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The Role of ncRNAs in Parasitic Plant Infection and Resistance Management in Tomato Breeding

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ABSTRACT

Tomato is one of the most important agricultural crops in the World and many biotic stresses exist affecting its production. Parasitic weeds in particular are important in tomato production, causing billions of dollars in losses. Although the problem is serious and widespread, control methods are restricted, relying mostly on chemicals with negative effects on the environment and human health. In this regard, biotechnological methods are gaining importance, especially non-coding RNAs. Even though not the full potential of non-coding RNAs is understood fully, they hold the potential to provide wide range of applications such as plant breeding, development of novel types of pesticide, and determination of gene function. Therefore, with new technology and new approaches the use of non-coding RNAs has a potential that can be a powerful alternative to deal with parasitic weed. In this review article, it was mainly focused on the mechanism of non-coding RNAs, their transfer mechanisms, potential usage areas and the possible role in plant breeding. Given these challenges, the role of ncRNAs in tomato improvement deserves closer attention, as outlined in this review.

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Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most consumed and produced vegetables in the world with the total production of 189.1 million tons (FAOSTAT, 2023). However, biotic and abiotic stress factors limit tomato production Especially parasitic weeds can be considered a major and complex problem (Cignitas et al., 2024). Conventional strategies, such as herbicide application and breeding, provide only limited success due to seed longevity and environmental constraints. In this context, innovative molecular approaches are required. In this regard, non-coding RNAs (ncRNA) have emerged as promising regulators of host-parasite interaction, offering new opportunities for developing resistant tomato varieties.

Non-coding RNAs including microRNAs play a vital role in response to biotic and abiotic stress factors in plant defense mechanisms (Nejat & Mantri, 2018). Therefore, they have enormous potential for plant breeding, especially strategic crops such as tomatoes. Tomatoes face numerous biotic stress factors such as fungi, viruses, nematodes, bacteria and weeds. Current studies have demonstrated that ncRNAs play a crucial role in the biotic stress response (Salman & Boyraz, 2017; Song et al., 2021). These miRNAs can regulate the plant response by either enhancing or reducing resistance (Basso et al., 2019). Some lncRNAs play a role in the signaling pathway such as abscisic acid (ABA) and brassinosteroid (BR) pathways (N. Li et al., 2022; Li et al., 2023).

Current ncRNA-based strategies can be categorized into three main approaches: marker-assisted selection (MAS), transgenic technologies including artificial microRNAs (amiRNAs), and gene silencing techniques such as Small Tandem Target Mimic (STTM). ncRNA-based MAS can be used in breeding programs to determine specific biotic or abiotic stress responses using expression profiles thus breeders can determine resistant or tolerant crops (Islam et al., 2023). This approach can be especially useful for polygenic traits (Li et al., 2023). Advanced genetic engineering techniques such as CRISPR/Cas have big potential for the improvement of stress-tolerant crops

(Ghosh & Dey, 2022). For example, ncRNAs-based strategies were useful for the enhancement of resistance against *Phytophthora infestans* and *Ralstonia solanacearum* diseases (Li et al., 2023; Wang et al., 2019).

Parasitic plants can manipulate the host physiology (Clarke et al., 2019) by exchanging macromolecules and RNAs (Kim & Westwood, 2015; LeBlanc et al., 2012). This in turn can induce the host's immune response utilizing the pathogenic signals. Management strategies can be collected under 4 main topics: Gene Silencing Techniques, Host-Induced Gene Silencing, Selection of Resistant Varieties and Integration of Transcriptomic Data. In gene silencing techniques ncRNA genes such as miRNA genes are directly targeted by genetic engineering techniques thus trying to obtain more resilient plants. In Host-Induced Gene Silencing, parasitic RNAs are targeted thus their parasitic genes can be silenced in this way parasitism can be reduced. In the Selection of Resistant Varieties, breeding programs focus on the resistance varieties that naturally express beneficial ncRNAs, which confer the resistance to host plant (Nandni et al., 2024; Yadav et al., 2024). In Integration of Transcriptomic Data, this technique is used for determination of candidate ncRNAs for further research and applications (Yadav et al., 2024). In this review, we summarize recent advances in understanding the regulatory roles of ncRNAs in plant immunity against parasitic weeds and discuss their potential implications for future tomato breeding strategies.

