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# Evaluation of higher plant virus resistance genes in the green alga, *Chlorella variabilis* NC64A, during the early phase of infection with *Paramecium bursaria* chlorella virus-1

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## Abstract

With growing industrial interest in algae plus their critical roles in aquatic systems, the need to understand the effects of algal pathogens is increasing. We examined a model algal host–virus system, *Chlorella variabilis* NC64A and virus, PBCV-1. *C. variabilis* encodes 375 homologs to genes involved in RNA silencing and in response to virus infection in higher plants. Illumina RNA-Seq data showed that 325 of these homologs were expressed in healthy and early PBCV-1 infected ( $\leq 60$  min) cells. For each of the RNA silencing genes to which homologs were found, mRNA transcripts were detected in healthy and infected cells. *C. variabilis*, like higher plants, may employ certain RNA silencing pathways to defend itself against virus infection. To our knowledge this is the first examination of RNA silencing genes in algae beyond core proteins, and the first analysis of their transcription during virus infection.

**Keywords:** Transcriptome, *Phycodnaviridae*, Phytoplankton, RNA silencing, RNA directed DNA methylation, Post-transcriptional gene silencing

## Introduction

Algae are currently receiving considerable attention as a biofuel source. Certain eukaryotic algae (e.g., *Nannochloropsis* and *Chlorella* species) can produce fuel compatible lipids at a rate significantly higher than oil crop plants (e.g., soybean and palm) (Brennan and Owende, 2010). Additionally, certain algae can grow in regions that are unsuitable for typical crop plants and/or in brackish water. However, it is likely that algae grown at a large scale will experience pathogens, including viruses. Viruses are significant pathogens in traditional crop production and viruses may limit algal biomass yields. Furthermore, algal viruses are potentially a greater problem than higher plant viruses because many plant viruses are vectored by insects, mites, nematodes, or fungi. Thus, two components are required for a viral disease outbreak in higher plants; in contrast, no known vectors are required to spread algal viruses.

The field of algal virology is relatively new and only a few algal viruses have been extensively characterized (e.g., Brussaard and Martinez, 2008; Mackinder et al., 2009; Nagasaki, 2008; Van Etten and Dunigan, 2012; Wilson et al., 2009). Consequently, the complete range of their activities is unknown. However, given the global impact of algae, it is clear that algal viruses play a significant role in the environment (Brussaard et al., 2008; Jacquet et al., 2010; Suttle, 2007; Wilhelm and Matteson, 2008). Most of the research on algal viruses has been

conducted on large dsDNA viruses that infect both freshwater and marine algae and are classified in the family *Phycodnaviridae*. ssRNA, dsRNA and ssDNA viruses have also been discovered in recent years that infect certain algae (Brussaard and Martinez, 2008; Nagasaki, 2008). Thus, a broad range of algae-infecting virus types exists in nature.

Viruses included in the *Phycodnaviridae* have genomes ranging from 160 to 560 kbp that contain up to 600 protein-encoding genes and many tRNA encoding genes (Van Etten et al., 2010; Wilson et al., 2009). One genus in the *Phycodnaviridae* consists of large icosahedral, plaque-forming viruses that infect unicellular, *Chlorella*-like green algae, genus *Chlorovirus*. Chloroviruses are present in freshwater environments throughout the world with titers as high as 100,000 plaque-forming units (PFU) ml<sup>-1</sup> of indigenous water, although titers are typically in the range of 1–100 PFU ml<sup>-1</sup> (Van Etten, 2003; Van Etten and Dunigan, 2012).

The prototype *Chlorovirus* is *Paramecium bursaria* chlorella virus-1 (PBCV-1), which infects *Chlorella variabilis* NC64A (formerly *Chlorella* NC64A). *C. variabilis* is an endosymbiont in the protozoan, *Paramecium bursaria*. *C. variabilis* can be grown independent of its partner in the laboratory, which allows plaque assays of the virus and synchronous infection of its host. These properties allow one to study the virus life cycle in some detail. Furthermore, both the PBCV-1 (Dunigan et al., 2012) and the *C. variabilis* (Blanc et al., 2010) genomes have been sequenced and annotated.

Previous studies on the initial steps of virus infection of *C. variabilis* established that PBCV-1 rapidly attaches to the host cell wall and degrades a portion of the cell wall at the point of attachment (Thiel et al., 2010; Van Etten and Dunigan, 2012). The viral membrane then presumably fuses with the host membrane, facilitating entry of the viral DNA and virion-associated proteins into the cell, leaving an empty capsid attached to the surface. PBCV-1 lacks a recognizable RNA polymerase gene and so circumstantial evidence suggests that the viral DNA quickly moves to the nucleus and steals the host transcription machinery. As reported here, certain early viral transcripts were detected by 7 min post infection (p. i.). Another early event that occurs during this time frame is that host chromosomal DNA begins to be degraded, presumably by PBCV-1 encoded and packaged DNA restriction endonucleases (Agarkova et al., 2006). The early stages of infection end when viral DNA synthesis begins, ~60–90 min p.i. (Meints et al., 1986). Therefore, if the host cell is to initiate a response to virus infection it must do so within this early timeframe.

Although substantial information is available on the viral events associated with PBCV-1 infection (e.g. Thiel et al., 2010; Van Etten and Dunigan, 2012), very little is known about the initial response(s) of the host cell to virus infection. A related phycodnavirus, EhV-86, that infects the marine alga, *Emiliania huxleyi*, inhibits the host cell's programmed cell death (PCD) mechanism, which insures that the viruses have time to replicate (Bidle et al., 2007). Although *E. huxleyi*'s attempt to avoid EhV-86 replication through PCD ultimately results in cell death, it is clear that *E. huxleyi* has a means of resisting virus infection. The direct observations of developed resistance, the presence of viral genes in algal host genomes, and the apparent coevolution of algae and viruses in nature (Blanc et al., 2010; Derelle et al., 2008; Lindell et al., 2004; Monier et al., 2009; Thomas et al., 2011) all suggest that algae have mechanisms to avoid and/or limit virus infection.

Green algae and land plants share a common ancestry (Lewis and McCourt, 2004; Parfrey et al., 2010), and in higher land plants, the responses to virus infection, and to pathogens in general, have been studied extensively (e.g. Bari and Jones, 2009; Chisholm et al., 2006; Katiyar-Agarwal and Jin, 2010; Nimchuk et al., 2003; Soosaar et al., 2005). One mechanism, RNA silencing, active in both plants and animals, has the potential to be an important means of survival against virus infection in algae, particularly green algae (Cerutti and Casas-Mollano, 2006; Whitham et al., 2006). Presently RNA silencing has been best studied in the green alga *Chlamydomonas reinhardtii* (Cerutti et al., 2011; Schroda, 2006). However, no viruses have been found that infect this model alga, limiting its use for studying algal host-virus interactions. *C. variabilis* and PBCV-1 provide an ideal pair for examining the presence of RNA silencing genes in a host and their expression during virus infection. Despite *C. variabilis* being a competent host for PBCV-1 infection, the initial response of *C. variabilis* to infection might provide important information about a potential innate immune response to virus infection in these algae.

*Arabidopsis* is a well-studied model for understanding higher plant defenses, including RNA silencing (Aufsatz et al., 2002; Brodersen and Voinnet, 2006; Hammond et al., 2001; Matzke et al., 2009; Whitham et al., 2006). Key genes in the RNA silencing pathways such as argonautes (AGOs), dicer-like proteins (DCLs), and RNA dependent RNA polymerases (RdRPs) have been searched for in the genomes of 20 eukaryotic algae, covering a wide taxonomic range, including nine green algae (Cerutti et al., 2011). Though the presence of homologs to AGOs and DCLs suggests that RNA silencing may occur in *C. variabilis*, RNA silencing requires several other participants. In this manuscript we compile a more complete list of genes potentially involved in RNA silencing in *C. variabilis*

by searching for homologs to those known to be involved in RNA silencing in *Arabidopsis*. We also searched for homologs to other genes known to be induced by virus infection in *Arabidopsis* (Whitham et al., 2006). Furthermore, to discern whether or not *C. variabilis* utilizes these genes, we examined their expression in uninfected cells and in cells that were infected with PBCV-1 for 7, 14, 20, 40, and 60 min using RNA-seq Illumina data.

## Results and discussion

### Higher plant virus resistance genes in *C. variabilis*

Thirty-four RNA silencing genes that have been identified in higher plants, primarily *Arabidopsis* (plus two additions: helicases and ribonuclease family III members), and an additional 27 genes that are involved in response to virus infection in *Arabidopsis* (Brodersen and Voinnet, 2006; Matzke et al., 2009; Whitham et al., 2006) were used as queries against the *C. variabilis* genome using BLASTp. For these 61 genes and two general gene categories (see Table 1), 375 homologs were present in the *C. variabilis* genome, including 14 putative *Arabidopsis*-*C. variabilis* ortholog pairs identified by the reciprocal best BLASTp hit criterion (Table S1). Of the detected genes, 219 are homologs to those induced upon virus infection in *Arabidopsis*, while the remaining 156 are homologs to those involved in RNA silencing, with 73 of these being helicases and four possible DCLs classified as ribonuclease family III members (i.e. the two gene categories). Table S1 lists all of the genes searched for in the genome of *C. variabilis* and the corresponding list of homologs found along with the e-values supporting their similarity to the query sequences, putative orthologous genes are also noted.

While *C. variabilis* had homologs to many of the genes of interest, not all were detected using one or more *Arabidopsis* queries or even motif searches using MEME; 19 of the 61 were not detected. This indicates that either these genes are absent in *C. variabilis*, or are so divergent that they are not recognized by these methods. The fact that we found homologs to many of the genes of interest supports the practicality of using information gathered from higher plant studies to begin examining similar processes in green algae.

### How many of the 375 putative resistance genes are expressed during PBCV-1 infection?

The RNA-Seq approach (Mortazavi et al., 2008) produces millions of short cDNA reads that are mapped to a reference genome to obtain a genome-scale transcriptional map, which consists of the transcriptional structure and the expression level for each gene. We used the Illumina RNA-Seq method to gain insight into the transcriptional responses that are associated with infection of *C. variabilis* by PBCV-1. More than 105 million sequence reads, 50 bp in length, were generated from six time points during the first hour of infection - i.e., 0, 7, 14, 20, 40 and 60 min p.i. The sequence reads were aligned onto the *C. variabilis* genome and then analyzed to measure gene expression levels. We used this data to analyze the changes in transcription activity of the 375 resistance genes during PBCV-1 infection. The global results of the RNA-Seq study will be presented in a separate paper (Rowe et al., in preparation). Briefly, of *C. variabilis*'s 9792 genes, 16 had no read mapped to them at any point during infection suggesting that they were not expressed under the conditions of the study. An additional 1867 had read numbers below 50 at any point and were designated as weakly expressed. Of the remaining 7909 genes, 5335 did not display any differential expression  $\leq 2$ -fold change during infection after read count normalization. The remaining 2574 genes exhibited  $\geq 2$ -fold changes with

**Table 1.** List of gene groups examined in the genome and transcriptomes of *C. variabilis*. Transcriptomes were of healthy/uninfected cells ( $T=0$ ) and of cells infected with PBCV-1 for up to 60 minutes. Loci listed are of *Arabidopsis* genes used to search *C. variabilis*'s genome. Numbers in the "Homologs" column reflect the number of homologs found in the *C. variabilis* genome. When no homologs were detected in *C. variabilis*, we noted the results of searching all the currently sequenced genomes of other green algae. Numbers in the "Expressed" column reflect the number of homologs detected at all time points. Numbers provided in the "Up- or Down-Regulation" column reflect only those homologs whose expression changed 2-fold or greater, as compared to  $T=0$  expression (the absence of a number indicates no change in expression  $\geq 2$ -fold).

Protein	TAIR locus	Homologs	Expressed	Up- or Down-regulation	Description	Reference
RNA silencing present in <i>C. variabilis</i> genome						
Argonaute 1 & 4 (AGO1 and 4)	AT1G48410 and AT2G27040	1	1	1 Up	Work within the RISC, bind to siRNAs and miRNAs, involved in RdDM and PTGS	1
ChromoMeThylase 3 (CMT3)	AT1G69770	4	3		Involved in CNG and CNN methylation, main methylase involved in non-CG methylation maintenance, likely controlled by SUVH4, SUVH5, SUVH6, and possible more in Arabidopsis	2
CLaSsY1 (CLSY1)	AT3G42670	18 that overlap with DRD1	17 that overlap with DRD1	2 Up	SNF2-like chromatin remodeling protein, required for proper localization of RDR2, possible role in a step between NRPD1 and RDR2 to produce siRNAs and spread transgene silencing	3
DiCer-Like 1, 2, 3, and 4 (DCL1-4)	AT1G01040, AT3G03300, AT3G43920, and AT5G20320	1	1		Produce 21–24 nt RNAs from longer substrates, differ based on specificity of substrates and cleavage sites	4
Defective in RNA-directed DNA methylation 1 (DRD1)	AT2G16390	21	19	3 Up	Putative SWI2/SNF2-like chromatin remodeling protein, essential for RdDM, works with Pol V to signal DRM2, needed for adding and removing methylation in response to the presence and absence, respectively, of RNA signals	5
Domains Rearranged Methylase 2 (DRM2)	AT5G14620	1	1		Involved in CG, CNG, and CNN methylation, major de novo DNA methyltransferase in RdDM, signaled by Pol V, along with DRM1 likely works with MET1 for full de novo CG methylation	6
EXoRiboNuclease 4 (XRN4)	AT1G54490	2	2		5'-3' exoribonuclease, involved in ethylene response, can work to suppress PTGS, affects siRNA and miRNA decay, degrades and allows accumulation of certain transcripts based on sequence and functional category	7
HASTY	AT3G05040	1	1		Member of importin/exportin family, involved in miRNA transport out of nucleus	8
Helicase	n/a	73	70	8 Up / 9 Down	As a domain within dicers may act to unwind siRNA precursor, as a group of proteins functions in all aspects of RNA metabolism, may also function in protein degradation, some are required for RNA silencing	9
Histone Deacetylase 6	AT5G63110	9	7	2 Down	1 of 2 histone modifying enzymes within RdDM, removes acetylate groups from lysine residues in N-termini of histones, reinforces CG methylation induced by RNA, physically interacts with MET1, may play additional roles in silencing not mediated by RNA, may provide free histone lysines to KYP for DNA methylation	10
Hua ENhancer 2 (HEN2)	AT2G06990	11	10	3 Up	Putative DEXH-box RNA helicase, involved in RNA metabolism, likely involved in degradation of improperly sliced mRNAs	11
KrYPTonite (KYP) aka SUVH4	AT5G13960	6	6	1 Down	A histone H3K9 methyltransferase, 1 of 2 histone modifying enzymes within RdDM, maintains cytosine methylation primarily in CNGs, may receive free histone lysines from HDA6 for DNA methylation	12
KU70	AT1G16970	1	1		Forms a heterodimer complex with KU80, interacts with and stimulates WEX's exonuclease activity, may also be involved in repairing dsDNA breaks	13
KU80	AT1G48050	1	1	1 Up	Forms a heterodimer complex with KU70, interacts with and stimulates WEX's exonuclease activity, may also be involved in repairing dsDNA breaks	14
METHyltransferase 1 (MET1)	AT5G49160	2+4 that overlap with CMT3	2+3 that overlap with CMT3	1 Up (without overlap)	Maintains CG methylation, physically interacts with HDA6, likely works with DRM1 and DRM2 for full de novo CG methylation <sup>15</sup>	15
Nuclear RNA Polymerase D2 (NRPD2) aka NRPD2A or DRD2 or NRPE2	AT3G23780	3	3		Second largest subunit of Pol IV and Pol V (a catalytic subunit), involved in producing and amplifying siRNAs when part of Pol IV, involved in signaling de novo methylation when part of Pol V and joining with DRD1	16
Nuclear RNA Polymerase E5 (NRPE5)	AT3G57080	2	1		A non-catalytic subunit of Pol V, involved in signaling de novo methylation when part of Pol V and joining with DRD1	17



**Table 1, continued.** List of gene groups examined in the genome and transcriptomes of *C. variabilis*.

Protein	TAIR locus	Homologs	Expressed	Up- or Down-regulation	Description	Reference
Ribonuclease Family III	n/a	4	4	3 Up	Cleave dsRNA into different size classes of RNA, include DCL (4 classes) and non-DCL members	18
Silencing DEfective 3 (SDE3)	AT1G05460	7	6	2 Up / 1 Down	An SF1 family member, may remove secondary structures in target transcripts, may amplify secondary siRNAs for transmitting PTGS signal, in <i>Drosophila</i> is required for RISC assembly	19
SErrate (SE)	AT2G27100	1	1		Physically interacts with DCL1 and HYL1 in miRNA pathway to process pri-miRNAs, helps to stabilize pri-miRNAs	20
SUppressor of Variegation 3–9 Homolog protein 2 (SUVH2)	AT2G33290	4 that overlap with KYP	4 that overlap with KYP	1 Down	Possess H3K9, H3K27, and HK20 methylation activity	21
SUppressor of Variegation 3–9 Homolog protein 5 (SUVH5)	AT2G35160	1+6 that overlap with KYP and 1 with SUVR3	1+6 that overlap with KYP and 1 with SUVR3	1 Down (overlaps with KYP)	Helps maintain H3K9 methylation, may control CMT3, with KYP controls transposons	22
SUppressor of Variegation 3–9 Related protein 3 (SUVR3)	AT3G03750	2+3 that overlap with KRY	2+3 that overlap with KRY		Histone-lysine N-methyltransferase, involved in histone-lysine and peptidyl-lysine methylation	23
Werner-like EXonuclease (WEX)	AT4G13870	2	2	1 Up / 1 Down	DEDD superfamily of 3'-5' exonucleases member, forms a complex with KU70/80 heterodimer which stimulates exonuclease activity, required for PTGS	24
RNA Silencing absent from <i>C. variabilis</i> genome						
Domains Rearranged Methylase 1 (DRM1)	AT5G15380	Not present			Involved in CG, CNG, and CNN methylation, major de novo DNA methyltransferase in RdDM, signaled by Pol V, along with DRM2 likely works with MET1 for full de novo CG methylation	25
Hua Enhancer 1 (HEN1)	AT4G20910	Not present			Methylates siRNAs and miRNAs at the 3' end to protect from uridylation, works after DCLs and before AGO1 in PTGS pathways	26
HYponastic Leaves 1 (HYL1)	AT1G09700	Not present			Nuclear dsRNA binding protein, physically interacts with DCL1, HYL1, and SE in miRNA pathway to process pri-miRNAs, likely aids in correct positioning of DCL1	27
Nuclear RNA Polymerase D 1 (NRPD1) aka SDE4 or NRPD1a	AT1G63020	Present in all (generally 3 per genome)			1 of 2 alternative largest subunits of Pol IV, involved in producing and amplifying siRNAs when part of Pol IV	28
Nuclear RNA Polymerase E 1 (NRPE1) aka DRD3 or NRPE1 or NRPD1b	AT2G40030	(Same protein family as above)			Largest subunit of Pol V, involved in signaling de novo methylation when part of Pol V and joining with DRD1	29
Nuclear RNA Polymerase D4/E4 (NRPD4/NRPE4)	AT4G15950	Not present			A non-catalytic subunit of Pols IV and V, involved in producing and amplifying siRNAs when part of Pol IV, involved in signaling de novo methylation when part of Pol V and joining with DRD1	30
Nuclear RNA Polymerase D7 (NRPD7)	AT3G22900	Not present			A non-catalytic subunit of Pol IV, involved in producing and amplifying siRNAs when part of Pol IV	31
Nuclear RNA Polymerase E7 (NRPE7)	AT4G14660	(Same protein family as above)			A non-catalytic subunit of Pol V, involved in signaling de novo methylation when part of Pol V and joining with DRD1	32
RNA Dependent RNA Polymerase 2 (RDR2)	AT4G11130	Not present			Important for RdDM, critical (with DCL3) for production of certain siRNAs, not required for tasiRNAs or miRNAs production	33
RNA Dependent RNA Polymerase 6 (RDR6)	AT3G49500	Only 1 ortholog in <i>Coccomyxa</i> sp. C-169 (homologous to RDR2).			Works with SGS3 to produce dsRNA for DCL4 to cleave into 21nt siRNAs, may depend on SGS3	34
Suppressor of Gene Silencing 3 (SGS3)	AT5G23570	Not present			Binds and protects cleaved transcript from degradation prior to RDR6 action, interacts with RDR6	35
SUppressor of Variegation 3–9 Homolog protein 6 (SUVH6)	AT2G22740	Present in most (including <i>C. variabilis</i> ) <sup>a</sup>			Helps maintain H3K9 methylation, may control CMT3, with KYP controls dsRNA from transcribed inverted repeats	36

