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Review

Resistance Management through Brassica Crop–TuMV–Aphid Interactions: Retrospect and Prospects

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Abstract: Turnip mosaic virus (TuMV) is an important threat to the yield and quality of brassica crops in China, and has brought serious losses to brassica crops in the Far East, including China and the north. Aphids (Hemiptera, Aphidoidea) are the main mediators of TuMV transmission in field production, and not only have strong virus transmission ability (small individuals, strong concealment, and strong fecundity), but are also influenced by the environment, making them difficult to control. Till now, there have been few studies on the resistance to aphids in brassica crops, which depended mainly on pesticide control in agriculture production. However, the control effect was temporarily effective, which also brought environmental pollution, pesticide residues in food products, and destroyed the ecological balance. This study reviews the relationship among brassica crop–TuMV, TuMV–aphid, and brassica crop–aphid interactions, and reveals the influence factors (light, temperature, and CO_2 concentration) on brassica crop–TuMV–aphid interactions, summarizing the current research status and main scientific problems about brassica crop–TuMV–aphid interactions. It may provide theoretical guidance for opening up new ways of aphid and TuMV management in brassica crops.

Keywords: aphids; brassica crops; TuMV; interaction; resistance

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1. Introduction

Turnip mosaic virus (TuMV) is the main virus causing crop disease in China, North America, and parts of Europe. Crops in these regions have been seriously harmed by TuMV, second only to cucumber mosaic virus (CMV) [1], ultimately leading to a major loss of brassica crops. The plants affected by TuMV show slight leaf stunting and even withering of the entire plant, seriously affecting yield and quality [2]. Aphids are the main pests of brassica crops and are the transmission mediator of TuMV, with at least 89 species of aphids spreading the virus in a non-persistent manner [3]. The transmission mode of TuMV and its extensive variation lead to its very difficult prevention and control. The traditional prevention effect of chemical pesticides is temporarily effective, which could cause great harm to the environment. Therefore, the cultivation and promotion of resistance varieties is one of the most economical and effective measures for preventing and controlling TuMV.

There is no doubt that plants were challenged by numerous pathogens and herbivores in both natural and agricultural environments, and these threats often exist simultaneously [4]. Most plant viruses need mediators to be transmitted, and insects are the most important types of mediators. Most of these vectors are hemipterans, such as aphids, whiteflies, thrips, leafhoppers, planthoppers, wood lice, and so on [5]. Aphids are the main mode of TuMV transmission among brassica plants. Liu et al. [6] successfully analyzed the molecular mechanism of reciprocal symbiosis between plant viruses and insects, discovered the cooperative invasion molecular mechanism of *bemisia tabaci-geminivirus* for the first time in the world, and expanded the research scope of plant virology, which put forward a new theory of virus–insect–crop interactions. There is much research performing studies on virus–plant interactions, but little research on the molecular and genetic mechanisms of mediating plant–virus–vector interactions exists [7,8]. There are some studies on TuMV that are focused on the interactions between TuMV and aphids, TuMV and crops, and crops and aphids, but there are few studies on brassica crop–TuMV–aphid interactions. This study reviews brassica crop–TuMV, TuMV–aphid, and brassica crop–aphid interactions, and clarifies the link among brassica crops, TuMV, and aphids. Further excavating the interactions of the three species (brassica crop–TuMV–aphid) could not only be helpful to exploring the mechanism of species formation and constructing the co-evolution model among insects, TuMV, and plants, but also coordinate the relationship between brassica crops' resistance and biological control in production, which would provide theoretical guidance for opening up new methods for aphid and TuMV management.