The Mechanism of ncRNAs

Although 75% of the genes can be transcribed into RNA, only 2% of them can be translated into proteins in eukaryotic genomes (Djebali et al., 2012). Noncoding RNAs have been called junk or dark matter for a long time. However, they have become important for the last 2 decades because their functions have been emerging in this period. Small RNAs (sRNAs, 18–30 nt), medium-sized ncRNAs (31-200 nt), and long noncoding RNAs (lncRNAs, > 200 nt), belonging to the ncRNAs family which are enormous. Especially, micro RNAs have a crucial role for post-transcriptional regulation of gene expression (Fei et al., 2013; Gutbrod & Martienssen, 2020; Song et al., 2019; H. Zhang et al., 2018). If it is focused on the miRNA biogenesis, it can be seen clearly that 3 main enzyme, they are: RNA polymerase II, which it transcribes the miRNAs from miRNA genes (MIRs) and then secondly dicer-like (DCL) proteins process the miRNAs and finally they are integrated to Argonaute (AGO) proteins thus this structure can do degradation or translation inhibition (Song et al., 2019). ncRNA molecules have an enormous usage area in almost all organisms such as humans, crops and livestock. NcRNA based genetic engineering methods exhibit vigorous tools for the find out gene function, develop novel therapeutic strategies and new plant breeding methods. RNAi, CRISPR-Cas systems, Circular RNAs (circRNAs), Antisense Oligonucleotides (ASOs), Small Nucleolar RNAs (snoRNAs), Ribozymes and RNA Aptamers and Long Non-coding RNAs (lncRNAs) are some methods of ncRNAs based methods. These methods are both useful and effective methods. Some studies are given in table 1.

Table 1: Some studies that are utilized by ncRNAs in plants

Moreover, artificial microRNAs (AmiRNAs), firstly used more than two decades in human cell but its use is relatively novel in plants. Generally these studies are clustered on the insect resistance, abiotic stress tolerance and virus resistance in different species such as tomato, wheat and arabidopsis (Shi et al., 2018; Y. Zhang et al., 2018).

However, there are not sufficient number of studies the interaction between parasitic plants and crops. Therefore, we focus on this topic. The main purposes of this article are making play of this issue and the discussing on the future opportunities in terms of plant breeding.

The Mechanism of RNAi

The phenomenon of RNAi is an endogenous process that has a crucial role in the silencing of genes at the transcriptional and post-transcriptional stages. It was first discovered in the 1990s at the Petunia plants. Researchers observed co-suppression in both gene and transgene when they tried to overexpress chalcone synthase in petals (Napoli et al., 1990). Moreover, Fire et al. (1998) observed post-transcriptional silencing after the dsRNA injection in the cytosol. The presence of dsRNA induced the silencing in cytoplasm (Bramlett et al., 2020). The dsRNAs are prepared into small interfering RNAs (siRNAs) via DICER-type ribonucleases (DICER). These siRNAs are included in RISC (RNA-induced silencing complex), a protein complex. Afterwards, this complex acts as a guide for repression or cleavage to complementary mRNA (Dubrovina & Kiselev, 2019).

The Regulation of Trans-Kingdom RNA Interference

The phenomenon of trans-kingdom RNAi includes many steps; (a) intracellular generation, (b) sorting of sRNAs, (c) release and uptake of mobile sRNAs, (d) the affiliation of into silencing complex and (e) gene silencing. These steps are crucial for the silencing mechanism, and each step has a vital role. Moreover, all steps are the underlying of Host Induced Gene Silencing (HIGS). This system may be named as a plant immunity system. Plants use this system for the response of pathogen attacks (Duan et al., 2012).