**Table 1, continued.** List of gene groups examined in the genome and transcriptomes of *C. variabilis*.

Protein	TAIR locus	Homologs	Expressed	Up- or Down-regulation	Description	Reference
Virus induced (in <i>Arabidopsis</i> ) present in <i>C. variabilis</i> genome						
Aldo-Keto reductase	AT2G37770	11	8	1 Down	An NADPH-dependent aldo-keto reductase, accepts a wide range of substrates, primary role may be to detoxify stress-related ketones and aldehydes, upregulated under different stresses including infection	37
Alpha/Beta-hydrolases Superfamily	AT2G39420	2	1	1 Down	Members share same $\alpha/\beta$ -sheet with 8 strands connected by helices fold, family consists of cellular and secreted proteins, larger ones found in eukaryotes, in plants smaller ones tend to be soluble	38
Calmodulin 2, 5, and Calmodulin-like MSS3	AT2G41110, AT2G27030, AT2G43290	16	11	3 Up	Signal various pathways including stress responses, activate and inactive proteins via $Ca^{2+}$ binding	39
Calreticulin 3	AT1G08450	2	2	2 Down	Involved in signaling via $Ca^{2+}$ binding, known to be localized to the ER with PDIs but may have an extra-ER location, may act as chaperones	40
Chitinase, Class IV and putative	AT3G54420 and AT2G43570	1	1		Pathogenesis-related 3 protein family, involved in and possibly involved in defense against fungi, nematodes, and insects, may act to loosen cell walls	41
Cytochrome P450	AT2G45570	12	9	5 Up	Has $e^-$ carrier and monooxygenase activities, involved in response to phosphate and water limitation, expressed during the hypersensitive response and various processes leading to cell death	42
Glucose-6-phosphate Dehydrogenase 2 and 3	AT5G13110 and AT1G24280	2	2		Rate-limiting enzyme within the pentose phosphate pathway, provides major source of NADPH in the cell	43
Glutathione S-transferase 16 and Phi 16	AT2G02930 and AT4G02520	1	1		Within phi class of glutathione s-transferases, specific to plants, involved in defense response to fungi, regulation controlled by multiple mechanisms	44
Heat Shock Protein 70	AT3G12580 and AT5G02490	12	12	1 Up / 4 Down	Central to network of chaperones and folding catalysts, assists refolding of non-native proteins, prevents aggregations, involved in responses to heat, bacteria, viruses, and increases in unfolded proteins in the ER lumen	45
Heat Shock Protein 83	AT5G52640	5	5		Involved in protein folding, trafficking, and degradation, signal transduction, cell cycle control, and in defense response to bacteria, possibly involved in stress adaptation in <i>Arabidopsis</i>	46
Pathogenesis-related Gene 1	AT2G14610	3	1		Pathogenesis-related 1 protein family, involved in defense activity against oomycetes, activated by chemical treatment, attack by insect, or infection	47
Polyubiquitin 4 and 10	AT5G20620 and AT5G05320	10	8	2 Up	Contains multiple, linked ubiquitin coding regions, involved in protein degradation	48
Protein Disulfide Isomerase (PDI)	AT3G54960	8	8		Forms and breaks disulfide bonds, involved in metabolism, protein folding, cellular redox homeostasis, and in the response to endoplasmic reticulum stress	49
Protein Phosphatase 2C	AT4G08260 and AT3G27140	8	7	1 Up / 2 Down	Within group B of protein phosphatases M family within protein serine/threonine phosphatases class, likely has high substrate specificity, strongly induced by stress	50
Putative Protein Kinase	AT2G31880, and AT5G13290	97	79	15 Up / 3 Down	Involved in regulation of multiple cell death and plant resistance signaling pathways via phosphorylation	51
Senescence-related Gene 1 (SRG1)	AT1G17020	6	5	1 Up	Member of the Fe(II)/ascorbate oxidase superfamily, oxidoreductase activity, may be involved in cell wall modification in abscission zones	52
SUMO-activating Enzyme 1A (SAE1A)	AT4G24940	4	4	1 Up	Necessary for catalysis, involved in sumolation, responds to abiotic stresses, may be directly involved in plant pathogenesis	53
Thioredoxin H-type 1, 3, 4, and 5	AT3G51030, AT5G42980, AT1G19730, and AT1G45145	13 + 2 that overlap with PDI and 1 with Calmodulin 2	11 + 2 that overlap with PDI and 1 with Calmodulin 2	1 Up / 4 Down (without overlap)	All belong to subgroup 1, reduce disulfide bonds in other proteins, reduced by NADPH mediated by NADPH-reductase, may be involved in protection against oxidative stress and in regulating redox-dependent signaling cascades, may be involved in nitrogen and carbon metabolism and in self-incompatibility	54
Tyrosine Aminotransferase 3	AT2G24850	5	5		Converts tyrosine to p-hydroxyphenylpyruvate, involved in production of radical scavengers, induced by jasmonate, methyl jasmonate, coronatine, methyl-12-oxophytodieneic acid, and wounding	55
WRKY 6	AT1G62300	1	1	1 Up	A key regulator of plant innate immunity, involved in senescence, response to herbivory and bacteria, boron and phosphate limitation, and chitin	56

**Table 1, continued.** List of gene groups examined in the genome and transcriptomes of *C. variabilis*.

Protein	TAIR locus	Homologs	Expressed	Up- or Down-regulation	Description	Reference
Virus induced (in <i>Arabidopsis</i> ) absent from <i>C. variabilis</i> genome						
Beta-1,3-glucanase	AT3G57260	Not present			Member of pathogenesis-related 2 protein family, may aid in generating signaling molecules for downstream defense mechanisms, may degrade microbial cell walls, may block virus transport	57
Copper/Zinc Superoxide Dismutase Copper Chaperone	AT1G12520	Orthologs in <i>Ostreococcus</i> and <i>Micromonas</i> spp.			Assists in Cu incorporation and catalysis of disulfide bond formation to lead to the activation of copper/zinc superoxide dismutase	58
Glutamate Receptor 2.7	AT2G29120	Not present			Member of putative ligand-gated ion channel subunit family, involved in ion transport, homeostasis of Ca <sup>2+</sup> , systemic acquired resistance, and in the responses to light and ER stress	59
Metalloproteinase	AT1G24140	Not present			Binds Zn, has metalloendopeptidase and peptidase activity, involved in ER unfolded protein response	60
Pathogenesis-related Gene 5/ Thaumatin-like	AT1G75040	Not present			Pathogenesis-related 5 protein family, may function in signal transduction, associated with antifungal activity	61
Pectin Methyltransferase	AT1G11580	Not present			Catalyzes pectin deesterification, shows ribosome-inactivating protein activity, involved in cell wall modification	62
Senescence-associated Gene 21 (SAG21)	AT4G02380	Not present			Involved in response to and tolerance of reactive oxygen species, induced by dehydration and ethylene treatment	63

References 1=Brodersen and Voinnet (2006), Höck and Meister (2008), 2=Brodersen and Voinnet (2006); Ebbs and Bender (2006), Huettel et al. (2007), Lindroth et al. (2001), 3=Smith et al. (2007), 4=Olmedo and Guzman (2008), 5=Huettel et al. (2007), 6=Aufsatz et al. (2004), Huettel et al. (2007); Singh et al. (2008), 7=Gregory et al. (2008), Rymarquis et al. (2011), Souret et al. (2004), Swarbreck et al. (2007), 8=Brodersen and Voinnet (2006), Park et al. (2005), Swarbreck et al. (2007), 9=Boisvert and Simard (2008), Linder and Owttrim (2009), Olmedo and Guzman (2008), 10=Huettel et al. (2007), Kim et al. (2012), 11=Jackson et al. (2002); Linder and Owttrim (2009); Swarbreck et al. (2007); Western et al. (2002), 12=Brodersen and Voinnet (2006), Huettel et al. (2007); Jackson et al. (2004), 13=Downs and Jackson (2004); Li et al. (2005), Lieber et al. (2003); Swarbreck et al. (2007), 14=Downs and Jackson (2004); Li et al. (2005); Lieber et al. (2003); Swarbreck et al. (2007), 15=Aufsatz et al. (2004); Huettel et al. (2007), Kim et al. (2012), 16=Huettel et al. (2007); Matzke et al. (2009), 17=Matzke et al. (2009); Swarbreck et al. (2007), 18=Olmedo and Guzman (2008), 19=Brodersen and Voinnet (2006); Linder and Owttrim (2009), 20=Swarbreck et al. (2007); Xie et al. (2010), 21=Naumann et al. (2005), 22=Ebbs et al. (2005); Ebbs and Bender (2006); Jackson et al. (2004), 23=Swarbreck et al. (2007), 24=Brodersen and Voinnet (2006); Glazov et al. (2003); Swarbreck et al. (2007), 25=Aufsatz et al. (2004); Huettel et al. (2007); Singh et al. (2008); Swarbreck et al. (2007), 26=Brodersen and Voinnet (2006); Jack (2002); Swarbreck et al. (2007), 27=Brodersen and Voinnet (2006), Swarbreck et al. (2007), Xie et al. (2010), 28=Huettel et al. (2007), Matzke et al. (2009), Swarbreck et al. (2007), 29=Huettel et al. (2007), Matzke et al. (2009); Swarbreck et al. (2007), 30=Matzke et al. (2009); Swarbreck et al. (2007), 31=Matzke et al. (2009), Swarbreck et al. (2007), 32=Matzke et al. (2009), Swarbreck et al. (2007), 33=Kurihara et al. (2008); Lu et al. (2006); Xie et al. (2004), 34=Béclin et al. (2002); Kumakura et al. (2009), 35=Béclin et al. (2002), Kumakura et al. (2009), 36=Ebbs et al. (2005), Ebbs and Bender (2006), Jackson et al. (2004), 37=Simpson et al. (2009), 38=Koschorreck et al. (2005); Swarbreck et al. (2007), 39=Reddy et al. (2011), 40=Crofts and Denecke (1998), 41=Van Loon et al. (2006), 42=Godiard et al. (1998), Swarbreck et al. (2007), 43=Stanton (2012), Swarbreck et al. (2007), 44=Swarbreck et al. (2007); Wagner et al. (2002), 45=Aparicio et al. (2005), Huang and Xu (2008), Noe'i et al. (2007), Swarbreck et al. (2007), 46=Huang and Xu (2008); Swarbreck et al. (2007), Takahashi et al. (1992), 47=Van Loon et al. (2006), 48=Swarbreck et al. (2007), 49=Swarbreck et al. (2007), 50=Schweighofer et al. (2004), 51=Gao et al. (2009); Swarbreck et al. (2007), 52=Callard et al. (1996), Swarbreck et al. (2007), 53=Kurepa et al. (2003), Miura et al. (2007); Saracco et al. (2007), 54=Gelhay et al. (2004), Swarbreck et al. (2007), 55=Sandorf and Holländer-Czytoko (2002), 56=Robatzek and Somssich (2001), Rushton et al. (2010), Swarbreck et al. (2007), 57=Van Loon et al. (2006), 58=Brown et al. (2004); Casareno et al. (1998); Furukawa et al. (2004), Huang et al. (2012), Lamb et al. (2001), 59=Swarbreck et al. (2007), 60=Swarbreck et al. (2007), 61=Van Loon et al. (2006), 62=De-la-Peña et al. (2008), and 63=Miller et al. (1999), Swarbreck et al. (2007)

a. In this study, we disqualified SUVH6 homologs found in *C. variabilis* based on lack of SUVH6-specific domains and greater homology of these sequences to KYP, SUVH2, SUVR3, and SUVH5 homologs.

approximately half showing up-regulation and half showing down-regulation.

Table 2 summarizes the homologs detected in the genome and transcriptomes of *C. variabilis*. Of the 375 genes of interest coded by *C. variabilis*, 325 were expressed in healthy cells and during the first 60 min of infection. Transcripts for another 48 genes were detected, but at low levels (<50 mapped reads) and were not included in our counts of expressed genes, two more had no reads at any point. Of the 325 expressed genes, 85 had expression levels that changed  $\geq 2$ -fold during the course of the infection. A hierarchical clustering analysis revealed two broad expression patterns (Figure 1): within the 85 variable genes, 31 were globally down-regulated, while the remaining 54 were up-regulated genes. Table S2 lists all 375 genes of interest and their normalized read counts over the six time points of the infection.

### RNA silencing

One process that is expected to be utilized for virus resistance by *C. variabilis* is RNA silencing. RNA silencing serves a variety of biological purposes aside from defense against virus infections. However, it appears that viral defense is an ancestral function (Cerutti and Casas-Mollano, 2006). Because of the ancestral development of RNA silencing, the critical role it can play in defense against viruses in higher plants, and the evolutionary connection between green algae and higher plants, we looked for RNA silencing genes in the *C. variabilis* genome that were homologous to those studied in *Arabidopsis* (Brodersen and Voinnet, 2006; Matzke et al., 2009). There are several pathways that fall under the term RNA silencing, which in plants can be grouped under either RNA-directed DNA methylation (RdDM) or post-transcriptional gene silencing (PTGS)



**Table 2.** Summary of *Arabidopsis* genes used as queries against the *C. variabilis* genome, homologs detected in the *C. variabilis* genome, homologs expressed, and homologs that undergo 2-fold or greater changes during infection.

Gene class	Number of <i>Arabidopsis</i> genes	Number of <i>C. variabilis</i> homologs of <i>Arabidopsis</i> genes	Expressed in healthy <i>C. variabilis</i>	Number of <i>C. variabilis</i> genes with 2-fold difference in expression during infection
RNA silencing	34+2 gene categories	156	145	23 Up-regulated 14 Down-regulated
Virus induced (in <i>Arabidopsis</i> )	27	219	180	31 Up-regulated 17 Down-regulated

(Aufsatz et al., 2002; Brodersen and Voinnet, 2006; Ghildiyal and Zamore, 2009; Hammond et al., 2001; Matzke et al., 2009).

The different RNA silencing pathways are not mutually exclusive and share several key proteins: e.g., dicers or dicer-like proteins (DCLs), argonaunts (AGOs), and RNA-dependent RNA polymerases (RdRPs) (Cerutti and Casas-Mollano, 2006; Höck and Meister, 2008). Figures 2–6 present simplified schematics of our current understanding of these pathways. It should be noted that RdRPs are not critical for RNA silencing in all organisms. One pertinent example is another green alga, *Chlamydomonas reinhardtii*, which like *C. variabilis*, lacks a recognizable RdRP. However, RNA silencing has been demonstrated in *C. reinhardtii* as well as other organisms that lack RdRPs (Cerutti and Casas-Mollano, 2006). Of the 36 genes and gene categories we examined, homologs for 24 were present in *C. variabilis*, including nine putative orthologs (AGO1, DCL1, MET1, HASTY, HEN2, SUVH3, KU70, KU80, and WEX), and of the 156 homologs detected, 145 were expressed. It should be noted that the pathway positions of a number of genes involved in RNA silencing are not known.

*C. variabilis* has one putative ortholog each of a DCL (homologous to DCLs 1–4, orthologous to DCL1) and an AGO (homologous to AGOs 1 and 4, orthologous to AGO1), both of which were expressed in uninfected cells and in the first 60 min of PBCV-1 infection. The AGO was >2-fold up-regulated. Four additional genes had high similarity with DCLs, however they lacked some of the domains required to classify them as DCLs. Consequently, we categorized them under the broader term as members of the ribonuclease family III. This family of proteins cleaves dsRNA into different size classes of RNA and contains both DCL and non-DCL members; the structures of the latter are simpler than those of DCLs and the functions of only a few are currently known (Olmedo and Guzman, 2008). DCLs are highly variable in regards to their amino acid sequences and the organization of their domains. Moreover, the DCLs of some organisms, whose RNA silencing activity has been confirmed, do not contain all the domains of a typical dicer (Cerutti and Casas-Mollano, 2006). Because of this, we included the four ribonuclease family III members in our examination. All four of these were expressed during infection, with three up-regulated. It is possible that these ribonucleases function as dicers for *C. variabilis*. It should be noted that PBCV-1 also encodes a functional ribonuclease III gene that is expressed very early in virus infection (Zhang et al., 2003).

Additionally, DCLs have a helicase domain. Although this domain is not always required and its specific function is unknown, it is predicted to unwind the precursor to small interfering RNAs (siRNAs) (Boisvert and Simard, 2008; Olmedo and Guzman, 2008). As proteins, helicases can function in all aspects of RNA metabolism, including roles in RNA silencing (Linder and Owttrim, 2009). Therefore, we also examined 73 helicases present in the *C. variabilis* genome. Seventy of these helicases were expressed, eight of which were up-regulated and nine of which were down-regulated.

