REVIEW OF LITERATURE
CHAPTER II

REVIEW OF LITERATURE

Rice (Oryza sativa L.) is the principal food crop of more than half of the world's population and nearly 30% of human energy is derived from this single plant species. It is grown in 115 countries over an area of 1.5 billion hectares with a worldwide production of 596 million ton but to meet food demands of the burgeoning population, there is a need for 60 per cent more rice production by 2020 (Paroda and Tomar, 1997).

Drought is of the major factor that limit plant growth and productivity. In spite of surge in literature on drought tolerance in crop during the past two decades, practical progress in breeding for drought tolerance has not been significant. Drought, therefore requires an analytical approach of dissection and studying the contribution of trait components using the quantitative trait loci (QTLs) model. This approach is particularly suited to crop like rice for which dense genetic linkage maps with a variety of DNA markers are already available. Most studies on drought tolerance deal with evaluating specific traits logically related to crop performance under drought. A molecular genetic analysis is more effective if conducted on individual traits (and even their components) before crop performance is considered. Thus, it is important to phenotype for specific traits or responses under managed nursery as green house condition, besides subsequent field evaluations under
drought in target regions. A strong demonstrated linkage between traits in relation to crop performance in the target environment is a crucial step before advocating marker-assisted selection (MAS).

Molecular markers serve as tools for a large number of applications ranging from localization of a gene to improvement of plant varieties by marker-assisted selection. It is also evident that these markers have been improved over the last two decades to provide easy, fast and automated assistance to scientists and breeders. Genome analysis based on molecular markers has generated a vast amount of information and a number of databases are being generated to preserve and popularize it.

2.1 Flowering

Cheema et al. (1988) reported that both additive and non-additive gene effects influenced the days to flowering. Manuel and Palanisamy (1989), Dhaliwal and Sharma (1990) and Nilakantapillai and Ramchandran (1990) found that the preponderance of additive gene action for days to flowering.

Ramalihgam et al. (1993) observed preponderance of non-additive gene action for days to flowering. Singh et al. (1993) studied the inheritance pattern of photoperiod sensitivity in F1s and F2s from 6 intervarital crosses. They observed that the qualitative photoperiodic responses showed photosensitive being dominant over photoinsensitivity. In this study a plant was considered for photosensitive that
flowered during short day lengths while photoinsensitive was considered for plants flower at long day length.

Yamamoto et al. (1996) reported on the basis of their experiment on heading date that two major QTLs have been found to be single Mendelian loci.

Veldboom and Lee (1996) studies were conducted to investigate the ability to detect quantitative trait loci (QTL) for flowering and plant stature traits in two diverse environments, and to assess the genetic relationship of QTL for correlated traits. A single-cross of elite inbreds Mo17 and H99 was used to produce a population of 150 F2: 3 lines. More QTLs were identified in the stress environment for anthesis and silk emergence, but the other traits had equivalent numbers of QTL detected in each environment. All QTL identified in the non-stress environment and all QTL identified in the stress environment were also detected in the mean environment.

Kang et al. (1998) detected total 5 significant QTLs (LOD-2.0) for 2 traits. 4 QTLs, significantly affecting days to heading were on chromosome 1, 3, 6 and 7 with 39.7% phenotypic variation, only one QTL was detected significantly influencing culm length on chromosome 1 with 59% total phenotypic variation.

Jinhua et al. (1998) reported that seven QTL were significantly associated with days to heading. The phenotypic variance ($R^2$) explained
by this individual QTL ranged from 3.00 to 15.21% of phenotypic variation.

Rae et al. (1999) worked on a cross between *Brassica oleracea var. italica* and *B. oleracea var. alboglabra* [B. *alboglabra]* observed 11 QTL on chromosomes 01, 02, 03, 05 and 09, five of which mapped to similar regions to five of the six found in a previous analysis of doubled haploid lines from the same cross. Several of the QTL were linked closely in repulsion.