According to previous studies, miRNAs can be transported throughout the phloem, contributing to plant growth and resistance to environmental stress (Kehr & Kragler, 2018). Obligate parasitic plants can contact the host using their haustoria. This trafficking is used for not only water and nutrients but also RNAs (Shahid et al., 2018). Considering this information, it was observed that some miRNAs, coming from the *Cuscuta campestris*, can target mRNAs of the host and can cause the downregulation of some genes. This circumstance was observedbetween *Arabidopsis thaliana* and *Cuscuta campestris*. It was indicated that the downregulation of target genes leads to notable growth of *C. campestris* so it may be said that miRNAs can be trans-species regulators for the gene of hosts, and they may be used for facilitating parasitism by parasitic plants.

Table 1. Some studies that are utilized by ncRNAs in plants

Method	Study	Mechanism	Result	Reference
RNA Interference (RNAi)	RNAi-mediated resistance to Potato Virus Y (PVY) in tobacco plants	Transgenic tobacco plants were engineered to express hairpin RNA constructs corresponding to the PVY genome. The hairpin RNA is processed into siRNAs by the plant's cellular machinery, which then targets and degrades PVY RNA.	The transgenic plants exhibited significant resistance to PVY infection, demonstrating the effectiveness of RNAi in conferring viral resistance in plants	(Yin et al., 2019)
CRISPR-Cas Systems	CRISPR-Cas9 mediated the knockout of the OsPYL9 gene in rice.	The OsPYL9 gene, involved in abscisic acid (ABA) signaling, was targeted by CRISPR-Cas9. ABA is a plant hormone that regulates drought response. Knocking out OsPYL9 was hypothesized to enhance drought tolerance.	The edited rice plants exhibited improved drought tolerance without compromising growth, indicating that CRISPR-Cas9 can be used to enhance stress resistance in crops.	(Y. Li et al., 2022)
Long non-coding RNAs (lncRNAs)	Role of lncRNA COOLAIR in *Arabidopsis thaliana*.	COOLAIR, a lncRNA transcribed from the FLOWERING LOCUS C (FLC) gene, was shown to regulate flowering time by modulating FLC expression. FLC is a major repressor of flowering.	Altering the expression of COOLAIR influenced flowering time, demonstrating how lncRNAs can regulate important developmental processes in plants.	(Tian et al., 2019)
Ribozymes and RNA Aptamers	Use of hammerhead ribozymes to control gene expression in tobacco.	Hammerhead ribozymes were engineered to target specific mRNAs in tobacco plants, leading to their cleavage and subsequent degradation.	This approach effectively reduced the expression of target genes, showcasing the potential of ribozymes for precise gene regulation in plants.	(Abdeeva et al., 2019)
Antisense Oligonucleotides (ASOs)	Antisense oligonucleotides targeting the DCL1 gene in *Arabidopsis thaliana*.	ASOs complementary to the DCL1 mRNA were introduced into plants to inhibit its expression. DCL1 is involved in miRNA processing.	The reduced expression of DCL1 led to altered levels of several miRNAs, affecting various developmental processes and stress responses.	(Priti et al., 2022)
Circular RNAs (circRNAs)	Identification and functional analysis of circRNAs in *Oryza sativa* (rice).	High-throughput sequencing and bioinformatics were used to identify circRNAs in rice, followed by functional studies to determine their roles.	Several circRNAs were found to be involved in stress responses and developmental processes, providing insights into the regulatory roles of circRNAs in plants.	(Bhavya et al., 2022)

On the other hand, it was observed that the entire of these transcripts were not transported to the host. Therefore, although it was not about concentration, this circumstance is a question that is waiting for solving (Roney et al., 2007; Shahid et al., 2018). Furthermore, there are some studies that reveal the trafficking between host and parasite. Thanks to these studies, it can be found out the effect of the ncRNAs on other organisms. For example, according to (Wu et al., 2022) there is a huge lncRNA trafficking between dodder and soybean. Their study reveals that 365 dodder lncRNAs and 14 soybean lncRNAs can move in a bidirectional manner. These circumstances can lead to the effecting of some metabolic activities on both sides such as metabolic process, catalytic activity, signaling, and response to stimulus.

