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Plant Immune System: Plant Disease Resistance Genes and its Applications

Shashi Prabha[1], Ashwani Yadav[1], Akanksha Sharma[1], Hemant Kumar Yadav[2], Sujit Kumar[1] and Rajendra Kumar[1]*

[1]U.P. Council of Agricultural Research, Lucknow, Uttar Pradesh, India.
[2]National Botanical Research Institute, Lucknow, Uttar Pradesh, India.

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Globally, the various plant diseases cause significant losses in plant productivity. The estimated loss caused by plant pathogens is approximately 10 to 20%. The losses are about 20% in developed countries and 30-45% in developing countries. The main class of pathogens causing plant diseases includes bacteria, fungi, insects, nematodes and viruses. In nature plants have some kinds of defence system to protect themselves against these pathogens. The defence system of plant is mediated by the disease resistance *(R)* genes. In plant, *R* genes direct the recognition of pathogen components which is encoded by avirulence genes *(Avr).* The interaction between disease resistance *(R)* genes and their corresponding pathogen avirulence *(Avr)* genes are the key for identification of a plant is resistance or susceptible to a pathogen attack. This review summarizes the various types of *R* genes reported and characterized in important plants to understand the plant defence systems.

Keywords: Resistance gene *(R),* Plant defence system, Avr and Pathogenesis related proteins.

Resistance Gene (*R* genes)

Plants have developed immune systems to combat the pathogens attacks. The immune systems involve two modes to destroy the invading pathogens. The first one includes transmembrane pattern recognition receptors (PRRs) mode. The PRRs belong to the family of receptor like proteins (RLPs) and recognize conserved microbial patterns[1]. RRRs act in response to slowly evolving microbial associated molecular patterns (MAMPS) or pathogen associated molecular patterns (PAMPs) such as flagellin[2]. Flagellin is the structural protein of bacteria that forms the major component of flagellar filaments. The flagellin has PAMPs that can be predicted by plant, leading to activation of defence response. The second mode uses the polymorphic Nucleotide Binding (NB) and Leucine-Rich Repeats (NB-LRR) protein products encoded by *R* genes. Resistance proteins (*R*-proteins) are the second line of defence system present in all the plants. These proteins provide the resistance against different pathogens by recognizing the effector molecules of pathogens. Specific effectors molecules produced by pathogens are directly recognized by different *R* proteins. The mechanism of defence is mediated by the disease resistance proteins that function is identification of pathogen effectors.

Flor, 1971 performed inherent analyses of plants and pathogens and defined a model known as gene for gene model. In this model it has been predicted that *R* gene may function as receptor to recognize the pathogen derived elicitor encoded by *Avr* genes. Flor, 1971) studied the interaction

* To whom all correspondence should be addressed.
Fax : +91-522-2721627, PBX Phone: 0522- 2721626;
E-mail: rajendrak64@yahoo.co.in

between flax and the fungal pathogen (*Melampsora lini*) and reported that flax genes for resistance were dominant and rust genes for virulence were recessive and finally concluded that pathogens contain a mixture of molecules encoded by dominant avirulence (*Avr*) genes that generate defence responses in plants carrying the corresponding *R* gene[3]. This model predicted that plant resistance will occur only when a plant possesses a dominant resistance gene (*R*) and the pathogen expresses the complementary functional avirulence gene (*Avr*). The pathogen avirulence genes are referred to as effector genes and have disease causing ability[4]. Different bacterial and fungal pathogens contain diverse sets of effectors molecules and *Avr* genes[5].

The most important class of *R* genes consist of a nucleotide binding domain (NB) and leucine rich repeat (LRR) domains and are referred to as NB-LRR *R* genes. The NB domain binds either GTP/GDP or ATP/ADP and the LRR domain is involved in protein-protein interactions. The most important function of LRR domain is disease resistant. Large number NBS of coding sequence have been isolated from different plant species by genome wide analysis methods. In papaya and *Cucumis sativus* 50 NBS coding sequence[6,7] and in *Oryza sativa* 653 NBS coding sequence have been isolated[8].

Applications of *R* genes in major plants

Mildew resistance locus (*MLO)* genes are present as small family in the genomes of all higher plants. *MLO* genes family exists in plants and exhibits resistance against the wide variety of pathogens. Various members of *MLO* gene family may play an essential role against phytopathogenic fungus in dicots. Presently, 15 *MLO* genes in *Arabidopsis*, 9 in maize, 12 in rice and 17 in grapes have been reported [9-12]. The details of major *R* genes reported in important plants are summarized below:

R* genes in *Arabidopsis* (*Arabidopsis thaliana)

