Multiple nucleotide sequence alignments were performed using CLustalW implemented in MEGA version 11. Phylogenetic neighbor-joining (NJ) trees were constructed based on the coat protein sequences with 1000 bootstrap replicates. The best-fitting model of substitution, determined by MEGA 11 (Tamura et al. 2013), was JC and K2+G. Pairwise nucleotide comparisons were conducted using Sequence Demarcation Tool version 1.2 (SDT v1.2) to calculate the nucleotide sequence identity matrix. Furthermore, potential recombination signals in the selected sequences were analyzed using seven algorithms (GENECONV, Bootscan, Chimaera, MaxChi, SiScan, 3Seq, and RDP) implemented in Recombination Detection Program version 4.97 (Martin et al. 2015).

Mechanical transmission:

Nicotiana rustica seedlings at the 3-4 leaf stage were selected for inoculation with an infected tomato sample to investigate mixed infections. The inoculum was prepared by grinding the infected sample in 0.1 M potassium phosphate buffer (pH 7.0) and mechanically inoculated onto *N. rustica* plants that were pre-treated with carborundum. The inoculated plants were then placed in an insect-proof greenhouse with a temperature of 25°C and a photoperiod of 16:8 (light: dark) for a duration of 2 weeks. Subsequently, symptomatic leaves were collected from the inoculated plants and tested using RT-PCR with specific primers to detect the presence of the targeted viruses.

Results

Greenhouse observation, sequencing and phylogenetic relationships/analysis

Naturally infected tomato plants exhibited characteristic symptoms of leaf mosaic, leaf deformation, and shoestring (Figure 1).