#### RNA directed DNA methylation

In RNA-directed DNA methylation (RdDM), Pol IV (NRPD2+NRPD1+NRPD4/E4+NRPD7) generates ssRNA

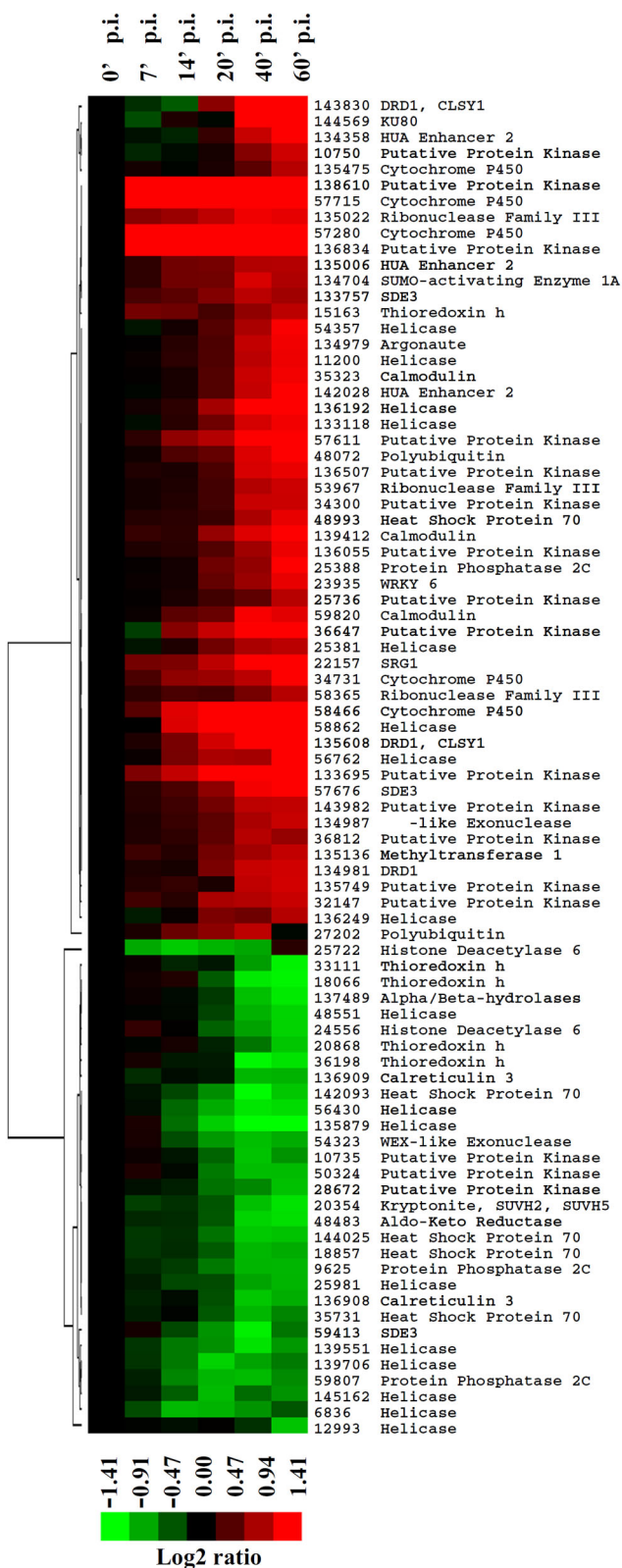
transcripts from targeted DNA that may be slightly methylated or possibly from nascent RNA. These transcripts are converted into dsRNA by the RNA dependent RNA polymerase, RDR2. CLSY1, which may work in the nucleus with Pol IV, is required for proper localization of RDR2. The dsRNA is further processed into 24 nt siRNAs by DCL3, which can then further direct the cleavage of nascent transcripts. These transcripts also may guide proteins such as HDA6, which physically interacts with MET1, SUVH2, and KYP, which together with SUVH5 and SUVH6 likely control CMT3 (which is also involved). DRD1, along with Pol V (NRPD2+NRPE1+NRPD4/E4+NRPE5+NRPE7), which physically interacts with AGO4, signals *de novo* methylation of DNA via DRM2 (Brodersen and Voinnet, 2006; Ebbs and Bender, 2006; Huettel et al., 2007; Matzke et al., 2009) (see Figure 2).

During infection, *C. variabilis* expressed the three NRPD2 subunits of Pol IV and Pol V that are present in the genome along with one of the two NRPE5 subunits of Pol V that are also present. The remaining subunits of both Pol IV and Pol V were not identified in the genome. RDR2 was not present in the genome, but 17 of the 18 CLSY1 genes (homology shared with DRD1) were expressed, two of which are up-regulated. Seven of the nine HDA6s (two down-regulated) were expressed. Both MET1 genes (those without similarity to CMT3) were expressed, with one up-regulated. All six KYPs and all four SUVH2s (which share homology with each other) were expressed, one of which was down-regulated during infection. The one SUVH5 (without similarity to KYP) and three of the four CMT3s were expressed without change over the first 60 min of infection. SUVH6 was not present in the genome. Nineteen of the 21 DRD1 genes were expressed. Two of these do not share homology with CLSY1 and one of these was up-regulated along with the two mentioned earlier. Lastly, the one DRM2 was expressed.

For those homologs not found in the genome, *C. variabilis* might use other proteins for the same function. NRPD2 joins with several subunits to form Pol IV and Pol V, respectively. It is curious that all three NRPD2 homologs were expressed, despite only one other subunit (specific to Pol V) being present in the genome. If the missing subunits are vital to Pol IV and/or Pol V function, then what is the purpose in expending the energy to make a portion of either polymerase? Moreover, nearly all other participants in this pathway were present and expressed. Though certainly not definitive, this suggests that a Pol V-like protein, may be functioning in the cell. If this pathway is indeed utilized, perhaps this simplified Pol V functions in Pol IV's place as well, or one of the NRPD2s is sufficient for Pol IV function.

#### Post-transcriptional gene silencing

Several types of RNA silencing pathways fall into the category of post-transcriptional gene silencing (PTGS). *C. variabilis* only encodes some of the genes involved in these pathways, but nearly all were expressed during infection. In the transacting short interfering RNA (tasiRNA) pathway (Figure 3), *Arabidopsis* uses AGO1 loaded into the RNA-induced silencing complex (RISC) to guide the cleavage of primary tasiRNA (pri-tasiRNA). One fragment is used as a template by RDR6, which



**Figure 1.** Transcriptome response of 85 *C. variabilis* genes during PBCV-1 infection. Hierarchical clustering of genes having a 2-fold change for at least one time point compared with 0 min p.i.. Scale of the expression log<sub>2</sub> ratio changes is indicated by a color bar at the bottom. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

works with SGS3, to produce dsRNA, which is then processed by DCL4, and the resulting siRNAs are subsequently methyl-

ated by HEN1 (Brodersen and Voinnet, 2006). Aside from homologs to AGO1 and DCL4, no other members of this pathway were detected in the genome. In the micro RNA (miRNA) pathway (Figure 4), pri-miRNA is processed by DCL1, HYL1, HEN1, and SE into mature, methylated miRNA. HASTY is thought to facilitate the nuclear export of miRNAs, which are then incorporated into RISC leading to translation inhibition and/or degradation via XRN4 (Brodersen and Voinnet, 2006; Park et al., 2005). Healthy and infected *C. variabilis* expressed both SE and HASTY (one homolog each) and both of its XRN4 homologs. Homologs for HYL1 or HEN1 were not detected in the genome.

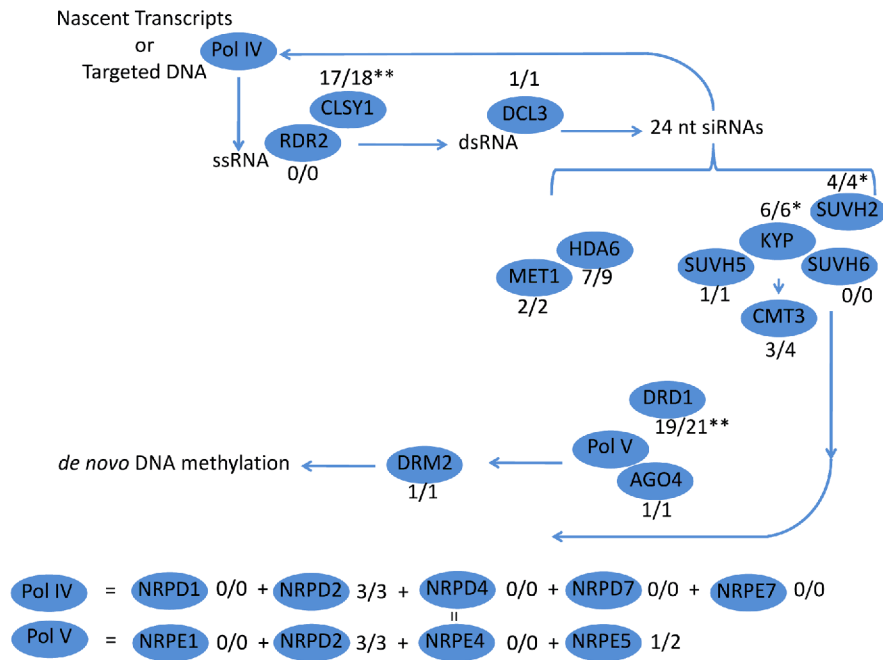
XRN4 is a 5' to 3' exoribonuclease that works in several pathways, and degrades certain RNAs based on sequence or functional category (Gregory et al., 2008; Rymarquis et al., 2011; Souret et al., 2004). When this or any other means are not used to degrade atypical RNAs, the Sense-PTGS (S-PTGS) pathway can be triggered (Figure 5). dsRNAs are produced by RDR6, SGS3, SDE3, and possibly WEX with the heterodimer, KU70/80. Subsequently, a DCL (possibly DCL4) works to produce siRNAs that HEN1 methylates. RDR6 can then either produce more dsRNA via transitivity or AGO1 along with RISC can use the siRNAs to guide the cleavage of targeted RNAs (Brodersen and Voinnet, 2006). Again, *C. variabilis* lacks RDR6, SGS3, and HEN1, but the remaining genes involved in this pathway are present in the genome and expressed during infection. Both XRN4s were expressed. Six out of seven SDE3 genes were expressed, two were up-regulated, and one down-regulated during infection. Both WEXs and each KU70 and KU80 homologs were expressed. One WEX and the one KU80 were up-regulated and the other WEX was down-regulated. Lastly within the PTGS category, the Inverted Repeat-PTGS (IR-PTGS) pathway (Figure 6) employs DCLs (probably DCL3 and DCL4), HEN1, and AGO1. Though *C. variabilis* does not possess a homolog for HEN1, both its DCL and AGO1 homologs were expressed during infection, the latter being up-regulated.

### Other genes of interest

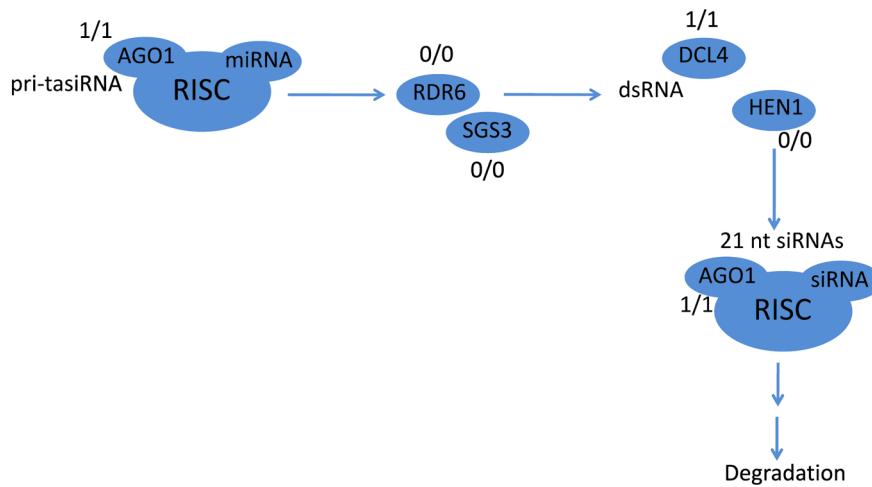
Because RNA silencing is not required for living in certain organisms (Cerutti and Casas-Mollano, 2006), and because even if it is used by *C. variabilis*, it may not be triggered by virus infection, we examined other genes that respond to virus infection in *Arabidopsis*. However, their specific roles, if any, in the plant's defense is unknown. Homologs for 27 such genes were searched for in *C. variabilis* and 20 were detected. To maintain a focused analysis we limited our examination of genes outside of RNA silencing to these 27 genes, though we acknowledge that there are a number of other genes known to be involved in pathogen response and/or resistance in higher plants. Of those 219 homologs found in *C. variabilis*, 180 were expressed in both healthy and infected cells (five of these being putative orthologs). And of these 180, 31 were up-regulated and 17 were down-regulated  $\geq 2$ -fold (Table 2). Some known functions of the homologs detected include: stress response, signaling, redox reactions, protein folding, and protein degradation (Table 1). With approximately 25% of the expressed genes experiencing a significant change in expression during infection it is likely that these genes may also be involved in *C. variabilis*'s response to virus infection or are targeted by PBCV-1 as part of its survival strategy.

### Conclusions

To our knowledge, this is the first examination of higher plant defense genes in an alga (beyond core RNA silencing genes). That many RNA silencing genes were not only found, but expressed, suggests that some of the RNA silencing path-



**Figure 2.** Schematic of the current understanding of known proteins involved in the RNA directed DNA Methylation pathway. Numbers represent numbers of homologs expressed/numbers of homologs present in the *C. variabilis* genome. \* and \*\* indicate shared homology.



**Figure 3.** Schematic of the current understanding of known proteins involved in the transacting short interfering RNA pathway. Numbers represent numbers of homologs expressed/numbers of homologs present in the *C. variabilis* genome.

ways may be utilized by *C. variabilis*. In particular, RNA directed DNA methylation and Sense post-transcriptional gene silencing are strong candidate pathways. Indeed RNA directed DNA methylation is an important defense strategy against DNA viruses in higher plants (Wang et al., 2012), though we admit that our DNA virus is quite different from known plant DNA viruses. We cannot definitively state that these pathways are employed by *C. variabilis* in an attempt to fend off virus infection. In its endosymbiont state, *C. variabilis*, is protected from virus infection and therefore relieved of pressure to evolve a defense mechanism. However, the finding that a quarter of the RNA silencing genes showed significantly altered expression during infection, suggests that they may be utilized for this purpose. The absence of certain homologs, in the *C. variabilis* genome, does not necessarily mean the true absence of a protein serving their function. Homologs to most of these same proteins were absent from all currently sequenced green algae. The seemingly va-

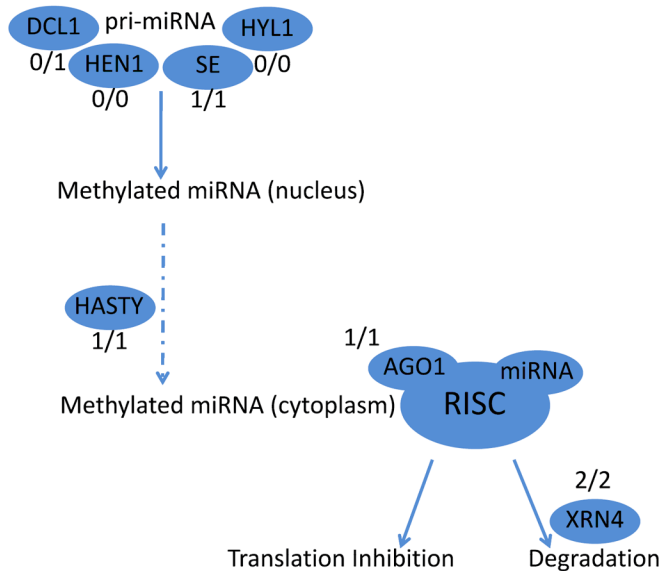
cant roles could be played by proteins encoded by genes too different from those in higher plants to be detected by our means, or these roles could be filled by presently detected proteins serving more than their known functions. The same can be suggested for the additional, potential defense genes we examined in this study.

The majority of genes known to be induced by virus infection in *Arabidopsis* were also expressed by *C. variabilis*, but only 31 out of 180 were up-regulated by at least a 2-fold expression ratio. These genes may serve similar virus-defense functions. Additionally, these results point to differences between green algae and land plants. With less than a quarter up-regulated during infection, one possible conclusion is that land plants have more sophisticated responses than green algae. Another possibility is that the virus is able to overwhelm the host before a successful defense using this/these means can be mounted.

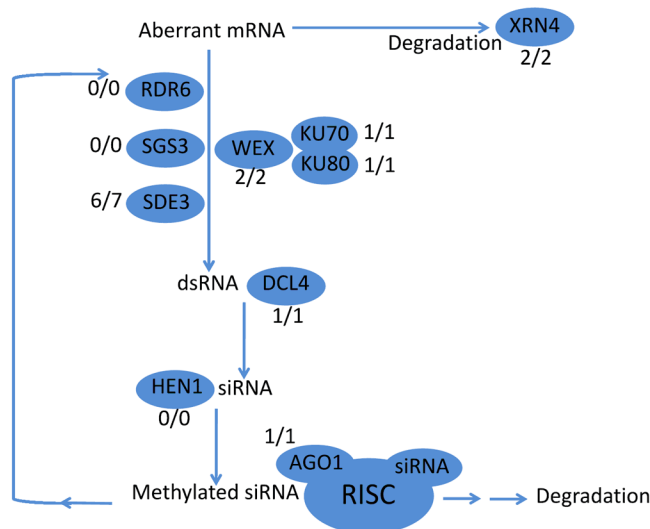
Though PBCV-1 still produced a successful infection, our analyses have narrowed the list of genes possibly involved



in virus defense and have highlighted possible mechanisms not only for defense, but also for the host cell's routine regulation of gene expression. In regards to defense strategies, it is likely that green algae share more in common with higher land plants than RNA silencing alone. These studies provide additional evidence that the further examination of green algae using *Arabidopsis* as a model can be reasonable and productive. Moreover, these evaluations provide a foundation for future comparisons between virus defense mechanisms and those present in the Plant Kingdom.



**Figure 4.** Schematic of the current understanding of known proteins involved in the micro RNA pathway. Numbers represent numbers of homologs expressed/numbers of homologs present in the *C. variabilis* genome.



**Figure 5.** Schematic of the current understanding of known proteins involved in the Sense Post-Transcriptional Gene Silencing pathway. Numbers represent numbers of homologs expressed/numbers of homologs present in the *C. variabilis* genome.



**Figure 6.** Schematic of the current understanding of known proteins involved in the Inverted Repeat Post-Transcriptional Gene Silencing pathway. Numbers represent numbers of homologs expressed/numbers of homologs present in the *C. variabilis* genome.

## Materials and methods

### Strains and culture conditions

The growth of PBCV-1 host *C. variabilis* NC64A on MBBM medium and the production and purification of PBCV-1 have been described (Van Etten et al., 1983).  $3 \times 10^9$  exponentially growing cells were pelleted by centrifugation after exposure to PBCV-1 (MOI=5). Cells were immediately flash frozen in liquid nitrogen and stored at  $-80^\circ\text{C}$  until further processing. The durations of infection lasted for 7, 14, 20, 40, and 60 min. Cells for the 0 min. p.i. time point were not exposed to PBCV-1 until after flash freezing.

### Isolation and sequencing of RNA from uninfected and PBCV-1 infected *C. variabilis*

The frozen *C. variabilis* cells were re-suspended in 3 ml of Trizol reagent (Invitrogen). From each sample, three aliquots, each 0.3 ml were collected from the above Trizol-cell suspension, mixed with additional 0.7 ml Trizol reagent. Total RNA was then extracted following the standard Trizol/RNeasy column procedure (Qiagen) and pooled as one sample. RNA qualities were assessed using an Agilent BioAnalyzer 2100 system (Agilent Technologies).

The RNA-seq library was constructed from 10  $\mu\text{g}$  of total RNA extracted for each time point using the mRNA-seq Sample Preparation Kit (RS-100-0801) according to the manufacturer's instructions (Illumina). RNA was subjected to poly(A) selection using Sera-Mag Magnetic Oligo-dT Beads followed by fragmentation and then used for cDNA synthesis with random hexamers. The cDNA product then underwent end repair, A-tailing, adapter ligation, and PCR amplification. Each library was sequenced using an Illumina GAIIx sequencer on one lane of the flow cell, generating 15.8–19.7 million 51-nt single-end reads for each time point.

### Transcriptome analysis

Reads were aligned simultaneously onto the *C. variabilis* and PBCV-1 genomes using BOWTIE2 (Langmead and Salzberg, 2012), and TOPHAT2 (Trapnell et al., 2009) for aligning reads spanning exon junctions. Only alignments that had no more than two mismatches with the reference sequence were retained. When a read produced more than one valid alignment, the genomic region producing the best alignment score was considered as its point of origin. Reads producing more than one alignment with identical best scores were considered as originating inside a repeated sequence and were discarded in subsequent per-gene read count analyses. For each time point we mapped 8.6–13.0 million reads to single copy sequences on the *C. variabilis* genome.

