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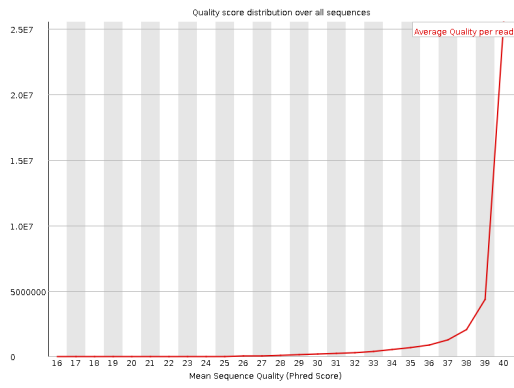
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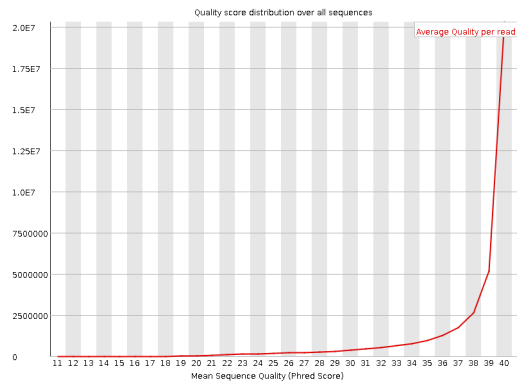
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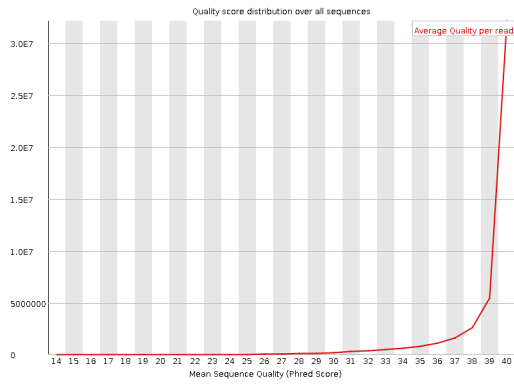
APPENDIX I



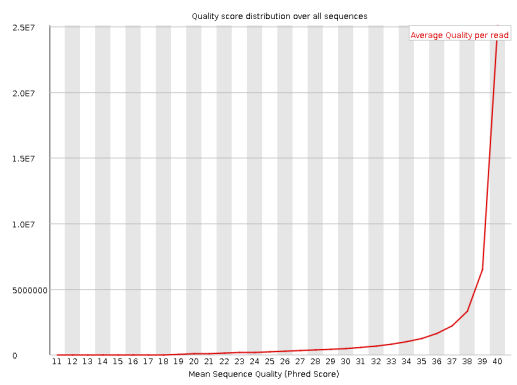
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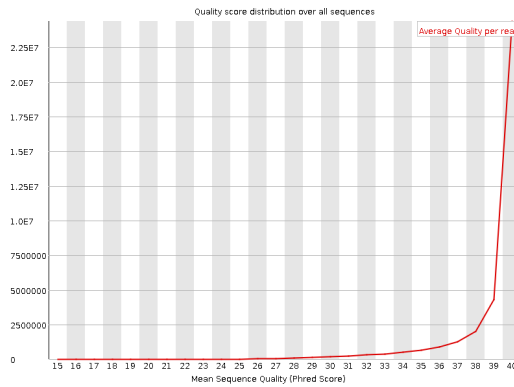
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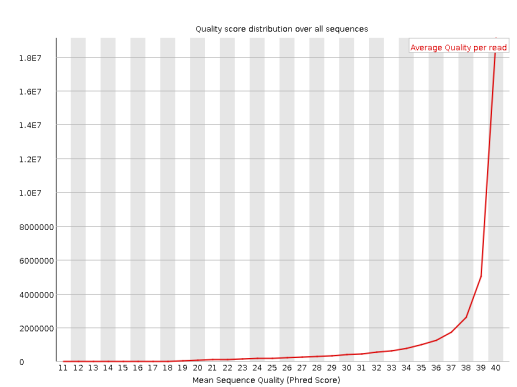
Control2_R1



Control2_R2

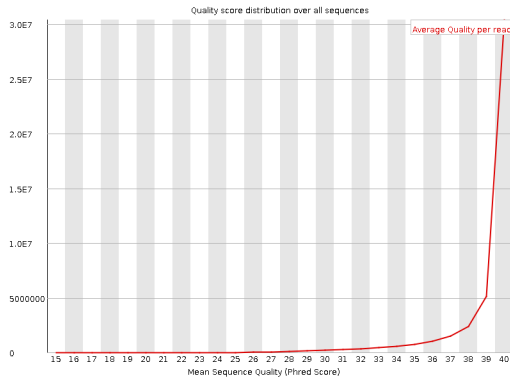


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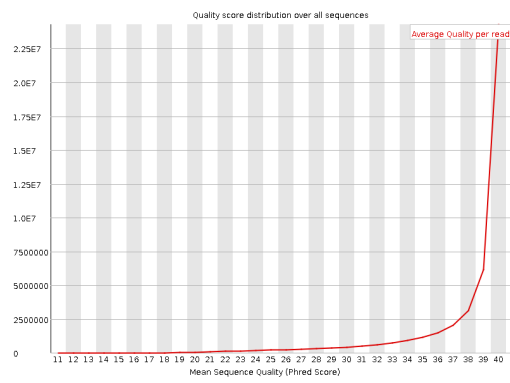


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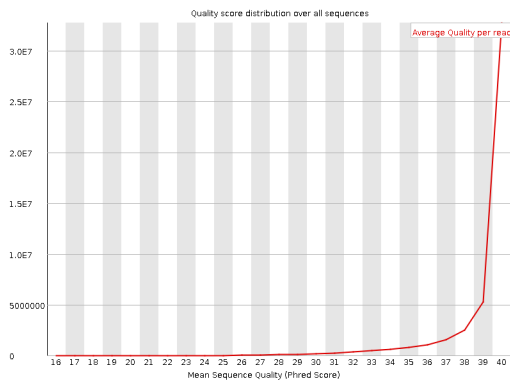
The per sequence quality score of the control samples



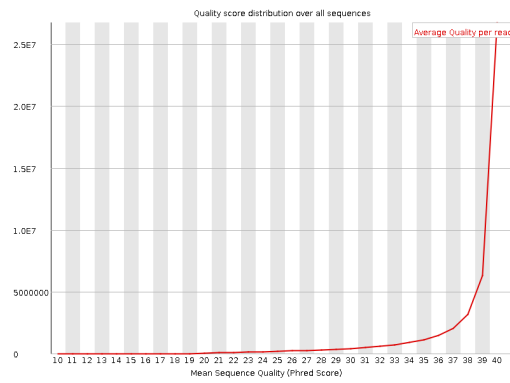
TMB-infested1_R1



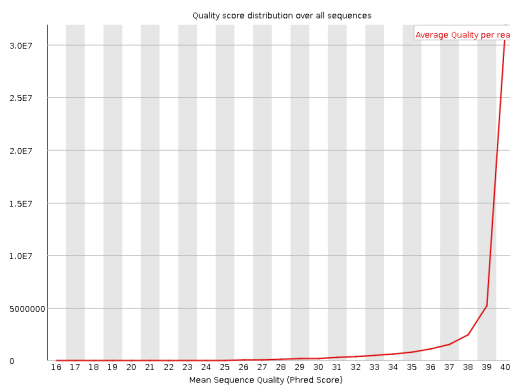
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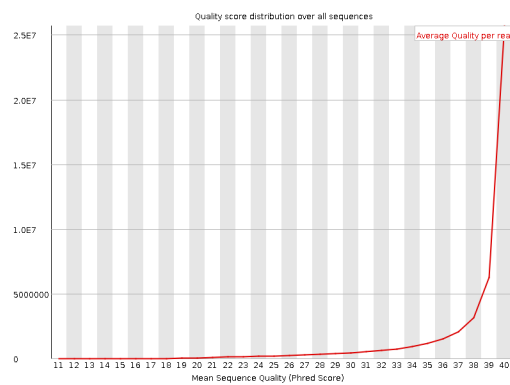
TMB-infested2_R1