Meyer *et al.,* (2003) identified over 149 resistance genes encoding NBS-LRR class in *Arabidopsis* using *in silico* analysis[13]. NBS-LRR locus contains different allelic forms that can confer resistance to different class of pathogens. Disease resistance gene *RPS6* was identified in *Arabidopsis*[14] and locus has been mapped on chromosome 5. *RPS6* gene exhibits disease resistant against the *Pseudomonas syringae*[15]. Various members of *MLO* gene families in *Arabidopsis* include *AtMLO2, AtMLO6* and *AtMLO12* play essential role in resistance to disease. The *AtMLO2* gene reduced susceptibility to *Golovinomyces orontii*. Two other *Arabidopsis* genes such as *AtMLO12* and *AtMLO6* were mutated with *AtMLO2* and which showed resistance to the powdery mildew[10]. Apart from *MLO* gene family, other resistance gene *RPW8* works against the powdery mildew disease in *Arabidopsis* which has an amino terminal transmembrane domain and CC domain. In *Arabidopsis thaliana* locus contains two dominant R genes are *RPW8.1* and *RPW8.2*. *RPW8.1* and *RPW8.2* genes confer resistance to powdery mildew disease caused by fungi *Erysiphe cruciferarum*[16].

Ashfield *et al.,* (2003) cloned *Rpg1-b* resistance gene from soybean and compared this gene with *RPM1* resistance gene from *Arabidopsis* and found that *Rpg1-b* gene of soybean and *RPM1* gene of *Arabiodpsis thalina* mediate recognition of same effector protein from *Pseudomonas syringae.* Both the genes *RPM1* and *Rpg1-b* belong to the coiled-coil NBS-LRR class of *R* genes[17]. The three *PEN1, PEN2* and *PEN3* proteins encoded by genes and acts as essential components in cell wall-based defence against powdery mildew *Blumeria graminis* fsp. *Hordei*[18].

R* genes in rice *(Oryza sativa)

Bacterial blight is one of the most serious disease of rice worldwide caused by *Xanthomonas oryzae pv. oryzae (Xoo)* which causes loss of productivity upto 81%[19]. Resistance to bacterial blight regulated by disease *R* genes and defence responsive genes. Thirty eight resistance genes for bacterial blight have been identified and utilized in rice breeding programs [20]. Five of them includes *Xa1*[21], *Xa21*[22], *Xa5* [23], *Xa26*[24] and *Xa7*[25] have been cloned. The gene *Xa 5* have been widely used globally for gene pyramiding to develop rice resistance varieties [26,27,20].

Blast disease of rice is another disease caused by *Magnaporthe grisea* fungus[28]. Till date 96 genes for blast resistance have been identified and mapped[29]. Several *R* genes are clustered in specifically on chromosome 6, 9, 11 and 12 in rice genome [30,31]. *Rirlb* gene belongs to defence related gene family that has been identified in cereals [32]. Many blast resistance genes have been

successfully introgressed into elite breeding lines using gene pyramiding approach. For example, the variety Pusa1602 (PRR78+*Piz5*) and Pusa1603 (PRR78+*Pi54*) lines were developed by incorporating the blast resistance genes *Piz-5* and *Pi54*, using a marker assisted backcrossing (MABC) breeding[33]**.** The Rongfeng B hybrid rice line was also developed through MABC breeding[34]**.** The blast resistance *Pi* genes (*Pi-7(t)*, *Pi-d(t)1* and *Pir2-3(t)* and *qLN2* QTL) from the Pongsu Seribu 1 rice variety was introduced into popular Malaysian mega rice variety MR263 [29]**.**

R* gene in tomato (*Solanum lycopersicum)

Tomato is one of the important vegetable crops worldwide .The tomato *Pto* gene is resistance gene encoding a serine/threonine protein kinase (PK) and shows resistance to *Pseudomonas syringae.* pv. tomato that express by the avirulence gene *Avr* Pto. Many family of *MLO* genes have been cloned in *Arabidopsis*, tomato and pea [9,35.] Whole genome of tomato have available and provides all the information which are related to structural features and phylogenetic relationship of the *MLO* gene family. In tomato 17 MLO genes are identified by bioinformatics methods[36].

By the biotechnological methods transgenic tomato has produced that shows resistance to wide varieties of pathogens. *Mi* gene has introduced into the cultivated *Lycopesicon esculentum* tomato from its natural relative *L. peravianum* cultivar [37]. Mi-1 encodes a cytoplasmic NBS-LRR-CC protein. The Mi locus localized at chromosome 6. Mi locus contains two highly homologous genes such as *Mi-1.1* and *Mi-1.2* or *Mi-1* genes. These genes effective against nematodes, oomycetes and fungi[38]. In the pepper *Bs2 R* gene shows resistance against the bacterial spot disease caused by the bacterium *Xanthomonas campestris. X. campestris* is also pathogen of tomato. This *Bs2 R* gene has been cloned from pepper into tomato that encodes a NB-LRR protein of *R* genes. Transgenic tomato carries *Bs2* and effective against *X. campestris.*