2. Interactions between Brassica Crops and TuMV

Brassica crops include six species ("U-triangle" theory), *B. rapa* (AA genome, 2n = 2x = 20), *B. nigra* (BB genome, 2n = 2x = 16), *B. oleracea* (CC genome, 2n = 2x = 18), *B. napus* (AACC genome, 2n = 4x = 36), *B. juncea* (AABB genome, 2n = 4x = 38), and *B. carinata* (BBCC genome, 2n = 4x = 34) [9]. TuMV disease was first described in *B. rapa* in 1921 in the USA [10]. The TuMV virion could invade the cells from the injured tissues in brassica crops, and TuMV would use the host factors to undergo the process of shelling and genome replication. The virion first released a large amount of coat protein (CP) and a positive-strand RNA of the virus for translation, and the virus's own RNA-dependent RNA polymerase (RdRp) converted the positive-strand RNA chain into negative-strand RNA, then using the negative-strand RNA as a template to synthesize positive-strand RNA. Positive-strand RNA, or other components of the virus, further complete cell-to-cell transport in phloem using the eukaryotic translation initiation factor 4E (eIF4E) or eukaryotic translation initiation factor 4E isoform (eIF(iso)4E) [3]. Plant viruses can travel long distances through the microtubule system in systemic infections [11]. Short-distance transport could leech on to the plasmodesmata [12]. Virions can be transported from one tissue to other tissues by the microtubule system and the plasmodesmata, which would lead to a whole-plant infection by viruses.

In recent years, nearly 20 TuMV-resistant genes/loci have been mapped and cloned in brassica crops, most of which were mapped on the A genome, with a few being mapped on the C genome [13–30]. The resistance gene to TuMV on the B genome has not been reported. The *retr01* gene, resistance TuMV C4 isolate, was mapped and cloned in *B. rapa*, which would encode the eIF(iso)4E protein [16]. Similar to *retr01*, the *retr02* gene was also mapped and cloned in *B. rapa*, which would also encode the eIF(iso)4E protein [22]; the *retr01* and *retr02* genes were the same allele-encoding eIF(iso)4E.a protein. Unlike *retr01* and *retr02*, the *retr03* genes were mapped and cloned in *B. juncea*, which could encode the eIF2Bβ protein [30]. It is worth noting that the *retr01*, *retr02,* and *retr03* genes could encode the eIF proteins. Eukaryotic translation initiation factors (eIFs) (i.e., eIF4E, eIF(iso)4E, eIF4G, and eIF(iso)4G) are important resistance genes for TuMV, which play critical roles in potyviral infection [31]. The eIF4G, the multi-subunit eIF3, and the 40S ribosomal subunit could form the initiation ternary complex, or the 43S initiation complex, which could facilitate the eIF4F complex formation. In all eukaryotic organisms, the eIF4E amino acids are highly conserved, which could interact with the mRNA 5′ cap structure [32]. Similarly, the eIF4G, which could interact with eIF4E, only recognizes a conserved motif, and the eIF4F complex (eIF4G/eIF4E) forms to initiate the mRNA translation initiation in plants [33]. The eIF4F complex is composed of the eIF4E and eIF4G, and the eIF(iso)4F complex is composed of the eIF(iso)4E and eIF(iso)4G; these complexes are involved in the binding of the mRNA cap and ribosome recruitment in the initial steps of translation [34]. Jenner et al. [35] found that TuMV could use both eIF4E and eIF(iso)4E from *B. rapa* for replication and, for the first time, that TuMV could use eIF4E and eIF(iso)4E from multiple loci of a single host plant. In addition, TuMV isolates were classified into 12 pathotypes, as determined in the *B. napus* lines, TuMV CHN2/3 and C4 isolates belonging to pathotype 3, the UK1 isolate belonging to pathotype 1, and CDN1 belonging to pathotype 4, which are three serious TuMV types. Li et al. [36] reported that the results from the yeast two-hybrid (Y2H) and bimolecular fluorescence complementation (BiFC) assays suggested that TuMV C4/CDN1/UK1/CHN2/CHN3 isolates all could not interact with the eIF4Es, which indicated that the five TuMV isolates could not use the eIF4Es-to-RNA replication and eIF4Es were resistant to the five TuMV isolates. TuMV C4/CHN2/CHN3 isolates could interact with eIF(iso)4E.a, but could not interact with eIF(iso)4E.c, which implied that the eIF(iso)4E.c was resistant to the TuMV C4/CHN2/CHN3 isolates, and that the eIF(iso)4E.a was susceptible to the three TuMV isolates. In addition, the TuMV CDN1/UK1 isolates were the opposite of the TuMV C4/CHN2/CHN3 isolates, which could interact with eIF(iso)4E.c, but could not interact with eIF(iso)4E.a, proving that the eIF(iso)4E.a is resistant to the TuMV CDN1/UK1 isolates and that the eIF(iso)4E.c is susceptible to the two TuMV isolates [36,37].

