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Review Article

The application of Quantitative Trait Loci (QTL) mapping in crop improvement

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QTL mapping is process of locating genes with effects on quantitative traits using molecular markers. It is basic research activity requiring careful planning of crosses and high precision phenotyping. It is used to offer direct mean to investigate the number of genes influencing the trait, to find out the location of the gene and to know the effect of dosage of these genes on variation of the trait. Genetic mapping is the first step to map based cloning. It is used for DNA based Marker Assisted Selection (MAS) and carrying out study on linkage between genes of interest. Genetic properties Of QTL, environmental factors, experimental errors in phenotyping and size of population are main factors affecting the QTL detection. The environment directly affects the expression of quantitative traits and when some experiments are conducted on the same sites for various seasons, it helps to detect the effects of environments on the QTL having influence on the traits of interest.

Key words: Quantitative trait locus, linkage, polymerase chain reaction, marker assisted selection, deoxyribonucleic acid sequences

INTRODUCTION

QTL mapping is process of locating genes with effects on quantitative traits using molecular markers. There are two types of traits, one type is quantitative type and another type is qualitative type. Here, quantitative type show continuous variation and qualitative type show discontinuous variation. Qualitative type is generally governed by few genes or single genes and fall into a few distinct phenotypic classes called as discrete classes. These classes can predict the genotypes of the individuals. Molecular markers are ideal to study QTL's and to map QTL's, which can be effectively used in MAS. It can be defined as the marker-facilitated genetic dissection of variation of complex phenotypes through appropriate experimental design and statistical analyses of segregating materials (Angaji, 2009).

QTL mapping is basic research activity requiring careful planning of crosses and high precision phenotyping. A major breakthrough in the characterization of quantitative traits that created opportunities to select for QTLs was initiated by the development of DNA (or molecular) markers in the 1980s. Therefor the objective of this review paper to highlight of the application of comparative genome and QTL mapping in plant breeding.

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Importance of QTL mapping

QTL mapping is used to offer direct mean to investigate the number of genes influencing the trait, to find out the location of the gene and to know the effect of dosage of these genes on variation of the trait. Genetic mapping is the first step to map based cloning. It is used for DNA based Marker Assisted Selection (MAS) and carrying out study on linkage between genes of interest (Shaukeen Khan, 2015).

Basic prerequisites for successful QTL mapping

There should be focus on lines which are easy to observe in a good screen. Traits should be derived where difference between susceptible and resistant mapping populations from crosses between highly resistant and highly susceptible lines is there. Use highly reliable screening systems that are known to differentiate resistant from susceptible lines (Shaukeen, 2015). Analysis should be based on the means of repeated screens rather than single trials. Ensure that repeatability of your screen is as high as possible (0.7 or higher).

A mapping population generated from phenotypically contrasting parents, saturated linkage map based on molecular markers, reliable phenotypic screening of mapping population and appropriate statistical package to analysis the genotypic information in combination with phenotypic information for

QTL detection are the basic requirements of QTL mapping.

QTL mapping strategies

All marker-based mapping experiments have same basic strategy. First of all, we will choose parents which are different for a character. Now, Screen the two parents for marker loci for polymorphism. To create mapping populations like includes F2 population, back crosses, recombinant inbred lines, and double haploids lines. Phenotype screening. Contrast the mean of the MM and mm lines at every marker locus. If difference between mean of the MM and mm lines is more, there will be more chance of QTL detection. To declare QTL where (MM-mm) is greatest (Bennetzen, 2002). The basic Principle is the segregation of marker locus and QTL generation after generation. Co segregation is due to linkage between marker and QTL to determine the linkage partition the mapping population into different genotypic classes based on progeny testing.

Factors affecting power of QTL mapping

The detection of QTLs in a segregating population is affected by several factors. Among these; genetic properties of QTL, environmental factors, experimental errors in phenotyping and size of population are main factors affecting the QTL detection (Bernardo et al., 2015). The environment directly affects the expression of quantitative traits and when some experiments are conducted on the same sites for various seasons, it helps to detect the effects of environments on the QTL having influence on the traits of interest (George, 2003). The population size directly influences the QTL mapping studies (Tanksley, 1995). A larger sized population results in the more precise mapping and also facilitates the detection of the QTLs with less pronounced effects (Tanksley, 1993). The experimental errors include the errors arising from imprecise phenotyping and genotyping. Non accurate phenotypic data and errors in genotypic data influence the distance between markers (Hackett, 2002). Since the following are basic:

Number of genes controlling the target traits and their position: Position of gene on chromosome affects the success of QTL mapping. If genes will remain close to concerned genetic marker, there will be more chance of detection of target traits or target gene (Deynze, 1995a). It is based on banding pattern of markers used. If genes will remain away from concerned genetic marker, there will be more chance of crossing over.

