Indian Journal of Plant Sciences ISSN: 2319–3824(Online)
An Open Access, Online International Journal Available at http://www.cibtech.org/jps.htm
2016 Vol.5 (3) July-September, pp. 30-36/Thakur et al.
Review Article

MOLECULAR MAPPING FOR LATE BLIGHT DISEASE RESISTANCE IN POTATO

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ABSTRACT
Mapping resistance gene is usually accomplished by phenotyping a segregating population for the resistance trait and genotyping it using a large number of markers. Strict environmental regulations on the application of chemicals for pest and disease control lead to promote plant breeding for disease resistance as the most environmentally friendly and effective way to limit pathogen epidemics. Studies of plant microbe interaction and genome mapping have led to a significant increase in the understanding of both qualitative, quantitative resistance and many *Solanum* species have been recognized as sources of late blight resistance. Fortunately, with the molecular markers it is possible to detect and locate several genomic regions affecting quantitative traits in segregating populations of potato. Currently, microsatellite and AFLP markers remain a standard for linkage map construction. The review on mapping of quantitative resistance will highlight the basis for using Marker Assisted Selection to introgress resistance alleles from wild species to improve late blight resistance.

Keywords: *Late Blight, Genetic Mapping, Potato, AFLP, SSR*

INTRODUCTION
Plants are attacked by a wide range of pathogens including viruses, bacteria, oomycetes, fungi, nematodes, and insects (Strange and Scott, 2005). Over 100 years of work on the genetics and breeding of resistance to *P. infestans* in potato has generated wealth information on this host–pathogen system (Umaerus and Umaerus, 1994).

As potato cultivated in different regions of the world is severely affected by a number of diseases incited by fungi, bacteria, viruses, nematodes and phytoplasmas which reduce the production in both quality and quantity through their adverse effects (Qamar and Khan, 2003). Today, several hundred pests and pathogens are recognized as causes of potato disease and decline. Late blight is considered the most important disease (Bisht *et al.,* 1997). Potato crop has great economic importance due to its utility for human consumption, animal feed and a source of starch and alcohol (Struik and Wiersema, 1999). Potato late blight is one of the most devastating plant diseases worldwide and is feared globally by farmers and industry. Apparently potato breeding and selection for resistance was an important activity in Ireland during the decades following the famine.

Effective management of late blight requires implementation of an integrated disease management. Today late blight is controlled by a combination of sanitary measures, crop rotation, resistant varieties and chemical treatment. Commercial potato production would hardly exist without routine use of fungicides. However, decreasing the chemical impact on the environment is now on the agenda. Moreover, applying fungicides is expensive with costs for chemicals and fuel. Although chemical control provide effective protection but their application is compromised by environmental effects. Also, there should be little chance of the pathogen quickly developing resistance to it. In recent times, of the various means of control available (Thakur, 2007). Adoption of resistant varieties also leads to a reduction in fungicide use (Bradshaw *et al*., 1995). At the beginning of the 20th century researchers discovered that many wild *Solanum* species contain resistance genes, numerous genes conferring vertical and horizontal resistance have been identified, promising improvement of crop quality (Gebhardt and Valkonen, 2001).

Breeding for Late Blight Resistance

Breeding for late blight resistance was stimulated in the mid 19th century by the disastrous consequences of *Phytophthora* epidemics in the USA and Europe. In the early 20th century, potato late blight resistance research started using wild *Solanum* species from South and Central America in breeding programs. Initially special attention was given to *S. demissum* as the main resistance source (Malcolmson and Black, 1966). To date at least 11 specificities (*R1-R11*) have been identified in *S. demissum*, four of which (*R1, R2, R3* and *R10*) have been introgressed by breeders up to the cultivar level (Tan *et al.*, 2008). Many minor quantitative trait loci have been identified (Lehtinen *et al.*, 2008). Niederhauser (1991) noted that much information has been accumulated on the use of race-specific R-genes but very little is known about the more durable general resistance such as what basic chemical and physical factors contribute to this type of resistance and how such factors are genetically controlled. According to Bradshaw (2008) four types of general resistance is now recognized: Late maturity is one trait often associated with general resistance. Some QTLs have been defined in the potato genome, which have a large effect on general resistance.

Vertical and horizontal resistance genes differ from each other. However, the general view today is that the defense reactions in the plant to *P. infestans* are of quantitative rather than qualitative nature (Desender *et al.*, 2007). The HR, traditionally associated with R-gene mediated resistance has been observed in all types of interactions between *P. infestans* and its host. However, the timing and the number of HR responding cells suggest a correlation between resistance level and HR effectiveness (Vleeshouwers *et al.*, 2000), implying a central role for HR in all resistance interactions. DNA markers have been integrated into breeding programs to aid in selection for R genes and quantitative resistance (Oberhagemann *et al*., 1999).