The tomato *I-3* gene is a novel gene for resistance to Fusarium wilt disease caused by *Fusarium oxysporum* f. sp. *lycopersici (Fol)* races 3. *I-3* encodes an SRLK (S-receptor-like kinase) reveals a new pathway for Fol resistance and confer *Avr3*-dependent resistance to Fol race 3[39.] Tomato yellow leaf curl virus causes disease in tomato worldwide. *Ty-2* resistance gene shows resistance against virus. By bioinformatics techniques, 22 disease-resistance candidate genes of *Ty-2* were recognized. These genes involve not only in of in tomato growth and development but also responses to various stresses[40].

***R* gene in barley (*Hordeum vulgare L.*)**

Mildew resistance locus o *(MLO)* is a novel class of plant integral membrane proteins *Mlo* gene is control element of plant pathogene resistant. *MLO* gene family may play an important role in defence system resistance against the variety of plant pathogens. Tucker *et al.,* (2013) found many *R* genes such as *Mla-9, Ml-ra*, *Mla-6* and the combinations of *Mla-1* plus *Mla-A12* and *Mla-6* plus *Mla-14* and *Mla-13* plus *MlRu3* together with the recessive resistance gene *mlo-5* in barley against powdery mildew caused by the fungus *Blumeria graminis* f. sp. *hordei (Bgh)* in Western Australia[41].

Many diseases are mostly seen in barley likes leaf rust, stem rust and loose smut diseases. Leaf rust disease is caused by *Puccinia hordei* (fungus) in barley. *Rph23* additive adult plant resistance gene is a new resistance gene to leaf rust in barley. This gene was identified from a doubled haploid population resulting from an intercross between and Australian barley varieties Franklin (F) and Yerong (Y). *Rph23* leaf rust gene has been mapped on 7HS chromosome [42]**.** Stem rust disease caused by *Puccinia graminis f. sp. tritici*. *Rpg1* gene provides durable protection against stem rust that loss in widely grown barley cultivars. An *Rpg1* gene encodes a receptor kinase like protein with two tandem protein kinase domains (A novel class of plant resistance genes)[43]**.** *Rpg5* is another stem rust resistance gene shows dominant resistance against rye stem rust in barley[44]**.** Zhou *et al.,* (2014) studied on association mapping of stem rust race TTKSK resistance in US barley breeding germplasm. They used 3000 cultivars for resistance at seedling stage as well as adult plant stage. In seedling stage two SNP markers on chromosome 7 H (11_21491 and 12_30528) were found which linked with resistance and resistance QTL was Rpg-qtl-7H-12_30528. In adult stage two SNP markers on chromosome 5H (11_11355 and 12_31427) were found which linked with resistance and resistance QTL was Rpg-qtl-5H-11_11355[45]. Zang *et al.,* (2015) identified smut

resistance gene *Un8* and was mapped on long arm of chromosome 5 (1HL)[46].

_R_ gene in wheat (*Triticum aestivum* L.)

Various types of diseases are found in wheat such as leaf rust, stem rust and stripe rust caused by different types of microorganisms. Leaf rust disease is caused by the fungus *Puccinia triticin*a Eriks. is widespread diseases of bread wheat (*Triticum aestivum* L.) worldwide[47,48]. Charpe *et al*., (2012) work on marker assisted gene pyramiding of leaf rust resistance genes *Lr*9, *Lr*24 and *Lr*28 in a bread wheat cultivar HD 2329 against virulent pathotypes of leaf rust 77-5 (121R63-1) and achieved that all genes showed a high degree of seedling and adult plant resistance[49]. Wang *et al*., (2014) studied on genetic analysis and molecular mapping of leaf rust resistance genes in the wheat line 5R618 bred at china. In this study they crossed between wheat line 5R618 (resistance) and Zhengzhou5389 (susceptible) with Chinese *P. triticina* pathotype THJP and found that *Lr5R* gene showed resistance to *P. triticina* and *Lr5R* gene was located on the 3DL chromosome. They concluded that *Lr5R* is novel leaf rust resistance gene[50]. Shahin *et al.,* (2015) performed research on relationship between partial resistance and heritage of adult plant leaf rust resistance gene *Lr46* in six bread wheat varieties such as Gemmeiza 9, Giza 168 and Gemmeiza 7, Gemmeiza 1, Sakha 93 and Sids 1 and found two varieties like Giza 168 and Gemmeiza 9 have three leaf rust genes *i.e. Lr*45, *Lr*46 and *Lr*47 and other four varieties do not contain any leaf rust gene after segregation of F_2 plant[51].