3. Interactions between Brassica Crops and Aphids

The relationship between insects and plants has always been a frontier research hotspot, including insect behavior, plant defense, chemical ecology, physiological ecology, molecular ecology, and evolutionary biology. It was of great significance for revealing the insect-selection mechanism, and exploring new strategies and techniques for insect behavior regulation [38].

Plant volatiles play an important role between plants and the environment, acting as a language for communication and interaction between plants and environments. Plant volatiles account for 1% of secondary plant metabolites and are mainly represented by terpenoids, phenylpropanoids/benzenoids, fatty acid derivatives, and amino acid derivatives [39]. When leaves are mechanically wounded, injured by pathogens, or damaged by herbivores, the unique smell produced is named "green leaf volatiles" (GLVs). GLVs are the main body of plant volatiles [40]. GLVs consist mainly of six carbon (C6) compounds, including aldehydes, alcohols, and esters [39], which come mainly from the linolenic acid degradation pathway (Figure S1) [41]. The precursors of this pathway are, mainly, octadecane unsaturated fatty acids, such as linoleic acid (LA) and linolenic acid (Le A) [42]. 13-hydroperoxide is generated by the directional oxidation of lipoxygenase (LOX) at its ^{13}C; then, it is cleaved into cis-3-hexenal under the action of hydroperoxide lyase (HPL). On the one hand, cis-3-hexenal is transformed into trans-2-hexenal by isomerization; on the other hand, under the action of ADH, aldehydes could be selectively reduced to corresponding alcohols, and eventually form esters with acyl coenzyme (CoA) under the action of alcohol acyl transferase (AAT) [43]. Generally, growing plants could produce a sufficient amount of GLVs, but this could be enhanced by biotic stressor. These volatile cues were benefited by natural enemies of herbivores.

3.1. Sensitive Olfactory System Facilitating Aphids Invading Brassica Crops

It is difficult to control TuMV because it is transmitted mainly in a non-persistent mode by at least 89 aphid species [44]. Specifically, TuMV is introduced into plant cells via the stylet of aphids in a typical non-persistent transmission mode during aphid probing or feeding. Aphids are one of the most destructive pests in brassica crops. The virus level of plants in the aphid environment was significantly higher than that for those without aphids [45]. Because of aphids' natural advantages, winged aphids have a stronger transmission ability and a wider transmission range than wingless aphids. Through sucking plant juices and secreting honeydew, aphids can spread a variety of plant viruses, causing more serious losses to agricultural production which are far more harmful than those caused by themselves [46]. Aphids need to find suitable hosts, so they have a complex and sensitive olfactory system. The developed olfactory system of aphids can accurately determine the volatiles of host plants and select suitable hosts.