Resistance is considered durable if it remains effective when used for many years over a substantial area. Likewise, although many putative quantitative trait loci to potato late blight have been identified using anonymous markers (Leonards-schipper *et al.*, 1994), it has been difficult to demonstrate that these QTLs truly corresponds to defense genes and the estimated location of the QTL can span several cM. R-genes have long history of unstable resistance due to continuous changes in the pathogen (Fry and Goodwin, 1997) and they can interfere with the recognition of horizontal resistance (Landeo and Turkensteen, 1989). On the other hand horizontal resistance to late blight is a quantitative trait, understood to be non race specific, effective against all variants of the pathogen, and therefore, more stable and durable (Luo *et al.*, 2001). The mRNA RT-PCR differential display method was used to compare the gene expression patterns of a resistant hybrid with that of a susceptible one (Lozoya *et al*., 2007).

Source of Resistance to Late Blight

Besides *S. demissum*, other wild *Solanum* species have been recognized as sources of late blight resistance. The described *R* loci include *Rpi-ber1* (initially named *Rber*) from *S. berthaultii*on chromosome X (Ewing *et al*., 2000), *RB*/*Rpi-blb1*, *Rpi-blb2* and *Rpi-blb3* from *S. bulbocastanum*on chromosome VIII, VIand IV, respectively (Lokossou *et al*., 2009), *Rpi-pnt1* (initially named *Rpi1*, Kuhl *et al*., 2001) from *S. pinnatisectum*on chromosome VII, *Rpi-mcq1* (initially named *Rpi-moc1*, from *S. mochiquense*on chromosome IXand *Rpi-phu1* from *S. phureja*on chromosome IX (Sliwka *et al*., 2007). In addition, several QTL involved in resistance to late blight have been reported, both in cultivated potato and in wild species, e.g. *S. microdontum* (Tan *et al.*, 2008), *S. paucissectum* and *S. phureja*on chromosome VII and XII. The studies of Landeo *et al*., (2000) implicated that the most advanced source of horizontal resistance to late blight at CIP (Population B3) derives from population A which contains R genes. The potato germplasm collection at the Vavilov Institute of Plant Industry in St. Petersburg, Russia, contains more than 9300 accessions, including wild and cultivated species, cultivars, and inter-specific hybrids. More than 2650 accessions are *S. andigenum* (Kiru *et al*., 2005).

Phenotyping and Genotyping

Disease resistance assays conducted in growth chambers and greenhouses can permit rapid, environmentally controlled evaluation of many plant genotypes and pathogen isolates (Naess *et al*., 2001). Disease assays conducted in growth chambers with detached leaflets or whole plants are employed to help

control environmental conditions and permit efficient testing of large numbers of genotypes (Kassa and Beyene, 2001). Phenotypic data from field trials for the full population were used to select the most resistant and susceptible plants of diploid population for use in screening of markers associated with resistance. The two groups were significantly different as indicated by their mean AUDPCs under field conditions (Smart *et al.*, 2007; Rodriguez *et al.*, 2008).

Since the early 1950s, the development of Genetics has been exponential with several milestones, including determination of DNA as the genetic material in 1944, discovery of the double helix structure of DNA in 1953, the development of electrophoretic assays of isozymes (Semagn *et al.*, 2006). Genetic mapping also known as linkage mapping or meiotic mapping is one of the various applications of molecular markers in any species (Collard *et al.*, 2005). To be useful for all these purposes, a genetic linkage map has to follow technical and methodological criteria such as simplicity, robustness, transferability, speed and cost effectiveness (Tierney and Lamour, 2005). A population used for gene mapping is commonly called as a mapping population which is usually obtained from controlled crosses. The parents of mapping populations must have sufficient variations for the traits of interest at both the DNA sequence and the phenotypic level (Singh and Parsanna, 2008; Ferreira *et al.*, 2006) and different maps are generated for different populations of same species (Paterson *et al.*, 2000).