TMB-infested2_R2

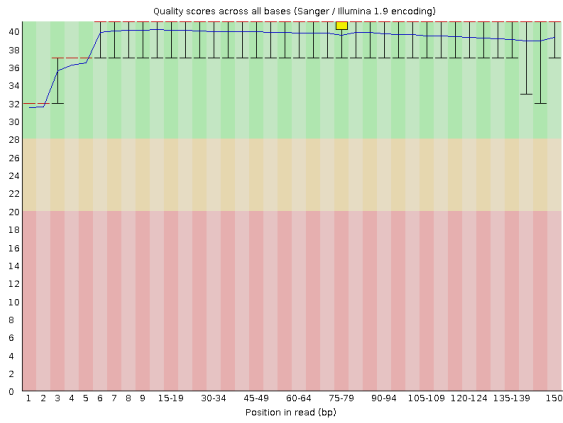


TMB-infested3_R1

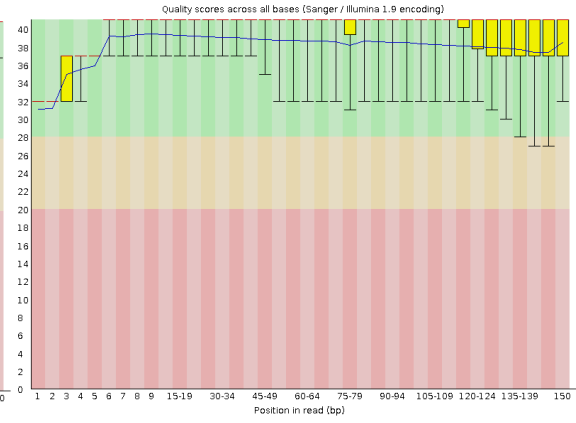


TMB-infested3_R2

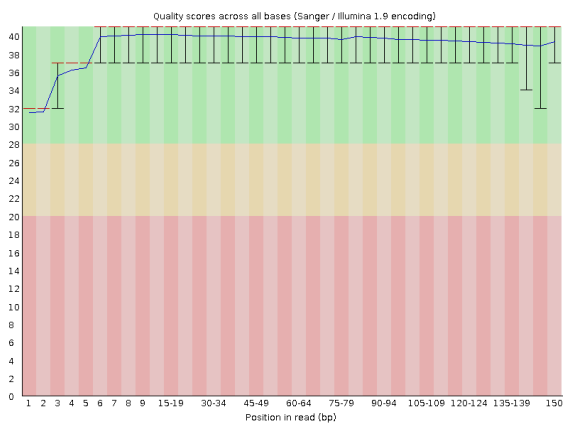
The per sequence quality score of the TMB-infested samples