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MN882030Solaum bycopersicumEgypt39070022, AMN882041Solaum bycopersicumNetherlands39070023, EMN882042Solaum bycopersicumNetherlands39563361, BMN882043Solaum bycopersicumNetherlands3941546, B-2MN882050Solaum bycopersicumNetherlands3941641, A-1MN882053Solaum bycopersicumNetherlands3941646, B-1MN882055Solaum bycopersicumNetherlands39941644, A-1MN882055Solaum bycopersicumNetherlands39942052, AMN882052Solaum bycopersicumNetherlands39962052, AMN882052Solaum bycopersicumNetherlands399620424, BMT018320Solaum bycopersicumChinaToBRFV-SDMT11866Copsicum amuumTurksyTBRFV-Ant-PepMW114091Solaum bycopersicumEgypt33314743MW114092Solaum bycopersicumEgypt3387206, 2MW114094Solaum bycopersicumNetherlands387356, 2MW114094Solaum bycopersicumNetherlands36733668, 2MW11411Solaum bycopersicumNetherlands3673366, 2MW114111Solaum bycopersicumNetherlands3673366, 2MW114114Solaum bycopersicumNetherlands3673366, 2MW114115Solaum bycopersicumNetherlands3673366, 2MW114114Solaum bycopersicumNetherlands3688922, 2MW114115Solaum bycopersicumNetherlands3685922, 1MW11	MN882028	Solanum lycopersicum	Netherlands	39070014_A
MN882041Solaum bycopersicumNetherlands39503361_AMN882042Solaum bycopersicumNetherlands39503361_AMN882045Solaum bycopersicumNetherlands39503361_BMN882045Solaum bycopersicumNetherlands3941630_B-2MN882053Solaum bycopersicumNetherlands3941641_A-1MN882059Solaum bycopersicumNetherlands39401664_BMN882059Solaum bycopersicumNetherlands39602442_BMN882059Solaum bycopersicumNetherlands39602442_BMN882059Solaum bycopersicumChinaT08RFV-SDMN882050Solaum bycopersicumChina108RFV-SDM100273Solaum bycopersicumChina108RFV-SDM111820Solaum bycopersicumEgypt33314743MV314091Solaum bycopersicumEgypt33314743MV314092Solaum bycopersicumEgypt33337205_2MV314094Solaum bycopersicumNetherlands3858922_1MV314094Solaum bycopersicumNetherlands3858922_1MV314111Solaum bycopersicumNetherlands3858922_1MV314112Solaum bycopersicumNetherlands3858992_2MV314112Solaum bycopersicumNetherlands3658371_2MV314112Solaum bycopersicumNetherlands3658974_1MV314113Solaum bycopersicumNetherlands306235_AMV314112Solaum bycopersicumNetherlands305333_3MV314123Solaum bycopersicum<	MN882030	Solanum lycopersicum	Egypt	39070022_A
MN882042 Solarum bycopersicum Netherlands 395G3361_A MN882043 Solarum bycopersicum Netherlands 395G3361_B MN882050 Solarum bycopersicum Netherlands 394150_B-P-2 MN882050 Solarum bycopersicum Netherlands 394161_A-1 MN882053 Solarum bycopersicum Netherlands 394164_B MN882056 Solarum bycopersicum Netherlands 3964244_B MN882062 Solarum bycopersicum Netherlands 3962055_A MN882062 Solarum bycopersicum China ToBRFV-SD MT018320 Solarum bycopersicum China 618975_2 MW114091 Solarum bycopersicum Egypt 3331743 MW114092 Solarum bycopersicum Pen 3673568_2 MW114094 Solarum bycopersicum Netherlands 3673368_2 MW1408 Solarum bycopersicum Netherlands 3673368_2 MW14091 Solarum bycopersicum Netherlands 3673368_2 MW14108 Solarum bycopersicum Netherlands 3673368_2 <td>MN882041</td> <td>Solanum lycopersicum</td> <td>Netherlands</td> <td>39070153_E</td>	MN882041	Solanum lycopersicum	Netherlands	39070153_E
MN882043Solaram lycopersicumNetherlands395G3361_BMN882050Solaram lycopersicumNetherlands395G3361_BMN882053Solaram lycopersicumNetherlands3941696_B-2MN882053Solaram lycopersicumNetherlands3941664_BMN882059Solaram lycopersicumNetherlands3962442_BMN882059Solaram lycopersicumNetherlands3962442_BMN882050Solaram lycopersicumNetherlands3962442_BMT00273Solaram lycopersicumChinaT08RV-SDMT118260Solaram lycopersicumChina108RV-S2MV314091Solaram lycopersicumEgypt3261782_2MV314092Solaram lycopersicumEgypt33314743MV314094Solaram lycopersicumPeru30783571_2MV314094Solaram lycopersicumNetherlands38589922_1MV314111Solaram lycopersicumNetherlands38589922_1MV314112Solaram lycopersicumNetherlands38589922_1MV314113Solaram lycopersicumNetherlands38589922_1MV314123Solaram lycopersicumNetherlands306235_AMV314113Solaram lycopersicumNetherlands305333_3MV314123Solaram lycopersicumNetherlands3054333_3MV314110Solaram lycopersicumNetherlands3054333_3MV314110Solaram lycopersicumNetherlands3064500_1MV314123Solaram lycopersicumNetherlands3064500_1MV314124 <td>MN882042</td> <td>Solanum lycopersicum</td> <td>Netherlands</td> <td>39563361_A</td>	MN882042	Solanum lycopersicum	Netherlands	39563361_A