Genetic dissection and breeding for such traits is a difficult task. Fortunately, with the molecular markers it is possible to detect and locate several genomic regions affecting quantitative traits in segregating populations. First, markers can aid selection on target alleles whose effects are difficult to observe phenotypically. Second, marker can be used to select for rare progeny in which recombination near the target gene have produced chromosomes that contain the target allele. Third, markers that are unlinked to a target allele can also be useful in marker assisted back crossing by permitting selection for those progeny with higher proportions of the recurrent parent genetic background. A number of methods for the detection of DNA polymorphism have recently been reported. So far one of the most useful techniques in this respect seems to be PCR (Segman *et al.*, 2006). The first large scale efforts to produce genetic maps were performed using RFLP markers, the best known genetic markers at the time. With the development of polymerase chain reaction (PCR) - based markers, the strategy in linkage mapping dramatically shifts to this marker system. Currently, microsatellite markers remain a standard for linkage map construction. The advantages of SSRs are well documented (Ashkenazi *et al.*, 2001; Raker and Spooner, 2002), as well as genome mapping and specific phenotypes mapping (Ghislain *et al.*, 2001). However, the high development cost and effort required to obtain working SSR primers for a given species has restricted their use to only a few of the agriculturally important crops (Squirrell, 2003). High-density genetic linkage maps with 5000 microsatellite markers have also been constructed in mammals (Luo *et al.*, 2001). RAPD and SSR markers were used to construct a partial genetic linkage map in a potato (McCord, 2010).

Multi-locus molecular marker techniques, such as AFLP (Vos *et al.*, 1995), can be used to generate large numbers of markers in a relatively short time, facilitating the construction of dense genetic linkage maps (Bryan *et al.*, 2002; Chalmers *et al.*, 2001). AFLP markers are highly polymorphic, reproducible and provide good genome coverage (Isidore *et al.*, 2003). Simulated annealing into the methodology for ordering the molecular markers in linkage groups was introduced (Blanco and Valverde, 2005).

Interval mapping of QTL for resistance to late blight, height, and maturity was performed on a tetraploid full-sib family of potato (Zhang *et al.*, 2010). The logarithm of odds value or LOD score is the ratio of probability that two loci are linked with a given recombination value over a probability that two are not linked (Stam, 1993a). The critical LOD scores used to establish linkage groups and to calculate map distances are linklod or maplod (Stam, 1993b; Luo *et al.*, 2001).

Linkage Analysis and Map Construction

Inrecent years, advances in computer technology have led to an increasing interest in extending linkage analysis and quantitative trait locus mapping methods from diploid to polyploid plant species, which display complex polysomic inheritance (Gallais, 2003; Mackay, 2001). Once a QTL for a trait is detected, it can enable accurate selection from the gene from the donor parent and accelerate recovery of the recurrent parent genome (Frisch *et al.*, 1999).

Several computer packages are presently available for genetic linkage mapping but the most widely used are JoinMap (Stam, 1993a and b), MAPMAKER/EXP, LINKAGE and Map Manager QTX. A study has been conducted to construct an ultra-dense genetic linkage map of potato using the new computer software Recombination Counting and Ordering (Van Os *et al*., 2005a and b). JoinMap is one of the most widely used software tools for the estimation of genetic maps. At each step of the algorithm, a goodness-of-fit statistic.

The new approach follows (Jansen *et al*., 2001), maximizing a multipoint likelihood objective function using Gibbs sampling to estimate multipoint recombination frequencies, simulated annealing as a marker order search strategy, and spatial sampling to escape from local optima. A genetic map of potato (*S. tuberosum* L.) integrating molecular markers with morphological and isozyme markers was constructed using a backcross (Jacobs *et al.*, 1995). MapQTL version 3.0 (Van Ooijen and Maliepaard, 1996a, b) is a Powerful tool for QTL analysis. It is available for many platforms (MS-DOS, Unix, Macintosh, VMS) (China papers, 2011). In one of recent study, QTL mapping for late blight resistance in a diploid mapping population of 126 F1 of Solanumspegazzinii (susceptible) × S. chacoense (resistant) was done and significant AFLP loci were placed onto the 12 linkage group of potato covering a total map length of 6548.1 cM. identified two QTL located on linkage groups IX and X revealed the presence of potential new geneticloci in the diploid potato family contributing to quantitative resistance against late blight (Chakrabarti *et al.*, 2014).

CONCLUSION

The mapping of quantitative resistance provides the basis for using MAS to introgress resistance alleles from wild species to improve late blight resistance. Recent empirical studies have confirmed that MAS for favorable alleles at QTLs controlling traits with low-to-moderate heritability can result in appreciable selection gains. Both simulated and empirical results indicate that MAS can be superior to phenotypic selection for low heritability traits, particularly when traits are difficult or costly to phenotype. Even modest improvements in disease resistance can delay or eliminate the need for fungicide applications. Models predicting late blight disease development in potato include cultivar resistance level as an important factor. Using MAS to pyramid quantitative resistance QTLs and qualitative R genes in carefully selected combinations within the same cultivar may enhance the durability of resistance by limiting the growth of any *P. infestans* isolates that overcome the R genes.

ACKNOWLEDGEMENT

We are grateful to ICAR-Central Potato Research Institute, Shimla and Himachal Pradesh University, Shimla for their useful collaboration.

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