



Review Paper

Involvement of Disease Resistant Quantitative trait loci (QTLs) and resistant (R) Genes in key Signaling pathways of *Arabidopsis thaliana* during pathogen infection: An Overview

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Available online at: www.isca.in, www.isca.me

Received 30th July 2013, revised 11th August 2013, accepted 12th September 2013

Abstract

Plant must continuously defend themselves against attack from fungi, bacteria, viruses, invertebrates etc. The regulating mechanism of any plant pathogen interaction is complex and dynamic. Plants possess both preformed and an inducible defense mechanism. Many resistant genes (R) are present within the chromosome of *Arabidopsis thaliana* which help in resistance activity against pathogens. In *A. thaliana*, the disease resistant genes (R) are extremely polymorphic confer parasite recognition and are found at several loci. Quantitative trait loci study in *A. thaliana* will provide knowledge on number of quantitative resistant loci involved in complex disease resistance, interactions between pathogen biology, plant development and biochemistry. The main QTL approach in *A. thaliana* is based on rapid developments in marker technology, statistical methodology will help in identifying the same kind of complex disease resistant loci in other crop plants. The *A. thaliana* genome carries diverse resistant genes are found in several loci linked with salicylic acid, jasmonic acid and ethylene signaling pathways. The present review focus on presence of disease resistant QTLs and genes linked in signaling pathways in *A. thaliana* during pathogen invasion as well as interaction.

Keywords: *Arabidopsis thaliana*, QTLs, SA, JA, ET, Resistant gene (R), Avirulence gene(Avr)

Introduction

Arabidopsis thaliana belongs from family Brassicaceae is a preferred model plant for genomic studies due to its short life cycle, small size as well as a known genome sequence. The entire reported 25,496 genes of *A. thaliana* with a genome size of 125 megabases are distributed over five chromosomes¹. The incorporation of disease resistant genes of *A. thaliana* in to agronomically important crops will be one of the most economically effective method for controlling plant diseases. In this context, the present study on the identification of resistant genes of *A. thaliana* and its positions on different chromosomes loci are enumerated in this review. The hypothesis mentioning on “gene for gene resistance” aptly defines “The pathogen avirulent (*avr*) gene and the plant resistant genes(R) are fully interacted during pathogen interaction”². Another type of defense mechanism in *A. thaliana* on innate immunity is the receptor mediated due to pathogen associated molecular patterns and leucine rich repeat receptor kinases³. In *A. thaliana*, disease resistant genes (R) were interconnected with salicylate, jasmonate and ethylene signaling molecules. Mutation in disease resistant genes activate or suppress any one of three signaling pathways in *Arabidopsis*. The three main signaling pathways of salicylate, jasmonate and ethylene dependent resistance responses are mutually inhibitory in case of *A. thaliana*⁴. *A. thaliana* is under a constant threat of infection with many biotrophic and necrotrophic pathogens as

well as viruses such as *Pseudomonas syringae*, *Peronospora parasitica*, *Ralstonia solanacearum*, *Xanthomonas campestris*, *Albugo candida*, *Alternaria brassicicola*, *Fusarium oxysporum*, *Tobacco etch virus*, *Cucumber mosaic virus*, *Cauliflower mosaic virus*, *Heterodera schachtii* and *Pythium* species etc.

Brief idea on *Arabidopsis thaliana* disease resistant genes

In *A. thaliana*, Based on structural motif and interacting domain, seven distinct classes of resistant genes (R) are acting against specific pathogen. Short description of this disease resistant genes of *A. thaliana* are given below in table 1. *A. thaliana* contain a large number of disease resistant genes are characterized structurally with nucleotide binding sites, leucine rich repeat region, tir-domain, a putative coiled coil domain. The *A. thaliana* contains the total eighty five number of tir-nbs-lrr genes at sixty four loci, thirty six numbers of cc-nbs-lrr genes at thirty loci. The nbs-lrr classes are without tir or cc domain at their N -terminus present seven times at six loci, fifteen truncated tir -nbs-lrr genes lack lrr at ten loci, six numbers of cc-nbs genes at five loci⁵. In *Arabidopsis* genome forty six numbers of disease resistant genes are single tons and fifty are in pairs in given below in table 2.

Table-1
Seven distinct classes of disease resistant genes in *Arabidopsis thaliana* are given below

Class	Gene	Structure	References
1	IRE1/bZIP60	Defining myrotilation motif / serine/threonine kinase catalytic domain	159
2	ADR1,RPS2	Leucine rich repeat domain(LRR)/RPS2 binding site domain(NBS)/ N-TerminaLeucin Zippedomain/Coiledcoildomain	160,161
3	RLM3,WRR4,RPP5, RPP2A,RPP2B, TAO1	Similar to Class 2 but instead of an LZ or CC domain contains a domain that is Toll like / Interleukin1 domain/ TIR domain	80,162,70,163
4	RPP27	LRR domain in extracellular, transmembrane domain in single and a small cytoplasmic tail proteins are called RLPs.	121
5	RLK1/RLK4/RLK5, FLS2/RLK3/ERECTA	Cytoplasmic Serine/Threonine kinase domain/Extracellular LRR domain/and a Transmembrane domain(TM) . These genes are called receptor like kinases	164 165 166
6	RPW8	Small cytoplasmic proteins and contain a coiled colied domain	17
7	Small cytoplasmic protein not anchored in Plasmamembrane/ contains two tandem protein kinase domains.		
A few proteins in <i>Arabidopsis thaliana</i> are not categorized in to one of these seven classes			

Table-2
Resistant genes are distributed between chromosomes of *Arabidopsis thaliana* are given below

Chromosome	Number of disease resistant genes
1	49
2	2
3	16
4	28
5	55

The *Arabidopsis* genome initiative (2000)

Brief idea on *Arabidopsis thaliana* pathosystem

The eighteenth century is the beginning of the scientific emergence of plant pathology. In *A. thaliana*, the defense mechanism is guided by a complex signaling network. In plant species, a relatively small proportion of pathogens successfully invade it as well as spread diseases. The hypersensitive response generated by invading phyto-pathogen. Then the hypersensitive response leads to triggers nonspecific resistance known as systemic acquired resistance. Both the response work each other during different pathogen infection. The name of diseases caused by different pathogens in *A. thaliana* are given below in table-3.