Stem rust, another rust disease caused by *Puccinia graminis* f. sp. *tritici* (Pgt) is serious diseases of wheat (*Triticum aestivum* L.) worldwide. Yadav *et al*., (2015) applied marker assisted backcrossing method and transferred the three stem rust resistant genes *Sr25*, *SrWeb* and *Sr50* from the CIMMYT breeding line PMBWIR4 into the wheat cv. HUW234 (popular Indian wheat cultivar) and found that improved version of wheat cv. HUW234 showed superior resistance as compared to source cultivar against stem rust[52].

Stripe rust is caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*) is one of the most damaging diseases of wheat. Various stripe rust resistance genes have been mapped on chromosome 2B such as *Yr5*, *Yr7*, *Yr27*, *Yr31*, *YrSp, YrV23*, *YrQz*, *YrTp1* and *YrCN19* [53-55]. These genes show resistance to all or to a few races of *P. striiformis* f. sp. *tritici*.**.** Stripe rust resistance gene *Yr51* has been mapped on 4AL chromosome and showed resistance against Australian pathotypes of *Puccinia striiformis* f. sp. *tritici* [56]**.** Zhou *et al.,* (2014) studied on identification of stripe rust gene *Yr59* to stripe rust in wheat germplasm PI 178759 of Washington state, USA. In this research they crossed between wheat germplasm PI 178759 and Avocet susceptible with *P. striiformis* f. sp. *tritici*. They identified that wheat germplasm PI 178759 was high temperature adult resistance (HTAP) and has been mapped on long arm of 7B chromosome[57].

_R_ gene in Maize (*Zea mays*)

Various types of diseases are found in maize such as *Aspergillus* ear rot, *Gibberella* ear rot and *Diplodia* ear rot caused by different types of microorganisms. *Aspergillus* ear rot is caused by fungus *Aspergillus flavus* which produces a mycotoxin called as aflatoxin. Several researches have reported that QTLs show resistance to aflatoxin accumulation[58-60] and to *Aspergillus* ear rot [59]**.** *Gibberella* ear rot is caused by the fungus *Gibberella zeae* and *Fusraium graminearum***.** Ali *et al.,* (2005) studied and identified 11 QTLs shows resistance to *Gibberella* ear rot disease[61]. *Diplodia* ear rot disease is caused by *Stenocarpella maydis*. Olatinwo *et al.,* (1998) suggested that non additive gene play an important role for resistant to *diplodia* ear rot disease[62] and Dorrance *et al*., (1998) suggested that general and specific additive gene play an important role in resistant against this disease[63].

_R_ gene in Linseed (*Linum usitatissimum)*

L6 resistance gene encodes NBS-LRR class of *R* gene that confers race specific resistance to strains of flax rust (*Melampsora lini*) that carry avirulence alleles of the *AvrL567* gene [64]**.** The resistance genes *L5, L6, L7, M, P* and *P2* and the corresponding avirulence gene have been cloned and currently avirulence/virulence genes at four loci, *AvrL567, AvrM, AvrP4* and *AvrP/AvrP123* have been cloned. [65]**.** Genes at the M locus in flax *(Linum usitatissimum)* that confer resistance to flax rust *(Melampsora lini).* Two other functional resistance genes *M1* and *M3* have cloned at this locus by candidate gene approaches and transposon tagging methods. *M1* and *M3* belongs to family of

the nucleotide binding site, leucine-rich repeat (NBS-LRR) of *R* gene [66]. 147 NBS-LRR genes identified that encode *R* gene to detect pathogens and to induce defense responses[67].

Various diseases are found in linseed which causes loss in its productivity includes rust caused by *Melomsora lini*, powdery mildew caused by *Oidium lini, Alternaria* blight caused by *Alternaria lini* and wilt caused by *Fusarium oxysporum*. Some disease resistance varieties of linseed have been developed and they show resistance to rust, powdery mildew, *Alternaria* blight, wilt and budfly diseases. LCK-9216 and LMH-16-5 varieties show resistance to powdery mildew and rust and moderate resistance to *Alternaria* blight and budfly but LMH-16-5 variety also shows moderate resistance to wilt. Jawahar Linseed-9 variety shows resistance to powdery mildew, rust and wilt and are tolerant to *Alternaria* blight. LMH-62 variety shows resistance to powdery mildew, rust and wilt[68]. PKV NL-260 variety shows moderate resistance to powdery mildew, *Alternaria* and budfly. NL-142 variety is moderate susceptible to *Alternaria* blight, wilt and rust and moderate resistance to bud fly and powdery mildew. NL-165 variety is moderate susceptible to *Alternaria* blight and resistance to leaf minor and moderate resistance to powdery mildew, wilt and budfly[69]. Surbhi (Kl-1) and Nagarkot (KL-31) varieties show resistance to rust, drought and powdery mildew. Jeevan (DPL-21) and Janaki (KL-43) varieties show resistance to rust, wilt and powdery mildew. Himalini variety shows fairly resistance to powdery mildew, wilt and resistance to rust. Him Alsi-I (KL-187) variety shows resistance to blight rust and wilt[70].