Of the 9776 host predicted genes, 1867 had raw read counts <50 in all time points and were discarded from subsequent analysis. The remaining 7909 genes had their read counts normalized for library size using the DESeq method (Anders and Huber, 2010). Clustering analysis and visualization of the results was done using the CLUSTER and TREE-VIEW programs (Eisen et al., 1998).

## Defense gene selection

Amino acid sequences of RNA silencing genes in *Arabidopsis* (Brodersen and Voinnet, 2006; Matzke et al., 2009) were obtained from NCBI and TAIR databases and used as queries in BLASTp searches against JGI's Model Proteins of *C. variabilis* (Altschul et al., 1990). In a similar manner, amino acid sequences of genes induced by both negative and positive sense RNA viruses in *Arabidopsis* (Whitham et al., 2006) were also used as query sequences. An alignment e-value of  $1e^{-5}$  was set as the cutoff value. Helicases were added to the list of genes of interest and were found by searching the *C. variabilis* genome annotation. Focus was placed on the presence of required domains and the "probable function" of the protein in question annotated as helicase activity. Additionally, the list of protein kinase homologs was supplemented with protein kinases found in the same manner. For those proteins to which no homologs could be found, the MEME Suite (<http://meme.sdsc.edu/meme/intro.html>) was used to generate motifs based on sequences from other eukaryotes and also higher plants (multiple sets of MEME-based motifs/queries were generated) (Bailey et al., 2009). Detected homologs were classified based on the query sequences used to find them with the exception of the DCL homologs. Most of the DCL homologs detected lack several of the domains possessed by typical dicers. Therefore they were reclassified with the more broad description of ribonuclease family III members leaving the description of DCL to indicate the presence of all expected domains.

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Table S1. List of all homologs present in the genome of *C. variabilis* that are related to *Arabidopsis* genes involved in RNA silencing and those induced by viruses along with the *Arabidopsis* query protein and resulting e-value. E-value corresponds to the BLASTp result from searching JGI's model proteins of *C. variabilis* with *Arabidopsis* query sequences obtained from NCBI.

Description	NC64A		Arabidopsis query		e-value	Query ID	e-value	Query ID	e-value	Query ID	KEGG Identifier/Gene Name of Putative Ortholog		
	protein ID	Location	e-value	ID								e-value	Query ID
Aldo-Keto Reductase	13275	98: 6623-8081	2.95E-34	ABH07515.1									
Aldo-Keto Reductase	19238	2: 160719-162867	1.15E-39	ABH07515.1									
Aldo-Keto Reductase	22713	9: 1215450-1217363	4.96E-34	ABH07515.1									
Aldo-Keto Reductase	23295	10: 248509-251473	1.97E-06	ABH07515.1									
Aldo-Keto Reductase	29451	2: 459876-462891	4.76E-09	ABH07515.1									
Aldo-Keto Reductase	32425	21: 177192-180599	6.27E-54	ABH07515.1									
Aldo-Keto Reductase	48483	2: 1634716-1636765	7.62E-07	ABH07515.1									
Aldo-Keto Reductase	135662	14: 660806-662514	2.68E-10	ABH07515.1									
Aldo-Keto Reductase	138560	21: 162828-165994	1.79E-48	ABH07515.1									
Aldo-Keto Reductase	138982	27: 237586-246204	3.23E-57	ABH07515.1									
Aldo-Keto Reductase	142101	5: 836109-839391	3.18E-58	ABH07515.1									
Alpha/Beta-hydrolases Superfamily	137489	19: 938177-940197	1.30E-09	BAH20221.1									
Alpha/Beta-hydrolases Superfamily	144404	9: 1236571-1240373	8.12E-08	BAH20221.1									
Argonaute 1, Argonaute 4	<b>134979*</b>	<b>12: 1196437-1201802</b>	8.10E-42	O04379.1 (AGO1)	1.29E-13	AEC07929.1 (AGO4)					AT1G48410 / AGO1		
Calmodulin 2	14319	14: 60837-61013	1.07E-08	AAD12000.1									
Calmodulin 2	20239	4: 1072482-1077234	1.30E-09	AAD12000.1									
Calmodulin 2	134855	12: 759894-760952	4.66E-10	AAD12000.1									
Calmodulin 2	140699	33: 152877-154191	1.00E-05	AAD12000.1									
Calmodulin 2	145399	9: 756050-760569	1.59E-06	AAD12000.1									
Calmodulin 2, Calmodulin 5	139412	27: 459029-466133	8.40E-09	AAD12000.1	2.66E-07	AEC10248.1							
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	30247	5: 68267-72106	8.69E-23	AAD12000.1	3.13E-17	AEC10248.1	3.13E-17	AAM10136.1					
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	35323	9: 88317-893109	4.46E-06	AAD12000.1	6.22E-06	AEC10248.1	6.22E-06	AAM10136.1					
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	36361	16: 719127-724229	1.28E-19	AAD12000.1	2.70E-16	AEC10248.1	2.70E-16	AAM10136.1					
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	55421	35: 299573-300582	1.79E-21	AAD12000.1	1.22E-11	AEC10248.1	1.22E-11	AAM10136.1					
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	59820	32: 135884-137740	3.99E-84	AAD12000.1	1.90E-20	AEC10248.1	1.90E-20	AAM10136.1					
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	133793	10: 331318-335491	5.61E-09	AAD12000.1	2.31E-07	AEC10248.1	2.31E-07	AAM10136.1					
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	134284	11: 400754-401635	1.79E-06	AAD12000.1	1.38E-08	AEC10248.1	1.38E-08	AAM10136.1					
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	140078	28: 409928-411688	8.43E-46	AAD12000.1	1.22E-12	AEC10248.1	1.22E-12	AAM10136.1					
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	141326	4: 1226609-1233339	5.92E-12	AAD12000.1	5.80E-08	AEC10248.1	5.80E-08	AAM10136.1					
Calmodulin 2, Thioredoxin h (H3)	135979	15: 248703-252371	1.19E-09	AAD12000.1	3.93E-07	AED94897.1 (H3)							
Calreticulin 3	136908	18: 50803-53418	1.11E-34	AE228293.1									
Calreticulin 3	136909	18: 53842-57368	5.76E-40	AE228293.1									
Chitinase Class IV, Chitinase (putative)	48490	2: 2027624-2032362	2.50E-40	AAQ62423.1	5.71E-30	AEC10291.1							
Chromomethylase 3, Methyltransferase 1	50474	3: 2164815-2172644	1.66E-15	AE334973.1 (CMT3)	1.68E-15	AAK69756.1 (CMT3)	5.85E-19	AED95777.1 (MET1)					
Chromomethylase 3, Methyltransferase 1	52630	11: 1243193-1254336	2.19E-40	AE334973.1 (CMT3)	2.25E-46	AAK69756.1 (CMT3)	1.23E-31	AED95777.1 (MET1)					
Chromomethylase 3, Methyltransferase 1	<b>137705*</b>	<b>2: 650015-660109</b>	5.37E-34	AE334973.1 (CMT3)	5.48E-34	AAK69756.1 (CMT3)	0.00E+00	AED95777.1 (MET1)			AT5G49160 / MET1		
Chromomethylase 3, Methyltransferase 1	139634	25: 666943-672028	3.87E-09	AE334973.1 (CMT3)	3.89E-09	AAK69756.1 (CMT3)	1.51E-19	AED95777.1 (MET1)					
Cytochrome P450	34731	9: 173438-175321	2.07E-14	O64637.1									
Cytochrome P450	51247	6: 419824-424285	1.88E-25	O64637.1									
Cytochrome P450	56217	14: 743147-745976	7.43E-08	O64637.1									
Cytochrome P450	57280	8: 663160-667834	1.10E-12	O64637.1									
Cytochrome P450	57715	14: 245827-252078	3.78E-09	O64637.1									
Cytochrome P450	58466	22: 377198-3382589	2.64E-28	O64637.1									
Cytochrome P450	134405	11: 839531-843188	5.09E-11	O64637.1									
Cytochrome P450	135113	14: 481516-486826	3.02E-10	O64637.1									
Cytochrome P450	135119	14: 660806-662514	1.43E-06	O64637.1									
Cytochrome P450	135122	14: 9115779-917917	1.80E-07	O64637.1									
Cytochrome P450	135475	14: 43719-46755	8.53E-16	O64637.1									
Cytochrome P450	138471	20: 806491-811354	1.54E-17	O64637.1									
Dicer-like (DCL1, DCL2, DCL3, DCL4)	<b>143199*</b>	<b>7: 1702610-1709370</b>	1.60E-117	AEE27221.1	2.77E-82	AEE73926.1 (DCL2)	1.03E-61	AEE77843.1 (DCL3)	2.93E-57	ABF19799.1 (DCL3)	1.57E-75	P84634.2 (DCL4)	AT1G01040 / DCL1
Domains Rearranged Methylase 2 (DRM2)	139582	3: 1194661-1198767	7.67E-06	O9M548.1 (DRM2)									
DRD1	9749	13: 428961-432049	5.84E-10	AEC06492.1									
DRD1	134981	12: 1205513-1211041	1.02E-05	AEC06492.1									
DRD1	143831	8: 1728281-1729234	5.40E-06	AEC06492.1									
DRD1, CLSY1	9310	2: 1137820-1140699	1.76E-08	AEC06492.1	4.87E-14	NP_189853 (CLSY)							
DRD1, CLSY1	21780	6: 408699-409472	6.70E-10	AEC06492.1	1.21E-06	NP_189853 (CLSY)							
DRD1, CLSY1	22847	9: 1001773-1005155	4.45E-18	AEC06492.1	2.61E-18	NP_189853 (CLSY)							
DRD1, CLSY1	34395	4: 1289738-1297719	1.71E-14	AEC06492.1	4.76E-18	NP_189853 (CLSY)							
DRD1, CLSY1	49470	1: 1119468-1126328	2.32E-22	AEC06492.1	7.00E-27	NP_189853 (CLSY)							
DRD1, CLSY1	56509	1: 1193929-1203561	1.76E-12	AEC06492.1	2.04E-12	NP_189853 (CLSY)							
DRD1, CLSY1	57917	11: 100668-105366	3.76E-07	AEC06492.1	8.29E-06	NP_189853 (CLSY)							
DRD1, CLSY1	135608	14: 481516-486826	3.09E-08	AEC06492.1	7.83E-08	NP_189853 (CLSY)							
DRD1, CLSY1	136777	17: 699264-708220	4.88E-20	AEC06492.1	4.14E-15	NP_189853 (CLSY)							
DRD1, CLSY1	136836	17: 932064-935354	2.86E-06	AEC06492.1	2.90E-10	NP_189853 (CLSY)							
DRD1, CLSY1	136932	18: 108310-118274	3.07E-11	AEC06492.1	6.38E-07	NP_189853 (CLSY)							
DRD1, CLSY1	137064	18: 578020-590656	4.45E-24	AEC06492.1	1.22E-30	NP_189853 (CLSY)							
DRD1, CLSY1	138032	2: 1794099-1804297	1.74E-06	AEC06492.1	3.17E-06	NP_189853 (CLSY)							
DRD1, CLSY1	140806	3: 1766466-1768453	4.24E-07	AEC06492.1	1.21E-06	NP_189853 (CLSY)							
DRD1, CLSY1	142147	4: 1157534-1163749	1.51E-06	AEC06492.1	6.76E-08	NP_189853 (CLSY)							
DRD1, CLSY1	142431	4: 2153086-2156465	1.63E-07	AEC06492.1	6.38E-07	NP_189853 (CLSY)							
DRD1, CLSY1	143830	6: 1405615-1409502	2.61E-09	AEC06492.1	4.12E-16	NP_189853 (CLSY)							
DRD1, CLSY1	144734	8: 256528-269262	2.53E-10	AEC06492.1	1.80E-16	NP_189853 (CLSY)							
Glucose-6-phosphate 1-dehydrogenase	36395	16: 1128024-1132745	2.44E-132	AE30511.1	9.44E-131	AED91851.1							
Glucose-6-phosphate 1-dehydrogenase	<b>134643*</b>	<b>12: 94280-97424</b>	0.00E+00	AEE20511.1	0.00E+00	AED91851.1						AT5G13110 / G6PD2	
Glutathione S-transferase 16	57549	7: 1560203-1562813	3.58E-06	ABD94077									
HASTY	<b>139890*</b>	<b>3: 1919274-1921512</b>	8.83E-68	NP_187155.2	1.15E-67	AAO34666.1						AT3G05040 / HST	

Heat Shock Protein 70, Hsc 70 protein	18857 2: 125949-127239	9.20E-40 AEE75218.1	3.85E-27 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	19454 3: 989551-992157	2.41E-51 AEE75218.1	2.99E-50 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	<b>32920*</b> 26: 392386-396631	0.00E+00 AEE75218.1	0.00E+00 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	35731 12: 193215-198231	4.20E-76 AEE75218.1	7.68E-71 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	36653 19: 678818-685275	8.12E-132 AEE75218.1	4.79E-131 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	48993 1: 1119468-1126328	0.00E+00 AEE75218.1	2.03E-174 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	56032 4: 924604-929108	0.00E+00 AEE75218.1	0.00E+00 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	57615 8: 718979-727783	0.00E+00 AEE75218.1	0.00E+00 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	137436 19: 767959-773941	2.57E-23 AEE75218.1	1.90E-22 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	142093 4: 929357-932671	1.07E-29 AEE75218.1	3.09E-29 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	144025 65: 26-3185	3.01E-113 AEE75218.1	2.24E-166 AAP37770.1
Heat Shock Protein 70, Hsc 70 protein	145242 9: 179690-183562	1.46E-128 AEE75218.1	2.17E-123 AAP37770.1
Heat Shock Protein 83	19360 2: 136408-137707	3.12E-36 P27323.3	
Heat Shock Protein 83	57527 7: 1224913-123322	1.68E-145 P27323.3	
Heat Shock Protein 83	59468 65: 3417-10734	1.90E-70 P27323.3	
Heat Shock Protein 83	134150 106: 7213-7856	1.11E-06 P27323.3	
Heat Shock Protein 83	140066 28: 361484-368639	4.23E-87 P27323.3	
Helicase	6836 5: 2142867-2146197		
Helicase	11200 3: 345557-347008		
Helicase	12993 18: 754470-755600		
Helicase	14687 14: 1088606-1089406		
Helicase	16802 14: 1038617-1040826		
Helicase	19567 3: 1053241-1057277		
Helicase	20835 5: 189976-193636		
Helicase	23258 10: 647099-650975		
Helicase	25381 15: 1125352-1128559		
Helicase	25981 18: 261643-265486		
Helicase	26393 20: 279686-282659	1.14E-06 AEE27221.1	
Helicase	28127 31: 406161-411022		
Helicase	28229 32: 309237-313007		
Helicase	29172 1: 647917-651743		
Helicase	30080 4: 1271234-1275793		
Helicase	31911 15: 417063-423814		
Helicase	33556 1: 1429007-1434817		
Helicase	33628 1: 2182787-2187237		
Helicase	34017 3: 192057-196244		
Helicase	34665 5: 712295-714804		
Helicase	35936 13: 786044-790325		
Helicase	36420 17: 428243-431524		
Helicase	36787 21: 828015-831869	1.88E-07 P84634.2 (DCL4)	
Helicase	36987 24: 332182-335699		
Helicase	48551 3: 1476980-1479283		
Helicase	50422 3: 1750103-1760404		
Helicase	51440 9: 76437-88386		
Helicase	51607 7: 1157372-1160390		
Helicase	51983 9: 76437-88386		
Helicase	54357 21: 745556-755111		
Helicase	55365 14: 743147-745976		
Helicase	56077 5: 990014-992974		
Helicase	56430 1: 95364-101279		
Helicase	56582 1: 2300951-2306768		
Helicase	56762 2: 1742997-1747201		
Helicase	56765 2: 1853785-1865813		
Helicase	57434 6: 1594681-1601788		
Helicase	57565 7: 1800091-1809526		
Helicase	57890 10: 1348919-1352391		
Helicase	58353 15: 324855-329093		
Helicase	58455 16: 689199-695224		
Helicase	58635 18: 803302-807473		
Helicase	58862 27: 66760-71085		
Helicase	59105 26: 195166-198291		
Helicase	59143 27: 66760-71085		
Helicase	59259 31: 230818-261110		
Helicase	59745 19: 531803-536730		
Helicase	133108 1: 901279-905631		
Helicase	133118 1: 946609-955040		
Helicase	133956 10: 915180-920226		
Helicase	134628 12: 40567-46062		
Helicase	135424 13: 1251202-1253608		
Helicase	135879 14: 1339476-1341915		
Helicase	136192 15: 982002-988383		
Helicase	136249 15: 1184413-1188877		
Helicase	136793 17: 755811-762818		
Helicase	137419 19: 721550-723571		
Helicase	137613 2: 300764-309819		
Helicase	137841 2: 1156367-1165132		
Helicase	137938 2: 1485487-1492814		
Helicase	137960 2: 1564336-1574691		
Helicase	138311 20: 227947-237782		