3.2. Two Ways for Brassica Crops' Defense against Aphids

The mechanism of brassica crops' defense against aphids can be divided into two types: constitutive defense and induced defense [47,48]. Constitutive defense is a form of direct defense, which means that, before aphid invasion, brassica crops possessed the defense characteristics to prevent aphids from feeding. When aphids reach the plant surface, the plant secretes a hydrophobic waxy layer, including non-volatile secondary metabolites and volatile and semi-volatile components (such as monoterpenes and glycosides), which can attract or repel aphids [49]. For example, trichomes are the unique structure of epidermal tissue in most plants [50]. Their main function is to resist the invasion of pathogens, mechanically block the movement of aphids on the plant surface, and secrete mucus or toxins to resist aphids [51]. Induced defense refers to a defense characteristic of plants, after being attacked by aphids, which can be divided into direct defense and indirect defense [52]. Induced direct defense is the physiological and biochemical changes of plants induced by aphids feeding, and is a direct defense against aphids. For example, in 1980, phytoalexin was defined as a kind of small-molecule disease-resistant compound synthesized and accumulated after plant disease [53]. Camalexin (3-thiazol-20-yl-indole) is a phytoalexin that was first isolated from a plant in the Brassicaceae family [54] and that has a crucial role in defense against fungal and bacterial pathogens [55,56]. Additionally, Kuśnierczyk et al. [57] confirmed that aphids' fitness was impaired by camalexin accumulation, as revealed by assays comparing aphid fecundity on WT and camalexin-deficient pad3 mutants. Induced indirect defense refers to when aphids or other stress signals induce plants to produce volatile organic compounds (VOCs) to attract parasitic and predatory natural enemies for defense. Herbivore-induced plant volatiles (HIPVs) are the most important compounds in plant volatiles which can be used as clues for indirect defense [58], and they have been shown to be various between populations/germplasms from the same plant species [59,60].

3.3. Special Volatiles Released after Being Attacked by Aphids

Aphids mainly use host volatiles to identify various hosts through the olfactory system [61]. The olfactory response of aphids to plant volatiles is an important step in identifying hosts for feeding [62]. Plant volatile information compounds can be divided into constitutive and induced VOCs, according to the presence or absence of pest induction.

Plant volatiles are often mixed with a variety of substances, and volatiles with different components and concentrations can be recognized by specific insects; thus, plant volatiles are chemical signals for host recognition by herbivorous insects. They can influence searches for mates, host selection, foraging, and egg-laying decisions [63,64]. For example, due to changes in volatile organic compounds, insects laid few eggs on clubroot-infected canola plants [65]. The VOC mixture may vary by the species of the herbivore, the plant species, the environmental conditions, and the number of herbivore species attacking the plant [66]. When brassica crops are harmed by herbivorous insects, they release other VOCs [67] that are different from those released by uninfected plants to regulate the relationship among brassica plants, herbivorous insects, and natural enemy insects. However, not only plants are infected with herbivores, but also pathogens. For example, there is information on insects choosing uninoculated pathogens, not inoculated canola, for oviposition [65]. Allyl isothiocyanates released by cruciferous plants have a strong attractive effect on *diaeretiella rapae* (Hymenoptera: Braconidae), and the sinigrin released by these plants is a chemical clue for *D.rapae* to find hosts [68,69]. Glucosinolate derivatives released by Brassica crops may be more attractive to parasitic wasps [70].

The volatiles produced and released by plants after they were attacked by insects are called herbivore-induced plant volatiles (HIPVs). The composition of HIPVs is very complex, including alkanes, olefins, alcohols, aldehydes, ketones, ethers, esters, hydroxy acids, organic acids, terpenes, and so on [58,71]. HIPVs play a key role in the complex plant–insect interactions [72]. Herbivorous insects can use HIPVs to find suitable host plants to avoid plant-induced defense and insect intraspecific or interspecific competition [73–75]. Moreover, predatory or parasitic natural enemy insects use HIPVs to search and locate prey or hosts [71,76–78]. HIPVs are not only perceived and used by insects, but also recognized by neighboring homologous or heterogeneous plants to predict the attack of herbivorous insects and prepare for defense against potential insect pests [79,80].