MN882045Solarum (vcopersicumNetherlands39563388_BMN882050Solarum (vcopersicumNetherlands3994161_A-1MN882053Solarum (vcopersicumNetherlands3994168_BMN882054Solarum (vcopersicumNetherlands3996242_BMN882052Solarum (vcopersicumUSACA18-01MT002973Solarum (vcopersicumUSACA18-01MT018200Solarum (vcopersicumChinaToRRFV-Ant-PepMT118666Capsicum annumTurkeyTBRFV-Ant-PepMW314091Solarum (vcopersicumEgypt3207982MW314092Solarum (vcopersicumEgypt3314743MW314094Solarum (vcopersicumEgypt3378571_2MW314111Solarum (vcopersicumPeru36783571_2MW314112Solarum (vcopersicumNetherlands3858922_1MW314113Solarum (vcopersicumNetherlands3858922_1MW314114Solarum (vcopersicumNetherlands3858922_1MW314115Solarum (vcopersicumNetherlands3966433.3MW314116Solarum (vcopersicumNetherlands40002350.AMW314115Solarum (vcopersicumNetherlands40002350.AMW314116Solarum (vcopersicumNetherlands40002350.AMW314110Solarum (vcopersicumHetherlands40002350.AMW314110Solarum (vcopersicumHetherlands40002350.AMW314110Solarum (vcopersicumHetherlands40002350.AMW314110Solarum (vcope	MN882043	Solanum lycopersicum	Netherlands	39563361_B
MN882050Solanum lycopersicumNetherlands39941596_B-2MN882053Solanum lycopersicumNetherlands3994168, BMN882059Solanum lycopersicumNetherlands3996205_AMN882052Solanum lycopersicumNetherlands3996244_BMN882052Solanum lycopersicumNetherlands3996244_BMT018320Solanum lycopersicumUSACA18-01MT018320Solanum lycopersicumChinaGBRPV-SDMT118666Capsicum annumTurkeyTBRPV-Ant-PepMW314091Solanum lycopersicumEgypt3314743MW314092Solanum lycopersicumPeru36783668_2MW314094Solanum lycopersicumNetherlands3887571_2MW314112Solanum lycopersicumNetherlands3878668_2MW314113Solanum lycopersicumNetherlands3888992_1MW314114Solanum lycopersicumNetherlands3964343_3MW314119Solanum lycopersicumNetherlands3964343_3MW314119Solanum lycopersicumNetherlands40002385_AMW314119Solanum lycopersicumNetherlands40002385_AMW314119Solanum lycopersicumNetherlands40002385_AMW314119Solanum lycopersicumNetherlands40002385_AMW314119Solanum lycopersicumNetherlands40002385_AMW314119Solanum lycopersicumNetherlands40002385_AMW314119Solanum lycopersicumNetherlands40002385_AMW314110 <td>MN882045</td> <td>Solanum lycopersicum</td> <td>Netherlands</td> <td>39563388_B</td>	MN882045	Solanum lycopersicum	Netherlands	39563388_B
MN882053Solonum lycopersicumNetherlands39941641_A-1MN882059Solonum lycopersicumNetherlands39962055_AMN882052Solunum lycopersicumNetherlands39962055_AMN882052Solunum lycopersicumUSACA18-01MT01820Solunum lycopersicumUSACA18-01MT01820Solunum lycopersicumChinaTBRV-Ant-PepMW314091Solunum lycopersicumEgypt3207982MW314092Solunum lycopersicumEgypt3314743MW314094Solunum lycopersicumEgypt33726_2MW314098Solunum lycopersicumPeru36783571_2MW314111Solunum lycopersicumNetherlands3858922_1MW314112Solunum lycopersicumNetherlands3858922_1MW314113Solunum lycopersicumNetherlands3858922_1MW314119Solunum lycopersicumNetherlands3966433_3MW314123Solunum lycopersicumNetherlands40002350_AMW314132Solunum lycopersicumNetherlands40002350_AMW31410Solunum lycopersicumNetherlands40002350_AMW314110Solunum lycopersicumNetherlands40002350_AMW314123Solunum lycopersicumNetherlands40002350_AMW314110Solunum lycopersicumNetherlands40002350_AMW314124Solunum lycopersicumNetherlands40002350_AMW314130Solunum lycopersicumNetherlands40002350_AMW314131Solunum ly	MN882050	Solanum lycopersicum	Netherlands	39941596_B-2