Hereditability of the genes segregating in a mapping population: Generally characters governed by oligogenes or single genes are having high hereditability than governed by polygene.

Type of mapping population used in QTL mapping: Nonrandom mating population is required for QTL mapping. It is result of mutation, natural selection, random drift etc.

Size of mapping population used in QTL mapping: In large sample size, QTL with small effects cannot be observed but QTL with large effects can be observed. In small sample size also, QTL with small effects cannot be observed but QTL with major effects can be observed.

Type and number of markers in linkage maps: If there is more number of markers used, amount of precision of estimation of both QTL position and effect will be more. Here, co-dominant marker shows three types of genetic difference while dominant marker shows two types of genetic difference (Tarchini, 2000). so, co-dominant marker provide more information than dominant marker regarding recombination with in marker intervals.

Phenotyping of mapping population and sample size: The target quantitative traits are measured as precisely as possible and limited amounts of missing data can be tolerated. The power to resolve the QTL location is confined first by sample size and then by genetic marker coverage of the genome. Generally, the number of individuals in a sample might appear to be large but missing data or skewed allele frequencies in the population cause the effective sample size to diminish, thus sacrificing the statistical power (Dunford, 1995). Sometimes, it is must to sacrifice population size in favor of data quality and this trade off means that only major QTL (with relatively large effect) can be detected (Tikhonov, 1999). QTL Data is typically pooled over locations and replications to obtain a single quantitative trait for the line. It is also preferred to measure the target trait(s) in experiments conducted in multiple (and appropriate) locations to have a better understanding of the QTL x environment interaction, if any.

QTLs and the signature of selection: Orr (1998) developed a sign test that compares the number of plus alleles present in the high condition of a trait with a model of neutrality assuming either equal or differential allelic effects. Consequently, QTL data can provide evidence for the presence of directional selection, when one can demonstrate a polarity to allelic substitution (Yu, 2003).

Detection and locating of QTL: The construction and use of a near-isogenic line (NIL) for identification of high probability for QTLs (Eujayl, 2001). Initially, a donor and recurrent parent are crossed and subsequent repeated back crosses to recurrent parent lead to a reduction of the donor genome contribution. With Marker Assisted Selection (MAS), a panel of NILs that tile the genome can be constructed. The resulting panel members can be tested for a range of phenotypic traits for the detection and locating of QTL candidates (Eujayl, 2002).

Development of introgression lines: For development of introgression lines to define and map QTLs for crop improvement (Schauer et al., 2006). have mapped the metabolic and fruit-quality QTLs in tomato introgression lines previously developed through multiple rounds of self-and back-crossing (to the cultivated parent) between an elite cultivar, Solanum lycopersicum var. Roma, and a wild tomato plant, Solanum pennellii, to generate 76 independent introgression lines of tomato plants harboring chromosome segments from the wild relative. Selection of specific, homozygous, single, overlapping chromosome introgressions in this population both simplifies QTL localization and defines linked DNA markers for use in crop improvement (Han, 1997).

Statistical methods used for QTL mapping

Statistical methods for QTL mapping tests for QTL/trait association are often performed by the following methods:

Single marker approach

The single marker approach is also known as single factor analysis of variance or single point analysis. It is widely used method for quick scanning of whole genome to determine best QTLs. It is used for each marker locus which is free from other loci (Lin, 2000). Generally, this technique is unable to determine QTL position (Kantety, 2002). F-test is used for determination of significant differences between various genotypes groups. Some major limitations of this approach: the method cannot determine whether the markers are associated with one or more QTLs; Chance of QTL detection decreases with distance between marker and QTL. An effect of QTL is underestimated of confounding with recombination frequencies (Kilian, 1995). Its accuracy is less compare to other methods.

Simple Interval Mapping (SIM)

SIM was first proposed by Lander and Botstein 1989 and it is based on linkage map. It can be called as two marker approach. Here, QTL is determined in interval generated between two markers at various points. It gives more accurate results compare to single marker approach but less than CIM and MIM technique (Leister, 1998). In this technique, (Lin, 1995) likelihood ratio test is used to determine every QTL position in interval created by both markers. SIM is mostly preferred as it can be easily performed through statistical packages such as MAPMAKER/QTL.

Lander and Botstein, 1989 developed formulae for significance levels appropriate for interval mapping when the genome size, number of chromosomes, number of marker intervals, and the overall false positive rate desired are given (Scott, 2000). However, when various QTLs are segregating in a cross, SIM will not take into consideration genetic variance due to other. In such a case, SIM is having same limitation as in single marker analysis.