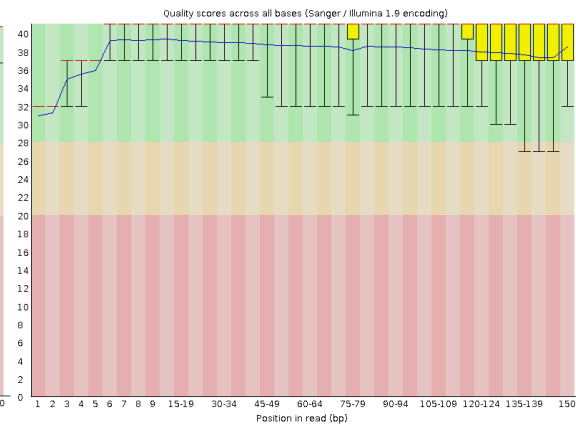
Control1_R1



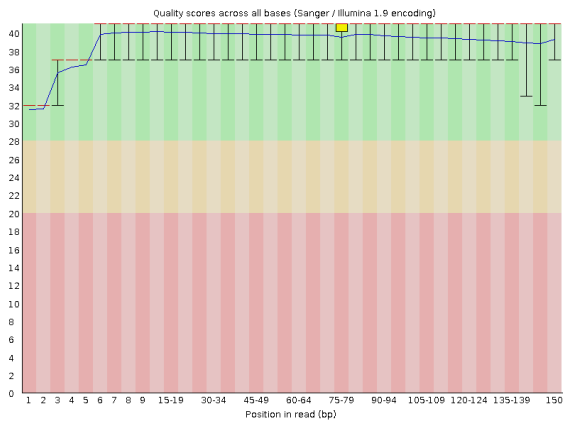
Control1_R2



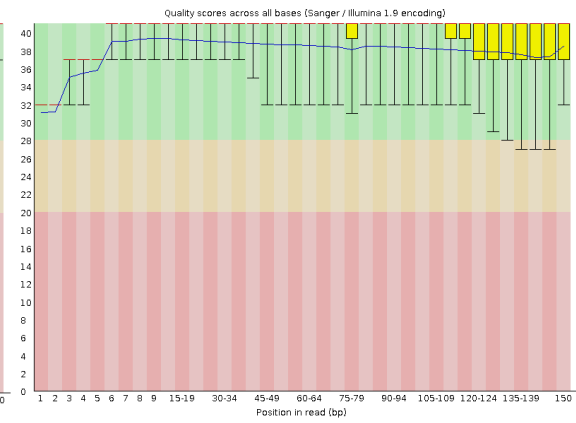
Control2_R1



Control2_R2

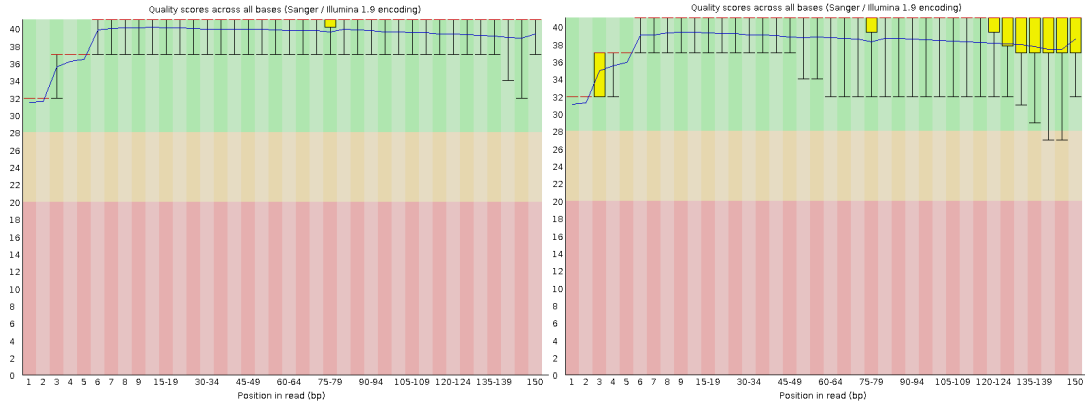


Control3_R1



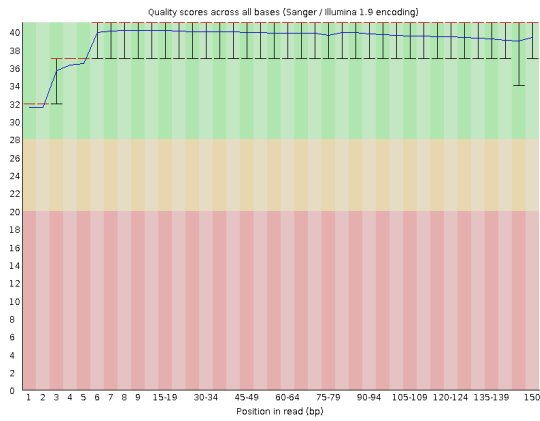
Control3_R2

The per base quality score of the control samples

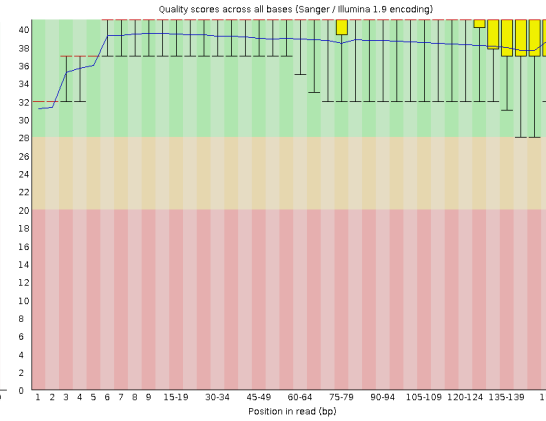


TMB-infested1_R1

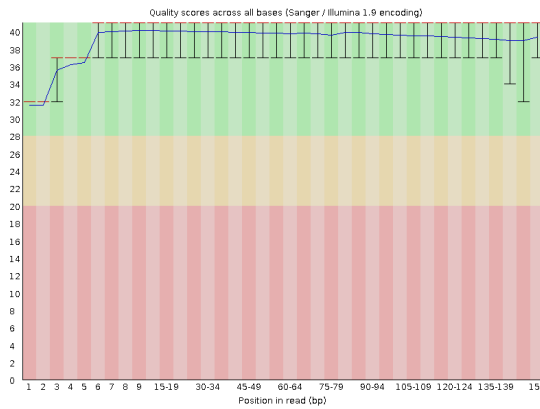
TMB-infested1_R2



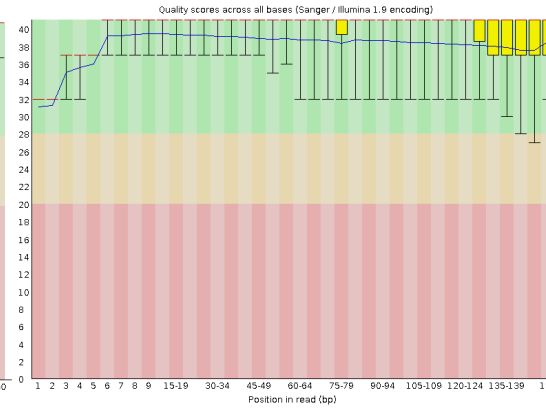
TMB-infested2_R1



TMB-infested2_R2



TMB-infested3_R1



TMB-infested3_R2

The per base quality score of the TMB-infested samples

APPENDIX II



Helopeltis theivora Responsive Transcriptomic Reprogramming Uncovers Long Non-coding RNAs as Possible Regulators of Primary and Secondary Metabolism in Tea Plant

Kuntala Sarma Bordoloi^{1,2} · Pooja Moni Baruah¹ · Bhaben Tanti¹ · Sarvajeet Singh Gill³ · Niraj Agarwala¹

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Abstract

Helopeltis theivora or the tea mosquito bug (TMB) is reportedly one of the most devastating pests of tea plant (*Camellia sinensis*) causing threat to the beverage crop. Long non-coding RNAs (lncRNAs) constitute a group of endogenous RNAs that play gene regulatory roles in eukaryotes. In the present study, 9502 lncRNAs were identified from healthy and TMB-infested *C. sinensis* tissues using high-throughput strand-specific RNA sequencing, out of which 80 lncRNAs got differentially expressed in response to TMB infestation. Determination of genes that could act as potential targets of lncRNAs revealed that the identified lncRNAs could possibly target as many as 5804 genes. Differential gene expression (DGE) analysis led to the identification of 3665 differentially expressed genes (DEGs), of which, the expression of 1767 genes got upregulated and 1898 genes got downregulated during tea plant's response to TMB. Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) enrichment analysis of DEGs and lncRNA-target genes have shown that TMB infestation might have triggered transcriptomic reprogramming leading to altered primary and secondary metabolism in *C. sinensis*. lncRNAs can act as competing endogenous RNAs (ceRNAs) to bind with common microRNA (miRNA) response elements (MREs) involving a competition between mRNAs and lncRNAs. We report 11 lncRNAs competing with 14 mRNAs to bind with 28 miRNAs forming the ceRNA network. The expression of 6 DEGs and 5 differentially expressed lncRNAs (DELs) has been validated by qRT-PCR.

Keywords Long non-coding RNA · *Camellia sinensis* · Transcriptome · *Helopeltis theivora* · High-throughput RNA sequencing · ceRNA

Introduction

Tea, being a perennial monocultured crop, attracts a huge number of insect pests thus limiting its production. Tea plant serves as a suitable host plant for a large range of insect pests and other algal, fungal, and bacterial pathogens which leads to serious loss of yield (Roy et al. 2015). However,

among the biotic agents causing stress in tea plants, the tea mosquito bug (TMB), *Helopeltis theivora* Waterhouse is one of the most devastating pests of *Camellia sinensis*. Large-scale and indiscriminate use of pesticides to manage TMB is not only adversely affecting the natural ecosystem but also creating problems of pesticide residue in made tea (Roy et al. 2009).

The genus *Helopeltis* has about 41 species (Schmitz 1968, 1988). But only three of them namely *H. antonii*, *H. theivora*, and *H. bradyi* are reported in India (Stonedahl 1991; Sundararaju 1996). In India, significant damages to the tea crop have been observed to be caused by *H. theivora*. TMB belongs to the group of sap-sucking mirids of the order Hemiptera. North-East India reports a significant loss of 15–20 lakh kgs of commercial tea each year due to TMB infestation. The TMB normally feeds on young shoots and new flushes. It sucks the sap from tissues through proboscis. Feeding of TMB results in the formation of a circular ring

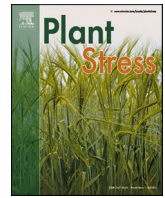
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✉ Niraj Agarwala
niraj_botany@gauhati.ac.in

¹ Department of Botany, Gauhati University, Gopinath Bordoloi Nagar, Guwahati, Assam 781014, India

² Mangaldai College, Upahupara, Mangaldai, Assam 784125, India

³ Centre for Biotechnology, Maharshi Dayanand University, Rohtak, Haryana 124001, India



Identification of circular RNAs in tea plant during *Helopeltis theivora* infestation

Kuntala Sarma Bordoloi^{a,b}, Pooja Moni Baruah^a, Niraj Agarwala^{a,*}

^a Department of Botany, Gauhati University, Gopinath Bordoloi Nagar, Guwahati, Assam 781014, India

^b Department of Botany, Mangaldai College, Upahupara, Mangaldai, Assam 784125, India

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ABSTRACT

The tea mosquito bug (TMB) or *Helopeltis theivora* has been reported as a significant tea pest that causes major tea crop loss. Circular RNAs (circRNAs) are a newly discovered group of the non-coding RNA (ncRNA) and are known to function in gene regulation process. Tea plant (*Camellia sinensis*) has not been explored for the detection of circRNAs during pest infestation. This is the first report of circRNAs identified in *C. sinensis* infested by a sap-sucking insect *H. theivora*. In total, we identified 709 circRNAs in six RNA-seq libraries. Analysis of the differential expression pattern revealed that 34 circRNAs got upregulated/downregulated in response to *H. theivora* attack. Functional annotation and enrichment analysis of the differentially expressed circRNAs showed that the circRNA-target genes were enriched in biological pathways like “tryptophan metabolism”, “biosynthesis of secondary metabolites”, “porphyrin metabolism”, “nucleocytoplasmic transport”, “N-glycan biosynthesis” etc. miRNA-mediated interaction analysis of the circRNAs also showed that 17 differentially expressed circRNAs could also act as “sponges” thus masking the miRNA-mRNA binding and subsequently repressing mRNA cleavage. These differentially expressed circRNAs were predicted to have the capacity to behave as endogenous target mimics (eTMs) for potential genes like aspartyl protease, phospholipase, lectin receptor etc.