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Helicase	138879	22: 432562-435855			
Helicase	139542	25: 354355-361481			
Helicase	139551	25: 402741-406942			
Helicase	139706	26: 194044-195214			
Helicase	142335	4: 1845225-1847715			
Helicase	142420	4: 2117325-2123225			
Helicase	142433	4: 2158583-2161193			
Helicase	142930	5: 836109-839391			
Helicase	144099	7: 135689-139618			
Helicase	144794	8: 470600-481344			
Helicase	145162	8: 1728281-1729234			
Histone Deacetylase 6	8472	11: 1140666-1144451	5.99E-159	AED97705.1	
Histone Deacetylase 6	9525	33: 354973-357391	7.79E-62	AED97705.1	
Histone Deacetylase 6	23482	11: 1456190-1459967	5.48E-144	AED97705.1	
Histone Deacetylase 6	23994	12: 1435094-1436460	2.12E-10	AED97705.1	
Histone Deacetylase 6	24556	13: 1161882-1164007	5.49E-18	AED97705.1	
Histone Deacetylase 6	25722	17: 7351-10169	1.62E-14	AED97705.1	
Histone Deacetylase 6	137274	19: 148103-149733	9.62E-10	AED97705.1	
Histone Deacetylase 6	140841	3: 1919274-1921512	4.88E-07	AED97705.1	
Histone Deacetylase 6	145535	9: 1236571-1240373	7.91E-139	AED97705.1	
HUA Enhancer 2	<b>28067*</b>	30: 366742-377171	0.00E+00	AAL11446.1	
HUA Enhancer 2	52598	11: 1031147-1044963	1.65E-12	AAL11446.1	
HUA Enhancer 2	134358	12: 272267-275086	3.12E-36	AAL11446.1	
HUA Enhancer 2	134899	13: 102047-103864	9.92E-08	AAL11446.1	
HUA Enhancer 2	135006	12: 1297082-1299755	6.70E-08	AAL11446.1	
HUA Enhancer 2	138793	22: 111256-127552	1.79E-14	AAL11446.1	
HUA Enhancer 2	140725	34: 133586-142626	1.17E-08	AAL11446.1	
HUA Enhancer 2	140958	3: 2390104-2403118	6.95E-08	AAL11446.1	
HUA Enhancer 2	141429	34: 133586-142626	0.00E+00	AAL11446.1	
HUA Enhancer 2	142028	4: 687758-696440	5.30E-68	AAL11446.1	
HUA Enhancer 2	144334	7: 960068-971038	2.40E-66	AAL11446.1	
Kryptonite, SUVH2, SUVH5	20354	4: 947867-952310	4.72E-13	AED91966.1 (KYP)	2.54E-11 AAK28967.1 (SUVH2) 2.59E-06 NP_181061.1 (SUVH5)
Kryptonite, SUVH2, SUVH5	25365	15: 841126-843132	1.45E-10	AED91966.1 (KYP)	AAK28967.1 (SUVH2) 8.09E-09 NP_181061.1 (SUVH5)
Kryptonite, SUVH2, SUVH5	142107	4: 978017-984445	1.61E-48	AED91966.1 (KYP)	2.11E-31 AAK28967.1 (SUVH2) 7.89E-34 NP_181061.1 (SUVH5)
Kryptonite, SUVH2, SUVH3, SUVH5	58236	14: 245827-252078	4.09E-44	AED91966.1 (KYP)	6.93E-10 NP_974212 (SUVH3) 1.66E-30 NP_181061.1 (SUVH5)
Kryptonite, SUVH3, SUVH5	18588	1: 2498872-2501312	1.34E-11	AED91966.1 (KYP)	2.40E-10 NP_974212 (SUVH3) 2.49E-10 NP_181061.1 (SUVH5)
Kryptonite, SUVH3, SUVH5	35816	12: 900000-901522	1.66E-12	AED91966.1 (KYP)	1.63E+08 NP_974212 (SUVH3) 9.50E-16 NP_181061.1 (SUVH5)
KU70	<b>53981*</b>	19: 39237-45448	1.34E-38	NP_564012.1	
KU80	<b>144569*</b>	7: 1702610-1709370	2.53E-29	NP_564520.1	
Methyltransferase 1	135136	13: 269730-275128	7.42E-08	AED95777.1	
Methyltransferase 1	137706	2: 660187-662714	4.19E-07	AED95777.1	
NRPE5	48698	6: 1164841-1166845	7.18E-28	NP_191267.1	
NRPE5	134695	12: 246327-247559	4.95E-25	NP_191267.1	
Nuclear RNA Polymerase D2A	19065	2: 2064779-2065281	6.47E-23	AEE76813.1	
Nuclear RNA Polymerase D2A	56318	23: 370562-377362	4.94E-115	AEE76813.1	
Nuclear RNA Polymerase D2A	59036	24: 642746-650052	7.12E-168	AEE76813.1	
Pathogenesis-related Gene 1	26372	22: 498098-498647	9.88E-14	AEC06314.1	
Pathogenesis-related Gene 1	135097	14: 43719-46755	3.75E-13	AEC06314.1	
Pathogenesis-related Gene 1	139641	25: 690334-692481	1.74E-06	AEC06314.1	
Polyubiquitin 4, Polyubiquitin 10	9815	16: 457831-458211	6.53E-42	AED92867.1 (4)	6.19E-42 AEE82505.1 (10)
Polyubiquitin 4, Polyubiquitin 10	14180	5: 883289-883585	7.25E-09	AED92867.1 (4)	7.09E-09 AEE82505.1 (10)
Polyubiquitin 4, Polyubiquitin 10	15978	4: 1795835-1796105	3.77E-26	AED92867.1 (4)	3.63E-26 AEE82505.1 (10)
Polyubiquitin 4, Polyubiquitin 10	24467	13: 880611-880970	1.11E-38	AED92867.1 (4)	1.05E-38 AEE82505.1 (10)
Polyubiquitin 4, Polyubiquitin 10	27202	24: 7266942-727267	5.11E-09	AED92867.1 (4)	5.01E-09 AEE82505.1 (10)
Polyubiquitin 4, Polyubiquitin 10	48072	1: 1099388-1100863	2.39E-11	AED92867.1 (4)	3.21E-11 AEE82505.1 (10)
Polyubiquitin 4, Polyubiquitin 10	48528	3: 738848-740288	9.50E-127	AED92867.1 (4)	8.21E-127 AEE82505.1 (10)
Polyubiquitin 4, Polyubiquitin 10	<b>51574*</b>	7: 864756-876994	0.00E+00	AED92867.1 (4)	0.00E+00 AEE82505.1 (10)
Polyubiquitin 4, Polyubiquitin 10	135983	16: 926266-929417	3.17E-26	AED92867.1 (4)	3.08E-12 AEE82505.1 (10)
Polyubiquitin 4, Polyubiquitin 10	136254	15: 1201071-1208628	5.81E-07	AED92867.1 (4)	5.71E-07 AEE82505.1 (10)
Protein Disulfide Isomerase	55742	162: 1215-3421	1.01E-10	BAH56959.1	
Protein Disulfide Isomerase	58416	16: 79490-81643	1.13E-07	BAH56959.1	
Protein Disulfide Isomerase	132941	1: 260599-263457	3.11E-10	BAH56959.1	
Protein Disulfide Isomerase	134783	12: 538010-540584	7.78E-06	BAH56959.1	
Protein Disulfide Isomerase	138016	2: 1738882-1742680	9.43E-07	BAH56959.1	
Protein Disulfide Isomerase	142831	5: 486435-489669	1.13E-34	BAH56959.1	
Protein Disulfide Isomerase, Thioredoxin h (H1, H3)	14696	2: 120132-121440	2.72E-29	BAH56959.1	6.34E-06 AEE78739.1 (H1) 9.07E-06 AED94897.1 (H3)
Protein Disulfide Isomerase, Thioredoxin h (H4)	136996	18: 358957-362257	3.74E-18	BAH56959.1	7.00E-06 AEE29892.1 (H4)
Protein Phosphatase 2C	9625	26: 21494-24388	3.91E-14	AEE82615.1	1.44E-13 AEE77272.1
Protein Phosphatase 2C	25388	15: 432881-434483	8.33E-08	AEE82615.1	
Protein Phosphatase 2C	35180	9: 889317-893109	5.71E-23	AEE82615.1	3.62E-19 AEE77272.1
Protein Phosphatase 2C	36133	14: 1117036-1118669	1.41E-10	AEE82615.1	5.80E-11 AEE77272.1
Protein Phosphatase 2C	58836	21: 948044-953534	4.59E-19	AEE82615.1	6.43E-18 AEE77272.1
Protein Phosphatase 2C	59087	26: 46483-49186	8.26E-07	AEE82615.1	
Protein Phosphatase 2C	59807	29: 103501-108236	1.45E-10	AEE82615.1	2.16E-12 AEE77272.1
Protein Phosphatase 2C	139942	27: 459029-466133	6.01E-09	AEE82615.1	7.20E-07 AEE77272.1
Putative Protein Kinase	7719	21: 687300-690782	1.77E-07	AAD32284.1	3.32E-06 AED91876.1
Putative Protein Kinase	10735	32: 240685-242438			
Putative Protein Kinase	10750	19: 795506-797518	8.60E-07	AAD32284.1	
Putative Protein Kinase	11223	14: 180180-181247	4.45E-08	AAD32284.1	

AT2G06990 / HEN2

AT1G16970 / KU70  
AT1G48050 / KU80

AT5G20620 / UBO4



Putative Protein Kinase	11382	5: 402200-403813	2.40E-08 AAD32284.1	3.42E-06 AED91876.1	1.89E-06 AED91877.1
Putative Protein Kinase	12761	11: 1109228-1110585	3.26E-07 AAD32284.1		
Putative Protein Kinase	13183	34: 275749-277025	8.29E-09 AAD32284.1		
Putative Protein Kinase	13410	11: 1300001-1300228	6.58E-06 AAD32284.1		
Putative Protein Kinase	13628	22: 666544-667659	1.38E-09 AAD32284.1		
Putative Protein Kinase	13683	45: 5892-6951	8.60E-06 AAD32284.1		
Putative Protein Kinase	13716	15: 513057-513977	5.36E-07 AAD32284.1		
Putative Protein Kinase	19632	3: 18315585-1831935	6.50E-11 AAD32284.1		
Putative Protein Kinase	19742	3: 18315585-1831935	7.52E-08 AAD32284.1		
Putative Protein Kinase	20808	5: 189976-193636	2.84E-08 AAD32284.1		
Putative Protein Kinase	21329	5: 2107905-2109147			
Putative Protein Kinase	21563	6: 2000876-2002079	1.59E-08 AAD32284.1		
Putative Protein Kinase	22641	9: 335071-336708	9.35E-13 AAD32284.1	3.06E-07 AED91876.1	
Putative Protein Kinase	22745	9: 1001773-1005155	3.35E-06 AAD32284.1	1.29E-07 AED91876.1	4.81E-06 AED91877.1
Putative Protein Kinase	23857	12: 925404-926052	1.84E-06 AAD32284.1		
Putative Protein Kinase	23988	12: 1380914-1382510	7.33E-08 AAD32284.1	1.78E-07 AED91876.1	1.58E-05 AED91877.1
Putative Protein Kinase	24076	12: 740656-741937	8.02E-12 AAD32284.1		
Putative Protein Kinase	24126	12: 740656-741937	8.11E-12 AAD32284.1	9.01E-11 AED91876.1	8.93E-06 AED91877.1
Putative Protein Kinase	25736	17: 906048-908316	1.50E-07 AAD32284.1		
Putative Protein Kinase	25821	19: 841228-843273	8.70E-06 AAD32284.1		
Putative Protein Kinase	26970	23: 135372-137307	2.49E-12 AAD32284.1	2.21E-10 AED91876.1	4.75E-06 AED91877.1
Putative Protein Kinase	28390	231: 95-830	1.81E-06 AAD32284.1		
Putative Protein Kinase	28672	38: 49333-52042	1.96E-11 AAD32284.1		
Putative Protein Kinase	29026	231: 95-830	2.17E-08 AAD32284.1		
Putative Protein Kinase	29775	3: 805404-807201	2.27E-10 AAD32284.1		
Putative Protein Kinase	29915	3: 1809976-1811344	9.32E-11 AAD32284.1		
Putative Protein Kinase	30642	7: 180275-182895	3.97E-14 AAD32284.1	1.87E-09 AED91876.1	
Putative Protein Kinase	30865	8: 1397728-1399552	6.41E-06 AAD32284.1		
Putative Protein Kinase	31062	10: 43317-45697	5.19 AAD32284.1	6.05E-11 AED91876.1	1.84E-06 AED91877.1
Putative Protein Kinase	32147	17: 995005-998691	3.32E-06 AAD32284.1		
Putative Protein Kinase	34300	4: 251161-253925	3.15E-12 AAD32284.1	5.30E-05 AED91876.1	3.01E-05 AED91877.1
Putative Protein Kinase	36647	19: 618576-621209	3.05E-06 AAD32284.1		
Putative Protein Kinase	36812	22: 16454-19399	1.48E-19 AAD32284.1	2.29E-12 AED91876.1	
Putative Protein Kinase	36848	22: 661067-663404	2.16E-14 AAD32284.1	4.72E-06 AED91876.1	
Putative Protein Kinase	37276	26: 450330-452767	6.85E-07 AAD32284.1	7.17E-05 AED91876.1	
Putative Protein Kinase	49225	29: 303296-306490	5.61E-10 AAD32284.1	3.27E-06 AED91876.1	
Putative Protein Kinase	49746	1: 3046695-3054721	8.45E-12 AAD32284.1	6.14E-11 AED91876.1	8.39E-06 AED91877.1
Putative Protein Kinase	50123	2: 2532250-2537111	3.65E-13 AAD32284.1	1.01E-11 AED91876.1	6.27E-06 AED91877.1
Putative Protein Kinase	50248	3: 1750103-1760404	2.84E-08 AAD32284.1		
Putative Protein Kinase	50324	3: 1169017-1172252			
Putative Protein Kinase	50622	6: 1918291-1921717	9.03E-19 AAD32284.1	1.53E-10 AED91876.1	
Putative Protein Kinase	51171	5: 2112874-2124092	1.69E-06 AAD32284.1		
Putative Protein Kinase	57033	4: 589172-595082	1.44E-07 AAD32284.1		
Putative Protein Kinase	57116	7: 1800091-1809526	2.08E-12 AAD32284.1	2.86E-10 AED91876.1	
Putative Protein Kinase	57611	11: 100668-105366	2.01E-15 AAD32284.1		
Putative Protein Kinase	58145	13: 420900-425357			
Putative Protein Kinase	58318	14: 1209189-1211763			
Putative Protein Kinase	58373	15: 526085-531347			
Putative Protein Kinase	58735	20: 319034-323755	3.79E-10 AAD32284.1		
Putative Protein Kinase	58858	22: 339871-346545	9.65E-16 AAD32284.1	1.90E-09 AED91876.1	
Putative Protein Kinase	58999	24: 370322-379069	2.01E-11 AAD32284.1	9.26E-10 AED91876.1	
Putative Protein Kinase	59518	653: 1332-1073	2.64E-12 AAD32284.1		
Putative Protein Kinase	59772	24: 518404-521846	5.08E-14 AAD32284.1		
Putative Protein Kinase	133695	10: 503420-504413	4.37E-15 AAD32284.1	1.33E-11 AED91876.1	6.12E-06 AED91877.1
Putative Protein Kinase	133720	10: 46072-50867	1.91E-11 AAD32284.1	1.46E-10 AED91876.1	4.08E-07 AED91877.1
Putative Protein Kinase	133852	10: 555379-560903	1.70E-06 AAD32284.1		
Putative Protein Kinase	134377	12: 538010-540584			
Putative Protein Kinase	134418	12: 928137-937028	7.69E-10 AAD32284.1	8.28E-06 AED91876.1	
Putative Protein Kinase	135749	15: 463999-470858	4.65E-06 AAD32284.1		
Putative Protein Kinase	135753	14: 930637-938200	6.41E-06 AAD32284.1		
Putative Protein Kinase	135759	14: 950314-953441	1.71E-08 AAD32284.1		
Putative Protein Kinase	136041	15: 463999-470858			
Putative Protein Kinase	136055	15: 519360-521098	4.77E-07 AAD32284.1		
Putative Protein Kinase	136066	15: 541171-548751	4.75E-13 AAD32284.1	1.68E-09 AED91876.1	
Putative Protein Kinase	136507	16: 926266-929417	2.18E-10 AAD32284.1	2.82E-05 AED91876.1	
Putative Protein Kinase	136568	16: 1159733-1165667	1.61E-16 AAD32284.1	3.40E-14 AED91876.1	
Putative Protein Kinase	136678	17: 322968-327068			
Putative Protein Kinase	136834	17: 918240-927913	3.14E-12 AAD32284.1		
Putative Protein Kinase	137363	19: 537377-546756	9.04E-07 AAD32284.1		
Putative Protein Kinase	137597	2: 246755-251331	1.39E-11 AAD32284.1		
Putative Protein Kinase	137604	2: 271806-273953	2.21E-10 AAD32284.1		
Putative Protein Kinase	137878	2: 1277636-1281499	2.38E-06 AAD32284.1		
Putative Protein Kinase	137935	2: 1472273-1476541	5.01E-07 AAD32284.1		
Putative Protein Kinase	138454	20: 735583-739763	4.31E-06 AAD32284.1		
Putative Protein Kinase	138610	25: 486039-489934	8.53E-11 AAD32284.1	7.85E-08 AED91876.1	
Putative Protein Kinase	138663	21: 606558-610574	5.07E-07 AAD32284.1		
Putative Protein Kinase	140646	3: 1194661-1198767	1.22E-12 AAD32284.1		
Putative Protein Kinase	140750	3: 1543901-1547815	1.16E-10 AAD32284.1		
Putative Protein Kinase	140983	30: 124829-138325			