MN882058Solanum lycopersicumNetherlands39941668_BMN882059Solanum lycopersicumNetherlands39962452_BMT002973Solanum lycopersicumUSACA18-01MT018320Solanum lycopersicumChinaT0BRV-SDMT118666Capsicum annuumTurkeyTBREV-Ant-PepMW314091Solanum lycopersicumEgypt33314743MW314092Solanum lycopersicumEgypt33317473MW314094Solanum lycopersicumEgypt33317473MW314094Solanum lycopersicumNetherlands38857902_2MW314094Solanum lycopersicumNetherlands3783668_2MW314111Solanum lycopersicumNetherlands36783668_2MW314112Solanum lycopersicumNetherlands36783668_2MW314113Solanum lycopersicumNetherlands38589922_1MW314114Solanum lycopersicumNetherlands3858992_2MW314123Solanum lycopersicumNetherlands40002350_AMW314124Solanum lycopersicumNetherlands4002350_AMW314125Solanum lycopersicumNetherlands40002350_AMW314126Solanum lycopersicumNetherlands40002350_AMW314110Solanum lycopersicumNetherlands40002350_AMW314110Solanum lycopersicumNetherlands40002350_AMW314110Solanum lycopersicumNetherlands40002350_AMW314110Solanum lycopersicumHeterlands40002350_AMW314110 <td< td=""><td>MN882053</td><td>Solanum lycopersicum</td><td>Netherlands</td><td>39941641_A-1</td></td<>	MN882053	Solanum lycopersicum	Netherlands	39941641_A-1
MN882059Solanum İycopersicumNetherlands3996205_AMN882062Solanum IycopersicumUSACA18-01MT102973Solanum IycopersicumChinaTDBRV-SDMT118666Capsicum annumTurkeyTBRV-Ant-PepMW314091Solanum IycopersicumChina6189975_2MW314092Solanum IycopersicumEgypt33617982MW314094Solanum IycopersicumEgypt33314743MW314094Solanum IycopersicumEgypt33314743MW314098Solanum IycopersicumPeru36783571_2MW314111Solanum IycopersicumNetherlands3857296_2MW314112Solanum IycopersicumNetherlands38589922_1MW314112Solanum IycopersicumNetherlands38589922_2MW314112Solanum IycopersicumNetherlands38589922_2MW314123Solanum IycopersicumNetherlands40002350_AMW314132Solanum IycopersicumNetherlands40002350_AMW314134Solanum IycopersicumChinaY2020_3MW314135Solanum IycopersicumChinaY2020_3MW31410Solanum IycopersicumChinaTom2M-J0MW31410Solanum IycopersicumChinaTom2M-J0MW31420Solanum IycopersicumBelgiumGBVC_ToBRFV_02MW31410Solanum IycopersicumHediands39630931MW314110Solanum IycopersicumHediands3963091MW31423Solanum IycopersicumHediands31963091 <td>MN882058</td> <td>Solanum lycopersicum</td> <td>Netherlands</td> <td>39941668 B</td>	MN882058	Solanum lycopersicum	Netherlands	39941668 B
MN882062Solamun lycopersicumNetherlands3996244_BMT002973Solamun lycopersicumChinaToBRV-SDMT118666Capsicum annuunTurkeyTBRFV-Anti-PepMW314091Solamun lycopersicumChina618975_2MW314092Solamun lycopersicumEgypt3331743MW314094Solamun lycopersicumEgypt33817296_2MW314094Solamun lycopersicumPeru36783664_2MW314094Solamun lycopersicumNetherlands3887296_2MW314111Solamun lycopersicumNetherlands36783668_2MW314112Solamun lycopersicumNetherlands36783668_2MW314113Solamun lycopersicumNetherlands38589922_1MW314119Solamun lycopersicumNetherlands3956343_3MW314123Solamun lycopersicumNetherlands40002385_AMW314136Solamun lycopersicumNetherlands40002385_AMW314110Solamun lycopersicumChinaY2020_3MW314110Solamun lycopersicumJordan3668794_1MZ438228Solamun lycopersicumJordan3668794_1MZ438228Solamun lycopersicumJordanTomL-JoNC238779Solamun lycopersicumJordan3668794_1MZ438228Solamun lycopersicumHeig3383730OM515235Solamun lycopersicumHeig33865691OM515236Solamun lycopersicumPeru36364500_1OM515248Solamun lycopersicumPeru36364500_1<	MN882059	Solanum lycopersicum	Netherlands	39962055 A
MT002973Solamun lycopersicumUSACA18-01MT018320Solamun lycopersicumChinaToBRFV-Ant-PepMW314091Solamun lycopersicumChina6189975_2MW314091Solamun lycopersicumEgypt33607982MW314092Solamun lycopersicumEgypt33314743MW314094Solamun lycopersicumEgypt336783571_2MW314098Solamun lycopersicumPeru36783571_2MW314111Solamun lycopersicumNetherlands38589022_1MW314112Solamun lycopersicumNetherlands38589922_2MW314113Solamun lycopersicumNetherlands39563433_3MW314123Solamun lycopersicumNetherlands4956433_3MW314123Solamun lycopersicumNetherlands40002385_AMW314124Solamun lycopersicumNetherlands40002385_AMW314125Solamun lycopersicumNetherlands40002385_AMW314110Solamun lycopersicumChinaY2020_3MW314110Solamun lycopersicumChinaTom2M-JoMZ438228Solamun hycopersicumJordanTom1-JoMZ438228Solamun hycopersicumHelgiumGBVC_ToBRFV_02MC028579Solamun hycopersicumHelgiumGBVC_ToBRFV_02MK31410Solamun hycopersicumPeru3634500_1OK515232Solamun hycopersicumHelgium3045031OK515245Solamun hycopersicumPeru3634501_1OK515245Solamun hycopersicumPeru4	MN882062	Solanum lycopersicum	Netherlands	39962442 B