Quantitative trait loci and disease resistant genes in *Arabidopsis thaliana* with different pathogens: Here, we focus many number of disease resistant gene loci present in five different chromosomes of *A. thaliana* against different pathogens and the resistant loci was given the name of pathogen. The disease resistant genes and quantitative trait loci of *A. thaliana*

are mapped in to five chromosomes .The map was given below in figure-1. (contain gene ID from TAIR, www.arabidopsis.org).

Table-3
***Arabidopsis thaliana* pathosystems¹⁶⁷**

Disease	Pathogen
Fungal	
1 Downy mildew	<i>Hyaloperonospora parasitica</i>
2 White blister	<i>Albugo candida</i>
3 Damping Off	<i>Pythium Species</i>
4 Dark leaf spot	<i>Alternaria brassicicola</i>
5 Powdery mildew	<i>E. cruciferarum,</i> <i>E.cichoracearum</i>
6 Vascular wilt	<i>F. oxysporum</i>
7 Leaf mold and Leaf spot	<i>Cladosporium</i>
8 Damping off or wire stem	<i>Thanatephorus cucumeris</i>
Bacterial	
9 Black rot on crucifers	<i>Xanthomonas campestris</i>
10.Bacterial speck on crucifers	<i>Pseudomonas syringae</i>
Viral	
11.Mild stunting	<i>Tobacco mosaic virus</i>
12. Mild stunting and desiccation	<i>Turnip crinkle virus</i>
13 Vein clearing and chlorotic spots	<i>Cauliflower mosaic virus</i>
Nematode	
14 Cyst nematode	<i>Heterodera schachtii</i>

Resistant towards *Erysiphe* species

The powdery mildew diseases are common plant diseases on agricultural and horticultural crops⁶. *A. thaliana* found to be infected with three powdery mildews called as *Erysiphe cichoracearum* (UCSC isolate), *Erysiphe cruciferarum* (UEA isolate) and *Erysiphe orontii*⁷. The resistance reaction phenotypes of *A. thaliana* was characterized and resistant loci were mapped. *A. thaliana* disease resistant genes shown resistance to few pathogenic strains of a particular type of pathogen. *A. thaliana* six accessions *Wa-1*, *Kas-1*, *Stw-0*, *Su-0*, *Sl-o* and *Te-0* were shown resistant to a wild isolate of the powdery mildew pathogen *Erysiphe cichoracearum*. *A. thaliana* contains five semi dominant powdery mildew disease resistant loci *RPW1*, *RPW2*, *RPW4*, *RPW5*. The name of loci are designed as *RPW* (recognition to powdery mildew). The loci are map to chromosomes 2, 3, 4 and 5 respectively and *RPW3* was a recessive resistant locus located on chromosome 3⁸. *A. thaliana* accessions *La-er* and *Ms-o* infected by two *Erysiphe* strains *Erysiphe cruciferarum* *UEA1* and *Erysiphe cichoracearum* *UCSC1*. The three dominant loci *RPW6*, *RPW7*, *RPW8* were identified in *A. thaliana* and mapped to chromosome 5, 3 and 3. *RPW7* and *RPW8* were found to be complex resistant loci with dual specificity⁹. *A. thaliana* *RPW8* locus contains two naturally polymorphic, dominant *RPW8.1* and *RPW8.2*, individually control resistance through salicylic acid dependent defenses. In *A. thaliana*, *RPW8* mediated resistance causes an oxidative burst, a hypersensitive reaction and induction of pathogenesis related gene-1 expression¹⁰. *A. thaliana* *RPW8* loci determines the frequency of powdery mildew disease in a heterogenous environments and potentially maintains genetic variation for resistance in natural populations¹¹. *RPW8.2* played the main role in post penetration resistance against *Golovinomyces cichoracearum* *UMSG1*^{12,13}. *A. thaliana* *RPW8* functions as a broad spectrum mildew disease resistance by targeting the extra haustorial membrane (EHM) of the invading pathogen¹⁴. *RPW8* may serve a "guardess" for *RAR1* and *EDS1*¹⁵. The nucleotide diversities were high at *RPW8.1* and *RPW8.2* in fifty one *A. thaliana* accessions as well as the identified mutations confer phenotypic variations. The presence of *RPW8* giving fitness benefits and costs effects in the presence and absence of the pathogens¹⁶. However, the origin of the powdery mildew disease locus obtained through sequence analysis of *RPW8* from *A. lyrata*, *Brassica rapa* and *Brassica oleraceae*¹⁷. In further experimental studies of *A. thaliana* *Ms-0* accession against *Golovinomyces* species indicates that *RPW8* loci contain two paralogous genes *RPW8.1* and *RPW8.2* confers resistance through salicylic acid signaling pathways. The 14-3-3 lambda is a positive regulator for *RPW8*¹⁸. *A. thaliana* *Col-0* accessions, *RPW8.2* interacts with phytochrome-associated protein phosphatase type 2C negatively regulates basal defense against powdery mildew¹⁹. The quantitative trait loci *RPW10*, *RPW11* and *RPW12* were confer resistant against powdery mildew disease in *A. thaliana* *Col-gl1xKas-1*. The QTL of *RPW-10* was mapped on chromosome-3, *RPW-11* occurred on chromosome -5 and *RPW-12* was mapped on the chromosome-