The role of EVs in RNA transfer

The understanding of the transportation of non-coding RNAs is crucial for the comprehensibility of the technologies of HIGS or SIGS. To arrive at RNAs from one cell to another cell without degradation, they need protection. This phenomenon is necessary for molecule uptake or export of cells. Although there are some studies about trans-kingdom ncRNAs between host and parasite, the mechanism is not elucidated completely. Particularly, recent studies demonstrate that extracellular vesicles (EVs) and non-vesicular fractions have a big potential for RNA-secreting in plants and mammals. The EVs are good transporters for bioactive cargo, such as proteins, lipids, nucleic acids, and metabolites. The EVs can be classed a vast scale in three groups; exosomes, microvesicles, and apoptotic vesicles (Kalluri & LeBleu, 2020; Théry et al., 2018; Yáñez-Mó et al., 2015). Although it is not completely clear in terms of the transportation of trans-kingdom ncRNAs, there are some findings about the presence of small RNAs in the EV fraction. For example, obtained apoplastic fluids from EVs of Arabidopsis include 10 to 17 nucleotide length RNAs as well as siRNAs and miRNAs (Baldrich et al., 2019) thought that these molecules are the product of sRNA degradation. On the other hand, there are some antitheses that support opposite ideas. For instance, a lack of prior protease treatment can lead to confusion of inside EVs and sRNAs outside EVs. Because they are both bound via RBPs (RNA-binding proteins). When protease and RNase are treated, circRNAs, extracellular RNAs and sRNAs are found in nonvesicular fractions (Zand Karimi et al., 2022).

Parasitic Plants and Their Interaction with Susceptible and Resistant Host

Plants are continuously challenged not only by microbial pathogens such as fungi, bacteria, and viruses, but also by parasitic plants. These parasitic weeds directly attach to host roots and extract water and nutrients, severely affecting plant growth and productivity. In response, host plants have developed a range of immune mechanisms to recognize and defend against such biotic threats. These plant immune responses are multilayered and involve complex signaling networks that mediate defense at both local and systemic levels. Particularly, microbe-associated molecular patterns (MAMPs) act an important role for plant defense against pathogens. These immune receptors are used for the detection of conserved structures of microbes such as bacterial flagellin or fungal chitin. Triggering of immune receptors, also termed as pattern recognition receptors (PRR) activates to some molecules such as secondary metabolites, ROS, some marker genes and stress-related phytohormones (Boller & Felix, 2009; Böhm et al., 2014; Kaiser et al., 2015).

In parasitic plants, haustorium has a crucial role for the up taking of nutrients, solutes, and carbohydrates but it is not used for it. It functions as a wire for the connection between the parasite and the host. Therefore, while it is up taking on some needs of parasitic plants it transfers some molecules to the host. For instance, according to (Haupt et al., 2001) 25 kDa protein can be successfully transferred to *Cuscuta*. Moreover, some studies showed that RNAs can be transferred as well (David-Schwartz et al., 2008; Roney et al., 2007; Westwood et al., 2009). These studies can be the appropriate approach for biotechnological methods that can be used for small RNAs transfer.