Maheswaran et al. (2000) identify putative quantitative trait loci (QTLs) associated with days to flowering (DTF) and photoperiod response in rice. Days to flowering of individual plants were evaluated under 10 h and 14 h day lengths, and loci associated with photoperiod sensitivity were identified based on the delay in flowering under the 14 h photoperiod (DTF at 14 h minus DTF at 10 h). An RFLP data set consisting of 127 markers provided the basis for the QTL analysis. Both single marker and interval analysis were used and interactions between putative QTLs were estimated based on two-way ANOVA. Out of 15 QTLs associated with DTF, only 4 were identified as influencing the response to photoperiod. Interactions between flowering QTLs indicated the complex nature of the control of flowering in rice.
2.2 Plant Height

Singh et al. (1979) reported that dwarfness behaves as monogenic recessive traits, functioning in association with modifier complexes of various strengths.

Lee et al. (1996) worked on a soyabean (Glycine max) population derived from a cross between Young and PI416937. 11 independent markers associated with plant height and the eight with lodging explained most of the genetic variability for these traits in combined analysis over locations. Of the 11 RFLP markers associated with plant height and the 8 with lodging, only two markers for plant height (Bl043 and A063a) and one for lodging (A169) were detected in all locations.

Li et al. (1997) identified 22 QTL for six agronomic traits which were significant in at least one environment, but only seven were significant in all three environments, seven were significant in two environments and eight could only be detected in a single environment. This indicated that G X environment interaction was trait dependent. QTL for spikelet and grain/panicle were common across environments while trait like heading data and plant height were more sensitive to the environment.

Lu-Chao Fu (1997) worked on doubled-haploid (DH) population derived from anther culture- was established from a cross between indica (Zhai-Ye-Qing 8) and japonica (Jing-Xi 17) rice varieties. A molecular
linkage map comprising of 137 markers was constructed based on this population which covered the rice genome at intervals of 14.8 cM on average. The linkage map was used to locate QTL for important agronomic traits as heading date, plant height, spikelets/panicle, grains/panicle, 1000-grain weight and percentage seed set, by interval mapping. Evidence of genotype X environment interaction was found by comparing QTL maps of the same population grown in three diverse environments. A total of 22 QTL for six agronomic traits were detected which were significant in at least one environment, but only seven were significant in all three environments; seven were significant in two environments and eight could only be detected in a single environment. QTL for spikelets and grains/panicle were common across environments while traits like heading date and plant height were more sensitive to the environment.

Jinhua et al. (1998) reported that six QTL on chromosome number 1, 4, 8, 9 and 12 were significantly associated with plant height. The phenotypic variation explained by each QTL ranged from 8.49 to 44.77%.

Yan-Ju Qiang et al. (1998) worked on a doubled haploid population of 123 lines from IR64/Azucena to dissect the developmental behavior and genotype by environment (G x E) interaction for plant height by conditional and unconditional quantitative trait loci (QTL) mapping methods in rice. It was shown that the number of QTL detected was different at various measuring stages. Some QTL could be detected at all
stages and some only at one or several stages. More QTL could be found on the basis of time-dependent measures of different stages.

Yan-JuQiang et al. (1999) a doubled haploid (DH) population of 123 lines from IR64/Azucena was used to analyse the genotype X environment (G x E) interaction for the following eight plant type traits in rice (*Oryza sativa*): maximum tiller number, tiller angle, flag leaf angle, panicle number, percentage of productive tillers, plant height, flag leaf length and flag leaf width. The total genetic effects were partitioned into genetic main effects and G x E interaction effects. These two kinds of predicted effects were used in mapping quantitative trait loci (QTLs). Four to nine QTLs affecting different plant type traits were detected. Results indicated that all common QTLs detected in both environments were controlled by genetic main effects and some also by G x E interaction effects. Some genomic regions identified significant QTL in only one environment; some also showed genetic main effects.

Hemamalini et al. (2000) reported that root morphology under well-watered conditions sampled on two occasions and under low-moisture stress was studied in a randomly chosen subset of 56 doubled haploid lines derived from a cross between IR64 and Azucena at two growth stages during the vegetative stage. In total 21 QTL for different traits were detected under low-moisture stress condition. While two QTL for plant height on chromosomes 1 and 3 were common.
2.3 Number of Tillers per Plant and Panicle Number

Tiller number and panicle number are positively correlated, even though the ratio of tiller to panicles may vary among cultivars and is subjected to environmental influences. The quantitative nature of tillering ability was indicated by Rao (1953).