2 in *A. thaliana*²⁰. A well developed pathosystem in between *A. thaliana* accessions *col-0* and *E. orontii* were observed. *A. thaliana* accession *columbia* infection with *E. orontii* leads to expression of defense related genes *PR1*, *BGL2*(*PR2*), *PR5* and *GST1*. *A. thaliana* mutants containing *Pad4-1*, *npr1-1*, *eds5-1* and a double *npr1-1 eds5-1* shows susceptibility to *E. orontii*²¹. *A. thaliana* mutants are displays enhanced disease resistance-1 to the fungus *E. cichoracearum*. The enhanced disease resistant mutant does not constitutively express the pathogenesis related genes of *PR-1*, *BGL2* or *PR5*. The *edr-1* was mapped to chromosome- 1²². In other way, *A. thaliana* mutant that shown enhanced disease resistance-2 to the *E. cichoracearum*. *A. thaliana* mutant in *edr-2* mediated resistance inhibits salicylic acid defense signaling in *npr1*, *pad4* and *sid-2*. *Edr2* gene locus was mapped on chromosome - 4²³. *A. thaliana* mutants constitutively express a vegetative storage protein-1(*VSP-1*) now called *Cev-1* were produced very smaller quantity that mediate jasmonate and ethylene signaling pathways and was mapped on chromosome-5²⁴. *A. thaliana* four mutant loci designated as powdery mildew resistant -1,-2,-3,-4 (*pmr-1*, *pmr-2*, *pmr-3*, *pmr-4*) were identified as susceptible to *E. cichoracearum*. *Pmr1* and *pmr2* were mapped to chromosome -1, *Pmr-4* was mapped to chromosome 4 and *Pmr-3* was mapped to chromosome 5²⁵. *Pmr-5* gene mutation rendered in *A. thaliana* resistance to the *E. cichoracearum* and *E. orontii*. Resistance in this mutant may be due to the loss of a susceptibility factor or to the activation of a novel form of defense²⁶. *Pmr-6* encodes a pectate lyase like protein is a susceptibility locus in *A. thaliana*. salicylic acid, jasmonic acid and ethylene signaling pathways are not involved in the *Pmr-6* gene mechanism²⁷. *A. thaliana* three mutants called *eds14*, *eds15*, *eds16* found to be highly disease susceptibility to *Erysiphe orontii*. *Eds16* was mapped to chromosome 1²⁸. *Pen-3* mutants of *A. thaliana* were resistant to *Erysiphe cichoracearum*. *Pen-3* loci was mapped to chromosome-1²⁹.

Resistant towards *Pseudomonas syringae*

The genetic tractability of both *A. thaliana* and *Pseudomonas syringae* shown a remarkable model for research on plant pathogen interactions. Tremendous progress had been made in understanding how plant *A. thaliana* recognizes *Pseudomonas syringae* *Avr* proteins and mounts effective defense against *A. thaliana* resistant loci *RPS2* shown significant defense against *RPM1*³⁰. In a map based cloning approach many *A. thaliana* *RPS2*, *RPM1*, *RPS4*, *RPS5* and *PBS1* were isolated where *PBS1* belongs to the nucleotide binding site leucine rich repeat class and *RPS2*, *RPM1* and *RPS5* proteins have coiled-coiled structures at their N termini and are classified in the CC subclass of NBS-LRR³¹⁻³⁶. In *A. thaliana* *RPS2* leucine-rich repeat domain determine very well interaction with *Pseudomonas syringae*³⁷. *RPS4* had a Toll Interleukin-1 receptor like homology along with other NBS-LRR proteins. The *Avr* gene products *AvrRpt2*, *AvrRpm1*, *AvrB*, *AvrRps4* and *AvrPphB* were believed to be delivered from bacteria into plant cell³⁸. *Avr* genes expression in the plant cell leads to

the HR dependent on the corresponding resistant genes³⁹. NDR1 mutation strongly affects resistance by a class of CC-NBS-LRR genes⁴⁰. NDR1 mutation affected *Pseudomonas syringae*, resistance by CC-NBS-LRRs class of gene name RPS2, RPM1 and RPS5 resistant genes where as resistance mediated RPS4. TIR-NBS-LRR was affected by EDS1 mutation but not by NDR1⁴¹. RPS2 was required for elicitation of hypersensitive (HR) response when *Pseudomonas syringae* was mounted. RPS2 was a quantitative trait loci mapped on the chromosome-4⁴². Five classes of mutants of *A.thaliana* were identified including mutations at RPS2, and mutations causing a “defense, no death” loss of HR phenotype, a lesion mimic mutant that also exhibited an hypersensitive response phenotype⁴³. *A. thaliana* was four hyper induced reaction gene family known as HIR1-HIR4. *A. thaliana* HIR1 and HIR2 form complexes with RPS2 reduced the growth of *Pseudomonas syringae* Pto Dc3000 by effector triggered immunity (ETI)⁴⁴. Mutational analysis of RPS2 gene encodes a 105kd protein revealed that the NBS and an N-terminal leucine zipper (LZ) motif were critical for RPS2 function⁴⁵. *A. thaliana* WIN3 gene requires PAD4 in the resistance pathways towards *Pseudomonas syringae* effector AvrRpt2. WIN3 gene accumulates salicylic acid during infection with *Pseudomonas syringae*⁴⁶. RPS4 was a disease resistant locus identified in *Arabidopsis* on chromosome-5⁴⁷. RPS3 was a disease resistance locus mapped on chromosome-3 using a previously cloned avirulence gene AvrB from a non-*Arabidopsis* soybean pathogen. *Pseudomonas syringae* pv *glycine* and RPG1 and RPS3 both confer AvrB-specific disease resistance, suggesting that these genes are homologous⁴⁸. EDS1 require a resistant gene loci for RPS4 against *Pseudomonas* bacteria expressing the avirulence gene AvrRps4⁴⁹. *A. thaliana* PAD4 gene mapped to chromosome-3⁵⁰. RPS5 was a disease resistance gene in *A. thaliana* with specificity AvrPph3 and was mapped to chromosome-1⁵¹. RPS6 was a disease resistant gene in *A. thaliana* against *Pseudomonas syringae*. RPS6 loci was mapped on chromosome 5⁵². In another experiment, Enhanced Disease Susceptibility-1 (EDS1) regulated by RPS4 and RPS6 provide basal resistance in *A.thaliana*⁵³. RPS6 belongs to TIR-NBS-LRR class of gene⁵⁴. A defense gene ELI3 expresses mRNA in *A. thaliana* leaves in response to *Pseudomonas syringae* strains, and this loci was mapped on chromosome-3⁵⁵. Fitness cost of RPM1 locus in *A. thaliana* fight the pathogen *Pseudomonas syringae* carrying AvrRPM1 or AvrB⁵⁶. AGO4 gene exert an effective resistance in *A. thaliana* against *Pseudomonas syringae*. AGO4 was one of the critical components in the transcriptional gene silencing pathway associated with siRNA that directs DNA methylation at specific loci⁵⁷. NHO1 was a gene in *A.thaliana* required for resistant against *pseudomonas syringae*⁵⁸. *A. thaliana* six ACBP3 genes ACBP1 to ACBP6 mediate defense to the bacterial pathogen *Pseudomonas syringae* pv *tomato* DC 3000⁵⁹. *A.thaliana* contains higher nicotinamide adenine dinucleotide play an important role in plant immunity by stimulating salicylic acid⁶⁰.