CONCLUSIONS

The main focus of the research is to manage the yield loss caused by diseases of plant at global level. Chemical management of plant diseases is simple and effective option. The most important difficulty associated with chemical management is environmental pollution and health hazards caused by toxic chemicals released during disease management. Chemical management gives good results for a few pathogens only, but bad results against other beneficial pathogens. Thus in order to recognize a sustainable agriculture and obtain high value products in terms of health safe, the use of resistance (tolerant) varieties have become a most important tool to reduce or decreases caused by various pathogens. Many varieties that are resistant to various pathogens are available for various plants.

Biotechnological tools are being used to make easy the existing disease management planning. The various molecular biology techniques are being used to assist the conventional breeding programme and to help in shorten the period required to grow resistance cultivar in various plants. In molecular biology techniques, molecular marker offer enormous scope for improving the efficiency of traditional plant breeding programme in which gene pyramiding and marker assisted backcrossing method are applied for obtaining disease resistance plants. Gene pyramiding with marker technology can combine into existing plant breeding programme to permit researchers to access, transmit and unite genes at a rate and with precision not before possible. Gene pyramiding is the method of combining more than one gene for resistance in a common genetic background through the repeated back crossing and selection with the virulence races of the pathogen. This technique is very effective in obtaining durable resistance to the pathogens. Molecular markers are used to detect the presence of desire character which is significantly important. Marker assisted backcrossing (MABC) is a specific and an efficient method to introgress a single locus controlling a trait of interest while retaining the important characteristics of the recurrent parent. MABC is superior to conventional backcrossing in accuracy and efficiency. MABC involves subsequent backcrossing to eliminate the genetic background of the donor while getting better genetic properties of recurrent parent as much as possible.