Subramaniam and Madhava (1973) reported that high tillering capacity was either by over dominance or dominance and number of productive tiller was under polygenic control.

Yan et al. (1998) worked on a doubled-haploid rice population of 123 lines from Azucena/IR64 was used for analyzing the developmental behaviour of tiller number by conditional and unconditional QTL mapping methods. It was indicated that the number of QTLs significantly affecting tiller number was different at different measuring stages. Many QTLs controlling tiller growth identified at the early stages were undetectable at the final stage. Only one QTL could be detected across the whole growth period.

Jinhua et al. (1998) reported only one significant QTL was associated with spikelets per plant on chromosome # 1 explained 4.23% of the phenotypic variation. Two QTL were identified for the number of panicle per plant on chromosome 1 and 2 which explained 3.81 of phenotypic variation.
Wu-Weiken et al. (1999) reported that five QTL were detected on chromosomes 1, 3 and 5. These QTL explained more than half of the genetic variance at the final observation. All the QTL displayed an S-shaped expression curve. Three QTL reached their highest expression rates during the active tillering stage, while the other two QTL achieved this either before or after the active tillering stage.

2.4 Panicle Length

Li (1975) reported that differences to panicle length are largely controlled by additive gene action.

IRRI (1967) reported that five genes control the panicle length in a cross between extreme parents.

Jinhu et al. (1998) reported that seven significant genomic regions were associated with panicle length on chromosome number 1, 2, 4, 8, 9 and 12 that explained 4.48-14.20% of observed phenotypic variation.

2.5 Grain Length and Breadth

Sasmal (1988) observed that heterosis for grain yield was associated with heterosis for grain length, grain breadth and panicle length.

Redofia and Mackill (1998) reported that 7 QTLs for grain length were identified, of which 2 each were found on chromosome 3 and 4 and one each on 2, 7 and 10 with particularly high LOD values and show 24 to 42% of phenotypic variation. For grain breadth 4 QTLs were identified
each on chromosome number 2, 3, 7, and 8 which explained 22 to 30% of phenotypic variation.

2.6 Length and Breadth Ratio

Ghosh (1993) predominance of additive effect was recorded for L/B ratio.

Redofia and Mackill (1998) reported that the grain shape measured as the ratio of length to breadth, was mostly controlled by loci on chromosome 3 and 7 and show 45% of the phenotypic variation.

2.7 Yield per Plant

Sasmal (1988) observed that heterosis for grain yield was associated with heterosis for grain length, grain breadth and panicle length.

Jinhua et al. (1998) reported that 6 QTLs were significantly associated with grain per plant, 2 QTL on chromosome number 8 and one each on 1, 2, 4 and 5 respectively, which explain 3.08 to 4.23% of phenotypic variation.

2.8 Yield Per Plot

Kumar and Rangaswamy (1984) and Kalaimani and Suadaram (1987) found non-additive gene action to be important for yield per plot.

Tanksley (1993); McCouch and Doerge (1995) concluded that the advent of molecular markers and maps makes it possible to identify
individual quantitative trait loci (QTL) associated with yield and its components, environmental stress tolerance, disease and insect resistance and quality traits in a variety of crop plants.

Jinhua et al. (1998) reported that 7 QTLs were identified for grain yield per plot in which 2 on chromosome on 8 and one each on 1, 2, 3, 4, 5 and 12 respectively which explain 2.56 to 5.16% of phenotypic variation.

2.9 Leaf Rolling Score

Singh and Singh (1989) reported that 4 types of leaf rolling during water stress were identified, rolling that originates from the tip and progresses to the base (vegetative to jointing stages); rolling of the entire leaf (jointing to reproductive stages); helical rolling often from the tip to the middle of the leaf (anthesis, rapid development of stress) and helical rolling towards the leaf base resulting in a non-helical shape (anthesis, slow development of stress).