MT018320Solanum lycopersicumChinaToBRFV-SDMT11866Capsicum annuamTurkeyTBRFV-Ant-PepMW314091Solanum lycopersicumEgypt32607982MW314092Solanum lycopersicumEgypt33314743MW314094Solanum lycopersicumEgypt33314743MW314098Solanum lycopersicumNetherlands33837296_2MW314111Solanum lycopersicumNetherlands36783571_2MW314112Solanum lycopersicumNetherlands36583668_2MW314113Solanum lycopersicumNetherlands38589922_1MW314119Solanum lycopersicumNetherlands38589922_2MW314113Solanum lycopersicumNetherlands39563433_3MW314113Solanum lycopersicumNetherlands40002350_AMW314132Solanum lycopersicumNetherlands40002350_AMW314110Solanum lycopersicumNetherlands40002350_AMW314110Solanum lycopersicumJordan36689794_1MZ94520Solanum lycopersicumJordanToml-JoMZ945420Solanum lycopersicumJordanToml-JoNC_028478Solanum lycopersicumJordanToml-BA21OK52457Solanum lycopersicumHeigiumGBVC_TOBRFV_02NC_028478Solanum lycopersicumPeru4073208_3OM515248Solanum lycopersicumPeru403353OM515245Solanum lycopersicumPeru4104821OM515244Solanum lycopersicumPeru <t< td=""><td>MT002973</td><td>Solanum lycopersicum</td><td>USA</td><td>CA18-01</td></t<>	MT002973	Solanum lycopersicum	USA	CA18-01
MT118666Capsicum annum ChinaTurkeyTBRFV-Ant-PepMW314091Solanum lycopersicumChina618975_2MW314092Solanum lycopersicumEgypt332407982MW314094Solanum lycopersicumEgypt3331743MW314095Solanum lycopersicumPeru36783668_2MW314111Solanum lycopersicumNetherlands36783668_2MW314112Solanum lycopersicumNetherlands3857920_2MW314113Solanum lycopersicumNetherlands38589922_1MW314113Solanum lycopersicumNetherlands38589922_1MW314112Solanum lycopersicumNetherlands39563433_3MW314112Solanum lycopersicumNetherlands39563433_3MW314112Solanum lycopersicumNetherlands40002385_AMW314113Solanum lycopersicumNetherlands40002385_AMW314110Solanum lycopersicumJordanTom2M-JoMW314110Solanum lycopersicumJordanTom2M-JoMW314110Solanum lycopersicumJordanTom2M-JoMW314110Solanum lycopersicumJordanTom2M-JoMW3228Solanum lycopersicumJordanTom2M-JoMW334110Solanum lycopersicumHeijumGBVC_TOBRFV_02NC.028478Solanum lycopersicumHeijumGBVC_TOBRFV_02NC.028478Solanum lycopersicumHeijum306333_3OM515232Solanum lycopersicumPeru40732089_3OM51524Solanum lycopersicum <t< td=""><td>MT018320</td><td>Solanum lycopersicum</td><td>China</td><td>ToBREV-SD</td></t<>	MT018320	Solanum lycopersicum	China	ToBREV-SD
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NW314092Solanum (yopersicumEgypt33607982MW314094Solanum (yopersicumEgypt33314743MW314098Solanum (yopersicumNetherlands33837296_2MW314111Solanum (yopersicumPeru36783571_2MW314112Solanum (yopersicumNetherlands3683686_2MW314113Solanum (yopersicumNetherlands3683686_2MW314114Solanum (yopersicumNetherlands38589922_1MW314112Solanum (yopersicumNetherlands39563433_3MW314123Solanum (yopersicumNetherlands40002350_AMW314136Solanum (yopersicumNetherlands40002350_AMW314110Solanum (yopersicumNetherlands4000235_AMW314110Solanum (yopersicumJordanTomL9M-J0MZ38228Solanum (yopersicumJordanTomL9M-J0MZ38228Solanum (yopersicumJordanTomL-J0MZ38228Solanum (yopersicumJordanTomL-J0OK539579Solanum (yopersicumHalyTomBA21OM515232Solanum (yopersicumPeru36364500_1OM515235Solanum (yopersicumPeru4073089_3OM515244Solanum (yopersicumPeru40364561OM515258Solanum (yopersicumPeru4036353OM515261Solanum (yopersicumNetherlands41903350OM515264Solanum (yopersicumNetherlands41903350OM515270Solanum (yopersicumNetherlands41903350 <t< td=""><td>MW31/091</td><td>Solanum lycopersicum</td><td>China</td><td>6189975 2</td></t<>	MW31/091	Solanum lycopersicum	China	6189975 2
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Table 1. Accession numbers and characteristics of 66 ToBRFV isolates retrieved from GenBank for phylogenetic analysis.