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REFERENCES

1. Beck, M., Heard, W., Mbengue, M., Robatzek, S. The INs and OUTs of pattern recognition receptors at the cell surface. *Curr Opin Plant Biol*., 2012; **15**:367–374.
2. Zipfel, C., Felix, G. Plants and animals: a different taste for microbes? *Curr. Opin. Plant Biol*., 2005; **8**: 353–360.
3. Flor, H.H. Current status of the gene-for-gene concept. *Annual Review of Phytopathology*., 1971; **9**:275-296.
4. Van Dijk, K., Fouts, D.E., Rehm, A.H., *et al.,* The *Avr* (effector) proteins HrmA (HopPsyA) and *Avr*Pto are secreted in culture from *Pseudomonas syringae* pathovars via the Hrp (type III) protein secretion system in a temperature- and pH-sensitive manner. *J. Bacteriol*., 1999; **181**:4790-4797.
5. Dou, D., Zhou, J.M. Phytopathogen effectors subverting host immunity: Different foes, similar battleground. *Cell Host Microbe.,* 2012; **12**: 484–495.
6. Porter, B.W., Paidi, M., Ming, R., *et al.,* Genome-wide analysis of *Carica papaya* reveals a small NBS resistance gene family. *Mol. Genet. Genomics.,* 2009; **281**:609–626.
7. Wan, H., Yuan, W., Bo, K., *et al.,* Genome-wide analysis of NBS-encoding disease resistance in *Cucumis sativus* and phylogenetic study of NBS-encoding genes in *Cucurbitaceae* crops. *BMC Genomics.,* 2013; **14**:109.
8. Shang, J., Tao, Y., Chen, X., *et al*., Identification of a new rice blast resistance gene, *Pid3*, by genome wide comparison of paired nucleotide-binding site leucine-rich repeat genes and their pseudogene alleles between the two sequenced rice genomes. *Genetics.,* 2009; **182**:1303–1311.
9. Devoto, A., Hartmann, H.A., Piffanelli, P., *et al.,* Molecular phylogeny and evolution of the plant-specific seven-transmembrane *MLO* family. *J Mol Evol.,* 2003; **56**: 77–88.
10. Consonni, C., Humphry, M.E., Hartmann, H.A., *et al.,* Conserved requirement for a plant host cell protein in powdery mildew pathogenesis. *Nat Genet.,* 2006; **38**: 716–720.
11. Liu, Q., Zhu, H. Molecular evolution of the *MLO* gene family in *Oryza sativa* and their functional divergence. *Gene.,* 2008; **409**: 1–10.
12. Feechan, A., Jermakow, A.M., Torregrosa, L., *et al.,* Identification of grapevine *MLO* gene candidates involved in susceptibility to powdery mildew. *Funct Plant Biol.,* 2008; **35**:1255–1266.
13. Meyers, B.C., Kozik, A., Griego, A., *et al.,* Genome-wide analysis of NBS-LRR–encoding genes in *Arabidopsis. The Plant Cell*., 2003; **15**(4): 809-834.
14. Kim, S.H., Kwon, S.I., Saha, D., *et al.,* Resistance to the *Pseudomonas syringae* effector *HopA1* is governed by the TIR-NBS-LRR protein *RPS6* and is enhanced by mutations in SRFR1. *Plant physiology*., 2009; **150**: 1723-1732.
15. Heidrich *et al*., *Arabidopsis EDS1* Connects Pathogen Effector Recognition to Cell Compartment Specific Immune Responses, *Science.,* 2011: **334** (6061):1401-4.
16. Xiao, S.Y., Ellwood, S., Calis, O., *et al.,* Broad-spectrum mildew resistance in *Arabidopsis thaliana* mediated by RPW8. *Science.,* 2001; **291**:118–120.
17. Ashfield, T., Bocian, A., Held, D., *et al.*, Genetic and physical localization of the soybean *Rpg1-b* disease resistance gene reveals a complex locus containing several tightly linked families of NBS-LRR genes. *Mol Plant Microbe Interact*., 2003; **16**:817-826.
18. Johansson, O.N., *et al.,* Role of the penetration-resistance genes *PEN1, PEN2* and *PEN3* in the hypersensitive response and race-specific resistance in *Arabidopsis thaliana. The Plant Journal*., 2014; **79**(3): 466–476.
19. Kumar, PN., Sujatha, K., Laha, G.S., *et al.,* Identification and fine-mapping of *Xa33,* a novel gene for resistance to *Xanthomonas oryzae* pv. *oryzae. Phytopathology*., 2012; **102**:222–228.
20. Suh, J.P., Jeung, J.U., Noh, T.H., *et al.,* Development of breeding lines with three pyramided resistance genes that confer broad-spectrum bacterial blight resistance and their molecular analysis in rice. *Rice.*, 2013; **6**: 5.
21. Yoshimura, S., Yamanouchi, U., Katayose, Y., *et al.,* Expression of *Xa1*, a bacterial blight-resistance gene in rice, is induced by bacterial inoculation. *Proc Natl Acad Sci USA.*, 1998; **95**:1663–1668.
22. Song, W.Y., Wang, G.L., Chen, L.L., *et al*., A receptor kinase-like protein encoded by the rice disease resistance gene. *Xa21*. *Science*. 1995; **270**:1804–1806.
23. Anjali, S.I., Susan R.M. The rice bacterial blight resistance gene *Xa5* encodes a novel form of disease resistance. *Molecular Plant-Microbe Interactions*., 2004; **17**: 1348-1354.
24. Sun, X., Cao Y., Yang, Z., *et al*., *Xa26*, a gene conferring resistance to *Xanthomonas oryzae* pv. *oryzae* in rice, encodes an LRR receptor kinase-like protein. *Plant J.*, 2004; **37**:517-527.
25. Gu, K.Y., Yang, B., Tian, D.S., Wu, L.F *et al.,* R-gene expression induced by a type-III effector triggers disease resistance in rice. *Nature.*, 2005; **435**:1122-1125.