Putative Protein Kinase	141030 4: 958371-960362	1.98E-06 AAD32284.1			
Putative Protein Kinase	141046 30: 462539-468900	1.42E-10 AAD32284.1			
Putative Protein Kinase	141147 4: 1157534-1163749	5.17E-06 AAD32284.1			
Putative Protein Kinase	141452 34: 243759-251281		4.31E-06 AED91876.1		
Putative Protein Kinase	141712 4: 2153086-2156465	9.43E-07 AAD32284.1			
Putative Protein Kinase	142162 4: 1226609-1233339	8.58E-08 AAD32284.1			
Putative Protein Kinase	142454 4: 2237941-2241471	7.04E-19 AAD32284.1	2.23E-14 AED91876.1	2.48E-06 AED91877.1	
Putative Protein Kinase	143307 8: 38320-45666	5.60E-06 AAD32284.1			
Putative Protein Kinase	143410 57: 1346-6789				
Putative Protein Kinase	143982 6: 1954260-1960953	2.16E-10 AAD32284.1			
Putative Protein Kinase	144329 7: 945706-949978		2.40E-06 AED91876.1		
Putative Protein Kinase	144680 8: 38320-45666	2.62E-17 AAD32284.1			
Putative Protein Kinase	145300 9: 350591-354108	2.35E-13 AAD32284.1			
Putative Protein Kinase	145350 9: 568581-574658	8.56E-17 AAD32284.1	6.41E-08 AED91876.1		
Ribonuclease Family III	53967 18: 1084410-1088740				
Ribonuclease Family III	58365 15: 447810-456220	2.19E-27 AEE27221.1	8.86E-20 AEE73926.1 (DCL2)	6.29E-13 AEE77843.1 (DCL3)	5.51E-06 AEE77843.1 (DCL3)
Ribonuclease Family III	133597 1: 2612970-2618913	5.06E-12 AEE27221.1	2.32E-11 AEE73926.1 (DCL2)	3.74E-06 AEE77843.1 (DCL3)	5.69E-12 ABF19799.1 (DCL3)
Ribonuclease Family III	135022 12: 1368827-1375310	1.18E-17 AEE27221.1	1.38E-15 AEE73926.1 (DCL2)	9.59E-09 AEE77843.1 (DCL3)	1.83E-06 ABF19799.1 (DCL3)
SDE3	57676 8: 1580240-1587082	5.18E-12 AAK40099.1			5.23E-06 ABF19799.1 (DCL3)
SDE3	58418 21: 948044-953534	6.49E-13 AAK40099.1			3.27E-20 P84634.2 (DCL4)
SDE3	59413 38: 180158-183538	1.54E-18 AAK40099.1			1.54E-07 P84634.2 (DCL4)
SDE3	133757 10: 168938-179243	4.94E-14 AAK40099.1			1.10E-18 P84634.2 (DCL4)
SDE3	133825 10: 447777-456602	5.54E-48 AAK40099.1			
SDE3	137486 19: 924077-932357	6.18E-14 AAK40099.1			
SDE3	142077 4: 2237941-2241471	1.52E-23 AAK40099.1			
SE	51470 7: 99916-103817	3.00E-28 O9ZDV0.2			
SRG1	9789 28: 232727-235181	4.71E-15 AEE29531.1			
SRG1	10090 43: 43560-45363	7.48E-18 AEE29531.1			
SRG1	20260 4: 849157-851839	1.01E-08 AEE29531.1			
SRG1	21158 5: 479661-481149	5.32E-10 AEE29531.1			
SRG1	22157 9: 335071-336708	2.45E-15 AEE29531.1			
SRG1	36779 21: 695622-69824	2.70E-15 AEE29531.1			
SUMO-activating Enzyme 1A	59425 39: 98022-120611	3.30E-15 AAN15413.1			
SUMO-activating Enzyme 1A	<b>134704*</b> 12: 272267-275086	7.25E-37 AAN15413.1			AT4G24940 / SAE1A
SUMO-activating Enzyme 1A	137823 2: 1098562-1102231	1.44E-13 AAN15413.1			
SUMO-activating Enzyme 1A	144742 8: 300825-305276	5.41E-08 AAN15413.1			
SUVH5	14389 18: 1044901-1045609	6.86E-07 NP_181061.1			
SUVR3	24455 13: 1213891-1214967		8.08E-07 NP_974212 (SUVR3)		
SUVR3, SUVH5	<b>137958*</b> 2: 1559569-1560869		1.87E-30 NP_974212 (SUVR3)	1.29E-06 NP_181061.1 (SUVH5)	AT3G03750 / SDG20
Thioredoxin h	14388 15: 147647-148271	5.13E-06 AEE32083.1 (H5)	3.55E-05 AEE78739.1 (H1)	2.18E-08 AEE29892.1 (H4)	4.32E-06 AED94897.1 (H3)
Thioredoxin h	15163 25: 391408-392203	8.54E-08 AEE32083.1 (H5)	1.30E-07 AEE78739.1 (H1)	1.89E-11 AEE29892.1 (H4)	2.20E-06 AED94897.1 (H3)
Thioredoxin h	20868 5: 1067392-1068011	2.86E-14 AEE32083.1 (H5)	1.04E-11 AEE78739.1 (H1)	2.51E-11 AEE29892.1 (H4)	2.07E-12 AED94897.1 (H3)
Thioredoxin h	26293 19: 841228-843273	1.31E-13 AEE32083.1 (H5)	9.20E-15 AEE78739.1 (H1)	7.73E-10 AEE29892.1 (H4)	2.07E-12 AED94897.1 (H3)
Thioredoxin h	26868 24: 7266942-727267	1.36E-08 AEE32083.1 (H5)	4.44E-09 AEE78739.1 (H1)	6.54E-07 AEE29892.1 (H4)	5.73E-06 AED94897.1 (H3)
Thioredoxin h	33111 30: 432462-435281	1.28E-10 AEE32083.1 (H5)	8.45E-14 AEE78739.1 (H1)	9.12E-16 AEE29892.1 (H4)	3.95E-10 AED94897.1 (H3)
Thioredoxin h	36198 15: 61048-62626	6.54E-09 AEE32083.1 (H5)	2.04E-11 AEE78739.1 (H1)	2.49E-10 AEE29892.1 (H4)	5.93E-07 AED94897.1 (H3)
Thioredoxin h	<b>133836*</b> 10: 503420-504413	6.92E-19 AEE32083.1 (H5)	1.38E-16 AEE78739.1 (H1)	2.27E-16 AEE29892.1 (H4)	1.50E-12 AED94897.1 (H3)
Thioredoxin h	134092 10: 1363797-1364986	2.80E-09 AEE32083.1 (H5)	2.55E-10 AEE78739.1 (H1)	3.03E-06 AEE29892.1 (H4)	1.11E-07 AED94897.1 (H3)
Thioredoxin h (H1, H3, H4)	52344 10: 937262-938427			1.99E-09 AEE29892.1 (H4)	1.04E-06 AED94897.1 (H3)
Thioredoxin h (H1, H3)	18066 1: 2507693-2509008		6.65E-10 AEE78739.1 (H1)		6.58E-10 AED94897.1 (H3)
Thioredoxin h (H4)	134198 11: 161469-165106			1.08E-07 AEE29892.1 (H4)	
Thioredoxin h (H4)	140512 3: 771978-774133			7.87E-08 AEE29892.1 (H4)	
Tyrosine Aminotransferase 3	22926 9: 1154912-1157688	6.10E-06 AAP31937.1			
Tyrosine Aminotransferase 3	29318 1: 2165190-2169064	3.09E-12 AAP31937.1			
Tyrosine Aminotransferase 3	48481 2: 1537999-1540528	4.70E-17 AAP31937.1			
Tyrosine Aminotransferase 3	56274 18: 497316-499922	7.57E-09 AAP31937.1			
Tyrosine Aminotransferase 3	57929 11: 211462-214768	2.12E-17 AAP31937.1			
Werner Syndrome-like Exonuclease (WEX)	54323 21: 531493-535556	4.66E-08 AEE83339.1	4.62E-08 NP_193123.2		
Werner Syndrome-like Exonuclease (WEX)	<b>134987*</b> 12: 1225937-1230473	6.27E-28 AEE83339.1	1.55E-25 NP_193123.2		AT4G13870 / WRNEXO
WRKY 6	23935 12: 631155-633289	2.30E-17 AEE33948.1			
XRN4	24310 12: 612192-614383	6.82E-111 AEE33109.1			
XRN4	143098 5: 1366952-1369829	2.91E-22 AEE33109.1			

\*Putative Ortholog to *A. thaliana* Gene

Table S2. List of all homologs present in the genome of *C. variabilis* that are related to *Arabidopsis* genes involved in RNA silencing and those induced by viruses along with the cluster into which they grouped, and the normalized expression values across all time points (T = 7 to T = 60).

Description	Protein ID	Location	Change in Expression	T = 0, Normalized	T = 7, Normalized	T = 14, Normalized	T = 20, Normalized	T = 40, Normalized	T = 60, Normalized
Argonaute 1, Argonaute 4	134979	12: 1196437-1201802	Up-Regulated (> 2-fold)	4923.7	4963.4	5715.4	6641.0	10456.9	12528.7
Calmodulin 2, Calmodulin 5	139412	27: 459029-466133	Up-Regulated (> 2-fold)	43.1	53.5	51.3	76.7	101.5	149.1
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	35323	9: 889317-893109	Up-Regulated (> 2-fold)	566.9	579.4	621.8	777.5	1230.8	1449.4
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	59820	32: 135884-137740	Up-Regulated (> 2-fold)	2556.7	2665.3	3630.7	3833.9	6639.3	6122.6
Cytochrome P450	34731	9: 173438-175321	Up-Regulated (> 2-fold)	30.6	40.9	53.1	55.6	62.6	103.4
Cytochrome P450	57280	8: 663160-667834	Up-Regulated (> 2-fold)	7.1	18.9	42.5	47.0	58.4	108.8
Cytochrome P450	57715	14: 245827-252078	Up-Regulated (> 2-fold)	2.4	25.2	77.8	117.9	116.8	163.9
Cytochrome P450	58466	22: 377198-3382589	Up-Regulated (> 2-fold)	14.1	19.7	33.6	43.1	58.4	87.3
Cytochrome P450	135475	14: 437199-46755	Up-Regulated (> 2-fold)	133.3	144.7	130.9	147.6	189.1	268.7
DRD1	134981	12: 1205513-1211041	Up-Regulated (> 2-fold)	381.8	426.9	417.5	612.6	821.9	854.3
DRD1, CLSY1	135608	14: 481516-486826	Up-Regulated (> 2-fold)	123.1	139.2	196.4	278.0	331.0	433.9
DRD1, CLSY1	143830	6: 1405615-1409502	Up-Regulated (> 2-fold)	37.6	31.4	26.5	64.2	111.3	114.2
Heat Shock Protein 70, Hsc 70 protein	48993	1: 1119468-1126328	Up-Regulated (> 2-fold)	120.7	139.2	142.4	150.5	232.3	295.5
Helicase	11200	3: 345557-347008	Up-Regulated (> 2-fold)	1070.2	1118.0	1271.9	1446.7	2196.0	2675.8
Helicase	25381	15: 1125352-1128559	Up-Regulated (> 2-fold)	59.6	55.0	67.2	92.0	115.4	122.2
Helicase	54357	21: 745556-755111	Up-Regulated (> 2-fold)	170.9	158.0	184.9	236.8	329.6	447.3
Helicase	56762	2: 1742997-1747201	Up-Regulated (> 2-fold)	73.7	77.0	116.7	141.9	139.1	198.8
Helicase	58862	27: 66760-71085	Up-Regulated (> 2-fold)	10.2	10.2	23.9	37.4	61.2	83.3
Helicase	133118	1: 946609-955040	Up-Regulated (> 2-fold)	97.2	92.8	114.1	149.6	221.1	247.2
Helicase	136192	15: 982002-988383	Up-Regulated (> 2-fold)	41.6	44.8	49.5	78.6	130.7	158.5
Helicase	136249	15: 1184413-1188877	Up-Regulated (> 2-fold)	76.8	69.2	79.6	124.6	118.2	154.5
HUA Enhancer 2	134358	12: 272267-275086	Up-Regulated (> 2-fold)	95.7	89.6	83.1	117.9	205.8	309.0
HUA Enhancer 2	135006	12: 1297082-1299755	Up-Regulated (> 2-fold)	32.1	38.5	49.5	50.8	64.0	64.5
HUA Enhancer 2	142028	4: 687758-696440	Up-Regulated (> 2-fold)	416.3	408.0	459.9	574.3	887.3	1159.2
KUB8	144569	7: 1702610-1709370	Up-Regulated (> 2-fold)	30.6	22.8	34.5	29.7	112.6	188.1
Methyltransferase 1	135136	13: 269730-275128	Up-Regulated (> 2-fold)	323.8	409.6	372.4	502.4	605.0	685.1
Polyubiquitin 4, Polyubiquitin 10	27202	24: 7266942-727267	Up-Regulated (> 2-fold)	243.8	271.2	365.3	418.0	506.2	237.8
Polyubiquitin 4, Polyubiquitin 10	48072	1: 1099388-1100863	Up-Regulated (> 2-fold)	17023.6	18154.6	23044.8	25070.3	39804.0	46094.2
Protein Phosphatase 2C	25388	15: 432881-434483	Up-Regulated (> 2-fold)	111.3	114.0	120.3	170.7	196.1	302.2
Putative Protein Kinase	10750	19: 795506-797518	Up-Regulated (> 2-fold)	104.3	90.4	99.9	114.1	173.8	231.0
Putative Protein Kinase	25736	17: 906048-908316	Up-Regulated (> 2-fold)	137.2	139.9	152.1	176.4	197.5	278.1
Putative Protein Kinase	32147	17: 995005-998691	Up-Regulated (> 2-fold)	51.0	65.3	59.3	98.7	101.5	110.1
Putative Protein Kinase	34300	4: 251161-253925	Up-Regulated (> 2-fold)	277.5	301.9	318.4	358.6	599.4	604.5
Putative Protein Kinase	36647	19: 618576-621209	Up-Regulated (> 2-fold)	25.9	20.4	43.3	55.6	127.9	142.4
Putative Protein Kinase	36812	22: 16454-19399	Up-Regulated (> 2-fold)	639.0	723.3	764.2	919.4	1290.6	1136.4
Putative Protein Kinase	57611	11: 100668-105366	Up-Regulated (> 2-fold)	8.6	10.2	15.0	17.3	57.0	81.9
Putative Protein Kinase	133695	10: 503420-504413	Up-Regulated (> 2-fold)	12.5	20.4	26.5	57.5	91.8	99.4
Putative Protein Kinase	135749	15: 463999-470858	Up-Regulated (> 2-fold)	94.1	108.5	115.0	104.5	197.5	212.2
Putative Protein Kinase	136055	15: 519360-521098	Up-Regulated (> 2-fold)	239.1	269.7	280.4	328.8	443.6	595.1
Putative Protein Kinase	136507	16: 926266-929417	Up-Regulated (> 2-fold)	42.3	48.0	46.9	56.6	97.4	104.8
Putative Protein Kinase	136834	17: 918240-927913	Up-Regulated (> 2-fold)	10.2	29.9	92.9	126.5	244.8	323.7
Putative Protein Kinase	138610	25: 486039-489934	Up-Regulated (> 2-fold)	0.5	9.4	29.2	32.6	64.0	102.1
Putative Protein Kinase	141147	4: 1157534-1163749	Up-Regulated (> 2-fold)	37.6	54.2	50.4	47.0	75.1	45.7
Putative Protein Kinase	143982	6: 1954260-1960953	Up-Regulated (> 2-fold)	926.7	1076.3	1177.2	1440.0	1923.4	1953.1
Ribonuclease Family III	53967	18: 1084410-1088740	Up-Regulated (> 2-fold)	220.3	239.0	248.5	285.7	438.1	483.6
Ribonuclease Family III	58365	15: 447810-456220	Up-Regulated (> 2-fold)	113.7	135.2	151.2	147.6	179.4	229.7
Ribonuclease Family III	135022	12: 1368827-1375310	Up-Regulated (> 2-fold)	221.1	373.5	401.5	459.2	559.1	537.3
SDE3	57676	8: 1580240-1587082	Up-Regulated (> 2-fold)	1005.9	1171.5	1347.0	1738.1	2575.6	2775.2
SDE3	133757	10: 168938-179243	Up-Regulated (> 2-fold)	416.3	551.1	589.1	688.4	853.9	776.4
SRG1	22157	9: 335071-336708	Up-Regulated (> 2-fold)	12.5	19.7	20.3	25.9	40.3	68.5
SUMO-activating Enzyme 1A	134704	12: 272267-275086	Up-Regulated (> 2-fold)	1502.2	1802.0	2315.5	2328.7	3475.4	2940.4
Thioredoxin h	15163	25: 391408-392203	Up-Regulated (> 2-fold)	46.3	72.3	70.8	60.4	80.7	95.4
Werner Syndrome-like Exonuclease (WEX)	134987	12: 1225937-1230473	Up-Regulated (> 2-fold)	231.3	260.2	288.3	331.7	446.4	498.4
WRKY 6	23935	12: 631155-633289	Up-Regulated (> 2-fold)	58.8	61.3	63.7	86.3	107.1	143.7
Aldo-Keto Reductase	48483	2: 1634716-1636765	Down-Regulated (> 2-fold)	1195.6	1028.4	1015.4	855.2	528.5	505.1
Alpha/Beta-hydrolases Superfamily	137489	19: 938177-940197	Down-Regulated (> 2-fold)	271.3	286.2	260.0	217.6	129.3	110.1
Calreticulin 3	136908	18: 50803-53418	Down-Regulated (> 2-fold)	3752.4	3265.9	3588.3	2749.6	1742.6	1915.5
Calreticulin 3	136909	18: 53842-57368	Down-Regulated (> 2-fold)	4311.4	3630.8	4101.3	3953.7	2125.0	2162.7
Heat Shock Protein 70, Hsc 70 protein	18857	2: 125949-127239	Down-Regulated (> 2-fold)	1398.7	1140.8	1181.7	985.6	689.8	720.0
Heat Shock Protein 70, Hsc 70 protein	35731	12: 193215-198231	Down-Regulated (> 2-fold)	3866.8	3446.8	3812.1	2748.6	1912.3	2311.8
Heat Shock Protein 70, Hsc 70 protein	142093	4: 929357-932671	Down-Regulated (> 2-fold)	503.3	468.6	385.6	290.5	190.5	233.7
Heat Shock Protein 70, Hsc 70 protein	144025	65: 26-3185	Down-Regulated (> 2-fold)	2871.1	2324.8	2398.7	1847.4	1322.6	1354.0
Helicase	6836	5: 2142867-2146197	Down-Regulated (> 2-fold)	236.8	176.9	115.9	118.9	133.5	170.6
Helicase	12993	18: 754470-755600	Down-Regulated (> 2-fold)	234.4	231.1	222.0	237.8	194.7	110.1
Helicase	25981	18: 261643-265486	Down-Regulated (> 2-fold)	810.7	729.6	615.6	605.9	429.7	403.0
Helicase	48551	3: 1476980-1479283	Down-Regulated (> 2-fold)	1735.1	1709.2	1680.5	1340.3	872.0	767.0