Accession number	Host	Country	Isolate
AY871068	Cucumber	Iran	SH17
AB042294	-	Indonesia	IA
U31219	Musca sp.	Hawaii	Hawaii
U20668	-	USA	Fny
AF127977	-	China	ĸ
AB008777	-	China	SD
AM183119	Solanum lycopersicum	Spain	Ri-8
FJ621496	Cucumis sativus	Poland	Woj
D10539	-	USA	М
AJ006988	-	China	P1
M22710	-	Japan	M22710
D12499	-	Japan	Y
AB049568	-	Japan	HL
D28489	-	Japan	CS
JF327832	Nicotiana tabacum	China	yunyan 87
DQ002876	-	Iran	DII
DQ002885	Cucumber	Iran	GI1
DQ002883	Squash	Iran	F13
X65017	-	China	HC210
EU414786	Petunia hybrida	China	ND2
AY429432	Arachishy pogaea	Netherlands	CA
EU414784	Nicotiana benthamiana	China	LW
AJ829779	Solanum lycopersicum	Spain	VAL90
AM183116	Solanum lycopersicum	Spain	Pl-1
Y10886	Solanum lycopersicum	Italy	Tfn
AJ829778	Solanum lycopersicum	Spain	BAR92
U31220	Musa	USA	Oahu
U20219	Solanum lycopersicum	USA	Ixora
JF279609	muskmelon	India	Bal-In
FJ168035	Capsicum annuum	India	Ch-Ada
X89652	Physalis minima	India	CP25
EF153733	Chrysanthemum morifolium	India	Lucknow
AF350450	Hyoscyamus muticus	India	L
HE583224	Cucumis sativus	India	Palampur
EF202597	Solanum lycopersicum	China	Tsh
AB368501	Solanum lycopersicum	Japan	PF
AF063610	-	USA	S
AF127976	-	USA	LS
EU191027	Lonicera caprifolium	Poland	WicDS
HM480051	Cucurbita pepo	Poland	C2
U10922	Spinacia oleracea	USA	DKRD