Background

Plants often undergo biotic stresses mainly posed by microbes such as bacteria, fungi and viruses as well as insect pests (Gull et al., 2019). The role of pattern recognition receptors (PRRs) come to play during plant's perception to herbivory. Plants recognize herbivory or insect attack through binding of PRRs with damage associated molecular patterns (DAMPs) released after wounding or herbivore associated molecular patterns (HAMPs) which are active components of herbivore/insect's salivary secretions. Sensing of HAMPs or PAMPs triggers the downstream signaling cascades in the plant cell like production of reactive oxygen species (ROS), rise in cytosolic Ca²⁺ concentration, membrane depolarization, MAPK cascade signaling. Defense signaling is a complicated process and involves multiple genes and their components. These early signaling events lead to reprogramming of defense hormonal pathways like those of salicylic acid (SA) and jasmonic acid (JA) and thereby defense is accomplished (Erb and Reymond, 2019). Previous reports provided evidence regarding the involvement of non-coding RNAs (ncRNAs) like long non-coding RNAs (lncRNAs) and

circular RNAs (circRNAs) in regulation of defense hormone signaling (Li et al., 2021; Zhang et al., 2020). With rapid development of high-throughput sequencing technology, a large number of ncRNAs like lncRNAs and miRNAs, were identified and confirmed as the crucial regulator for gene expression and biological function in different biological processes (Shafiq et al., 2015; Budak et al., 2020; Bordoloi and Agarwala, 2021; Bordoloi et al., 2021a,2021b; Baruah et al., 2021a;2021b). As an important gene expression regulator amongst ncRNAs, circRNAs are a novel class of endogenous ncRNAs characterized by the existence of a covalent bond linking the 3' and 5' ends. Different from the traditional linear RNAs terminated with 3' tails and 5' caps, circRNAs could form covalently closed ring structures by back-spliced circularization without 5'–3' polarities (Chen 2016). They arise as products of post-transcriptional mRNA maturation during splicing. Their formation take place when back splicing (head-to-tail splicing) occurring between downstream donor segment and upstream acceptor segment generates a covalently closed RNA molecule which is circular in form (Ashwal-Fluss et al., 2014; Suzuki and Tsukahara, 2014). They may derive from exons (exonic circRNA), introns (intronic

* Corresponding author.

E-mail address: niraj_botany@gauhati.ac.in (N. Agarwala).

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MicroRNAs in plant insect interaction and insect pest control

Kuntala Sarma Bordoloi, Niraj Agarwala*

Department of Botany, Gauhati University, Gopinath Bordoloi Nagar, Guwahati, Assam 781014, India

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RNAi

ABSTRACT

Insects are a threat to plants and cause havoc in considerable ways. Interestingly, a group of small non-coding RNAs called microRNAs (miRNAs) are found to be associated with the regulatory processes of plants both in pre and post-infestation scenarios either elevating or demoting expression levels of different genes involved in plant-insect interaction. Studies show roles of a number of miRNAs during plant-insect interaction targeting a range of genes from transcription factors (TFs) to genes involved in plant growth and development, from transmembrane receptors to molecules involved in various signalling pathways. The role of miRNAs in regulating phytohormone signalling show the complex interaction of miRNA/mRNA modules in plant-insect herbivory. Biotechnological approaches involving RNAi strategy prove to be successful in eradicating pests. In this review, we have discussed the progress made so far in understanding the role of miRNAs in plant insect interactions and artificial miRNA (amiRNA) mediated RNAi strategies used to combat the menace of insect pests in plants.

1. Introduction

Small non-coding RNAs (sRNAs) of ~20–30 nucleotides in length are found to control gene expression in eukaryotes by regulation of genes that share complementarity with the regulating sRNA molecules. These micromanagers of gene expression play an undeniable role in changing the expression patterns of genes in tissue-specific manner, thus controlling the overall metabolism and physiological processes of the organism (Bartel, 2004). Among the non-coding sRNAs, small-interfering RNAs (siRNAs) and microRNAs (miRNAs) are the major regulators in silencing the expression of certain genes. Although the mechanism of action of both siRNAs and miRNAs are almost similar but both of the classes of sRNAs follow different paths of biogenesis (Carthew and Sontheimer, 2009).

miRNAs are 19–24 nucleotides (~22 nt) long endogenous molecules, that serve as regulators of endogenous nucleic acids either by the degradation of complementary mRNA transcripts or by inhibiting the translation process (Bartel, 2004; Chen, 2005; Brodersen et al., 2008; Wang et al., 2019). The first miRNA identified was that of the *lin-4* product in the nematode *Caenorhabditis elegans* (Lee et al., 1993). In a pioneering work, it was seen that the *lin-4* gene doesn't code for any protein, rather some 22 nt and 61 nt long products were formed which had high complementarity with the 3' UTR of the transcript of the gene *lin-14*. The longer product acted as the precursor for the shorter product by folding itself into a stem loop structure. *Lin-4* gene products were seen

to repress the *lin-14* gene activity during larval developmental stages of *C. elegans* (Bartel, 2004; Lee et al., 1993; Wightman et al., 1993). Progressive studies revealed the role of miRNAs in different metabolic processes of both plants and animals. For instance, *Arabidopsis CAF* (Carpel Factory) gene which is homologous to Dicer proteins, codes for a protein with RNA helicase activity at the N-terminal domain and RNase III-like activity at the C-terminal domain. This *CAF* gene product was shown to associate with determinate floral development (Jacobsen et al., 1999) and miRNA processing activities in *Arabidopsis* (Reinhart et al., 2002). The *caf* mutants showed reduced accumulation of miRNAs (Reinhart et al., 2002) and indeterminate floral development in *Arabidopsis* (Jacobsen et al., 1999). The miRNA biogenesis and processing can be regulated by plants in response to external factors (Manavella et al., 2019).

miRNAs are synthesized by RNA-Pol II from non-coding regions of DNA, especially introns and very rarely from 5'UTR and 3'UTR regions (Carthew and Sontheimer, 2009). RNA-Pol II transcribes the regions of the DNA into long primary transcripts being capped and polyadenylated called the pri-miRNAs which then fold to form a looped double stranded structure (Carthew and Sontheimer, 2009; Pareek et al., 2015). The pri-miRNAs are then cut into 500–800 nucleotides long pre-miRNAs by an enzyme called DCL1 (Dicer Like 1) that has RNaseIII activity with the coordination of HYL1 (Hyponastic Leaves 1), a dsRNA binding protein and SE (Serrate), a zinc finger protein (Pareek et al., 2015; Zhu, 2008; Zhuo et al., 2013). The unstable pre-miRNAs are converted to miRNA:

* Corresponding author.

E-mail addresses: kuntalab@ Gauhati.ac.in (K.S. Bordoloi), niraj_botany@ Gauhati.ac.in (N. Agarwala).