Resistant towards *Peronospora parasitica*

A. thaliana accession *Wassilewskija*, the RPP1 was a complex loci contains four genetically linked recognition specificities and was mapped on chromosome 3⁶¹. In different accessions of *A.thaliana*, so many number of disease resistant loci RPP1 to RPP28 were mapped in presence of major recognition gene complexes on five chromosomes which were resistant to *Peronospora parasitica*⁶². RPP5 was a complex loci in *A. thaliana* *Ler* and *Col-O* haplotypes exhibits intra specific polymorphism play an important role in innate immunity.

The RPP5 gene complex exhibit high level polymorphism by extensive recombination between LRRs encode different numbers of LRRs⁶³. The *A. thaliana* different accessions interact with *Peronospora parasitica* *Noco2* isolate and four RPP loci were identified such as RPP14.1, RPP14.2 RPP14.3 and RPP 5.2. RPP14.1, RPP14.2. RPP14.3 resistant loci were mapped on chromosome 3 and RPP5.2 loci was mapped on chromosome 4⁶⁴.

RPP5 locus was respond to pathogens that disturb RNA silencing⁶⁵. Using gene chip *A.thaliana* genome array, three RPP genes called RPP4, RPP7 and RPP8 directed towards the pathogenic oomycete *Peronospora parasitica*. These common set of target genes controls the regulation of all three signaling pathways. Many defense genes predominantly encode putative signaling protein molecules that play an important role in defense⁶⁶. In *A. thaliana*, RPP1, RPP10, RPP14 loci were mapped to the same locus on the chromosome-3 which were resistant towards *P. parasitica* isolates Emoy2, Cala2 and *Noco2*. RPP1, RPP10, RPP14 were complex locus encodes Toll-Interleukin-1-Resistance –Nucleotide binding site to detect the four *Peronospora parasitica* isolates. The RPP13 loci was mapped to chromosome-3⁶⁷. Another two RPP resistance loci called as RPP7 and RPP8 in *A.thaliana* against *Peronospora parasitica* was mapped on chromosome-1 and chromosome-5. RPP7 and RPP8 loci resistant activity was not suppressed by mutations in either EDS1 or NDR1⁶⁸. RPP4 was mapped on chromosome-4⁶⁹. EDS1 require a subset of RPP2, RPP4, RPP5, RPP21 conferring resistance to the *Peronospora parasitica*⁷⁰. In *A. thaliana*, Ssi-1 (suppressor of salicylic acid insensitivity-1) dominant gene restores pathogenesis related gene like PR1, PR2, PR5 genes to *pseudomonas syringae* pv *tomato* and Ssi was mapped to chromosome 4⁷¹. *A. thaliana* mutants reduced susceptibility to the downy mildew pathogen *Hyaloperonospora parasitica* was studied and six dmr (downy mildew resistance) loci called as dmr1, dmr2, dmr3, dmr4, dmr5, dmr6 were identified⁷². In *A. thaliana*, recessive downy mildew resistant -1 allele (*Dmr1*) encodes homoserine kinase that was involved in resistance⁷³. *Hyaloperonospora Arabidopsis* ATR1 was interact with RPP1 leading to activation of plant disease resistance in *A. thaliana*⁷⁴.

Resistant towards *Botrytis cinerea*.

Botrytis cinerea is a necrotrophic fungi interact very well with *A.thaliana*. When *Botrytis cinerea* interact with *A thaliana* , antimicrobial compound camalexin accumulated which provides defense response.⁷⁵ *A. thaliana* three loci BOS2, BOS3 and BOS4 were identified as resistant loci against *Botrytis cinerea*. BOS2 BOS3 loci were mapped to chromosomes- 4 and -1 ..The BOS2, BOS3 and BOS4 loci influence camalexin levels and activate the ethylene and jasmonate signaling pathways⁷⁶.

Resistant towards *Albugo candida*

Biotrophic oomycete pathogen *Albugo candida* infects *A. thaliana* .The disease caused by *Albugo candida* bears its name white rust for the production of white sori⁷⁷. Three resistant loci called RAC-1(Recognition of *Albugo candida*), RAC-2 and RAC-3 were used to map and identify in accessions of *A.thaliana* accessions *Ksk1* and *Ksk-2* .⁷⁸ RAC -1 is a dominant loci of *Arabidopsis* accession *Ksk-1* mapped to chromosome 1 ,RAC-3 is closely linked to the RPP8/HRT on chromosome- 5, RAC-2 is a recessive resistant loci of *A. thaliana* accession *Ksk-2* mapped on chromosome- 3. The resistant gene WRR4 (White rust resistance) encodes a cytoplasmic toll interleukin receptor like nucleotide binding leucine rich repeat receptor like protein(TIR-NB-LRR) that confers a dominant, broad -spectrum, white rust resistance in *A. thaliana* accession *columbia*. This gene was mapped in chromosome 1. The WRR4 protein requires functional expression of the lipase like protein EDS1^{79,80}.

Resistant towards *Ralstonia solanacearum*

Ralstonia solanacearum is the causal agent of bacterial wilt of many important agricultural crops such as potato, tomato, banana, pepper and even trees such as eucalyptus etc.⁸¹. Two *A.thaliana* genes RRS1-S and RRS1-R involved in resistant towards the *Ralstonia solanacearum*⁸². RRS1 was mapped on chromosome- 5⁸³. *Arabidopsis thaliana* accessions Ler xCol-O accessions recombinant inbred lines showed that resistance was governed by at least three loci named as QRS1 (Quantitative resistance to *Ralstonia solanacearum*) and QRS2 on chromosome-2, QRS3 on chromosome- 5. ERECTA gene lies close to QRS1 mapped on chromosome 2⁸⁴. *A.thaliana* accessions Ws-O RRS1 and RPS4 function as resistant to *Ralstonia solanacearum*, *C. higginsianum* and *Pseudomonas syringae pv tomato strainDC3000*⁸⁵.