26. Sundaram, R.M., Vishnupriya, M.R., *et al.,* Marker assisted introgression of bacterial blight resistance in *Samba Mahsuri*, an elite indica rice variety. *Euphytica.,* 2008; **160**:411–422.
27. Kottapalli, K.R., Narasu, M.L., Jena, K.K. Effective strategy for pyramiding three bacterial blight resistance genes into fine grain rice cultivar, *Samba Mahsuri*, using sequence tagged site markers. *Biotechnol Lett.,* 2010; **32**:989–996.
28. Okuyama, Y., Kanzaki, H., Abe, A., *et al.,* A multifaceted genomics approach allows the isolation of the rice *Pia*-blast resistance gene consisting of two adjacent NBS-LRR protein genes. *Plant J.,* 2011; **66**: 467–479.
29. Hasan, M.M., Yusop, M.R., Ismail, M.R., *et al.,* Performance of yield and yield contributing characteristics of bc2 f3 population with addition of blast resistant gene. *Ciênc. Agrotec., Lavras.,* 2015; **39**(5):463-476.
30. Ashkani, S., Rafii, M.Y., Rasm, H.A., Latif, M.A. Genetic dissection of rice blast resistance by QTL mapping approach using an F3 population. *Molecular biology Reports*. 2013; **40**:2503-2515.
31. Ballinin, E., Morel, J.B., Droc, G., Price, A., Courtois, B., *et al.,* A genome wide meta analysis of rice blast resistance gene and quantitative trait loci provides new insights into partial and complete resistance. *Molecular plant microbe interaction*. 2008; **21**:859-868.
32. Mauch, F., Reimmann, C., Freydl, E., Schaffrath, U., Dudler, R. Characterization of the rice pathogen-related protein *Rir1a* and regulation of the corresponding gene. *Plant Mol Biol*., 1998: **38**(4):577-86.
33. Singh, V.K., Singh, A., Singh, S.P., *et al*., Incorporation of blast resistance into 'PRR78', an elite Basmati rice restorer line, through marker assisted backcross breeding. *Field Crops Res*., 2012; **128**:8–16.
34. Fu C, Wu T, Liu W, Wang F, *et al.,* Genetic improvement of resistance to blast and bacterial blight of the elite maintainer line Rongfeng B in hybrid rice (*Oryza sativa* L.) by using marker-assisted selection. *Afr J Biotechnol*., .2012; **11**:13104–13124.
35. Bai, Y., Pavan, S., Zheng, Z, Zappel, N.F., *et al.,* Naturally occurring broad-spectrum powdery mildew resistance in a central American tomato accession is caused by loss of *Mlo* function. *Mol Plant-Microbe Interact*., 2008; **21**: 30-39.
36. Chen, Y., Wang, Y., *et al*., Genome-wide analysis of the mildew resistance locus o (*MLO*) gene family in tomato (*Solanum lycopersicum* L.). *POJ.,* 2014; **7**(2):87-93.
37. Rossi, M., Goggin, F.L., Milligan, SB., *et al.,* The nematode resistance gene *Mi* of tomato confers resistance against the potato aphid. *Proc Natl Acad Sci U S A.*, 1998; **95**(17): 9750-4.
38. Dogimont, C., Bendahmane, A., Chovelon, V., Boissot, N. Host plant resistance to aphids in cultivated crops: genetic and molecular bases, and interactions with aphid populations. *C. R. Biol.* 2010; **333;** 566–573.
39. Catanzariti, A.M., Lim, G.T., Jones, D.A. The tomato *I-3* gene: Novel genes for resistance to Fusarium wilt disease. *New Phytol*., 2015; **207**(1):106-18.
40. Liu, Y.F., Wan, H.J., Wei, Y.P., *et al., In silico* analysis of gene content in tomato genomic regions mapped to the *Ty-2* resistance gene. *Genet Mol Res*., 2015; **14**(3):7947-56.
41. Tucker, M.A., Jayasena, K., Ellwood, S.R., Oliver, R.P. Pathotype variation of barley powdery mildew in Western Australia. *Australasian plant pathology*. 2013; **42**(5):617-623.
42. Singh, D., Racatos, P.D., Derevnina, L., *et al., Rph23:* A new designated additive adult plant resistance gene to leaf rust in barley on chromosome 7H. *Plant Breeding.,* 2015; **134**: 62–69.
43. Brueggeman, R., Rostoks, N., Kudrna, D., *et al.* The barley stem rust-resistance gene *Rpg1* is a novel disease-resistance gene with homology to receptor kinases. *Proc. Natl. Acad. Sci. U.S.A.,* 2002; **99**: 9328–9333.
44. Wang, X., Richards, J., Gross, T., *et al.,* The *rpg4*-mediated resistance to wheat stem rust (*Puccinia graminis*) in barley (*Hordeum vulgare*) requires *Rpg5*, a second NBS-LRR gene, and an actin depolymerization factor. *Molecular Plant-Microbe Interactions.,* 2013; **26**(4):407-418.
45. Zhou H, Steffenson B.J, Gary Muehlbauer G., *et al.,* Association mapping of stem rust race TTKSK resistance in US barley breeding germplasm. *Theor Appl Genet.,* 2014; **127**(6): 1293–1304.
46. Zang, W., Eckstein, P.E., Colin, M., *et al.,* Fine mapping and identification of a candidate gene for the barley Un8 true loose smut resistance gene. *Theor Appl Genet.* 2015; **128**(7):1343-57.
47. Oelke, L.M., Kolmer, J.A. Characterization of leaf rust resistance in hard red spring wheat cultivars. *Plant Disease.,* 2004; **88**(10):1127-1133.
48. Mebrate, S.A., Oerke, E.C., Dehne, H.W., Pillen, K. Mapping of the leaf rust resistance gene *Lr38* on wheat chromosome arm 6DL using SSR markers. *Euphytica*., 2008 ; **162**(3): 457-466.
49. Charpe, A., Koul, S., Gupta, S.K., *et al*., Marker assisted gene pyramiding of leaf rust resistance genes *Lr 9, Lr 24* and *Lr 28* in a bread wheat