Table 2. Accession numbers and characteristics of 42 CMV isolates retrieved from GenBank for phylogenetic analysis.



Figure 1.Natural and simultaneous infection of tomato plants by *tomato brown rugose fruit virus* (ToBRFV) and *cucumber mosaic virus* (CMV). Symptoms including of mosaic, shoestring, leaf deformation (Left), and blistering on leaves (Right).



A total of 10 tomato samples were selected and ToBRFV were detected in all samples. A 458 base pair fragment corresponding to the region of the coat protein gene was amplified in RT-PCR assay using ToBRFV-specific primers, (Figure 2).



Figure 2. Electrophoresis performed to analyze the RT-PCR products amplified using *tomato brown rugose fruit virus* and *cucumber mosaic virus* specific primer pairs. Lane M: 1 kb DNA ladder (marker), Lane 1: Sample amplified with ToBRFV primers, 2: Sample amplified with CMV primers, 3: Sample amplified with simultaneously infected by ToBRFV and CMV, 4: Negative control.

One sample was sequenced and sequence BLAST analysis and multiple alignment confirmed that the Iranian isolate shared 99.76% nucleotide sequence identity with other isolates in the GenBank. The obtained sequence was deposited in GenBank under the accession number of OM807073. Phylogenetic analysis based on the coat protein nucleotide sequences revealed the clustering of ToBRFV isolates into three distinct clades, with the Iranian isolate (Jol-F-2022) grouped within clade II alongside isolates from various countries, including Mexico, Turkey, Israel, China, Peru, Canada, the USA, Jordan, the Netherlands, Italy, Egypt, the State of Palestine, Germany, and the United Kingdom (Figure 3a). While general primers for the Orthotospovirus genus and specific primers for PMMoV and ToMV did not yield any amplification. Using CMV specific primers, a 657 base pair fragment of the CMV complete coat protein gene was successfully amplified in five samples (Figure 2). According to this, ToBRFV isolates was detected in a mixed infection with CMV in tomato samples. Comparative analysis of CMV nucleotide sequences (OM807074) with those in the GenBank revealed sequence identities ranging from 95.13%-98.85%. Phylogenetic analysis based on nucleotide sequence of coat protein gene grouped CMV isolates into three main clades. Clades were divided into subgroups, and the Iranian isolate (Spec-F-72) was clustered in subgroup IB with Bal-In, Ch-Ada, CP25, Lucknow, and L isolates from India (Figure 3b).

Pairwise nucleotide identity matrices, generated using the Sequence Demarcation Tool (SDT v1.2), indicated that ToBRFV and CMV shared sequence similarities of 99% to 100% and 75% to 97% with other isolates, respectively. Investigation of potential recombination events using RDP4 did not detect any recombination events in the coat protein sequences.

Mechanical transmission

At 15 days post-inoculation (dpi), the inoculated plants exhibited pronounced mosaic symptoms, confirming the successful infection. Verification of the infection was achieved through RT-PCR amplification using specific primers for both viruses, as depicted in Figure 4.



Figure 3 The neighbor joining phylogenetic trees (Distance-based) were generated to illustrate the relationship among 66 *tomato brown rugose fruit virus* (ToBRFV) isolates (Right) and 43 cucumber mosaic virus (CMV) isolates (left) based on their coat protein nucleotide sequences based on Jukes-Cantor method. Phylograms were constructed using MEGA11 with 1000 replicates. Bootstrap values (>50%) are indicated next to the branches. The Iranian ToBRFV and CMV isolates are specifically highlighted in red.





Figure 4 Severe mosaic symptoms were observed on *Nicotiana rustica* plants inoculated with ToBRFV and CMV, which appeared at 20 days post-inoculation (dpi).

Discussion

Viral diseases are major constraints on tomato production worldwide and cause significant yield and quality losses (Hansen & Lapidot 2012). Considering that many plant species can be infected by multiple viruses, finding more than one virus simultaneously in a plant is not unusual. Therefore, mixed infections can occur due to the broad host range of several viruses and the polyphagous nature of many plant virus vectors, which can transmit more than one virus to the plant. In nature, mixed infections are common and can be considered a rule rather than an exception, representing a potential source of variability due to recombination events (Scholthof *et al.* 2011; Luria *et al.* 2017; Singhal *et al.* 2021).

During a mixed infection, the involved viruses may interact with each other in a synergistic, neutral, or antagonistic manner. Precise diagnosis and comprehension of the genetic diversity and regional distribution of these viruses are vital for the effectiveness of disease management strategies. Interference with plant defense mechanisms by viral proteins is likely not the sole determinant of whether an interaction is synergistic or antagonistic: some proteins may facilitate replication, intercellular movement, and spread within the host of other viruses. For instance, in potato that can be concurrently infected by several viruses in addition to potyviruses, viral suppressor proteins of potyviruses play a role in increasing replication and enhancing plant symptoms by suppressing plant defense mechanisms against other viruses (Valli et al. 2018). Additional research is

imperative to unravel the molecular mechanisms that underlie symptom development and interactions between these viruses in mixed infections.