Resistant towards *Xanthomonas campestris*

Xanthomonas campestris PV campestris the causal agent of black rot crucifers⁸⁵. Four Quantitative resistant trait loci called RXC1, RXC2, RXC3, RXC4 (Reaction to *Xanthomonas campestris*) were identified through genetic analysis of *A. thaliana* Col-OxLer recombinant inbred lines. RXC1 loci was mapped on chromosome 2, a gene conferring tolerance to *Xanthomonas campestris 2D520*, RXC2 loci was mapped on

chromosome 5, RXC3 loci was mapped on chromosome 5 and RXC4 loci was mapped on chromosome 2 of *A. thaliana* in above inbred accessions⁸⁶. Another gene loci was identified in *Arabidopsis* against *Xanthomonas i.e. RXC5*⁸⁷.

Resistant towards *Trichoplusia ni*

The quantitative trait loci in *Trichoplusia ni* is strongly correlate with higher glucosinolate levels⁸⁸. TASTY locus was found to discover in *A.thaliana* on a chromosome-1 to know about susceptibility status of recombinant inbred lines⁸⁹. A myrosinase associated protein ESM1 loci was identified through map based cloning on chromosome -3 in *A. thaliana landesberg erecta x columbia accessions* inbred lines and found to be insect resistance⁹⁰.

Resistant towards *Leptosphaeria maculans*

A blackleg disease of Brassica oilcrops was caused by *Leptosphaeria maculans* is a hemi biotrophic fungi⁹¹ RLM1 (Resistance against *Leptosphaeria maculans*) and RLM2 were two *A. thaliana* TIR-NBS-LRR resistant genes effective against *Leptosphaeria maculans*⁹². RLM1 resistant loci in *Arabidopsis* accessions *Col-O*, *Ws-O* and *Cvi-1* was mapped on chromosome 1 and RLM2 resistant loci in *Col-0 x Ler-O*, and *Ler-2xCvi-1* was mapped on chromosome - 4. Loss of two RLM1 and RLM2 resistance loci in *A. thaliana Col-O x Ler-O* inbred lines showed susceptibility for *Leptosphaeria maculans*⁹³.

Resistant towards *Tobacco etch virus*

The *Tobacco etch virus* (TEV)-*Arabidopsis* model system for identification of host genes. From the model observation two points are identified i.e. first virus unable to encountered due to presence of resistant allele and second is the resistant genes act against a known viral genotype but not for polymorphic viral genotypes⁹⁴.

Three complex resistance loci RTM1 (Restricted to Tobacco etch virus movement) RTM2, RTM3 were observed through mutational analysis in *Arabidopsis accession Col-O* ecotype. RTM2 resistant loci was mapped on chromosome-5 of *A. thaliana Col-O* ecotype.RTM2 was a multi domain configuration which was homologous to thermal shock proteins .RTM1 loci was mapped on chromosome-1. RTM3 gene loci was mapped on chromosome 3 that encodes a new type of protein⁹⁵⁻⁹⁸.

Resistant towards *Cucumber mosaic virus*

Mutation in *ssi2* gene conferred enhanced resistant to cucumber mosaic virus in *A. thaliana* and is salicylic acid independent pathway⁹⁹. The RCY1 in the *A. thaliana* ecotype *C24* was associated with the hypersensitive response and mapped on chromosome- 5¹⁰⁰.

Resistant towards Turnip Crinkle Virus

A dominant *HRT* gene confers a hypersensitive response to Turnip crinkle virus (*TCV*) had been cloned from *Arabidopsis* ecotype *Dijon* (*Di17*) and was a LZ-NBS-LRR class resistant gene. *HRT* signaling pathway in *A. thaliana* is dependent on salicylic acid and is independent of NPR1, NDR1, ETR1, COI1 and perhaps of EDS1 and PAD4¹⁰¹. A locus in *A. thaliana* *Di17* × *Col-0* accession inbred lines designated *HRT* mapped on chromosome 5 which confers the ability to develop a hypersensitive response after *TCV* inoculation¹⁰².

A. thaliana cryptochrome (*CRY-2*) and Phototropin (*PHOT-2*) gave stability during *TCV* infection¹⁰³. *Arabidopsis* ecotype *Dijon* (*Di17*) was regulated by presence of two host genes *HRT* and *RRT* results development of hypersensitive response and was salicylic acid dependent¹⁰⁴. *CRT1* was a GHKL ATPase resistance to turnip crinkle virus in *A. thaliana* mediated through the *HRT* by developing HR failed to control virus replication¹⁰⁵.

Resistant towards cauliflower mosaic virus

Genetic variants of *Cauliflower mosaic virus* (*Camv*) and *A. thaliana* were characterized to identify mild and severe symptoms. Infections of a glabrous mutant (*g11*) of *A. thaliana* ecotype *columbia* (*Col-Ogl1*) by 30 *Camv* isolates. Thirteen isolates failed to cause symptoms and a greater variety of symptom type was observed in a single. *A. thaliana* ecotype infected with a typical *Camv* isolate *Cabb B-JI*¹⁰⁵. Two *A. thaliana* ecotype *Enkheim-2* (*En-2*) and *Bla-14* were resistant to systemic infection by cauliflower mosaic virus. *Cauliflower mosaic virus* resistance by a single semi dominant gene called *cauliflower mosaic virus* resistance -1 located at chromosome-1¹⁰⁶.

Resistant towards Tobacco ring spot nepo virus:

Tobacco ring spot virus resistance is display by many *Arabidopsis* ecotypes. *TTR-1* (Tolerance to Tobacco ring spot virus -1 gene) encoding a TIR-NBS-LRR protein. *TTR1* gene involved in SGT-dependent defense responses¹⁰⁷. *TTR1* was mapped to chromosome 5¹⁰⁸.

Resistant towards Plum pox poty virus and Spring beauty latent virus infection

A. thaliana accession *cvi-1* restrict to plum pox poty virus long distance movement controlled by a single recessive gene designated as *rpv1* which was mapped to chromosome -1¹⁰⁹. In several accessions of *A. thaliana*, symptom development in spring beauty latent virus (*SBLV*) were to designed a loci *SSB1* (Symptom development by *SBLV* infection) which shown resistant activity. This semi dominant loci *SSB1* was mapped to chromosome -5¹¹⁰.