McCouch and Doerge (1995) identified QTLs linked to drought avoidance in the field, based on visual leaf rolling under water deficit stress at three different growth stages. They found that 50% of the putative QTLs associated with root characters in the greenhouse study were mapped to the same chromosomal location as QTLs influencing drought avoidance in the field experiments.
Price et al. (1999) used a mapping population of 205 RILs derived from a cross between two drought resistant varieties Azucena and Bala, to identify genomic regions contributing to the drought resistance. Analyses of screens are conducted in the dry season at the International Rice Research Institute (IRRI) over two seasons and at the West Africa Rice Development Association (WARDA) over one season. Performance under drought was assessed visually as leaf rolling and leaf drying and by measuring relative water content. Using a combined RFLP and AFLP map with 134 markers, quantitative trait loci (Quantitative trait loci (QTLs)) with LOD>2.0 detected using composite interval mapping were found on all chromosomes except 4, 6, 8, and 11.

Blum et al. (1999) using DH F2 line population of rice (CT-9993-5-10-M/IR62266-42-6-2) reported that these lines differ significantly for all measured indicators of plant water status namely leaf rolling score, leaf depth score and relative water content (RWC). Leaf rolling is an index of turgar potential. The plant should maintain good turgar at low water status, which in turn allows physiological activity. Leaf rolling indicate that plant suffer from stress and did not sufficiently prevent moisture loss.

Courtois et al. (2000) QTLs controlling drought avoidance mechanisms were analysed in a doubled-haploid population of rice for leaf rolling, leaf drying, relative water content of leaves and relative growth rate under water stress were measured, the total number of QTLs
detected in all trials combined was 11 for leaf rolling, 10 for leaf drying, 11 for relative water content and 10 for relative growth rate under stress. Some of these QTLs were common across traits. Among the eleven possible QTLs for leaf rolling, three QTLs (on chromosomes 1, 5 and 9) were common across the three trials and four additional QTLs (on chromosomes 3, 4 and 9) were common across two trials. One QTL on chromosome 4 for leaf drying and one QTL on chromosome 1 for relative water content were common across two trials while no common QTL was identified for relative growth rate under stress.

Babu et al. (2002) using CT\IR population reported three QTLs for leaf rolling one on chromosome 1 and two on chromosome 11. The phenotypic correlation between the traits showed that the parameters of stress indicator were significantly correlated with plant phenology and production traits under stress. RWC was negatively correlated with leaf rolling, leaf drying, days to heading and spikelet fertility under stress. Two QTLs were also identified for relative water content (RWC) on chromosome 1 between RZ417-RM212 and ME2-12-RG532, respectively.

2.10 Relative Water Content

Tripathy et al. (2000) determined which genomic region is responsible for CMS. 104 rice (Oryza sativa) doubled haploid (DH) lines derived from a cross between CT9993-5-10-1-M and IR62266-42-6-2
were studied in the greenhouse. He observed that there was no significant difference \((P>0.05)\) in RWC between the two parental lines as well as among the 104 lines, indicating that all the plants were sampled at a uniform stress level. However, a significant difference \((P<0.05)\) in CMS was observed between the two parental lines and among the population. No significant correlation was found between CMS and RWC, indicating that the variation in CMS was genotypic in nature. The continuous distribution of CMS and its broad-sense heritability (34\%) indicates that CMS should be polygenic in nature. QTL analysis using composite interval mapping identified nine putative QTLs for CMS located on chromosomes 1, 3, 7, 8, 9, 11 and 12. The amount of phenotypic variation that was explained by individual QTLs ranged from 13.4\% to 42.1\%. Four significant \((P<0.05)\) pairs of digenic interactions between the detected QTLs for CMS were observed. The identification of QTLs for this important trait will be useful in breeding for the improvement of drought tolerance in rice.

2.11 Root Length

Champoux et al. (1995) worked on identification and mapping Quantitative trait loci (QTLs) associated with five parameters of rice root morphology as root thickness, root shoot ratio, root dry weight per tiller, deep root weight per tiller and maximum root length and to determine if these Quantitative trait loci (QTLs) are located in the same chromosomal regions as Quantitative trait loci (QTLs) associated with drought
tolerance using 203 RIL population derived from a cross between Co 39 and Moroberaken detected 14 Quantitative trait loci (QTLs) for root: shoot ratio and 18 Quantitative trait loci (QTLs) for root thickness. QTL analysis of greenhouse and field data was done using single-marker analysis (ANOVA) and interval analysis (MAPMAKER QTL). Most Quantitative trait loci (QTLs) that were identified were associated with root thickness, root: shoot ratio and root dry weight per tiller, and only a few with deep root weight.