The approach of artificial micro RNAs includes successful strategies for the control of parasitic plant infestations (Alakonya et al., 2012; Roney et al., 2007; Runo et al., 2011; Runo et al., 2012). There are some studies that demonstrate that this technology can be successfully applied. For example, (Alakonya et al., 2012) conducted to studies about targeting of SHOOT MERISTEMLESS-like (STM) by using phloem-specific RNAi-constructs in *Cuscuta pentagona.* The results reveal that small RNAs successfully transferred into *C. pentagona* haustoria and haustorium development were inhibited. Furthermore, different types of strategies can be created for example parasitic enzymes can be targeted as well (Bleischwitz et al., 2010) carried out this type of project they blocked the infestation-specific cysteine protease *Cuscuta*. In light of this information, numerous strategies can be determined by the exhibiting of blind spots of the parasitism mechanism. Although there are some hope-inspiring developments, the usage of these technologies needs to be optimized and a long process for put into practice.

Host Resistance to Parasitic Plants

The application of selective herbicides is not an entirely effective solution for the control of parasitic weeds, mainly due to the long-term viability of their seeds in the soil and the difficulty in targeting them without harming the host plant. One of the best solutions is the improvement of resistant varieties. However, there are some limitations in this topic such as genetic variation and limited information about molecular resistance mechanisms. Although such limitations exist, there is some knowledge that can be used for the improvement of strategies and can be put into practice. While pre-attachment resistance is defined as a decrease of seed germination and haustorial connection inhibition, post-attachment resistance is about the immune response after attachment of a parasitic plant (Yoder et al., 2009).

Various compounds, such as strigolactones, are known to stimulate the germination of parasitic plants; *Orobanche* species serve as a notable example. In addition to their role in parasitic seed germination, strigolactones are also

essential signaling molecules in the establishment of arbuscular mycorrhizal symbiosis. On the other hand, certain compounds such as the coumarin derivative scopoletin have been reported to inhibit the germination of *Orobanche cumana* in sunflower genotypes (Dor et al., 2016). In the light of this information different types of management strategies can be designed. Additionally, communication between host and parasite is crucial for susceptibility and resistance. For example, CUSCUTA RECEPTOR 1 (CuRe1) was identified in the *Solanum lycopersicum* but it is not the sole factor. The studies demonstrated that CuRe1 is lacking of intracellular kinase domain (Duriez et al., 2019; Hegenauer et al., 2016). Another resistance mechanism is the tissue-based mechanism. In this mechanism, when penetration is realized by haustoria its growing is inhibited. This mechanism is mainly based on the accumulation of callose, suberin, and lignin. Thus, it leads to the cell wall fortification in the infection site. This phenomenon was observed in the *O. cumana* resistance in sunflower and *O. crenata* resistance in Faba bean for the Callose deposition. Moreover, cell wall lignification was reported in the resistance of *C. campestris* in tomato and the resistance of Striga in rice (Albanova et al., 2023). Furthermore, according to (Amini et al., 2017) specific inhibitors of haustoria can be expressed as a defence mechanism against some parasitic plants for example specific cysteine protease inhibitors can be a response to *C. campestris* infection (Figure 1).

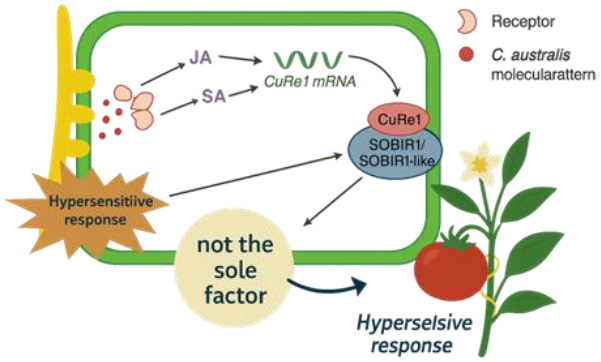

Figure 1. The mechanism of CUSCUTA RECEPTOR 1 (CuRe1) gene.