Resistant towards Fusarium oxysporum

Many QTLs which were genetically complex control natural variation in *A. thaliana* accessions *Bay-0* and *Shahdara* resistance to *Botrytis cinerea*. In *A. thaliana* *Ty-O* × *Col-O* six dominant RFO (resistance to *Fusarium oxysporum*) loci shows resistant activity towards *Fusarium oxysporum*. The name of six loci are RFO1 to RFO6 and might be represent more than one gene. The *A. thaliana* RFO loci were mapped on five chromosomes such as RFO1, RFO2 mapped on chromosome-1, chromosome -3 contain RFO3 loci, chromosome -4 contain RFO4 loci, chromosome- 5 contain RFO5 and RFO6 loci. RFO1 loci was the largest contributor resistant to *fusarium* races identical with a previously known gene called as *WAKL 22*¹¹¹. *A. thaliana* Thionin *Thi2.1* gene over expression involved in resistance to *Fusarium oxysporum*¹¹².

Resistant towards Heterodera schachtii

Heterodera are obligate sedentary endoparasites of agricultural crops. The relationship between nematodes and their host were well established. Seventy four different ecotypes of *Arabidopsis* were screened for their susceptibility towards *Heterodera schachtii* and consider *Arabidopsis* as a host for plant parasitic nematodes will provide a model system for the molecular genetic analysis of this interaction¹¹³. *Heterodera schachtii* and root knot *Meloidogyne incognita* expression levels of pathogenesis related genes PR-1 to PR5 were examined in the roots and leaves of *A. thaliana*. The PR3 and PR4 are expressed in jasmonic acid (JA)-dependent SAR. The PR-1, PR-2 and PR-5 were highly induced in roots as well as PR-3 is to a lesser¹¹⁴. The use of *Arabidopsis* as a susceptible host in which to study the induction and formation of syncytia by cyst nematodes will benefit greatly from the established expertise in *Arabidopsis* research. *Arabidopsis* provides a genetically tractable model system for the study of nematode CLE signaling, as well as role in defense. *HsCLE-1* and *HsCLE-2* were CLE like genes from *Heterodera schachtii* sharing highest similarity to *Arabidopsis thaliana* CLEs 1-7^{115, 116}.

Resistant towards Pythium irregulare

The resistance to *pythium* does not directly involve to the hypersensitive response but by jasmonate and ethylene signaling pathways¹¹⁷. *A. thaliana* mutant plants *fad3-2*, *fad 7-2*, *fad8* were deficient in jasmonate synthesis to demonstrate that jasmonate signaling was essential for protection against the *Pythium mastophorum*¹¹⁸. Six member genes of *propep1-6* was well studied in *A. thaliana*. Over expression of two family members *propep-1* and *propep-2* enhances resistance of *A. thaliana* plants against the pathogen oomycete *Pythium irregulare*¹¹⁹. The 23aa peptide activates the transcription of defensin gene *PDF1.2* and synthesis H_2O_2 and over expression of *Propep-1* confer resistance against a root pathogen *Pythium irregulare*¹²⁰.

Resistant towards *Cladosporium fulvum*

Receptor like proteins were leucine rich repeat proteins. In *A.thaliana* genome contains approximately 59 RLP family genes. The 17 genes of this family were present on chromosome -1 including CLV2, TMM, RPP27 and other 12 genes were present on chromosome 2, 16 number of genes on chromosome 3, 8 number of genes on chromosome- 4, 6 number of genes on chromosome -5¹²¹.

Resistant towards *Alternaria brassicicola*

Alternaria brassicicola with *A.thaliana* interaction helps to identify genes play an important role in resistance. Microarray experiment revealed that 168 genes are up regulated yet to be determined in resistance during an interaction between the *A.thaliana* ecotype col-0 and *Alternaria brassicicola*¹²². *A.thaliana* RESURRECTION -1(RST1) gene which was mapped on chromosome- 3 play a major role in defense. The RST1 gene of *A.thaliana* act as a negative regulator in jasmonic acid signaling¹²³.