Shashidhar et al. (1996) evaluated DH lines derived from a cross between Azucena mapping population in PVC tubes. The data was subjected to mapmaker analysis and found that a few RFLP loci cosegregated with root length (2 loci), shoot length (3 loci), total length (3 loci) and no of roots (2 loci). The allele pattern of plant was constructed with the RFLP data and transgressive segregants were studied for penetrating ability.

Pantuwan et al. (1997) worked on the root traits to increase drought resistance in lowland rainfed rice. The root system of 6 rice cultivars were studied in several rainfed lowland experiments at the Ubon Rice Research Centre. Use of steel tubes was done for soil-root sampling. Genotypes showed differences in root-mass density and root-length density at 10-30 cm depths. While those differences were rather small, they were associated with genotypic differences in water extraction.
from the subsoil, and also with visual estimation of retention of green leaves during a dry period.

Price and Tomos (1997) worked on the genetic dissection of root growth in rice and quantitative trait mapping using molecular markers. They worked on the genetic mapping of root growth traits in a F2 population of Bala and Azucena. RFLP between the two parents was 32% and a molecular map with 71 marker loci and 17 linkage groups covering 1280 cM was produced. Quantitative trait loci (QTLs) for eight root growth characteristics were mapped using phenotypic data obtained in a hydroponic screening. Quantitative trait loci (QTLs) for maximum root length after 3, 7, 14 and 21 days of growth were also revealed. One QTL for root volume and two QTL for adventitious root thickness were detected.

Yadav et al. (1997) worked on the mapping of genes controlling root morphology and root distribution in a DH population of rice. A DH population of 105 lines derived from an Indica (IR-64) and Japonica (cv. Azucena) cross was studied and the gene controlling the morphology and distribution (root thickness, maximum root length, total root wt., deep root wt. per tiller and deep root to shoot ratio) were mapped using RFLP markers. Most putative QTL activity was concentrated in fairly compact regions on chromosomes 1, 2, 3, 6, 7, 8 and 9, but was widely spread on chromosome 5 and largely absent on chromosomes 4, 10, 11 and 12.
Shen (1999) worked on developing near isogenic lines of IR-64 introgressed with Quantitative trait loci (QTLs) for deeper and thicker roots through marker assisted selection. Using IR 64 and Azucena as parents. Four segments on chromosomes 1, 2, 7, and 9 were initially targeted for single QTL selection. Four doubled-haploid lines with the proper allelic combinations at the targeted segments and less than 50% Azucena alleles in the rest of the genome were chosen as donors. These lines were backcrossed on IR64 up to the BC3F1 generation and then selfed. Marker-aided selection for the target segments was performed from BC1F1 up to BC3F2.

Kamoshita et al. (2000) identified only three QTLs for deep or thick root traits common across the two plantings. In CT 9993/IR 62266, seven common QTLs for deep or thick root traits were identified or bound, but four of them were the same for shoot dry weight or plant height, and suggested that potential genetic improvement of constitutive root traits of rained low land rice by introgression.

Zheng et al. (2000) detected one QTL located between RG04 and RG346 was found to influence both root penetration ability and root thickness and suggested that the identified consistent Quantitative trait loci (QTLs) could be used for marker assisted selection (MAS) for deep and thicker root with high root penetration. Twelve putative Quantitative trait loci (QTLs) were detected by interval mapping comprising four Quantitative trait loci (QTLs) for root penetration ability, four
Quantitative trait loci (QTLs) for root thickness, two Quantitative trait loci (QTLs) for penetrated root number, two Quantitative trait loci (QTLs) for total root number. These Quantitative trait loci (QTLs) individually explained $8.4\%$ to $16.4\%$ of the phenotypic variation. No QTL were detected for maximum penetrated root length by interval mapping.

Hemamalini et al. (2000) worked on molecular assisted tagging of morphological and physiological traits under contrasting moisture regime at peak of vegetative stage in rice. Root morphology under well watered condition sampled on two occasion and under moisture stress was studied in a randomly chosen subset of 56 DH lines derived from a cross between IR 64 and Azucena at two stage during vegetative growth.