One of the most enigmatic defense mechanisms is post-haustoria resistance. Mainly there are two different theories; firstly accumulation of mucilage blocks the transfer of nutrient and water uptake and secondly, specific proteins and small interfering RNAs play a role in the inhibition of parasitic activities (Pérez-de-Luque et al., 2006). On the other hand, the development of a successful barrier for haustoria formation seems to be a unique feature of resistant genotypes, for example, lignification based resistance was observed to *C. campestris* in Heinz tomato genotypes (Jhu et al., 2022) and callose based resistance was observed to *O. crenata* in pea cultivars (Pérez-de-Luque et al., 2006). It can be clearly seen that genetic based different types of resistance can be found to parasitic plants in each plant. In the light of this information, the resistance of parasitic plants depends on many factors. Therefore, when the management strategy is determined, this information needs to be considered. These resistance mechanisms often overlap with broader stress-response pathways, leading to cross-resistance.

Cross-Resistance to Parasitic Plants and Other Stresses

As it is known that cross-resistance and multiple resistance mechanisms exist in plants. Especially, abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA) act important roles in stress response mechanism against to biotic, abiotic or a combination of both (Sonkar et al., 2021). Therefore, the mechanism of stress responses is similar with another biotic stress mechanism in terms of parasitic plants.

There are mainly three main resistance mechanisms to parasitic plants and other biotic stress factors. SA and JA pathways are good examples for cross-resistance they both play crucial roles for the response to multiple stressors (Albanova et al., 2023). While both enzymes are induced by *C. pentagona* parasitism in tomato plants (Runyon et al., 2010). SA pathway is dominant over the JA pathway in the response mechanism of *Orobanche minor* parasitism in *Trifolium*. Furthermore, hypersensitive response (HR) is crucial for the plant-to-plant interaction. In this point, programmed cell death are the key mechanism for the prohibition of the formation of functional haustoria. There are two important examples in this context, tomato-cuscuta and sorghum-Striga. This mechanism is not only used to parasitic plants but also it is utilized to multiple plant pathogens as a response as well. As a result, it can be said that this represents a key mechanism of multiple resistance. Although there are some developments, the missing is observing of response to root and stem parasitic plants for the single host. This approach is important because there is differentiation between the hosts of Orobanchaceae and *Cuscuta* spp. and current literature is not sufficient for elucidation. This approach is important for the illumination of the resistance mechanism in the crops and the development of a crop, resistance to both parasitic plants would be exciting.

The tomato plant has good potential for becoming the model plant because it is host for both *Orobanche* and *Cuscuta* genus. Some mechanism was determined in tomatoes for example the lack of strigolactone can provide resistance to broomrapes but there is no correlation with resistance to dodder (Dor et al., 2011). Moreover, lignin-based resistance was observed but there is still no resistance mechanism for both parasitic plants. Therefore, it can be said that if the resistance mechanism to both parasitic plants can be elucidated, it would be useful for crop improvement.

Breeding strategies of Resistant Cultivars

In recent times, breeding strategies have been based on endogenous resistance in the plant. In classical breeding programs, this method may be useful, but it is hard because it needs a large population size and expensive facilities. For this purpose, marker-assisted selection (MAS) is becoming prominent, because as is known numerous studies have been conducted on the purpose of determination of QTLs, and resistance sources. These QTLs can be used in different breeding strategies. For instance, this strategy

gave good results in sorghum, maize, and sunflowers. One of the best sources of resistance is wild types because their genetic treasure contains much more resistance genes as regards the cultivated plants. Therefore, the finding of resistance-defining QTLs is more possible. Furthermore, the finding of resistance mechanisms is as important as resistance QTLs. Thus, genetic manipulation strategies can be paved, in this way target oriented, short term and low-cost breeding programs can be designed.

RNA sequencing technologies are both salient and useful technologies for elucidating the interaction between parasites and hosts. Thanks to this technology, the effects of effector-triggered immunity (ETI) and pathogen-triggered immunity (PTI) on different parasites have been identified thus some management strategies could be created using host-induced gene silencing (HIGS), an RNAi based method. Moreover, epigenetic regulations may be important for the adaptation to parasitic plants. Also, miRNAs may have an important role in adaptation. For example, the interaction between dodder and alfalfa was found out in terms of DNA methylation (Vaniushin et al., 1979).