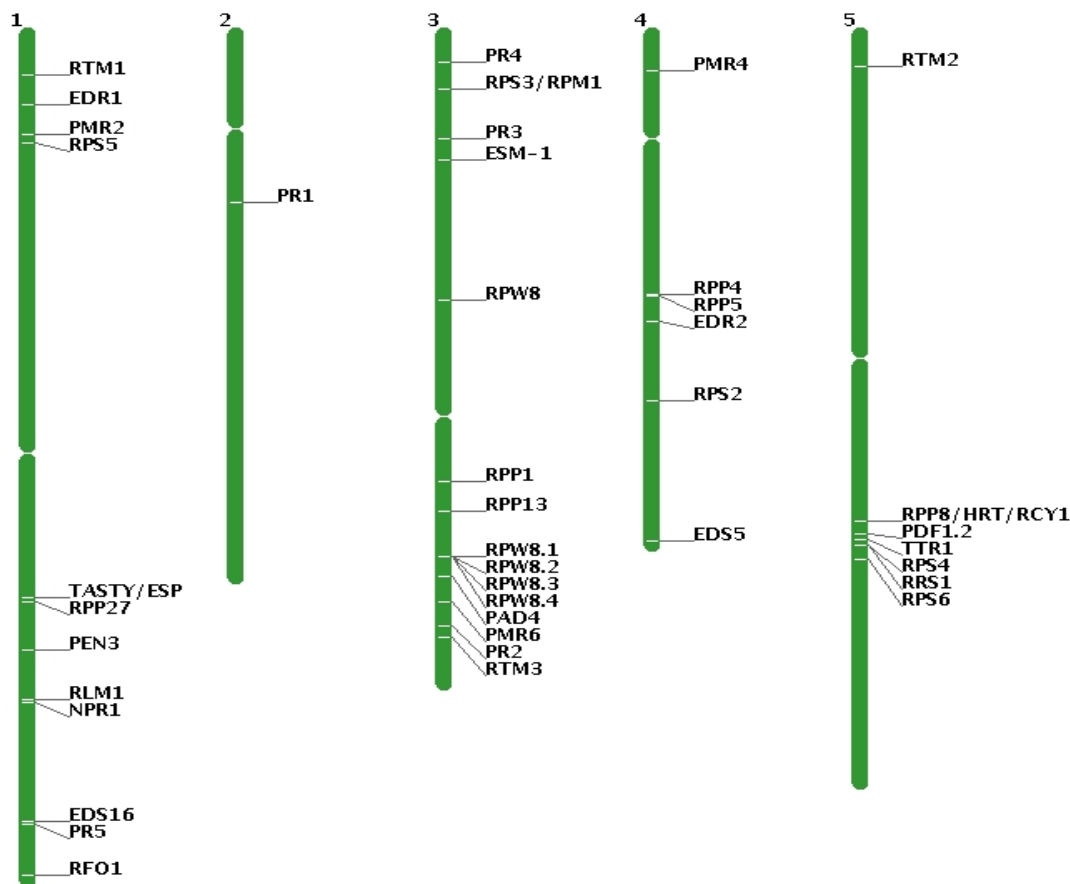


Figure-1

AT3G50450-RPW8.1 ; AT3G50460-RPW8.2; AT3G50470-RPW8.3; AT3G50480-RPW8.4; AT4G19040- EDR2; AT2G14610- PR1; AT3G54920- PMR6; AT4G03550-PMR4; AT5G44420 PDF1.2; AT1G11310 PMR2; AT4G39030 EDS5; AT1G64280 NPR1; AT1G74710 EDS16 AT5G45250 RPS4; AT4G26090 RPS2; AT1G59870 PEN3; AT3G07040 RPS3/RPM1; AT1G12220 RPS5; AT5G46470 RPS6; AT3G52430 PAD4; AT3G44480 RPP1; AT3G46530 RPP13; AT5G43470 RPP8/HRT/RCY1; AT4G16950 RPP5; AT4G16860 RPP4; AT1G54470 RPP27; AT3G26470 RPW8 ; AT5G45260 RRS1; AT1G05760 RTM1; AT5G04890 RTM2; AT3G58350 RTM3; AT1G54040 TASTY/ESP; AT3G14210 ESM-1; AT1G64070 RLM1; AT5G44870 TTR1; AT1G79670 RFO1; AT3G57260 PR2; AT3G12500 PR3; AT3G04720 PR4; AT1G75040 PR; AT1G08720 EDR1

[The QTLs and Genes are distributed in five chromosomes of *Arabidopsis thaliana*. The Gene ID of disease resistant genes from TAIR.(www.arabidopsis.org).The QTL map was based on gene ID.

Arabidopsis thaliana Salicylic acid, Jasmonic acid and Ethylene response genes during pathogen infection:

A.thaliana contains signaling molecules like salicylic acid, jasmonic acid and ethylene function in different ways. *A.thaliana* contains salicylic acid is a critical mediator in innate immunity and plays an important role in limiting the growth and reproduction of the virulent powdery mildew *Golovinomyces orontii* in *A. thaliana*¹²⁴. In *A. thaliana*, salicylic acid accumulates in pathogen challenged tissues and expression of pathogenesis related PR1,PR2 and PR5 genes. The *A. thaliana* containing NahG were low level of salicylic acid contents compared to the sid (salicylic acid induction deficient) mutants¹²⁵. *A. thaliana* Sid mutants express PR2, PR5 genes and accumulates camalexin during pathogen interaction¹²⁶. Salicylic acid signaling require NPR1 which was a nuclear transported protein involved in defense gene activation during systemic acquired resistance¹²⁷. The *A. thaliana* NIM1/NPR1 mutant was isolated that unavailed the network to establish systemic acquired resistance against *Peronospora parasitica* due to downstream signaling of salicylic acid^{128,129}. *A.thaliana* contains a number of genes such as PAD4,EDS5,NPR1,SGTb1,EDR1 in salicylic acid signaling pathways contribute resistance to powdery mildews. *A. thaliana* atg2-2 mutant required salicylic acid activating defense related genes resistance to *Golovinomyces cichoracearum*¹³. NPR1/NIM1 acting as a positive regulator of defense responses during pathogen interaction.PAD4 involved in salicylic acid signaling^{131,132}. Two separate signaling branches are EDS1 and PAD4 proteins with limited homology to lipases and other requires NDR1¹³³.The EDS1 and PAD4 pathway is associated with TIR-NBS-LRR proteins and the NDR1 pathway was typically associated with CC-NBS-LRR proteins. Snc1 was fully dependent on PAD4 but point mutation in Snc1 block the synthesis of salicylic acid¹³⁴. PR1, PR2, PR5 were set of genes activated in response to salicylic acid signaling and PDF1.2, PR3, PR4 were activated in response to jasmonic acid signaling pathway¹³⁵. *A. thaliana* Coi1 or Pad3 mutants requires phytoalexin camalexin and jasmonic acid for resistance against *Alternaria brassicicola*¹³⁶. In *A. thaliana*, the molecular cloning of genes involved in ethylene signaling had revealed a variety of signaling modules in the ethylene response pathways. Ethylene signaling in molecular and cellular details in *A. thaliana* will provide innovative tools for improving plant adaptability against pathogens. Ethylene receptors were membrane proteins and related to receptor proteins found in bacteria, algae and plants namely two component regulatory systems that initiates a series of phosphorylation reactions in response to external stimuli. In *A. thaliana*, ethylene was perceived by ETR1, ETR2,ERS1,ERS2 and EIN4 five family¹³⁷.CTR1, a Raf like kinase suppresses downstream ethylene responses in the absence of ethylene and vice versa in presence of ethylene. Signal transduction and subsequent gene expression continue by EIN2 and EIN3. The first *Arabidopsis* ethylene mutant was etr1-1¹³⁸.Ethylene insensitive *A. thaliana* reacted similarly to infection by *pythium* species and was identified by the ein2-1 mutants which were enhanced susceptibility. The etr1-1 mutants