Shen et al. (2001) conducted QTL analysis on root parameter in population of 105 DH lines from the cross of IR-64 and Azucena and introgressed segments of chromosome no. 4, carrying putative alleles enhancing root length, in IR-64 via molecular assisted backcrossing. Of the 29 resulting BC$_3$ derived introgression that were phenotyped only 11 had root characteristics that differ from the recurrent parent.

Hall (2001) pointed out that the selection for crop plants for most of the drought resistance traits as longest roots and highest level of osmotic adjustment is associated with depressed grain yield to a small extent.

2.12 Double Haploids
Recombinant inbred lines (RILs) developed via single seed descent and double haploid lines (DHL) generated from pollen/anther culture are homozygous and genetically uniform within each line. Large amounts of genetically identical seeds can be produced from RIL and DHL. Thus the RFLP mapping information and the seeds can be shared among scientists to map many traits of interest (McCouch and Doerge, 1995). Wang et al. (1994) first used an RIL population to map genes for blast resistance in rice. The same population was then used to map genes for drought avoidance (Champoux et al., 1995) and plant height (Huang et al., 1996) without the need of RFLP analysis.

Many studies have employed doubled haploid populations to construct genetic maps and locate QTLs (Albar et al., 1998; Yadav et al., 1997; Alam and Cho, 1998; Heun et al., 1991; Backes et al., 1995; Uzunova et al., 1995). In contrast to RILs, DH lines developed from anther culture can reach homozygosity after a single generation. Because the lines are genetically homozygous they can be propagated without further segregation. This characteristic allows for the precise measurement of quantitative traits by repeated trials and for a reduction of environmental covariance of the total phenotypic variance.

Doubled-haploid techniques also offer tremendous potential study of quantitative inheritance. Since all the alleles of DHLs are fixed, selection for quantitative characters is often more reliable than in
conventional populations (Choo et al., 1985). DHLs have also proven valuable in genetic studies on linkage relationships (Pickering and Devaux 1992), quantitative inheritance (Choo et al., 1985), pleiotropy and molecular mapping of the plant genome (Graner et al., 1991).

Haploids can be produced by means of various production techniques such as anther culture, interspecific hybridization, and so on. They formed doubled haploids after their chromosomes are doubled by colchicine. Using double haploid techniques, truly homozygous lines can be obtained from the gametes of F₁ hybrids; thereby the time required to develop new varieties may be shortened by 2-3 generations.

Guiderdoni et al. (1992) developed a double haploid population from a cross between IR-64 and Azucena. Many economically important characters, including grain shape, blast resistance, bacterial blight resistance, brown planthopper resistance, aroma, and drought tolerance are segregating in this population. An RFLP map of this population was established by Huang et al. (1994) from an initial population of 135 lines. Parents were evaluated for RFLP polymorphism using six restriction enzymes (Dra I, EcoRV, HindIII, ScaI, XbaI and EcoRI). This population has been used for mapping and analyzing major genes and QTLs for numerous agronomic characters (Albar et al., 1998; Alam and Cohen, 1998; Huang et al., 1997; Yadav et al., 1997). This mapping population also provides an excellent opportunity for characterizing QTLs for
bacterial blight resistance, because IR-64 has Xa-4 gene, which has been shown to be both polygenic and relatively durable.

2.13 Identification of QTLs

The concept of detecting QTLs using linked major gene is not new. Sax (1923) for the first time gave the concept of detecting QTLs using linked major gene. Today (1961) indicated the possibility of analyzing location of polygenes using linked marker. The progress in DNA marker and linkage map provided an efficient tool and method of mapping monogenic as well as polygenic traits (Paterson, 1995 and Tanksley, 1993).

In rice, a well-saturated genetic linkage map based on DNA markers has been developed (Causse et al, 1994 and McCouch et al., 1988). This has been used for the mapping of QTLs for various traits. Since the development of saturated linkage map, QTLs for various traits has been detected. The available literature on this aspect is being presented in the following section.

Xu, et al. (1995) developed a statistical technique and generalized computer software for interval mapping of quantitative trait loci (QTLs). QTLMAP-I, a program suitable for a low memory capacity computer for mapping population including F2s, backcrosses and double haploid. The method was used to map quantitative trait loci (QTLs) for wide compatibility, days to heading and grain number per panicle in rice.
Xu et al. (1995) using MAPMAKER/ QTL computer software, 11 quantitative loci (QTLs) were mapped for 4 traits: days to heading, tiller angle, spikelet number per panicle and Spikelet density.