Helicase	56430	1: 95364-101279	Down-Regulated (> 2-fold)	1245.8	1181.7	833.2	641.4	513.2	536.0
Helicase	135879	14: 1339476-1341915	Down-Regulated (> 2-fold)	1425.4	1582.7	933.1	643.3	481.2	498.4
Helicase	139551	25: 402741-406942	Down-Regulated (> 2-fold)	289.3	236.7	181.3	165.9	121.0	161.2
Helicase	139706	26: 194044-195214	Down-Regulated (> 2-fold)	337.9	276.7	211.4	149.6	179.4	210.9
Helicase	145162	8: 1728281-1729234	Down-Regulated (> 2-fold)	265.8	241.4	184.9	129.4	175.2	150.4
Histone Deacetylase 6	24556	13: 1161882-1164007	Down-Regulated (> 2-fold)	965.9	1174.6	978.2	664.4	516.0	428.5
Histone Deacetylase 6	25722	17: 7351-10169	Down-Regulated (> 2-fold)	42.3	22.0	19.5	21.1	22.3	49.7
Kryptonite, SUVH2, SUVH5	20354	4: 947867-952310	Down-Regulated (> 2-fold)	1192.5	932.5	994.1	855.2	568.8	498.4
Protein Phosphatase 2C	9625	26: 21494-24388	Down-Regulated (> 2-fold)	1022.4	873.5	814.6	641.4	509.0	506.4
Protein Phosphatase 2C	59807	29: 103501-108236	Down-Regulated (> 2-fold)	406.1	359.3	242.3	201.3	197.5	237.8
Putative Protein Kinase	10735	32: 240685-242438	Down-Regulated (> 2-fold)	229.7	240.6	211.4	155.3	108.5	130.3
Putative Protein Kinase	28672	38: 49333-52042	Down-Regulated (> 2-fold)	614.7	577.1	546.6	395.0	364.4	291.5
Putative Protein Kinase	50324	3: 1169017-1172252	Down-Regulated (> 2-fold)	221.9	250.0	214.9	139.0	107.1	107.5
SDE3	59413	38: 180158-183538	Down-Regulated (> 2-fold)	276.8	301.1	209.6	156.3	109.9	176.0
Thioredoxin h	20868	5: 1067392-1068011	Down-Regulated (> 2-fold)	385.7	379.0	420.1	337.5	244.8	180.0
Thioredoxin h	33111	30: 432462-435281	Down-Regulated (> 2-fold)	709.5	742.2	614.7	650.0	386.6	279.4
Thioredoxin h	36198	15: 61048-62626	Down-Regulated (> 2-fold)	199.1	217.0	182.2	180.2	76.5	83.3
Thioredoxin h (H1, H3)	18066	1: 2507693-2509008	Down-Regulated (> 2-fold)	1441.0	1546.5	1637.2	1014.3	586.9	560.1
Werner Syndrome-like Exonuclease (WEX)	54323	21: 531493-535556	Down-Regulated (> 2-fold)	1019.2	1118.8	758.9	563.7	489.5	525.2
Aldo-Keto Reductase	13275	98: 6623-8081	No Change in Expression	272.8	235.9	260.0	251.2	201.7	171.9
Aldo-Keto Reductase	19238	2: 160719-162867	No Change in Expression	83.1	85.7	89.3	79.6	87.6	88.7
Aldo-Keto Reductase	22713	9: 1215450-1217363	No Change in Expression	122.3	139.9	96.4	100.7	69.5	73.9
Aldo-Keto Reductase	29451	2: 459876-462891	No Change in Expression	171.7	169.8	198.1	177.4	132.1	161.2
Aldo-Keto Reductase	32425	21: 177192-180599	No Change in Expression	918.9	817.7	848.2	839.8	668.9	595.1
Aldo-Keto Reductase	135662	14: 660806-662514	No Change in Expression	40.0	37.7	37.1	45.1	34.8	43.0
Aldo-Keto Reductase	138560	21: 162828-165994	No Change in Expression	429.6	418.3	425.4	389.2	300.4	302.2
Calmodulin 2	20239	4: 1072482-1077234	No Change in Expression	1967.9	2026.1	2122.7	2385.3	1702.3	1260.0
Calmodulin 2	145399	9: 756050-760569	No Change in Expression	355.9	439.8	378.6	389.2	408.9	362.7
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	30247	5: 68267-72106	No Change in Expression	889.9	939.5	1099.4	1001.9	803.8	827.5
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	36351	16: 719127-724229	No Change in Expression	181.1	149.4	153.0	223.4	251.7	326.4
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	55421	35: 299573-300582	No Change in Expression	239.1	235.9	277.7	216.7	203.0	181.3
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	134284	11: 400754-401635	No Change in Expression	59.6	65.3	77.8	62.3	30.6	32.2
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	140078	28: 409928-411688	No Change in Expression	1259.9	1033.1	1207.3	1386.3	938.7	687.8
Calmodulin 2, Thioredoxin h (H3)	135979	15: 248703-252371	No Change in Expression	201.5	191.8	145.9	150.5	116.8	108.8
Chitinase Class IV, Chitinase (putative)	48490	2: 2027624-2032362	No Change in Expression	97.2	73.9	75.2	101.6	111.3	123.6
Chromomethylase 3, Methyltransferase 1	52630	11: 1243193-1254336	No Change in Expression	733.1	640.8	637.7	825.4	1179.3	1233.1
Chromomethylase 3, Methyltransferase 1	137705	2: 650015-660109	No Change in Expression	5054.6	4218.8	4087.1	5048.6	6533.6	7480.7
Chromomethylase 3, Methyltransferase 1	139634	25: 666943-672028	No Change in Expression	431.2	399.4	400.7	431.2	417.2	341.2
Cytochrome P450	51247	6: 419824-424285	No Change in Expression	862.4	835.0	772.1	742.0	637.0	533.3
Cytochrome P450	56217	14: 743147-745976	No Change in Expression	1766.4	1708.5	1879.5	1842.6	1312.8	961.8
Cytochrome P450	135122	14: 9115779-917917	No Change in Expression	1326.6	1449.8	1386.0	1561.7	1450.5	990.0
Cytochrome P450	138471	20: 806491-811354	No Change in Expression	701.7	786.2	850.9	892.6	828.9	659.5
Dicer-like (DCL1, DCL2, DCL3, DCL4)	143199	7: 1702610-1709370	No Change in Expression	154.5	166.7	161.0	212.8	286.5	283.4
Domains Rearranged Methylase 2 (DRM2)	139582	3: 1194661-1198767	No Change in Expression	281.5	326.3	366.2	395.0	471.5	396.3
DRD1	9749	13: 428961-432049	No Change in Expression	331.6	257.1	241.5	280.9	297.6	296.9
DRD1, CLSY1	21780	6: 408699-409472	No Change in Expression	58.8	59.8	66.3	73.8	64.0	68.5
DRD1, CLSY1	22847	9: 1001773-1005155	No Change in Expression	634.3	586.5	572.3	452.5	356.0	333.1
DRD1, CLSY1	34395	4: 1289738-1297719	No Change in Expression	5166.0	4433.5	4822.1	4306.5	3781.4	3781.3
DRD1, CLSY1	49470	1: 1119468-1126328	No Change in Expression	207.8	171.4	153.9	156.3	166.9	194.8
DRD1, CLSY1	56509	1: 1193929-1203561	No Change in Expression	531.6	404.1	378.6	389.2	399.1	480.9
DRD1, CLSY1	57917	11: 100668-105366	No Change in Expression	186.6	187.1	181.3	204.2	294.8	306.3
DRD1, CLSY1	136777	17: 699264-708220	No Change in Expression	249.3	242.9	240.6	272.3	317.1	373.4
DRD1, CLSY1	136836	17: 932064-935354	No Change in Expression	1329.7	1238.3	1170.2	1524.3	1691.1	1795.9
DRD1, CLSY1	136932	18: 108310-118274	No Change in Expression	219.5	186.3	170.7	207.1	193.3	216.3
DRD1, CLSY1	137064	18: 578020-590656	No Change in Expression	2697.8	2689.7	2872.8	3182.9	4034.5	4101.0
DRD1, CLSY1	138032	2: 1794099-1804297	No Change in Expression	139.6	118.7	129.1	172.6	196.1	261.9
DRD1, CLSY1	140806	3: 1766466-1768453	No Change in Expression	156.0	149.4	159.2	171.6	196.1	208.2
DRD1, CLSY1	142147	4: 1157534-1163749	No Change in Expression	376.3	267.3	355.6	397.9	500.7	609.8
DRD1, CLSY1	142431	4: 2153086-2156465	No Change in Expression	267.4	261.8	251.2	301.0	371.3	397.6
DRD1, CLSY1	144734	8: 256528-269262	No Change in Expression	323.8	294.0	251.2	272.3	367.2	385.5
Glucose-6-phosphate 1-dehydrogenase	36395	16: 1128024-1132745	No Change in Expression	348.1	381.3	430.7	333.6	276.8	233.7
Glucose-6-phosphate 1-dehydrogenase	134643	12: 94280-97424	No Change in Expression	1255.2	1337.4	1323.2	964.5	873.4	865.1
Glutathione S-transferase 16	57549	7: 1560203-1562813	No Change in Expression	70.6	103.8	106.1	69.0	65.4	72.5
HASTY	139890	3: 1919274-1921512	No Change in Expression	59.6	58.2	50.4	75.7	90.4	106.1
Heat Shock Protein 70, Hsc 70 protein	19454	3: 989551-992157	No Change in Expression	83.9	73.9	81.4	88.2	73.7	96.7
Heat Shock Protein 70, Hsc 70 protein	32920	26: 392386-396631	No Change in Expression	19162.4	18553.2	22678.7	23079.0	20136.4	15971.5
Heat Shock Protein 70, Hsc 70 protein	36653	19: 678818-685275	No Change in Expression	7531.4	7132.6	8232.6	9422.2	8637.8	8641.2
Heat Shock Protein 70, Hsc 70 protein	56032	4: 924604-929108	No Change in Expression	1755.4	1836.6	2324.4	2263.5	2241.9	2769.8
Heat Shock Protein 70, Hsc 70 protein	57615	8: 718979-727783	No Change in Expression	1121.2	898.6	949.9	1058.4	1152.9	1246.6
Heat Shock Protein 70, Hsc 70 protein	137436	19: 767959-773941	No Change in Expression	1753.9	1647.9	1516.0	1787.0	2097.2	2374.9

Heat Shock Protein 70, Hsc 70 protein	145242	9:	179690-183562	No Change in Expression	14120.3	13730.5	14559.2	10518.0	7423.7	8046.2
Heat Shock Protein 83	19360	2:	136408-137707	No Change in Expression	471.2	394.7	457.3	502.4	401.9	405.7
Heat Shock Protein 83	57527	7:	1224913-123322	No Change in Expression	11678.1	10901.7	13222.8	14644.3	12801.7	12534.0
Heat Shock Protein 83	59468	65:	3417-10734	No Change in Expression	1228.6	1028.4	1148.0	1168.7	908.1	977.9
Heat Shock Protein 83	134150	106:	7213-7856	No Change in Expression	1292.9	1116.4	1314.3	1578.0	1104.2	1242.5
Heat Shock Protein 83	140066	28:	361484-368639	No Change in Expression	3686.5	3248.7	3411.4	3057.3	2547.8	2662.4
Helicase	19567	3:	1053241-1057277	No Change in Expression	564.5	626.6	662.5	656.7	702.3	514.5
Helicase	20835	5:	189976-193636	No Change in Expression	3614.4	3980.6	3052.3	2322.0	2247.4	2365.5
Helicase	23258	10:	647099-650975	No Change in Expression	2436.8	2416.8	2291.7	2481.1	1792.6	1417.1
Helicase	26393	20:	279686-282659	No Change in Expression	643.7	642.3	557.2	442.9	367.2	394.9
Helicase	28127	31:	406161-411022	No Change in Expression	692.3	676.9	704.0	641.4	666.2	616.6
Helicase	28229	32:	309237-313007	No Change in Expression	1692.7	1775.3	1881.3	1928.0	1506.2	1239.8
Helicase	29172	1:	647917-651743	No Change in Expression	4336.5	4071.8	4891.1	4565.4	3425.4	3027.7
Helicase	30080	4:	1271234-1275793	No Change in Expression	7276.6	7158.5	7252.6	7369.6	7234.6	7036.0
Helicase	31911	15:	417063-423814	No Change in Expression	5134.6	5001.9	4846.0	4471.4	3816.2	3458.9
Helicase	33556	1:	1429007-1434817	No Change in Expression	1817.4	1746.2	1713.2	1799.5	1606.3	1775.8
Helicase	33628	1:	2182787-2187237	No Change in Expression	3318.0	3486.1	3357.4	2639.3	2503.3	2497.1
Helicase	34017	3:	192057-196244	No Change in Expression	176.4	184.8	156.6	152.4	196.1	217.6
Helicase	34665	5:	712295-714804	No Change in Expression	1184.7	1260.3	1353.2	1133.2	1115.4	1043.7
Helicase	35936	13:	786044-790325	No Change in Expression	620.9	560.6	602.3	678.8	916.5	879.8
Helicase	36420	17:	428243-431524	No Change in Expression	4604.6	4655.2	4582.4	3581.7	2899.7	2595.2
Helicase	36787	21:	828015-831869	No Change in Expression	8282.5	8600.4	6710.5	5162.7	5041.4	5014.3
Helicase	36987	24:	332182-335699	No Change in Expression	119.2	124.2	106.1	102.6	122.4	114.2
Helicase	50422	3:	1750103-1760404	No Change in Expression	688.4	675.4	580.2	667.3	621.7	729.4
Helicase	51440	9:	76437-88386	No Change in Expression	758.2	879.0	892.4	998.0	1001.3	819.4
Helicase	51607	7:	1157372-1160390	No Change in Expression	1303.8	1423.8	1206.4	1120.7	1207.2	1276.1
Helicase	51983	9:	76437-88386	No Change in Expression	290.9	233.5	212.3	232.0	243.4	232.4
Helicase	56077	5:	990014-992974	No Change in Expression	3166.7	2846.1	3321.2	3735.1	4049.8	2053.9
Helicase	56582	1:	2300951-2306768	No Change in Expression	2504.2	2227.4	2283.7	2284.7	2845.4	3211.8
Helicase	56765	2:	1853785-1865813	No Change in Expression	829.5	754.8	738.5	944.3	986.0	1022.2
Helicase	57434	6:	1594681-1601788	No Change in Expression	124.7	102.2	92.0	143.8	159.9	232.4
Helicase	57565	7:	1800091-1809526	No Change in Expression	117.6	111.6	86.7	106.4	116.8	170.6
Helicase	57890	10:	1348919-1352391	No Change in Expression	519.0	544.8	559.0	653.8	614.7	596.4
Helicase	58353	15:	324855-329093	No Change in Expression	1443.4	1444.3	1275.4	1247.3	1173.8	1128.3
Helicase	58455	16:	689199-695224	No Change in Expression	2748.8	2623.6	2350.9	1935.6	1649.4	1656.2
Helicase	58635	18:	803302-807473	No Change in Expression	3058.5	2660.6	2426.1	1777.4	1545.1	1739.5
Helicase	59105	26:	195166-198291	No Change in Expression	595.9	554.3	440.5	361.4	420.0	570.9
Helicase	59143	27:	66760-71085	No Change in Expression	4604.6	5359.6	4988.4	3677.6	3354.4	3082.8
Helicase	59259	31:	230818-261110	No Change in Expression	1306.2	1198.2	1272.8	1431.4	1610.5	1520.6
Helicase	59745	19:	531803-536730	No Change in Expression	17647.7	16383.2	17764.6	19505.9	20911.0	15853.2
Helicase	133108	1:	901279-905631	No Change in Expression	49.4	65.3	46.0	72.9	76.5	75.2
Helicase	133956	10:	915180-920226	No Change in Expression	148.2	122.6	122.1	132.3	119.6	133.0
Helicase	134628	12:	40567-46062	No Change in Expression	2365.4	2085.8	2079.4	2291.3	2896.9	3148.6
Helicase	135424	13:	1251202-1253608	No Change in Expression	1463.0	1332.6	1433.7	1645.1	1577.1	1524.6
Helicase	136793	17:	755811-762818	No Change in Expression	5465.5	5214.2	5663.3	5563.4	4596.4	3890.1
Helicase	137419	19:	721550-723571	No Change in Expression	234.4	235.1	139.7	123.7	134.9	119.6
Helicase	137613	2:	300764-309819	No Change in Expression	7098.6	6673.4	6882.9	6890.2	7147.0	7827.2
Helicase	137841	2:	1156367-1165132	No Change in Expression	1503.0	1504.0	1588.5	1907.8	2119.5	1397.0
Helicase	137938	2:	1485487-1492814	No Change in Expression	2453.2	2251.7	2101.5	2050.7	1504.8	1417.1
Helicase	137960	2:	1564336-1574691	No Change in Expression	820.9	628.2	641.2	699.9	713.4	779.1
Helicase	138311	20:	227947-237782	No Change in Expression	1842.5	2022.2	1826.4	1734.3	1557.6	1555.5
Helicase	138879	22:	432562-435855	No Change in Expression	354.4	430.8	400.7	325.0	283.7	270.0
Helicase	139542	25:	354355-361481	No Change in Expression	612.3	605.4	485.6	465.9	542.4	576.3
Helicase	142335	4:	1845225-1847715	No Change in Expression	1195.6	1276.0	1174.6	1115.0	638.3	647.5
Helicase	142420	4:	2117325-2123225	No Change in Expression	178.8	117.9	116.7	130.4	193.3	243.1
Helicase	142433	4:	2158583-2161193	No Change in Expression	203.8	217.0	185.7	246.4	286.5	341.2
Helicase	142930	5:	836109-839391	No Change in Expression	2610.0	2485.2	2503.0	2005.6	1693.9	1519.2
Helicase	144099	7:	135689-139618	No Change in Expression	333.2	383.7	398.0	436.2	535.4	476.9
Helicase	144794	8:	470600-481344	No Change in Expression	177.2	158.0	142.4	144.8	208.6	236.4
Histone Deacetylase 6	8472	11:	1140666-1144451	No Change in Expression	162.3	154.1	144.2	143.8	171.1	213.6
Histone Deacetylase 6	9525	33:	354973-357391	No Change in Expression	114.5	102.2	110.6	125.6	178.0	196.1
Histone Deacetylase 6	23482	11:	1456190-1459967	No Change in Expression	356.7	306.6	290.1	264.6	237.8	229.7
Histone Deacetylase 6	140841	3:	1919274-1921512	No Change in Expression	120.0	109.3	98.2	99.7	91.8	134.3
Histone Deacetylase 6	145535	9:	1236571-1240373	No Change in Expression	374.0	419.8	451.1	457.3	566.0	503.7
HUA Enhancer 2	28067	30:	366742-377171	No Change in Expression	637.4	586.5	511.2	567.6	502.1	513.1
HUA Enhancer 2	52598	11:	1031147-1044963	No Change in Expression	149.7	194.2	159.2	161.1	185.0	192.1
HUA Enhancer 2	134899	13:	102047-103864	No Change in Expression	530.0	591.2	635.9	721.9	541.0	549.4
HUA Enhancer 2	138793	22:	111256-127552	No Change in Expression	957.3	857.8	850.0	908.9	1108.4	1481.6
HUA Enhancer 2	140958	3:	2390104-2403118	No Change in Expression	4520.7	4009.7	4165.0	3944.1	3838.4	4152.0
HUA Enhancer 2	141429	34:	133586-142626	No Change in Expression	1624.5	1494.6	1448.8	1228.1	1115.4	1128.3