In the present study, symptoms such as mosaic, leaf narrowing, and leaf distortion were observed in greenhouse tomato plants under investigation. The observed symptoms, which can be induced by various viruses including Tomato brown rugose fruit virus (ToBRFV), Tomato mosaic virus (ToMV), and Cucumber mosaic virus (CMV), were examined through molecular assays and subsequently detected viruses were sequenced. Ultimately, the simultaneous presence of ToBRFV and CMV in these plants was confirmed. The simultaneous presence of CMV and ToBRFV in tomato plants has important implications for disease management and control strategies. Out of the 10 plants examined in this study, CMV was identified in five samples, while ToBRFV was detected in all samples. The increased prevalence of ToBRFV compared to CMV in greenhouse production systems is closely associated with various modes of virus transmission, including contaminated seeds, mechanical transmission, and transmission by pollinating bees. This highlights the urgency for additional efforts in managing this virus. On the other hand, CMV by itself can induce symptoms such as leaf mosaic, leaf distortion, growth inhibition, fruit malformation, and shoestring, leading to reduced tomato plant yield. Moreover, the severity of symptoms observed in mixed infections can be more pronounced when compared to single infections with either CMV or ToBRFV alone. However, to date, no study has been conducted on the simultaneous effect of these two viruses in experimental tomato plants. Mixed infection of ToBRFV and TSWV in pepper plants has also been reported previously (Esmaeilzadeh & Koolivand 2023). Nevertheless, their concurrent presence with ToBRFV in tomato and pepper plants and the assumption of synergistic interaction between these viruses could lead to significant losses in tomato and pepper crops yield. On the other hand, mixed infections should be considered a key factor influencing virus evolution.

Understanding the genetic diversity and evolution of CMV and ToBRFV is also crucial for developing effective control measures. Analysis of the coat protein gene of ToBRFV has revealed limited genetic diversity, which is consistent with the findings of Celik et al. 2022. However, in the case of CMV, isolates exhibit high diversity and are classified into two subgroups: I and II, with subgroup I further divided into IA and IB based on the sequence homology of their genomes (Sokhandan Bashir et al. 2006: Sokhandan Bashir et al. 2008; Stanković et al. 2021). The coat protein gene analysis of Iranian CMV isolates indicates subgroup IB, which has been associated with East Asian origins. The regional distribution and genetic variability of CMV isolates may also impact the dynamics of mixed infections. Our findings highlight the occurrence of mixed infections in tomato plants with ToBRFV and CMV, emphasizing the importance of understanding the viral dynamics and potential challenges faced in tomato cultivation (Scholthof et al. 2011; Smith 2014; Singhal et al. 2021).

Since in a mixed infection scenario, the diagnosis

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and identification of viral pathogens involved and the factors controlling the spread can be complicated, it is necessary to accurately detect and understand how to improve effective strategies. Although in this study, only concurrent infection of these two viruses was examined using RT-PCR with specific primers, efforts are underway to clarify the relationships between ToBRFV and CMV, as well as the molecular mechanisms that underlie the symptom development. This research is essential for understanding virus epidemiology and laying the foundation for the development of effective management strategies.

Recently, there has been an increase in studies examining mixed viral infections. This information can serve as a rich source of valuable insights for designing control measures that go beyond merely protection and are based on the antagonistic behavior between viruses. It can involve activating plant defense mechanisms (such as RNA silencing by the first virus and then preventing or reducing damage by the second virus) to effectively manage these complex interactions.

In summary, addressing mixed infections is crucial for sustainable tomato cultivation. To gain a better understanding of the possibility and implications of mixed infections between ToBRFV and CMV, further research and investigation are necessary. These studies may involve experimental inoculations, molecular detection methods, and in-depth characterization of symptom development and viral interactions in coinfected plants.

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