It is known that plants respond strongly when they are challenged a second time to the same stressor. For example, according to (Ibrahim, 2016) the germination rate was improved when seeds were challenged a second time to salinity stress. Moreover, these circumstances were observed for both biotic and abiotic stress. So, it can be said that if an organism is challenged a second time to any stressor, the next generation will be more tolerant. This phenomenon is called as systemic acquired resistance (SAR) (Durrant & Dong, 2004). Systemic acquired resistance is induced by stress-responsive genes and pathogen-related proteins. SAR, pathogen-associated molecular patterns (PAMP) and small interfering RNAs play crucial roles in plant response to pathogens (Deleris et al., 2016) thought that these mechanisms are directly related to epigenetic mechanisms. Moreover, some evidence reveals that there is a relationship between environmental stressors and epigenetic control (López Sánchez et al., 2021).

While traditional breeding remains vital, biotechnological approaches such as host-induced gene silencing (HIGS) provide complementary tools (Giudice et al., 2021).

The Usage Opportunity of Host Induced Gene Silencing in Parasitic Plant Management

In the last years, numerous studies have revealed that there is a small RNAs (sRNAs) exchange between the host and parasite (Buck et al., 2014; Hua et al., 2018; LaMonte et al., 2012; Shahid et al., 2018; Zhang et al., 2016). Therefore, it can be said that RNAi technology is becoming a powerful tool for crop improvement. Although some studies exist about the interaction between host and parasites such as nematodes, fungi and viruses, the number of studies about parasitic weeds are enough. Especially RNAi-based technologies such as spray-induced gene silencing (SIGS) and host-induced gene silencing (HIGS) can be useful. Particularly, it can be dwelled on host-induced gene silencing (HIGS). As it is mentioned before this method is RNAi-based method and because this technology is sequence specific, a specific site can be directly targeted thus parasitic organisms can be damaged. This could be a good endogenous mechanism for parasitic plant management.

The first step of HIGS is the determination of the target gene, which plays an important role in parasitism. For example, SaExp3 in *Striga* and TvQR1in *Triphysaria versicolor* can be good examples because they have directly played a role in parasitism (Bandaranayake et al., 2010; Bandaranayake et al., 2012; O'Malley & Lynn, 2000). Moreover, CYTOKININ RESPONSE FACTOR 5 (CKX5), WRI1 (ETHYLENE-RESPONSIVE TRANSCRIPTION FACTOR WRI1-LIKE), JASMONOYL-L-AMINO ACID SYNTHETASE GH3.5 (JAR1), GIBBERELLIN INSENSITIVE DWARF 1 (GID1), PYRABACTIN RESISTANCE-LIKE 8 (PYL8), and BIG (auxin transport protein), PECTINESTERASE 4 (PME4), POLYGALACTURONASE 5 (PGLR5), and BETA-DXYLOSIDASE 6 (BXL6), are involving to host-parasite interaction for the parasitism (Jiang et al., 2021).

The Usage of Non-Coding RNAs in Tomato Breeding

Double-stranded hairpin RNA (hpRNA), an RNAi-based technique can be considered as another powerful tool, they can target vital parasite genes. It is a point to take into consideration that when they are designed against parasitic plants, they do not show any phenotype in the host (Yoder et al., 2009). Another key point in this context is the determination of best parasite genes to silence. For this purpose, the parasitic plant genome project has considerable studies but as it is known that plant genomes are updating consistently, present data needs to be compared with current information (Westwood et al., 2012). In these purposes various micro RNAs have been determined for example MiR482 is directly target to NBS-LRR resistance genes so it can be said that it is a negative regulator for plant immune system also miR6022 and miR6024 have similar effect on the plant immune system (Li et al., 2023). Therefore, it can be said that numerous microRNAs or other non-coding RNAs have a crucial role for plant immune system both biotic and abiotic stress resistance. For this reason, non-coding RNAs have a huge potential for using in plant breeding (Jhu et al., 2023). The mechanism of Double-stranded hairpin RNA (hpRNA) demonstrated in Figure 2.