4. Interactions between TuMV and Aphids

4.1. Aphids Were the Main Mode of TuMV Transmission among Brassica Crops

Many plant viruses in the world are transmitted by insects [81,82]. Under natural conditions, at least 89 species of aphids transmit TuMV in a non-persistent way [83]. The plants, after being inoculated against TuMV, could release VOCs which may attract the aphids to feed the plants and transmit the TuMV to new plants (Figure 1). The virus with non-persistent transmission had no incubation period in the medium, did not replicate in the medium, and could not be transmitted vertically to the offspring, losing its ability to transmit the virus after molting [84]. The species of virus-transmitting aphids varied based on the location, most of which were peach aphids and radish buds, followed by cabbage aphids and cotton aphids [3,83]. When the aphids prick and absorb food, the virus is obtained at the same time. The plant tissue fluid was tested by the chemical receptors at the tip of the maxillary needle and the parapharyngeal region of the esophagus, and the virus was transmitted by piercing the phloem cells of other plants through the oral needle. The most effective measure to prevent and control the virus is to cut off the transmission process of insect mediators; another way could be to reduce the aphids' piercing damage. For example, brown seaweed extract-treated plants had a lower amount of piercing damage compared with control [85]. The study on the interactions between TuMV and aphids may be helpful to finding the key links in the prevention and control of TuMV.

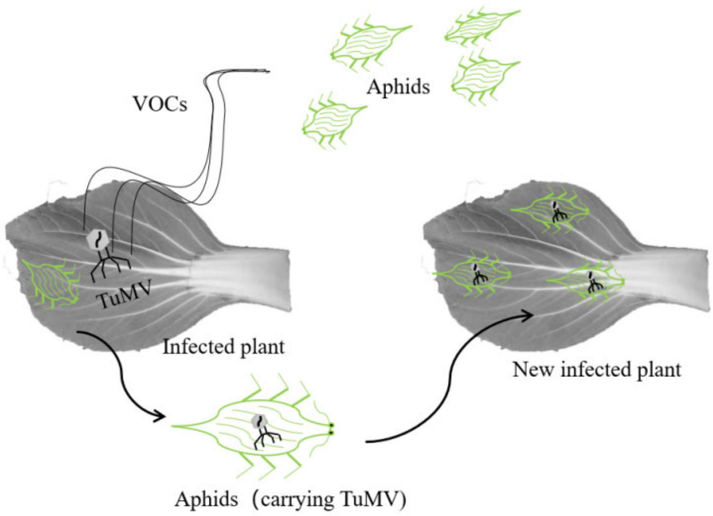

Figure 1. The mode of TuMV transmission in brassica crops by aphids.

4.2. The Effect of Virus on Aphids

In brassica crop–TuMV–aphid interactions, brassica crops would release chemical volatiles to regulate the behavior of aphids. The host plants, vectors, and viruses have become interdependent components in a complex pathological system [86]. Virus-infected plants were more attractive to insects than normal plants. Studies have shown that virus infection could affect the volatiles produced by plants and make infected plants more attractive to insects [54,70], and the behavior of a virus could manipulate the selection of a host by a vector insect. Previous studies have shown that there were significant differences in the drive ability of non-toxic vector insects and virulent vector insects to healthy plants and susceptible plants, and that non-toxic vector insects tend to feed on susceptible plants, while virulent vector insects tend to harm healthy plants [82,86]. Cucumber mosaic virus (CMV) could induce plants to produce volatile chemicals within 24 h, but the quality of host plants infected by cucumber mosaic virus becomes worse after 1–2 weeks, which promoted the transfer of mediators to virus-free host plants [87]. Recent research has shown that the specific substances of the allyl isothiocyanate Brassicaceae, which could attract aphids, may completely disappear after 3 weeks of TuMV infection in Chinese cabbage [88]. The study, including the biological characteristics, behavior, and influencing factors related to the transmission of TuMV by aphids, could provide ideas for the development of new technologies for the effective prevention and control of TuMV. Meanwhile, the biological control of aphids and the exploration of other environment-friendly control measures are also important methods for effective plant virus control. Mauck et al. [87,89] found that aphids may prefer plants infected by viruses because of olfactory perception. It was reported that green peach aphids preferred tobacco infected with TuMV and had higher fecundity on tobacco and *Arabidopsis thaliana* infected with TuMV [90].