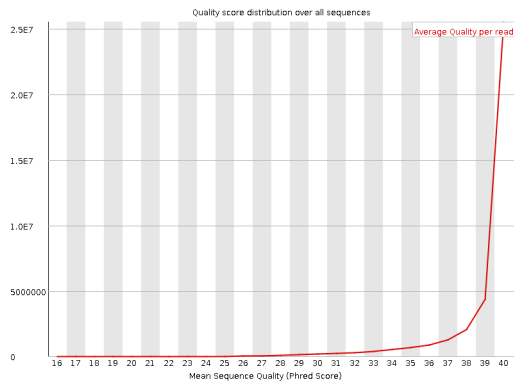
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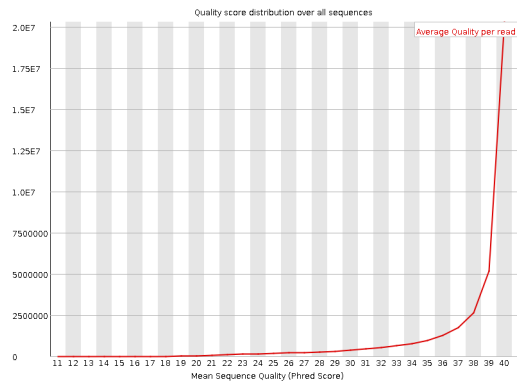
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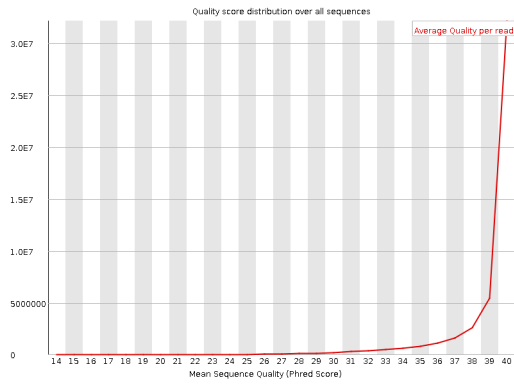
APPENDIX I



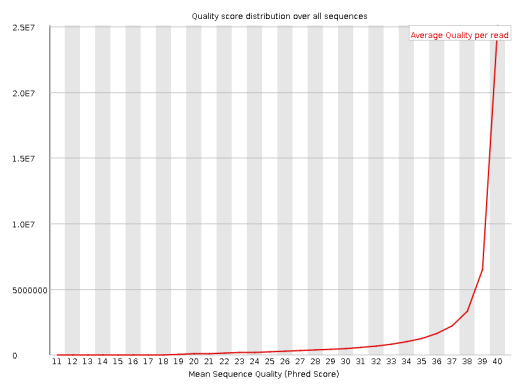
Control1_R1



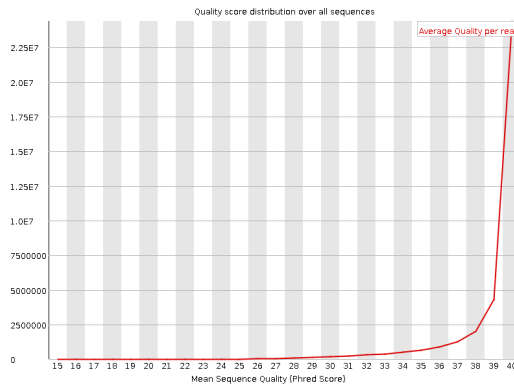
Control1_R2



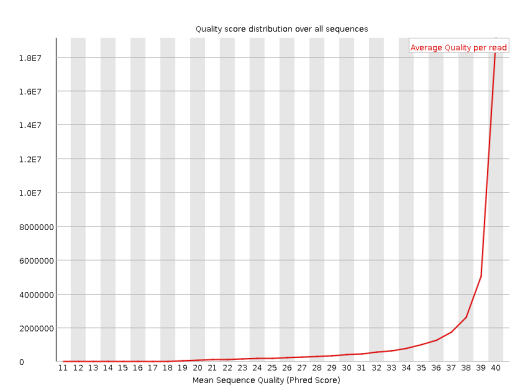
Control2_R1



Control2_R2

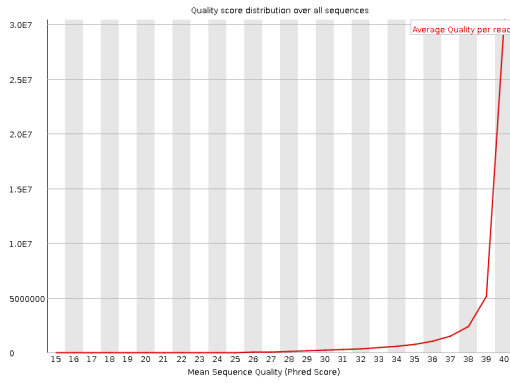


Control3_R1

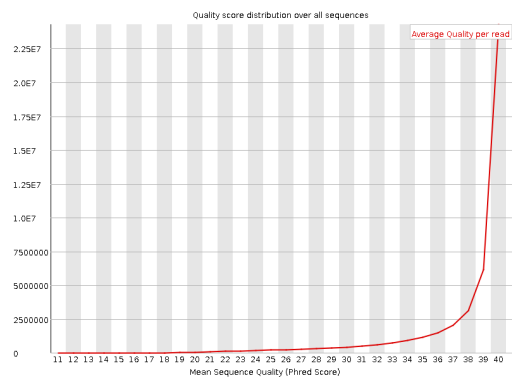


Control3_R2

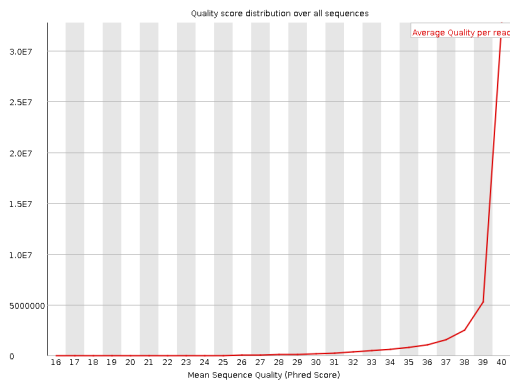
The per sequence quality score of the control samples



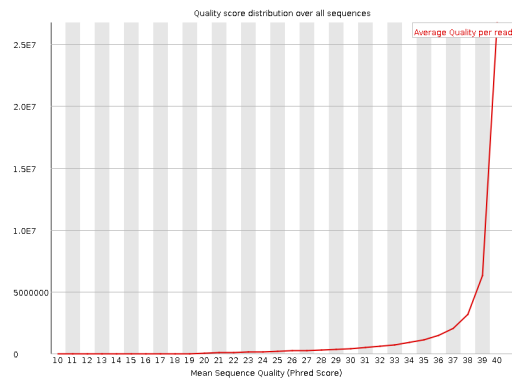
TMB-infested1_R1



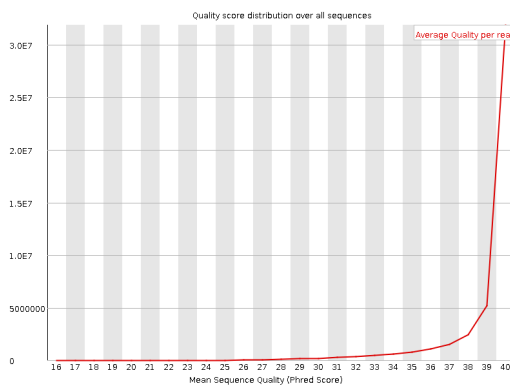
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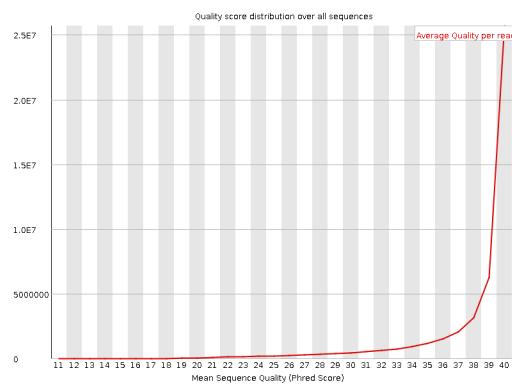
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TMB-infested2_R2