Lilley et al. (1996) conducted Quantitative trait loci (QTLs) analysis using single marker analysis (ANOVA) and interval analysis (MAPMAKER/QTL). The measurement obtained and the QTL identified were compared to root traits and leaf rolling score measured on the same line and one major locus was associated with osmotic adjustment.

Quarrie et al. (1996) worked on QTL analysis of stress responses as a method to study the importance of stress induced genes. Molecular marker technologies, using RFLPs and markers derived via the polymerase chain reaction, allow high density genetic maps to be prepared. These can be used to identify loci regulating expression of quantitative traits (QTL). Several RFLP markers revealed changes in allele frequencies as a result of recurrent selection for yield under drought. Some of the RFLP probes showing changes in allele frequencies had homologies with genes likely to be involved in plant stress responses.

Shashidhar et al. (1996) evaluated DH lines derived from a cross between IR 64 / Azucena mapping population in PVC tubes. The data was subjected to mapmaker analysis and we found that a few RFLP loci cosegregate with root length (2 loci), shoot length (3 loci), total length (3 loci) and number of root (2 loci). The allelic pattern of the plants were
constructed with the RFLP data and transgressive segregants were studied for predictive ability.

Grandillo and Tanksley (1996) molecular markers were used to map and characterize quantitative trait loci (QTLs) for several characters of agronomic and biological importance in an interspecific back cross of tomato and reported that the difference in fruit weight was controlled largely by a single major QTL. Digenic epistasis was not evident. Several regions of the genome showed effects on more than one trait.

Yan et al. (1998) suggested that the number of QTL detected was different at various measuring stages. Some QTL could be detected at all stages and some only at one or several stages. More QTL could be found on the basis of time dependent measures of different stages. Mapping QTL for genetic main effects and G X E interaction effects could help in determining the nature of QTLs X environment interaction for the development of quantitative traits.

Blum et al. (1999) developed a double haploid F2 line population of rice (cross of CT 9993-5-10-1-M / IR 62266-42-6-2, designated IR68586) for molecular mapping of drought tolerant traits in rice. They used 100 lines of this population for drought tolerance test.

Li et al. (1999) worked on identification of Quantitative trait loci (QTLs) in rice reported that in rice there appears two types, first that represents major genes that affects quantitative traits which are detected with large LOD score (>10). The second type includes most of the
Quantitative trait loci (QTLs) identified in rice, which have small effects and to be involved in epistasis and/or genotype environment interactions. Several important issues in QTL mapping such as background gene variation control, epistasis and genotype X environment interactions were addressed by mathematical comparison and computer simulation.

Tan et al. (1999) developed a path coefficient analysis method for detection of quantitative trait loci. The methods recently developed by combining multiple regression with interval mapping can overcome some inherent shortcomings of a single QTL model. However, multiple regression is not appropriate for linked marker due to redundant information generated by the more distant markers. Elimination of redundancy by using multiple regression can result in QTL detection bias. An alternative approach, path coefficient analysis (PCAN), is proposed here for QTL detection. This approach was investigated for genetic dissection of fertility restoration of cytoplastic male sterility of the wild abortive type in rice.

Xu et al. (1999) proposed simple statistical method for mapping quantitative trait loci-regression with means of flanking marker genotypes. This method uses the quantitative trait means of flanking marker genotypes as the dependent variable Y, and the coefficient of additive and dominance effect of putative QTL in an interval as independent variable X1 and X2. This method can be performed at any
position in a genome covered by markers. The effect and location of QTL can be estimated simultaneously. For increasing the estimation precision of QTL location, the interference of other relative QTL was controlled statistically as Zeng's composite interval mapping when scanning QTL in an interval.

Zhang et al. (2001) identified that RG 939, RG 476, RG 214 on chromosome # 4 are important in terms of drought tolerance in rice since it regulates plant height, yield and number of panicles under stress. These also harbour genomic regions having QTLs for RPI, BRT, thickness and dry weight of penetrated roots under simulated soil hardpans.