5. Brassica Crop–TuMV–Aphid Interactions

Previous studies have paid more attention to the pairwise interaction analysis among brassica crops, aphids, and TuMV. Pairwise interaction was the core of the interaction, in addition to the participation of some other factors, such as plant hormones, environment, microorganisms, and so on.

5.1. The Effect of Phytohormone on Brassica Crop–TuMV–Aphid Interactions

The destruction of a viral infection to the normal plant developmental physiology is often related to plant hormone accumulation [91]. Changes in phytohormones levels have always been related to changes in virus accumulation [92]. In the process of virus-plant interaction, hormone signal-mediated plant resistance plays an important role in regulating the process of virus occurrence (such as symptom development, virus replication, and virus movement, etc.) [91,93]. Among them, salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) are mainly involved in plant defense against pathogens [94], while auxin (AUX), gibberellic (GA), cytokinin (CTK), brassinolide (BR), and abscisic (ABA) also play a role in plant defense, but are mainly involved in plant growth and development [95]. Most insect or virus infections are controlled mainly by the resistance induced by SA [96,97]. However, some studies have found that JA-mediated resistance is also very important for regulating plant resistance to vector insects or plant viruses [98]. In addition, hormone signal-mediated plant resistance is also involved in the regulation of the interaction between plant viruses and vector insects [99–101]. Many studies have shown that at least three phytohormones, JA, SA, and ET, played an important role in orchestrating plant defense responses [102–104]. SA signals played a vital role in the defense response against a variety of pathogens [105,106], and SA could influence biotrophic pathogens specifically. For example, for a biotrophic pathogen, *Plasmodiophora brassicae* infection induced higher SA defenses in canola [65]. Meanwhile, the production of JA and ET were involved in the regulation of plant responses to herbivores, necrotrophic pathogens, and nonpathogenic microbes [105,107,108]. Virus infection could also alter JA and ET signaling [8,106,109,110].

5.2. The Resistance Mechanism between Virus and Host Plants

For cucumber mosaic virus (CMV) transmitted by aphids, it was found that its 2b protein interacted with the JAZ protein (Jasmonate ZIM-domain proteins, JAZs) to inhibit the JA pathway, and 26S proteasome was used to prevent the degradation of key suppressors of the JA signal pathway, thus enhancing the preference for mediator insects [111]. The 2b protein encoded by CMV could interact with the JAZs directly and inhibit the JA resistance pathway by inhibiting the degradation of the JAZs, so the plants infected by CMV were more attractive to insect aphids. At the same time, *Arabidopsis thaliana* plants with three mutants of *myc*^{234} were more attractive to aphids [101]. In particular, JA may be a key target for vector transmission because it is the main hormone involved in plant insect defense. For example, the occurrence of reactive oxygen species, pathogenesis-related (PR) proteins, corpus callosum deposition, and induced accumulation of allergic reactions were all related to SA biosynthesis and signal activation. The callose deposition may inhibit the ability of TuMV to infect the sieve tube, which is beneficial to the reproduction of green peach aphids. Previously, it was proved that inhibiting the production of callose induced by aphids in host plants was related to TuMV infection [90]. Recently, Casteel et al. [100] found that nucleo inclusion protease (NIa-Pro), encoded by TuMV, could manipulate the ethylene signal pathway of host plants to enhance the ability of green peach aphids. Improving insect performance would increase the number of viral vectors and promote the spread of viruses to new hosts [7,87,90,112]. Wang et al. [113] reported that the expression of *Nicotiana benthamiana* ALD1 (*NbALD1*) was induced by TuMV, and *NbALD1* could mediate resistance to turnip mosaic virus by regulating the accumulation of SA and ET pathways.

5.3. The Effect of Environmental Factors on Brassica Crop–TuMV–Aphid Interactions

In agriculture, the spread of diseases, the growth of crops, and the reproduction of aphids are affected by many environmental factors. Climatic change affects the crop yield, the dynamics of pests, and their regulation by natural enemies [114,115]. At present, the main external factors affecting the three interactions include light conditions, temperature, and CO_2 concentration. Predicting the combined effect of changing environmental conditions on disease is not straightforward [116,117]. For example, in Arabidopsis, the combination of heat, drought, and TuMV infection causes a more severe reduction in plant growth than each individual factor alone [118].