cultivar HD 2329. *J. Wheat Res*., 2012; **4** (1):20-28.
50. Wang, J., Shi, L., Zhu, L., Li, X., Liu, D. Genetic analysis and molecular mapping of leaf rust resistance genes in the wheat line 5R618. *Czech J. Genet. Plant Breed.,* 2014; **50**: 262–267.
51. Shahin, S.I., El-Orabey, W.M. Relationship between Partial Resistance and Inheritance of Adult Plant Resistance Gene *Lr 46* of Leaf Rust in Six Bread Wheat Varieties. *Advances in crop science and technology*., 2015; **3**:161.
52. Yadav, P.S., Mishra, V.K., Arun, B., *et al.,* Enhanced resistance in wheat against stem rust achieved by marker assisted backcrossing involving three independent *Sr* genes. *Current Plant Biology.*, 2015; **2**: 25-33.
53. Luo, P.G., Ren, Z.L., Zhang, H.Q., *et al.,* Identification, chromosomal location, and diagnostic markers for a new gene (*YrCN19*) for resistance to wheat stripe rust. *Phytopathology.*, 2005; **95**: 1266–1270.
54. Chen, X.M., Stephen, S.J., Roland, F.L. Chromosomal location of genes for resistance to *Puccinia striiformis* in seven wheat cultivars with resistance genes at the *Yr3* and *Yr4* loci. *Phytopathology*., 1996; **86**: 1228–1233.
55. Yin, X.G., Shang, X.W., Pang, B.S., *et al.,* Molecular mapping of two novel stripe rust resistance genes *YrTp1* and *YrTp2* in A-3 derived from *Triticum aestivum* × *Thinopyrum ponticum. Agricultural Sciences in China.*, 2006; **5**: 483–490.
56. Randhawa, M., Bansal, U., Valarik, M., *et al.,* Molecular mapping of stripe rust resistance gene *Yr51* in chromosome 4AL of wheat. *Theor Appl Genet.,* 2014; **127**: 317-324.
57. Zhou, X.L., Wang, M.N., Chen, X.M., *et al.,* Identification of *Yr59* Conferring high temperature adult plant resistance to stripe rust in wheat germplasm PI 178759. *Theor Appl Genet*., 2014; **127**(4):935-945.
58. Brooks, T.D., Williums, W.P., Windham, .GL., *et al.,* Quantitative trait loci contributing alfatoxin accumulation in the maize inbred Mp313E. *Crop science*., 2005; **45**:171-174.
59. Busboom, K.L., White DG. Inheritance of resistance to aflatoxin production and *Aspergillus* ear rot of corn from the cross of inbreds B73 and Oh516. *Phytopathology*., 2004; **94**: 1107-1115.
60. Paul, C.G., Naidoo, A., Forbes, V., *et al.,* Quantitative traits loci for low aflatoxin production in two related maize populations. *Theoretical and Applied Genetics.,* 2003; **107**: 263-270.
61. Ali, M.L., Taylor, J.H., Jie, L., *et al.,* Molecular mapping of QTLs for resistance to Gibberella ear rot, in corn, caused by *Fusarium graminearum. Genome.,* 2005; **48**(3): 521-33.
62. Olatinwo, R., Cardwell, K., Menkir, A., *et al*., Inheritance of resistance to *Stencarpella macrospora* ear rot of maize in the mid-altitude zone of Nigeria. *European Journal of plant pathology.,* 1998; **105**: 535-543.
63. Dorrance, A.E., Hinkelmann, K.H., Warren, H.L. Diallel analysis of diplodia ear rot resistance in maize. *Plant disease*., 1998; **82**(6):699-703.
64. Lawrence, G.J., Finnegan, E.J., Ayliffe, M.A., Ellis, J.G. The L6 gene for flax rust resistance is related to the *Arabidopsis* bacterial resistance gene *RPS2* and the tobacco viral resistance gene N. *Plant Cell*., 1995; **7**(8): 1195-1206.
65. Lawrence, G.J., Dodds, P.N., Ellis, J.G. Rust of Flax and Linseed Caused by *Melampsora Lini. Molecular Plant Pathology.,* 2007; **8**: 349–364.
66. Lawrence, G.J, Anderson, P.A., Dodds, P.N., Ellis, J.G. Relationships between Rust Resistance Genes at the *M* Locus in Flax. *Molecular Plant Pathology.,* 2010 **11**:19–32.
67. Kale, S.M., Pardeshi, V.C., Barvkar, V.T., *et al.,* Genome-wide identification and characterization of nucleotide binding site leucine-rich repeat genes in linseed reveal distinct patterns of gene structure. *Genome.,* 2013; **56**: 91–99.
68. Anonymous-a, 2014. http://www.pnbkrishi.com/linseedtech.htm (Accessed on 04-01-2014).
69. Anonymous-b, 2014. http://www.pdkv.ac.in/aicrpLinseed.php (Accessed on 04-01-2014).
70. Anonymous-c, 2014. http://agropedia.iitk.ac.in/content/linseed-varieties-and-its-characteristics (Accessed on 04-01-2014).