2.14 Molecular Linkage Map

The advent of molecular markers techniques facilitated the construction of linkage maps especially after the development of polymerase chain reaction (PCR)-based marker including Random Amplified Polymorphic DNA (RAPD) and Amplified Fragment Length Polymorphism (AFLP) markers and Simple Sequence Repeat (SSR) markers (Williams et al., 1990; Vos et al., 1995; McCouch et al., 1997; Chen et al., 1997; Temnykh et al., 2000).

Maps based on molecular markers have an inherent advantage over the classical linkage maps. DNA markers are widely used in the development of molecular linkage maps for different genomes because of their unique genomic position and behavior as single Mendelian transmission factors. In molecular linkage maps, the linear order and
relative genetic distances of linked DNA markers on individual chromosomes and the whole genome of an organism are determined genetically and represented graphically. DNA markers have an unlimited potential in number allowing saturated coverage of the genome.

McCouch et al. (1988) constructed the first RFLP map of rice consisting of 135 loci. The loci correspond to clones selected from a PstI rice genomic library made from the indica variety IR36. The map covered 1389 cM of rice genome and exceeded the classical map at that time by more than 20%. The map was generated from a cross between two cultivars IR34583 (indica) and Bulu Dalam (javanica).

A second map of rice was constructed based on an anther culture-derived population of IRAT177 (japonica) and Apura (indica) ( Tanksley et al., 1991). Saito et al. (1991) constructed another RFLP map based on a cross involving Kaslath (indica) and FL134 (japonica). Among the 347 RFLP, morphological, and biochemical markers examined, 82% were resolved as codominant alleles, the remaining 18% showed dominant/recessive (null) relationship. Saito’s map covers a total of 1836 cM width 347 loci and exceeds the classical genome map and McCouch’s RFLP map by 58.5% and 32.2% respectively.

Causse et al. (1994) worked on the rice QTL analysis using DNA markers based on a well saturated genetic linkage map to detect the genomic region associated with several traits exhibiting complex inheritance.
related to glycolysis and tricarboxylic acid cycle, which contribute to ATP production.

The first step towards cataloging and categorizing genetically complex abiotic stress responses is the rapid discovery of genes by large scale partial sequencing of randomly selected cDNA clones or expressed sequence tags (ESTs). Extensive EST collections already exist for Arabidopsis (Bevan et al., 1999) and rice (Goff 1999)). Large scale EST sequencing initiatives are also well under way for various crop spices (Walbot 1999) including cotton, Medicago truncatula, maize, soybean, tomato and sorghum and also for Loblolly pine (http://www.nf.gov/bio/awards/genome99.htm).

Cushman et al., 1999 reported that approximately more than 15% functionally unknown genes expressed than the unstressed plants in comparative sampling of approximately equal number of ESTs from the leaf tissue of well watered and salinity stressed M. crystallium.

Machuka et al., 1999 reported that most of the ESTs (69%) shared homology with known sequences, although many of the clones encoded proteins that are induced as part of the heat tolerance, cold acclimation, oxidative stress adaptation or xenobiotic detoxification response.

2.16 Identification of candidate genes

The gene encoding the CRYPTOCHROMOME2 photoreceptor was shown to be responsible for the phenotypic variation associated with a
flowering time QTL (El-Din El-Assal et al., 2001). In rice, three QTL have been identified as candidate genes (Kojima et al., 2002; Yano et al., 2000) whose function was known from studies of Arabidopsis.

Mingsheng Chen (2002) reported that recombination is suppressed severely in centromeric regions as well as on the short arms of chromosome 4 and 10. This integrated high-resolution physical map of rice genome will greatly facilitate whole genome sequencing by helping to identify a minimum tiling path of clones to sequence. Furthermore, the physical map will aid map based cloning of agronomically important genes and will provide an important tool for the comparative analysis of grass genomes.

Wang Xu-sheng (2005) conducted in silico analysis of candidate region flanked by the genetic markers RM212 and RM319 on chromosome # 1, proximal to semi dwarf (sd1) locus. A total of 175 annotated genes were identified from this region. These included 48 genes annotated by functional homology to known genes, 23 pseudogenes, 24 ab initio predicted genes supported by an alignment match to an EST of known function, and 80 hypothetical genes predicted solely by ab initio means. Among these, 16 candidate genes could potentially be involved in drought stress response.