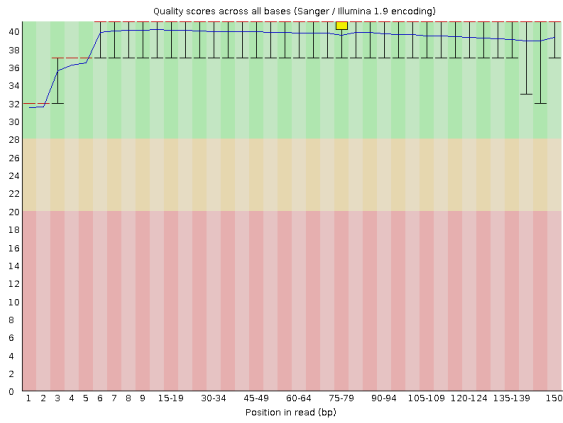


TMB-infested3_R1

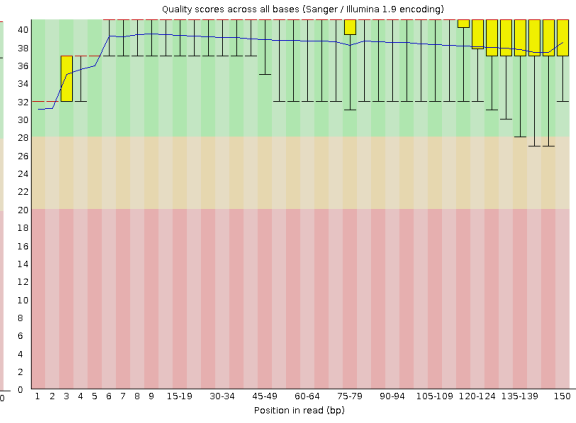


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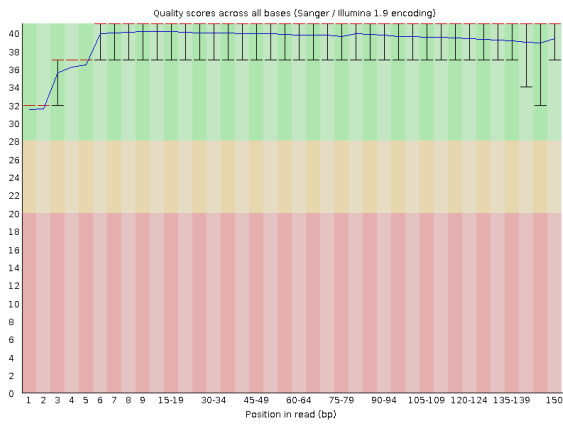
The per sequence quality score of the TMB-infested samples



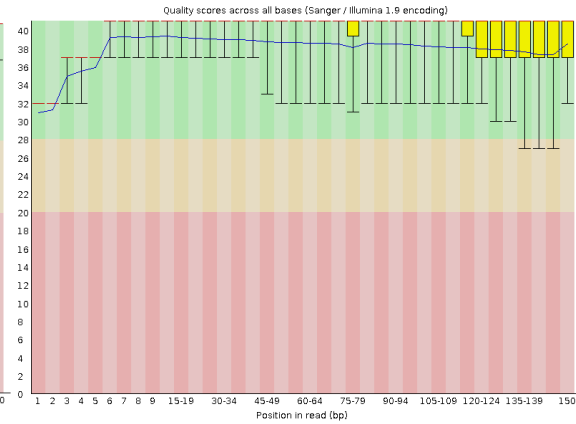
Control1_R1



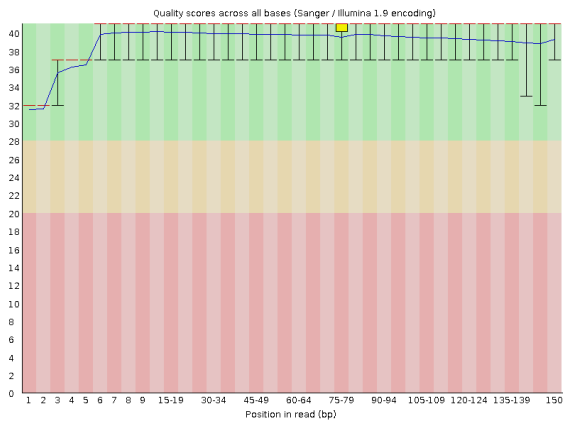
Control1_R2



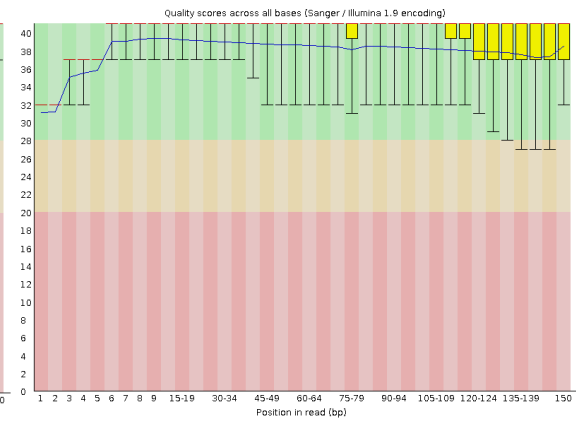
Control2_R1



Control2_R2

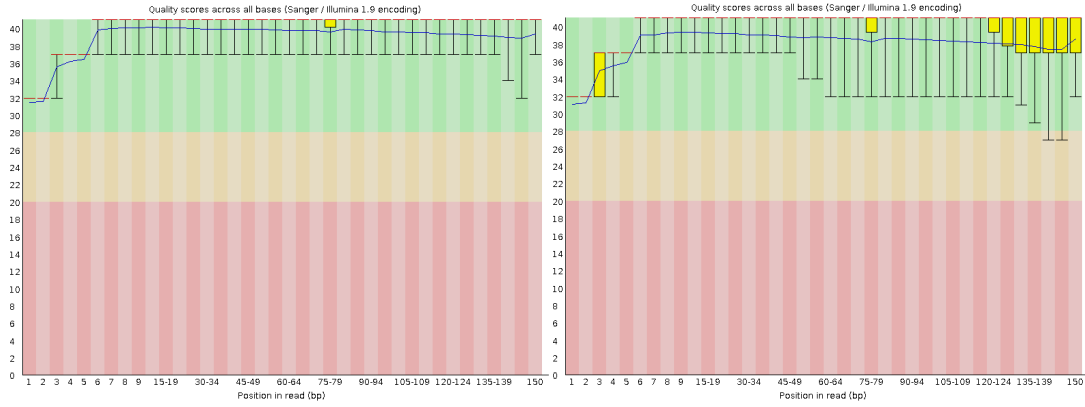


Control3_R1



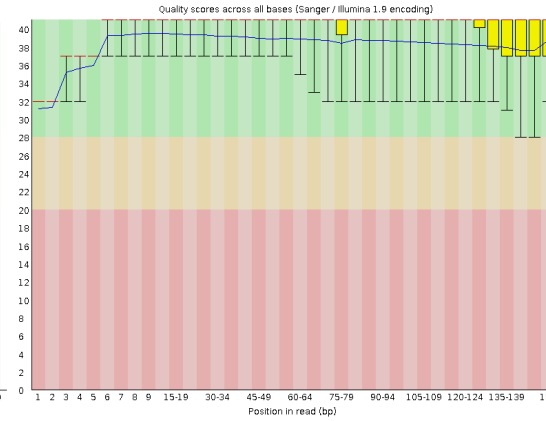
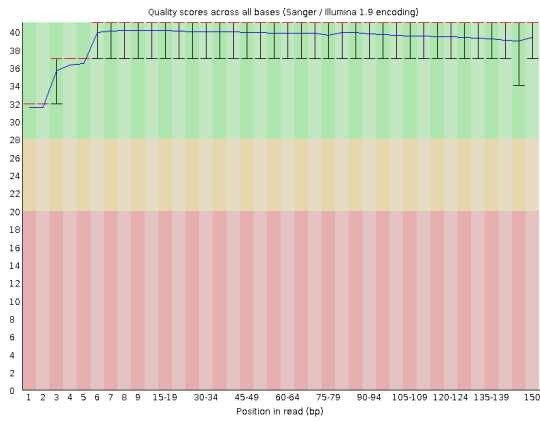
Control3_R2