5.3.1. Light Conditions Affecting Brassica Crop–TuMV–Aphid Interactions

As the most important energy source of plants, light not only provides energy in the process of plant growth, but also participates in the process of plant–pathogen interactions. Roberts and Paul [119] proved that the leaf tissues of plants growing in shade was more conducive to the growth and development of herbivorous insects, and shading could promote the infection of a series of pathogens. The mechanisms by which shading increases herbivory and disease severity could be complex. Insect herbivores were detected by the perception of damage-associated molecular patterns (DAMPs) as well as herbivore-associated molecular patterns (HAMPs) [106,120–123]. For example, in the case of microbial pathogens, shading could modify the microenvironmental factors, such as the leaf surface wetness [124]. Similarly, herbivorous insects could respond directly to changes in light levels, which may affect herbivores under natural conditions [125].

5.3.2. Temperature Affecting Brassica Crop–TuMV–Aphid Interactions

In the interactions among brassica crop–TuMV–aphid, temperature could affect the incidence or infection degree of TuMV by mediating aphids. High temperature and drought are beneficial to the reproduction and activity of aphids, but not conducive to the growth of brassica crop, and the crop disease resistance in such conditions is weak [126]. Aphids were the main media for the spread of virus diseases. Therefore, the virus disease in high-temperature and drought conditions is more serious. Research showed that the TuMV level was low, which may depend on the varied natural environment, and the change of temperature could break the interaction between TuMV–host [127]. Brassica crops are more likely to be infected with virus diseases in the seedling stage, and they are artificially inoculated when they have 3–4 true leaves; the infection rate of crops in this period was the highest. Therefore, brassica crops should be kept away from the periods of high temperature and drought.

5.3.3. CO_2 Concentration Affecting Brassica Crop–TuMV–Aphid Interactions

The concentration of CO_2 in the environment of brassica crops also greatly affects the spread of TuMV. Elevated concentrations of carbon dioxide or ozone activate salicylic acid signal-mediated plant resistance. The increase of carbon dioxide concentration down-regulates jasmonic acid resistance, while the increase of ozone concentration increases jasmonic acid resistance [128–130]. The increase of carbon dioxide concentration could enhance plant photosynthesis, causing the accumulation of plant ROS, affecting the expression of plant *NPR1* gene, and then regulating the response process of different hormone signals in plants.

6. Prospect

TuMV seriously affects the yield and quality of brassica crops in China. At present, the control of aphids depends mainly on chemical means, but the control effect of chemical pesticides is not environment-friendly, and brings environmental pollution and other problems which result in a threat to the ecological balance. Therefore, sustainable aphid management and disease control methods need to improve the yield and quality of brassica crops. At present, the studies on the interaction among brassica crop–TuMV–aphid focus mainly on the interaction between the two, the regulation of plant volatiles, and plant hormones. However, more study is needed, regarding the early prevention and the use of aphids' natural enemies to prevent the spread of viruses among crops. It is necessary to take some measures to control TuMV. There are many ways for brassica crops to defend against TuMV (Figure 2), such as physical defense (cell wall protections), chemical defense (metabolite inhibition), and gene defense (inhibition of DNA replication), which would be helpful for plant survival in the fight against diseases. TuMV could use the eIF genes from the host plant and interact with the VPg gene to survive in the plant, and aphids are one of the important transmission factors for transmitting TuMV from one plant to other plants (Figure 2) [36,37]. In recent years, with its continuous development, gene editing technology has been widely used in the control of insect-borne diseases and the cultivation of disease-resistant varieties [131]. Some research has reported that RNA viruses could be inhibited by the CRISPR/Cas system [132,133]. TuMV harbored a positive-stranded RNA genome of about 10,000 nucleotides, and the RNA genome was translated into a single large polyprotein which was subsequently cleaved by virus-encoded proteinases to yield at least ten functional proteins [134]. Cas13a, as part of a versatile, RNA-guided, RNA-targeting CRISPR/Cas system, has great potential for precise, robust, and scalable RNA-guided RNA-targeting applications [135]. The research which engineered the CRISPR/Cas13a RNA interference system revealed that CRISPR/Cas13a catalytic activities resulted in interference against TuMV-GFP in transient assays and in the stable overexpression lines of *Nicotiana benthamiana*, and that Cas13a could process long pre-crRNA transcripts into functional crRNAs, resulting in TuMV interference [131].