Composite Interval Mapping (CIM)

CIM 1986 and MQM techniques are developed by Jansen and Stam (1994).It is used to minimize effects of various linked QTLs. It is based on one QTL and other markers used as covariates. This technique gives more precise results and used to exclude bias due to another QTLs (non-target QTLs) linked to target QTL. It used to fit the parameters for a single QTL in one interval. The partial regression coefficient is used to determine genetic variance due to non-target QTLs (Nelson, 1995a). It considers a marker interval and a few other selected single markers in each QTL analysis, so that n-1 tests for interval-QTL associations are conducted on a chromosome with n markers.

The merits of CIM are as follows: mapping of multiple QTLs can be carried out by the search in one dimension; by using linked markers as covariates, the test is not affected by QTL out of region, thereby increasing the precision of QTL mapping; and by eliminating as much as the genetic variance produced by other QTL, the residual variance is reduced, thereby the efficiency of determination of QTL is increased. CIM is more efficient than SIM, but not widely used in QTL mapping as in SIM (Paterson, 1995).

Multi trait Interval Mapping (MIM)

It is recent method of QTL Mapping. Multiple Interval Mapping (MIM) is the extension of interval mapping to multiple QTLs, just as multiple regressions extends analysis of variance. It is used to map multiple QTLs. This method is potential tool for detection of QTL X QTL interaction (Collard, 2005) (Table 1).

Table 1. Advantages and disadvantages of most commonly-used DNA markers for QTL analysis.

Molecular (C) marker	Restriction Fragment Length Polymorphism (RFLP)	Random Amplified Polymorphic DNA (RAPD)	Simple Sequence Repeats(SSRs) or 'microsatellites'	Amplified Fragment Length Polymorphism (AFLP)
Codominant(C) or Dominant (D	Codominant	Dominant	Codominant	Dominant
Advantages	Robust, reliable, transferable across, populations	Rapid, simple , Inexpensive, multiple loci from a single primer possible, less DNA required	simple, Robust and reliable, transferable between, populations	Multiple loci, high levels of polymorphism produced
Disadvantages	Time-consuming, laborious, expensive, more DNA required, less polymorphism	Generally not transferable, less reproducibility	Time-consuming, laborious, usually require polyacrylamide electrophoresis	Complicated methodology, large DNA required

Merit and demerit of QTL mapping in plant breeding

QTL mapping is used to detect the genes which control the trait of interest (Mohan et al., 1997). It is very useful for the Genome-wide scan for QTLs detection in plants. Diseases are a big concern in agriculture and genes responsible for generation of resistance to these diseases can be detected by QTL mapping (Young et al., 1992). Some important drawbacks of QTL mapping include less allelic diversity, lower number of recombination events (Price, 2006), being time consuming in case of mapping population development (Neale, 2004) and specificity of the detected QTLs to a given population (Andersen et al., 2005) (Figure 1).

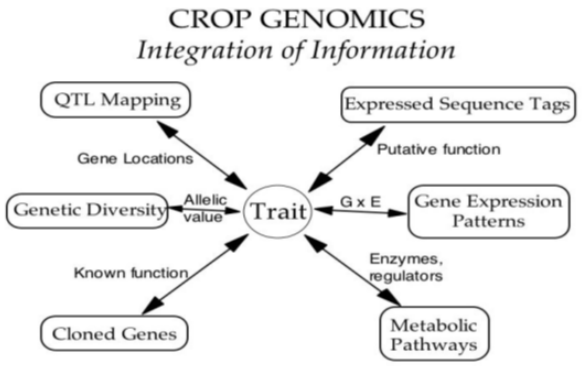

Figure 1. Crop genomics integration.

CONCLUSION

QTL mapping based on linkage and marker trait association can be effectively used for gene pyramiding, germ plasma screening of diversified material for abiotic (salinity, cold, salt, drought) and biotic stresses (disease, pest) etc. The identification and location of specific genes mediating quantitative characters is having great importance in plant breeding. Proper development and understanding of the statistical background is essential for QTL mapping. A quantitative trait which is controlled by several genes, all the genes having small affects, additive in nature and is more affected by environment. DNA markers are very useful for information about number and position of QTLs because they are highly polymorphic, abundant and co-dominant in nature. High resolution linkage maps based on various molecular markers are required for preparation of for QTL analysis. Proper development and understanding of the statistical background is essential for QTL mapping. The technique of Marker-assisted selection and QTL mapping should be adopted at large scale for all major crops.

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