The per base quality score of the control samples



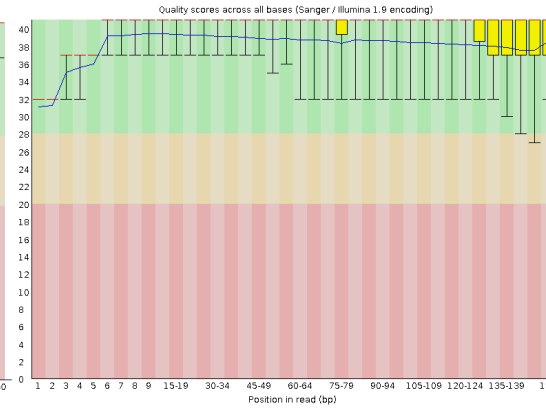
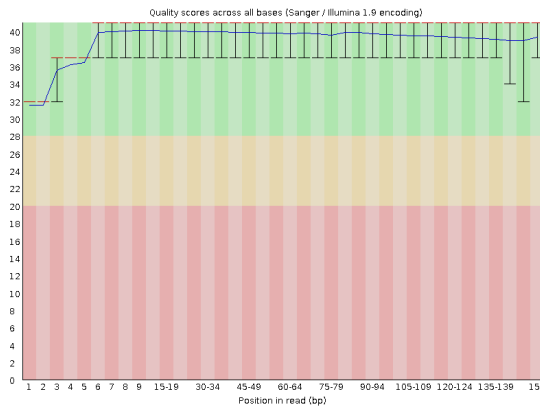
TMB-infested1_R1

TMB-infested1_R2



TMB-infested2_R1

TMB-infested2_R2



TMB-infested3_R1

TMB-infested3_R2

The per base quality score of the TMB-infested samples

APPENDIX II



Helopeltis theivora Responsive Transcriptomic Reprogramming Uncovers Long Non-coding RNAs as Possible Regulators of Primary and Secondary Metabolism in Tea Plant

Kuntala Sarma Bordoloi^{1,2} · Pooja Moni Baruah¹ · Bhaben Tanti¹ · Sarvajeet Singh Gill³ · Niraj Agarwala¹

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Abstract

Helopeltis theivora or the tea mosquito bug (TMB) is reportedly one of the most devastating pests of tea plant (*Camellia sinensis*) causing threat to the beverage crop. Long non-coding RNAs (lncRNAs) constitute a group of endogenous RNAs that play gene regulatory roles in eukaryotes. In the present study, 9502 lncRNAs were identified from healthy and TMB-infested *C. sinensis* tissues using high-throughput strand-specific RNA sequencing, out of which 80 lncRNAs got differentially expressed in response to TMB infestation. Determination of genes that could act as potential targets of lncRNAs revealed that the identified lncRNAs could possibly target as many as 5804 genes. Differential gene expression (DGE) analysis led to the identification of 3665 differentially expressed genes (DEGs), of which, the expression of 1767 genes got upregulated and 1898 genes got downregulated during tea plant's response to TMB. Gene Ontology (GO) and Kyoto Encyclopedia of Genes and Genomes (KEGG) enrichment analysis of DEGs and lncRNA-target genes have shown that TMB infestation might have triggered transcriptomic reprogramming leading to altered primary and secondary metabolism in *C. sinensis*. lncRNAs can act as competing endogenous RNAs (ceRNAs) to bind with common microRNA (miRNA) response elements (MREs) involving a competition between mRNAs and lncRNAs. We report 11 lncRNAs competing with 14 mRNAs to bind with 28 miRNAs forming the ceRNA network. The expression of 6 DEGs and 5 differentially expressed lncRNAs (DElNs) has been validated by qRT-PCR.

Keywords Long non-coding RNA · *Camellia sinensis* · Transcriptome · *Helopeltis theivora* · High-throughput RNA sequencing · ceRNA

Introduction

Tea, being a perennial monocultured crop, attracts a huge number of insect pests thus limiting its production. Tea plant serves as a suitable host plant for a large range of insect pests and other algal, fungal, and bacterial pathogens which leads to serious loss of yield (Roy et al. 2015). However,

among the biotic agents causing stress in tea plants, the tea mosquito bug (TMB), *Helopeltis theivora* Waterhouse is one of the most devastating pests of *Camellia sinensis*. Large-scale and indiscriminate use of pesticides to manage TMB is not only adversely affecting the natural ecosystem but also creating problems of pesticide residue in made tea (Roy et al. 2009).

The genus *Helopeltis* has about 41 species (Schmitz 1968, 1988). But only three of them namely *H. antonii*, *H. theivora*, and *H. bradyi* are reported in India (Stonedahl 1991; Sundararaju 1996). In India, significant damages to the tea crop have been observed to be caused by *H. theivora*. TMB belongs to the group of sap-sucking mirids of the order Hemiptera. North-East India reports a significant loss of 15–20 lakh kgs of commercial tea each year due to TMB infestation. The TMB normally feeds on young shoots and new flushes. It sucks the sap from tissues through proboscis. Feeding of TMB results in the formation of a circular ring

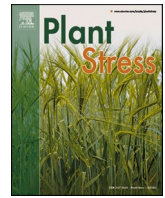
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✉ Niraj Agarwala
niraj_botany@gauhati.ac.in

¹ Department of Botany, Gauhati University, Gopinath Bordoloi Nagar, Guwahati, Assam 781014, India

² Mangaldai College, Upahupara, Mangaldai, Assam 784125, India

³ Centre for Biotechnology, Maharshi Dayanand University, Rohtak, Haryana 124001, India



Identification of circular RNAs in tea plant during *Helopeltis theivora* infestation

Kuntala Sarma Bordoloi^{a,b}, Pooja Moni Baruah^a, Niraj Agarwala^{a,*}

^a Department of Botany, Gauhati University, Gopinath Bordoloi Nagar, Guwahati, Assam 781014, India

^b Department of Botany, Mangaldai College, Upahupara, Mangaldai, Assam 784125, India

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 Plant-insect interaction

ABSTRACT

The tea mosquito bug (TMB) or *Helopeltis theivora* has been reported as a significant tea pest that causes major tea crop loss. Circular RNAs (circRNAs) are a newly discovered group of the non-coding RNA (ncRNA) and are known to function in gene regulation process. Tea plant (*Camellia sinensis*) has not been explored for the detection of circRNAs during pest infestation. This is the first report of circRNAs identified in *C. sinensis* infested by a sap-sucking insect *H. theivora*. In total, we identified 709 circRNAs in six RNA-seq libraries. Analysis of the differential expression pattern revealed that 34 circRNAs got upregulated/downregulated in response to *H. theivora* attack. Functional annotation and enrichment analysis of the differentially expressed circRNAs showed that the circRNA-target genes were enriched in biological pathways like “tryptophan metabolism”, “biosynthesis of secondary metabolites”, “porphyrin metabolism”, “nucleocytoplasmic transport”, “N-glycan biosynthesis” etc. miRNA-mediated interaction analysis of the circRNAs also showed that 17 differentially expressed circRNAs could also act as “sponges” thus masking the miRNA-mRNA binding and subsequently repressing mRNA cleavage. These differentially expressed circRNAs were predicted to have the capacity to behave as endogenous target mimics (eTMs) for potential genes like aspartyl protease, phospholipase, lectin receptor etc.