HUA Enhancer 2	144334	7: 960068-971038	No Change in Expression	115.3	123.4	108.8	126.5	164.1	202.8
Kryptonite, SUVH2, SUVH5	25365	15: 841126-843132	No Change in Expression	110.5	105.4	77.8	80.5	97.4	84.6
Kryptonite, SUVH2, SUVH5	142107	4: 978017-984445	No Change in Expression	225.8	158.8	179.5	242.6	333.8	377.5
Kryptonite, SUVH2, SUVH3, SUVH5	58236	14: 245827-252078	No Change in Expression	962.8	984.3	1113.5	1055.5	956.8	767.0
Kryptonite, SUVH3, SUVH5	18588	1: 2498872-2501312	No Change in Expression	314.4	277.5	330.8	373.9	358.8	325.1
Kryptonite, SUVH3, SUVH5	35816	12: 900000-901522	No Change in Expression	679.8	676.9	574.0	591.5	534.0	495.7
KU70	53981	19: 39237-45448	No Change in Expression	41.6	39.3	38.9	26.8	43.1	44.3
Methyltransferase 1	137706	2: 660187-662714	No Change in Expression	926.7	684.0	719.1	883.0	1080.6	1203.6
NRPE5	134695	12: 246327-247559	No Change in Expression	723.7	754.8	1024.2	896.4	488.1	405.7
Nuclear RNA Polymerase D2A	19065	2: 2064779-2065281	No Change in Expression	385.0	367.2	384.7	525.4	474.2	447.3
Nuclear RNA Polymerase D2A	56318	23: 370562-377362	No Change in Expression	2208.6	1798.9	1958.2	2059.3	2750.9	2643.6
Nuclear RNA Polymerase D2A	59036	24: 642746-650052	No Change in Expression	2151.4	1793.4	1876.8	2005.6	2029.1	1833.6
Pathogenesis-related Gene 1	139641	25: 690334-692481	No Change in Expression	101.9	91.2	89.3	101.6	93.2	96.7
Polyubiquitin 4, Polyubiquitin 10	9815	16: 457831-458211	No Change in Expression	327.7	312.1	410.4	350.9	308.7	288.8
Polyubiquitin 4, Polyubiquitin 10	15978	4: 1795835-1796105	No Change in Expression	2775.5	3272.2	4187.1	4272.0	4888.4	3788.0
Polyubiquitin 4, Polyubiquitin 10	24467	13: 880611-880970	No Change in Expression	548.8	559.0	628.9	596.3	510.4	440.6
Polyubiquitin 4, Polyubiquitin 10	48528	3: 738848-740288	No Change in Expression	729.1	703.7	935.8	949.1	898.4	801.9
Polyubiquitin 4, Polyubiquitin 10	51574	7: 864756-867994	No Change in Expression	4968.4	4959.5	5597.8	4797.4	3647.9	3683.2
Polyubiquitin 4, Polyubiquitin 10	136254	15: 1201071-1208628	No Change in Expression	450.0	369.5	301.6	335.5	386.6	440.6
Protein Disulfide Isomerase	58416	16: 79490-81643	No Change in Expression	109.0	88.8	94.6	96.8	109.9	130.3
Protein Disulfide Isomerase	132941	1: 260599-263457	No Change in Expression	608.4	527.6	447.5	455.4	422.8	464.8
Protein Disulfide Isomerase	134783	12: 538010-540584	No Change in Expression	208.6	174.5	168.0	175.4	137.7	142.4
Protein Disulfide Isomerase	138016	2: 1738882-1742680	No Change in Expression	575.5	423.8	496.2	488.9	368.5	326.4
Protein Disulfide Isomerase	142831	5: 486435-489669	No Change in Expression	1207.4	1238.3	1471.8	1618.3	1545.1	1274.8
Protein Disulfide Isomerase, Thioredoxin h (H1, H3)	14696	2: 120132-121440	No Change in Expression	1003.6	1010.3	1155.1	1157.2	752.4	569.5
Protein Disulfide Isomerase, Thioredoxin h (H4)	136996	18: 358957-362257	No Change in Expression	297.9	235.1	205.2	291.4	247.5	259.3
Protein Phosphatase 2C	36133	14: 1117036-1118669	No Change in Expression	209.3	209.1	174.2	190.8	157.2	133.0
Protein Phosphatase 2C	58836	21: 948044-953534	No Change in Expression	4378.8	5142.7	5852.5	5736.9	4724.3	3745.0
Protein Phosphatase 2C	59087	26: 46483-49186	No Change in Expression	272.8	209.9	256.5	343.2	452.0	495.7
Protein Phosphatase 2C	139942	27: 459029-466133	No Change in Expression	337.9	342.8	359.1	346.1	282.3	326.4
Putative Protein Kinase	7719	21: 687300-690782	No Change in Expression	204.6	133.7	143.3	115.0	109.9	146.4
Putative Protein Kinase	12761	11: 1109228-1110585	No Change in Expression	167.8	173.0	175.1	183.1	168.3	110.1
Putative Protein Kinase	13183	34: 275749-277025	No Change in Expression	269.7	320.0	296.3	344.2	349.1	244.5
Putative Protein Kinase	13628	22: 666544-667659	No Change in Expression	121.5	130.5	110.6	93.0	102.9	87.3
Putative Protein Kinase	13716	15: 513057-513977	No Change in Expression	41.6	48.0	56.6	42.2	47.3	81.9
Putative Protein Kinase	19742	3: 1831585-1831935	No Change in Expression	179.2	197.3	229.1	180.2	93.2	95.4
Putative Protein Kinase	21563	6: 2000876-2002079	No Change in Expression	453.2	452.1	498.8	487.0	564.6	592.4
Putative Protein Kinase	22641	9: 335071-336708	No Change in Expression	86.2	83.3	95.5	120.8	162.7	138.4
Putative Protein Kinase	23857	12: 925404-926052	No Change in Expression	56.4	68.4	66.3	65.2	48.7	68.5
Putative Protein Kinase	24126	12: 740656-741937	No Change in Expression	445.3	493.7	444.0	462.1	436.7	428.5
Putative Protein Kinase	26970	23: 135372-137307	No Change in Expression	87.0	73.1	88.4	86.3	122.4	130.3
Putative Protein Kinase	29026	231: 95-830	No Change in Expression	105.8	135.2	146.8	136.1	130.7	116.9
Putative Protein Kinase	29775	3: 805404-807201	No Change in Expression	660.9	711.5	721.7	790.0	579.9	452.7
Putative Protein Kinase	29915	3: 1809976-1811344	No Change in Expression	267.4	302.7	276.8	222.4	180.8	165.2
Putative Protein Kinase	30642	7: 180275-182895	No Change in Expression	149.7	144.7	119.4	109.3	96.0	122.2
Putative Protein Kinase	30865	8: 1397728-1399552	No Change in Expression	134.1	184.0	189.3	246.4	240.6	190.7
Putative Protein Kinase	31062	10: 43317-45697	No Change in Expression	44.7	42.5	31.8	26.8	34.8	25.5
Putative Protein Kinase	36848	22: 661067-663404	No Change in Expression	210.9	225.6	212.3	192.7	164.1	162.5
Putative Protein Kinase	37276	26: 450330-452767	No Change in Expression	263.4	284.6	295.4	297.2	356.0	374.8
Putative Protein Kinase	49225	29: 303296-306490	No Change in Expression	1058.4	893.1	905.7	767.9	645.3	593.7
Putative Protein Kinase	49746	1: 3046695-3054721	No Change in Expression	1473.2	1677.0	1553.1	1550.2	1490.9	1383.6
Putative Protein Kinase	50123	2: 2532250-2537111	No Change in Expression	642.9	677.7	681.0	702.7	538.2	497.0
Putative Protein Kinase	51171	5: 2112874-2124092	No Change in Expression	169.3	183.2	173.4	200.4	254.5	255.2
Putative Protein Kinase	57033	4: 589172-595082	No Change in Expression	405.3	522.8	573.1	534.0	486.8	454.0
Putative Protein Kinase	58145	13: 420900-425357	No Change in Expression	83.1	110.9	94.6	99.7	69.5	108.8
Putative Protein Kinase	58318	14: 1209189-1211763	No Change in Expression	1109.4	1031.5	1076.4	1066.1	840.0	789.8
Putative Protein Kinase	58373	15: 526085-531347	No Change in Expression	308.9	316.1	379.4	370.1	422.8	413.7
Putative Protein Kinase	58735	20: 319034-323755	No Change in Expression	597.4	573.9	649.2	622.2	518.7	488.9
Putative Protein Kinase	58858	22: 339871-346545	No Change in Expression	1254.4	1408.1	1355.0	1337.4	1148.7	940.3
Putative Protein Kinase	58999	24: 370322-379069	No Change in Expression	1526.5	1893.2	1966.2	2086.2	2433.8	2558.9
Putative Protein Kinase	59518	653: 1332-1073	No Change in Expression	163.9	151.7	168.9	124.6	100.1	107.5
Putative Protein Kinase	59772	24: 518404-521846	No Change in Expression	1329.7	1293.3	1245.3	1051.7	1122.3	1059.8
Putative Protein Kinase	133720	10: 46072-50867	No Change in Expression	170.1	162.0	168.0	209.0	271.2	274.0
Putative Protein Kinase	133852	10: 555379-560903	No Change in Expression	598.2	683.2	878.3	883.0	798.3	638.1
Putative Protein Kinase	134418	12: 928137-937028	No Change in Expression	41.6	46.4	52.2	46.0	65.4	53.7
Putative Protein Kinase	135753	14: 930637-938200	No Change in Expression	417.9	473.3	459.0	516.7	361.6	370.7
Putative Protein Kinase	135759	14: 950314-953441	No Change in Expression	129.4	99.1	129.1	127.5	109.9	131.6
Putative Protein Kinase	136041	15: 463999-470858	No Change in Expression	149.7	152.5	155.7	174.5	208.6	200.1
Putative Protein Kinase	136066	15: 541171-548751	No Change in Expression	414.0	528.3	541.3	491.8	453.4	549.4
Putative Protein Kinase	136568	16: 1159733-1165667	No Change in Expression	1067.1	1132.2	1092.3	958.7	802.5	824.8

Putative Protein Kinase	136678	17: 322968-327068	No Change in Expression	221.1	279.1	369.7	352.8	296.2	347.9
Putative Protein Kinase	137363	19: 537377-546756	No Change in Expression	1233.3	1157.3	957.0	873.4	777.4	818.1
Putative Protein Kinase	137597	2: 246755-251331	No Change in Expression	453.2	559.0	552.8	592.5	695.4	620.6
Putative Protein Kinase	137604	2: 271806-273953	No Change in Expression	116.8	116.4	130.0	127.5	153.0	127.6
Putative Protein Kinase	137878	2: 1277636-1281499	No Change in Expression	129.4	132.9	154.8	162.0	93.2	100.7
Putative Protein Kinase	137935	2: 1472273-1476541	No Change in Expression	139.6	119.5	121.2	158.2	173.8	228.4
Putative Protein Kinase	138454	20: 735583-739763	No Change in Expression	1954.6	2225.0	2111.2	1881.0	1833.0	1379.5
Putative Protein Kinase	138663	21: 606558-610574	No Change in Expression	396.7	397.8	449.3	430.5	314.3	295.5
Putative Protein Kinase	140646	3: 1194661-1198767	No Change in Expression	546.5	472.5	479.4	455.4	514.6	511.8
Putative Protein Kinase	140750	3: 1543901-1547815	No Change in Expression	2121.6	2368.9	2462.4	2466.8	1570.1	1081.3
Putative Protein Kinase	140983	30: 124829-138325	No Change in Expression	384.2	385.2	323.7	345.1	381.1	397.6
Putative Protein Kinase	141046	30: 462539-468900	No Change in Expression	340.3	426.9	371.5	441.0	401.9	470.1
Putative Protein Kinase	141452	34: 243759-251281	No Change in Expression	2597.5	3230.6	3481.3	4210.7	5155.4	4060.7
Putative Protein Kinase	142162	4: 1226609-1233339	No Change in Expression	322.2	489.0	508.6	467.9	528.5	493.0
Putative Protein Kinase	142454	4: 2237941-2241471	No Change in Expression	2080.8	2064.6	2352.7	2682.5	2713.3	2137.1
Putative Protein Kinase	143307	8: 38320-45666	No Change in Expression	47.8	36.2	49.5	41.2	45.9	75.2
Putative Protein Kinase	143410	57: 1346-6789	No Change in Expression	834.2	872.7	794.3	929.9	820.5	705.2
Putative Protein Kinase	144329	7: 945706-949978	No Change in Expression	40.8	61.3	55.7	62.3	66.8	76.6
Putative Protein Kinase	144680	8: 38320-45666	No Change in Expression	254.0	301.1	344.9	390.2	406.1	384.2
Putative Protein Kinase	145300	9: 350591-354108	No Change in Expression	124.7	140.7	142.4	159.1	146.0	166.6
Putative Protein Kinase	145350	9: 568581-574658	No Change in Expression	1435.6	1751.7	1797.2	2010.4	2083.3	1680.4
Ribonuclease Family III	133597	1: 2612970-2618913	No Change in Expression	165.4	144.7	168.0	154.4	158.5	188.1
SDE3	58418	21: 948044-953534	No Change in Expression	792.7	886.1	831.4	694.1	465.9	557.5
SDE3	133825	10: 447777-456602	No Change in Expression	2411.7	2502.5	1960.0	1963.4	1725.9	1775.8
SDE3	137486	19: 924077-932357	No Change in Expression	730.7	647.1	674.0	680.7	610.5	768.3
SE	51470	7: 99916-103817	No Change in Expression	688.4	640.8	554.6	568.5	453.4	522.5
SRG1	10090	43: 43560-45363	No Change in Expression	526.9	526.0	583.7	465.0	297.6	275.4
SRG1	20260	4: 849157-851839	No Change in Expression	493.2	426.9	513.0	533.0	331.0	331.8
SRG1	21158	5: 479661-481149	No Change in Expression	155.2	157.2	136.2	143.8	137.7	124.9
SRG1	36779	21: 695622-69824	No Change in Expression	95.7	90.4	93.8	70.0	62.6	59.1
SUMO-activating Enzyme 1A	59425	39: 98022-120611	No Change in Expression	1158.8	1285.5	1289.6	1204.1	1267.0	1257.3
SUMO-activating Enzyme 1A	137823	2: 1098562-1102231	No Change in Expression	56.4	33.0	46.9	38.3	54.2	60.4
SUMO-activating Enzyme 1A	144742	8: 300825-305276	No Change in Expression	512.0	410.4	459.0	584.8	732.9	709.2
SUVH5	14389	18: 1044901-1045609	No Change in Expression	109.0	125.8	123.8	103.5	96.0	104.8
SUVR3	24455	13: 1213891-1214967	No Change in Expression	51.7	37.7	40.7	39.3	68.1	102.1
SUVR3, SUVH5	137958	2: 1559569-1560869	No Change in Expression	116.0	126.6	126.5	156.3	155.8	186.7
Thioredoxin h	14388	15: 147647-148271	No Change in Expression	558.2	557.4	635.9	642.3	374.1	294.2
Thioredoxin h	26293	19: 841228-843273	No Change in Expression	825.6	793.3	855.3	1052.7	1203.0	1117.6
Thioredoxin h	133836	10: 503420-504413	No Change in Expression	1462.2	1597.6	2014.8	2154.2	2536.7	1371.5
Thioredoxin h (H1, H3, H4)	52344	10: 937262-938427	No Change in Expression	95.7	84.9	84.9	95.9	102.9	76.6
Thioredoxin h (H4)	134198	11: 161469-165106	No Change in Expression	530.0	534.6	442.2	407.5	389.4	429.8
Thioredoxin h (H4)	140512	3: 771978-774133	No Change in Expression	491.6	503.2	446.7	371.0	300.4	274.0
Tyrosine Aminotransferase 3	22926	9: 1154912-1157688	No Change in Expression	850.7	827.1	701.4	840.8	894.2	800.6
Tyrosine Aminotransferase 3	29318	1: 2165190-2169064	No Change in Expression	1873.0	1953.8	2105.0	1429.4	1226.6	1466.8
Tyrosine Aminotransferase 3	48481	2: 1537999-1540528	No Change in Expression	609.2	681.7	680.2	686.4	621.7	483.6
Tyrosine Aminotransferase 3	56274	18: 497316-499922	No Change in Expression	176.4	165.1	201.7	159.1	140.5	108.8
Tyrosine Aminotransferase 3	57929	11: 211462-214768	No Change in Expression	100.4	75.5	77.8	94.0	91.8	142.4
XRN4	24310	12: 612192-614383	No Change in Expression	958.1	884.5	660.7	493.7	511.8	482.2
XRN4	143098	5: 1366952-1369829	No Change in Expression	1123.5	1251.7	1210.0	943.4	713.4	697.2
Aldo-Keto Reductase	23295	10: 248509-251473	Not Expressed*	25.1	22.8	14.2	10.5	22.3	22.8
Aldo-Keto Reductase	138982	27: 237586-246204	Not Expressed*	0.5	6.3	11.5	20.1	34.8	28.2
Aldo-Keto Reductase	142101	5: 836109-839391	Not Expressed*	2.4	3.9	2.7	5.8	4.2	17.5
Alpha/Beta-hydrolases Superfamily	144404	9: 1236571-1240373	Not Expressed*	0.8	3.1	5.3	9.6	20.9	24.2
Calmodulin 2	14319	14: 60837-61013	Not Expressed*	0.5	0.5	0.5	1.0	4.2	1.3
Calmodulin 2	134855	12: 759894-760952	Not Expressed*	14.1	11.0	13.3	12.5	26.4	37.6
Calmodulin 2	140699	33: 152877-154191	Not Expressed*	14.9	18.9	31.0	30.7	61.2	41.6
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	133793	10: 331318-335491	Not Expressed*	16.5	14.9	23.9	13.4	27.8	34.9
Calmodulin 2, Calmodulin 5, Calmodulin-like MSS3	141326	4: 1226609-1233339	Not Expressed*	5.5	7.9	16.8	12.5	16.7	16.1
Chromomethylase 3, Methyltransferase 1	50474	3: 2164815-2172644	Not Expressed*	22.0	24.4	31.8	28.8	33.4	59.1
Cytochrome P450	134405	11: 839531-843188	Not Expressed*	4.7	7.1	8.0	14.4	20.9	34.9
Cytochrome P450	135113	14: 481516-486826	Not Expressed*	3.1	7.9	6.2	7.7	7.0	9.4
Cytochrome P450	135119	14: 660806-662514	Not Expressed*	0.5	6.3	2.7	1.9	4.2	8.1
DRD1	143831	8: 1728281-1729234	Not Expressed*	14.1	12.6	15.9	23.0	50.1	48.4
DRD1, CLSY1	9310	2: 1137820-1140699	Not Expressed*	0.8	0.5	3.5	16.3	41.7	49.7
Helicase	14687	14: 1088606-1089406	Not Expressed*	7.1	7.1	8.8	12.5	16.7	24.2
Helicase	16802	14: 1038617-1040826	Not Expressed*	6.3	6.3	15.0	14.4	22.3	25.5
Helicase	55365	14: 743147-745976	Not Expressed*	18.8	18.1	24.8	30.7	25.0	44.3
Histone Deacetylase 6	23994	12: 1435094-1436460	Not Expressed*	16.5	15.7	19.5	21.1	30.6	36.3
Histone Deacetylase 6	137274	19: 148103-149733	Not Expressed*	9.4	6.3	3.5	13.4	8.3	32.2
HUA Enhancer 2	140725	34: 133586-142626	Not Expressed*	0.5	0.5	1.8	3.8	26.4	34.9

NRPE5	48698	6: 1164841-1166845	Not Expressed*	1.6	9.4	15.9	24.9	30.6	41.6
Pathogenesis-related Gene 1	26372	22: 498098-498647	Not Expressed*	11.8	15.7	25.6	30.7	33.4	33.6
Pathogenesis-related Gene 1	135097	14: 43719-46755	Not Expressed*	0.5	0.8	0.5	0.5	7.0	2.7
Polyubiquitin 4, Polyubiquitin 10	14180	5: 883289-883585	Not Expressed*	4.7	2.4	2.7	5.8	4.2	12.1
Polyubiquitin 4, Polyubiquitin 10	135983	16: 926266-929417	Not Expressed*	14.1	17.3	27.4	19.2	16.7	28.2
Protein Disulfide Isomerase	55742	162: 1215-3421	Not Expressed*	24.3	22.8	19.5	21.1	30.6	52.4
Protein Phosphatase 2C	35180	9: 889317-893109	Not Expressed*	7.1	7.1	8.0	8.6	15.3	18.8
Putative Protein Kinase	11223	14: 180180-181247	Not Expressed*	6.3	7.1	7.1	12.5	16.7	40.3
Putative Protein Kinase	11382	5: 402200-403813	Not Expressed*	0.5	0.5	1.8	1.9	16.7	9.4
Putative Protein Kinase	19632	3: 18315585-1831935	Not Expressed*	3.9	6.3	8.0	17.3	8.3	20.1
Putative Protein Kinase	20808	5: 189976-193636	Not Expressed*	21.2	32.2	42.5	32.6	41.7	34.9
Putative Protein Kinase	21329	5: 2107905-2109147	Not Expressed*	25.9	22.8	23.9	24.9	27.8	37.6
Putative Protein Kinase	22745	9: 1001773-1005155	Not Expressed*	0.8	3.9	7.1	11.5	13.9	22.8
Putative Protein Kinase	23988	12: 1380914-1382510	Not Expressed*	9.4	7.9	7.1	12.5	29.2	45.7
Putative Protein Kinase	24076	12: 740656-741937	Not Expressed*	0.5	0.8	1.8	2.9	5.6	6.7
Putative Protein Kinase	25821	19: 841228-843273	Not Expressed*	0.8	1.6	0.9	2.9	4.2	8.1
Putative Protein Kinase	28390	231: 95-830	Not Expressed*	7.1	6.3	7.1	5.8	13.9	8.1
Putative Protein Kinase	50248	3: 1750103-1760404	Not Expressed*	0.8	0.8	1.8	4.8	2.8	5.4
Putative Protein Kinase	50622	6: 1918291-1921717	Not Expressed*	1.6	3.9	16.8	24.9	37.5	61.8
Putative Protein Kinase	57116	7: 1800091-1809526	Not Expressed*	3.9	14.2	14.2	12.5	23.6	52.4
Putative Protein Kinase	134377	12: 538010-540584	Not Expressed*	1.6	3.9	7.1	5.8	18.1	40.3
Putative Protein Kinase	141030	4: 958371-960362	Not Expressed*	16.5	21.2	23.9	24.0	27.8	37.6
Putative Protein Kinase	141712	4: 2153086-2156465	Not Expressed*	7.1	11.8	7.1	25.9	40.3	49.7
SDE3	142077	4: 2237941-2241471	Not Expressed*	0.5	0.5	2.7	2.9	4.2	21.5
SRG1	9789	28: 232727-235181	Not Expressed*	3.9	1.6	5.3	17.3	26.4	55.1
Thioredoxin h	26868	24: 7266942-727267	Not Expressed*	1.6	6.3	2.7	7.7	5.6	8.1
Thioredoxin h	134092	10: 1363797-1364986	Not Expressed*	3.1	8.6	8.0	7.7	7.0	17.5

Expression Values Were Too Low (<50 mapped reads)\*

Putative Protein Kinase	13410	11: 1300001-1300228	Not Detected At Any Point
Putative Protein Kinase	13683	45: 5892-6951	Not Detected At Any Point