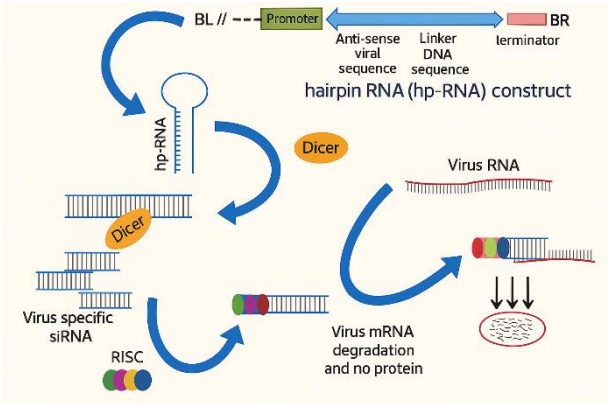

Figure 2. The mechanism of Double-stranded hairpin RNA (hpRNA)

There is an ongoing debate on an argument about whether the molecules can be transferred from host to parasitic plants (LeBlanc et al., 2012). However, tomato and pumpkin examples reveal that RNAs of the host can be transferred via haustoria and these molecules can be detected across 30 cm of haustoria using RT-PCR (Roney et al., 2007). This evidence can be associated with the phylogeny of the host and parasite as well (Clarke et al., 2019). These findings also demonstrate the trafficking between host and parasite in evolutionary timescale. For instance, *atp1*, a mitochondrial gene and its homolog were found in both *Plantago* and its parasite *Cuscuta* (Mower et al., 2004).

The success of RNAi-based strategies depends on the direct targeting of desired traits. If a strategy negatively affects the required traits such as yield or fruit quality, it will not be successful. Therefore, it can be said that the determination of vital genes in parasitic plants. For this reason, they can be searched on the open-source databases. The Parasitic Plant Genome Project, (Westwood et al., 2010) can be useful for the researchers also http://www.jgi.doe.gov/, https://blast.ncbi.nlm.nih.gov/Blast.cgi and https://www.ncbi.nlm.nih.gov/ may be useful tools for the researchers as well.

Taken together, these approaches highlight both the promise and challenges of ncRNA-based technologies in tomato breeding.

Conclusions

As a result, parasitic weeds are really an enormous problem in agricultural production. It is known that there are numerous different management methods such as herbicide usage, breeding and other biotechnological methods. Although these methods are partly successful, mutations and variable climate conditions restrict their efficiency. Therefore, divergent methods are becoming important day by day. For instance, non-coding RNAs are a relatively novel approach in this field.

Non-coding RNAs are a relatively brand-new topic in weed science. Despite the fact that there is much research in some fields such as nematodes, fungi, viruses etc., many different mechanisms between host and parasitic plants could not be exposed. Therefore, the main source of motivation was remarking on this review article. Especially, HIGS and SIGS topics will become important. When new investigations are revealed, these technologies will become significant for both pesticide and plant breeding industries.

Declarations

Ethical Approval Certificate

This study did not involve any experiments on animals or human participants and therefore did not require ethical approval.

Author Contribution Statement

Halim Can Kayikci: Conceptualization, study design, supervision, data collection and/or processing, data analysis and/or interpretation, literature search, writing the original draft, critical review

Esra Cignitas: Conceptualization, study design, data collection and/or processing, data analysis and/or interpretation, literature search, supervision, critical review, submission and revision

Alparslan Karabeniz: Conceptualization, study design, supervision, data collection and/or processing, data analysis and/or interpretation, literature search, writing, critical review, submission and revision

Nedim Mutlu: Supervision, literature search, critical review, submission and revision

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Conflict of Interest

The authors declare no conflict of interest.

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