appeared to be as resistant as wild type *Arabidopsis*¹³⁹. Ethylene insensitive ein 2-1 mutants showed reduced disease severity after inoculation with bacterial leaf pathogens *Pseudomonas syringae* or *Xanthomonas campestris* in *A. thaliana*¹⁴⁰. but *Arabidopsis* etr1 and etr2 mutants indicates enhanced susceptibility¹⁴¹. EIN2 was required the systemic induction of genes PDF1.2, PR3 and PR4 in the ethylene insensitive *Arabidopsis* mutant ein2-1. *A. thaliana* mutant ein2-1 shown enhanced susceptibility towards *Botrytis cinerea* than wild type¹⁴². Ethylene response factor-1(erf1) is a regulator of ethylene after pathogen attack in *Arabidopsis* and drives the activation of defense related genes such as pr4 and pdf1.2 and its over expression positively confers resistant to *Fusarium oxysporum*, *Plectosphaerella cucumerina* and several necrotrophic fungi¹⁴³. Pdf1.2 regulated by apetala 2/ethylene response factor transcription factor ora59¹⁴⁴. The *Arabidopsis* ein2-1 an ethylene insensitive mutant shown delay in wilt disease development caused by the *Ralstonia solanacearum*¹⁴⁵. During ethylene signaling, *A. thaliana* increases susceptibility to the Egyptian cotton worm *Spodoptera literallis* but not against diamond back moth *Plutella xylostella*. The *Arabidopsis* hookless1 (hls1) and ein2 mutant affects ethylene signaling conferred resistance to Egyptian cotton worm *Spodoptera littoralis*¹⁴⁶. ISR1 locus on chromosome 3 controlling *Rhizobacteria* such as *Pseudomonas fluorescens WCS417r* involved in ethylene signaling in *A. thaliana*¹⁴⁷. In *A. thaliana* mutant etr1-1 shown enhanced resistant activity against *Verticillium dahlia* due to increased accumulation of the PR1, PR2, PR5, GSTF1 (*Glutathiones transferase*), GSTU16, CHI-1, (Chitinase),CHI-2 and Myb 75 genes¹⁴⁸. Jasmonic acid control defense gene expression through large scale transcriptional reprogramming. Jasmonic acid was necessary for defense gene expression in response to various microbial pathogens and arthropod herbivores. *Arabidopsis* plants were showed expression of the jasmonic acid responsive genes lox2, pdf1.2 and vsp by *Pseudomonas syringae pv tomato dc3000*. Npr1 found to be essential for salicylic acid mediated defense gene expression¹⁴⁹. Npr1 was a key regulatory pathogen in the systemic acquired resistance. In *Arabidopsis* systemic acquired resistance were effective through parallel activation of npr1 dependent defense response against *Pseudomonas syringae pv tomato*¹⁵⁰.The interaction between npr1 and ethylene modulate in defense response upon pathogen. Ethylene and jasmonic acid signaling in the *A. thaliana* ssi 1 mutants affect the npr1 independent expression of pdf1.2 and pr1 leads to susceptibility towards *Pseudomonas syringae* and *Peronospora parasitica*¹⁵¹. Two jasmonate signaling mutants Jin1 and Jin4 (Jasmonate - insensitive) shown increased in resistant activity in *Arabidopsis* upon treatment with biotrophic pathogen *Pseudomonas syringae* and necrotrophic pathogen *Botrytis cinerae*¹⁵². Due to lack in the production of jasmonic acid *A. thaliana* several fatty acid desaturase (fad3/fad7/fad8), coronatine insensitive 1.

Coi1 and jasmonic acid resistant-1(jar1), jin- 1 (jasmonate insensitive -1 gene) mutants shown high susceptibility to a variety of pathogens *Botrytis cinerae*, *Fusarium oxysporum*

,*Pythium* species, *Alternaria brassicicola* and the bacterial pathogen *Erwinia carotovora*, *Pseudomonas syringae* pv *tomato*.¹⁵⁴ Jasmonic acid dependent genes like plant defensin 1.2 (pdf1.2); thionin 2.1 (thi2.1), hevein like protein (hel) and chitinase b(chi-b) were involved in Jasmonic acid pathway dependent defense responses for resistant against biotrophic fungus *E.cichoracearum*, *Pseudomonas syringae* pv *maucicola*.¹⁵⁵ The *Arabidopsis* gene coi-1 required for jasmonic acid signaling pathways.¹⁵⁶ Ein2 gene act as a defense response in *Arabidopsis* against *Botrytis cinerea*. A subset of pathogen resistant genes in *Arabidopsis* comprising pr-3, pr-4 and pr-12(pdf1.2) genes coregulate the jasmonate and ethylene signaling pathways. These genes encode antimicrobial proteins. Additional study on EIN2 and COI1 mutants confirm at least two separate signal transduction pathways is essential for resistance against different pathogens, one that is salicylic acid dependent and other one was jasmonic acid or ethylene dependent. Fumonisin, is a toxin produced by the fungus *Fusarium moniliforme* interplay between different signaling components in the control of hypersensitive response.¹⁵⁷ Bos2, bos3 and bos4 (*Botrytis cinerea* susceptibility) mutants accumulate reduced levels of camalexin than wild type and responsiveness to ethylene and jasmonate. Genetic evidence found that cev1(vsp1) stimulates both the jasmonic acid and ethylene signal pathways through coi1 (Coronatine insensitive-1), an essential component of the jasmonic acid signaling pathways and etr1 encodes the ethylene receptor. The *A.thaliana* mutants npr1, eds5, ein2 and jar1 disrupt the salicylic acid, jasmonic acid and ethylene and cpr1, cpr5, cpr6 mutants constitutively activate these pathways identified by epistasis analysis.¹⁵⁸

Conclusion

The identification of disease resistant genes and gene loci in *A. thaliana* is an input knowledge to built agriculture. The Resistance genes from *Arabidopsis* are introduced in to different crop species and these varieties of crop species are used in agriculture farming. In other way, our environment should clean from pesticides, herbicides and different poisonous chemicals used for pathogen killing in crop varieties. The disease resistant genes which were identified in *Arabidopsis* can help to study of different protein classes related to other crop resistant gene loci encoding protein classes. The *A.thaliana* resistant genes involved in signaling pathways is a source of finding for this same link in other crop varieties. Three basic knowledge can be obtained from mapping and analyzing the pathways involved in resistant genes are (A)Resistance (B) Susceptibility (C) Signaling network of genes. This presentation and findings help to develop agriculture.

Acknowledgement

Thanks to CSIR, India provided me research opportunity in NBRI, Lucknow under Dr Samir V. Sawant, Principal Scientist. Also thanks to Dr C.S. Mohanty, Dr S.N. Jena in NBRI,

Lucknow, Uttarpradesh and Dr R.K. Hazra, Regional Medical Research Centre, Bhubaneswar, Odisha.

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