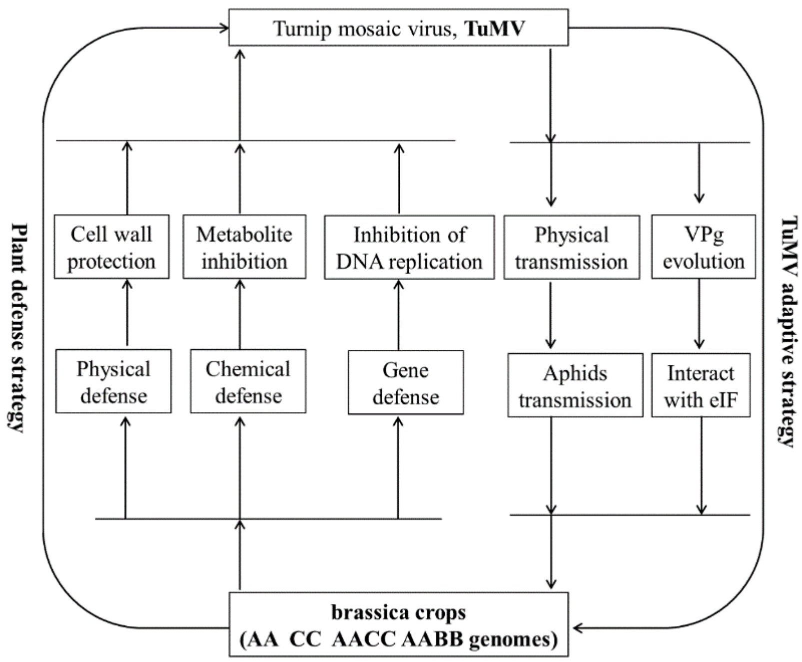

Figure 2. The interaction ways between brassica crops and TuMV.

At present, the brassica crop–TuMV–aphid interactions with the environmental factors have become a major topic for multidisciplinary development in the world; however, some questions need further investigation: (i) the impact on the ecosystem from brassica crop–TuMV–aphid interactions. TuMV could directly or indirectly modify the behavior of insects, change the characteristics of host plants, and facilitate the transmission of viruses within the host. From the ecological level, the change of insect behavior and plant characteristics by viruses could not only affect the growth, development, reproduction, and feeding behavior of insects, but also affect the entire biological community of the ecosystem; (ii) Omics big data analysis brings unprecedented opportunities and challenges to brassica crop–TuMV–aphid interactions. Through comprehensive comparisons of the disease, crop genome, proteome, and microbe, the key factors changing in the process of virus infection should receive more attention, clarifying the transcriptional regulation pathways, adjusting the relationship between the interactions, and improving the crop yields, quality, and disease resistance, thereby providing a new plant-protection scheme; (iii) exploring the comprehensive control strategy of TuMV disease control. From the study on the pathogenicity of the virus itself in the interactions between viruses and plants, viruses, and insects, it was necessary to further clarify the TuMV virome study, which reveals the interaction mechanism in the pathogenicity and disease process; (iiii) the establishment of environmental protection and pollution-free defense measures for aphids and TuMV control, based on genome editing technology, should be pursued.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/horticulturae8030247/s1, Figure S1: Biosynthetic pathway of green leaf volatiles (GLVs).

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