Background

Plants often undergo biotic stresses mainly posed by microbes such as bacteria, fungi and viruses as well as insect pests (Gull et al., 2019). The role of pattern recognition receptors (PRRs) come to play during plant's perception to herbivory. Plants recognize herbivory or insect attack through binding of PRRs with damage associated molecular patterns (DAMPs) released after wounding or herbivore associated molecular patterns (HAMPs) which are active components of herbivore/insect's salivary secretions. Sensing of HAMPs or PAMPs triggers the downstream signaling cascades in the plant cell like production of reactive oxygen species (ROS), rise in cytosolic Ca²⁺ concentration, membrane depolarization, MAPK cascade signaling. Defense signaling is a complicated process and involves multiple genes and their components. These early signaling events lead to reprogramming of defense hormonal pathways like those of salicylic acid (SA) and jasmonic acid (JA) and thereby defense is accomplished (Erb and Reymond, 2019). Previous reports provided evidence regarding the involvement of non-coding RNAs (ncRNAs) like long non-coding RNAs (lncRNAs) and

circular RNAs (circRNAs) in regulation of defense hormone signaling (Li et al., 2021; Zhang et al., 2020). With rapid development of high-throughput sequencing technology, a large number of ncRNAs like lncRNAs and miRNAs, were identified and confirmed as the crucial regulator for gene expression and biological function in different biological processes (Shafiq et al., 2015; Budak et al., 2020; Bordoloi and Agarwala, 2021; Bordoloi et al., 2021a,2021b; Baruah et al., 2021a;2021b). As an important gene expression regulator amongst ncRNAs, circRNAs are a novel class of endogenous ncRNAs characterized by the existence of a covalent bond linking the 3' and 5' ends. Different from the traditional linear RNAs terminated with 3' tails and 5' caps, circRNAs could form covalently closed ring structures by back-spliced circularization without 5'–3' polarities (Chen 2016). They arise as products of post-transcriptional mRNA maturation during splicing. Their formation take place when back splicing (head-to-tail splicing) occurring between downstream donor segment and upstream acceptor segment generates a covalently closed RNA molecule which is circular in form (Ashwal-Fluss et al., 2014; Suzuki and Tsukahara, 2014). They may derive from exons (exonic circRNA), introns (intronic

* Corresponding author.

E-mail address: niraj_botany@gauhati.ac.in (N. Agarwala).

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MicroRNAs in plant insect interaction and insect pest control

Kuntala Sarma Bordoloi, Niraj Agarwala*

Department of Botany, Gauhati University, Gopinath Bordoloi Nagar, Guwahati, Assam 781014, India

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Defense
Salicylic acid
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Plant-insect interaction
RNAi

ABSTRACT

Insects are a threat to plants and cause havoc in considerable ways. Interestingly, a group of small non-coding RNAs called microRNAs (miRNAs) are found to be associated with the regulatory processes of plants both in pre and post-infestation scenarios either elevating or demoting expression levels of different genes involved in plant-insect interaction. Studies show roles of a number of miRNAs during plant-insect interaction targeting a range of genes from transcription factors (TFs) to genes involved in plant growth and development, from transmembrane receptors to molecules involved in various signalling pathways. The role of miRNAs in regulating phytohormone signalling show the complex interaction of miRNA/mRNA modules in plant-insect herbivory. Biotechnological approaches involving RNAi strategy prove to be successful in eradicating pests. In this review, we have discussed the progress made so far in understanding the role of miRNAs in plant insect interactions and artificial miRNA (amiRNA) mediated RNAi strategies used to combat the menace of insect pests in plants.

1. Introduction

Small non-coding RNAs (sRNAs) of ~20–30 nucleotides in length are found to control gene expression in eukaryotes by regulation of genes that share complementarity with the regulating sRNA molecules. These micromanagers of gene expression play an undeniable role in changing the expression patterns of genes in tissue-specific manner, thus controlling the overall metabolism and physiological processes of the organism (Bartel, 2004). Among the non-coding sRNAs, small-interfering RNAs (siRNAs) and microRNAs (miRNAs) are the major regulators in silencing the expression of certain genes. Although the mechanism of action of both siRNAs and miRNAs are almost similar but both of the classes of sRNAs follow different paths of biogenesis (Carthew and Sontheimer, 2009).

miRNAs are 19–24 nucleotides (~22 nt) long endogenous molecules, that serve as regulators of endogenous nucleic acids either by the degradation of complementary mRNA transcripts or by inhibiting the translation process (Bartel, 2004; Chen, 2005; Brodersen et al., 2008; Wang et al., 2019). The first miRNA identified was that of the *lin-4* product in the nematode *Caenorhabditis elegans* (Lee et al., 1993). In a pioneering work, it was seen that the *lin-4* gene doesn't code for any protein, rather some 22 nt and 61 nt long products were formed which had high complementarity with the 3' UTR of the transcript of the gene *lin-14*. The longer product acted as the precursor for the shorter product by folding itself into a stem loop structure. *Lin-4* gene products were seen

to repress the *lin-14* gene activity during larval developmental stages of *C. elegans* (Bartel, 2004; Lee et al., 1993; Wightman et al., 1993). Progressive studies revealed the role of miRNAs in different metabolic processes of both plants and animals. For instance, *Arabidopsis CAF* (Carpel Factory) gene which is homologous to Dicer proteins, codes for a protein with RNA helicase activity at the N-terminal domain and RNase III-like activity at the C-terminal domain. This *CAF* gene product was shown to associate with determinate floral development (Jacobsen et al., 1999) and miRNA processing activities in *Arabidopsis* (Reinhart et al., 2002). The *caf* mutants showed reduced accumulation of miRNAs (Reinhart et al., 2002) and indeterminate floral development in *Arabidopsis* (Jacobsen et al., 1999). The miRNA biogenesis and processing can be regulated by plants in response to external factors (Manavella et al., 2019).

miRNAs are synthesized by RNA-Pol II from non-coding regions of DNA, especially introns and very rarely from 5'UTR and 3'UTR regions (Carthew and Sontheimer, 2009). RNA-Pol II transcribes the regions of the DNA into long primary transcripts being capped and polyadenylated called the pri-miRNAs which then fold to form a looped double stranded structure (Carthew and Sontheimer, 2009; Pareek et al., 2015). The pri-miRNAs are then cut into 500–800 nucleotides long pre-miRNAs by an enzyme called DCL1 (Dicer Like 1) that has RNaseIII activity with the coordination of HYL1 (Hyponastic Leaves 1), a dsRNA binding protein and SE (Serrate), a zinc finger protein (Pareek et al., 2015; Zhu, 2008; Zhuo et al., 2013). The unstable pre-miRNAs are converted to miRNA:

* Corresponding author.

E-mail addresses: kuntalab@ Gauhati.ac.in (K.S. Bordoloi), niraj_botany@ Gauhati.ac.in (N. Agarwala).

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