MARKER-ASSISTED SELECTION FOR TERMINAL DROUGHT TOLERANCE IN PEARL MILLET [*Pennisetum glaucum* (L.) R. Br.]

By

P. SATHISH KUMAR

RE FOR PLANT BREEDING AND GENETICS
/IIL NADU AGRICULTURAL UNIVERSITY
COIMBATORE – 641 003

2004

MARKER-ASSISTED SELECTION FOR TERMINAL DROUGHT TOLERANCE IN PEARL MILLET [*Pennisetum glaucum* (L.) R. Br.

Thesis submitted in part fulfilment of the requirements for the award of the degree of **Doctor of Philosophy in Plant Breeding and Genetics** to the Tamil Nadu Agricultural University, Coimbatore.

P. SATHISH KUMAR
I. D. No. 00-810-005

CENTRE FOR PLANT BREEDING AND GENETICS
TAMIL NADU AGRICULTURAL UNIVERSITY
COIMBATORE – 641 003

2004

CERTIFICATE

This is to certify that the thesis entitled " **MARKER-ASSISTED SELECTION FOR TERMINAL DROUGHT TOLERANCE IN PEARL MILLET (*Pennisetum glaucum* (L.) R. Br.)**" submitted in part fulfilment of the requirements for the degree of **Doctor of Philosophy** in **Plant Breeding and Genetics** to the Tamil Nadu Agricultural University, Coimbatore is a record of *bonafide* research work carried out by **Mr. P. SATHISH KUMAR** under my supervision and guidance and that no part of this thesis has been submitted for the award of any other degree, diploma, fellowship or other similar titles or prizes and that the work has not been published in part or full in any scientific or popular journal or magazine.

Place : Coimbatore
Date : 02.08.04

V. MURALIDHARAN
(Chairman)

Approved by

Chairman : **V. MURALIDHARAN** 08/11/04

Co-Chairman : **C. T. HASH**
ICRISAT

Members : **T.S. RAVEENDRAN**

D. VEERARAGAVATHATHAM

M. JAYAPRAGASAM

Date: External Examiner:

ACKNOWLEDGEMENT

I sincerely acknowledge and thank

Dr. C.T. Hash (Principal scientist, Molecular breeding, ICRISAT), who pictured the concept of this study and supported through the DFID project. He offered meticulous guidance and sustained encouragements throughout the period

Dr. V. Muralidharan (Professor, Department of Oil seeds and Chairman of the Advisory Committee) and Dr. N. Subbaraman (Professor, RRC, Kovilankulam) for the inspiration and help to take the research project at ICRISAT

Dr. T.S. Raveendran (Director, CPBG) and Dr. C. Surendran (Ex-Director, CPBG) for offering full support all through the course of my study

Dr. T.S. Raveendran (Director, CPBG), Dr. D. Veeraragavathatham (Director, Planning and Monitoring), Dr. M. Jayapragasam (Professor, Bio-chemistry) members of the Advisory Committee for the guidance received during the preparation of the thesis

Dr. Francis R. Bidinger, ICRISAT, Dr. Rattan S Yadav, IGER, Dr. Maria Kolesnikova-Allen, IITA, Tracy S. Pittaway, IGER, Dr. Subash Chandra, ICRISAT, Dr. V. Mahalakhsmi, IITA, Dr. Emma Mace, DPI&F, Dr. N. Manivannan, TNAU, Dr. M. Kumar, TNAU, Dr. V. Gomathi, TNAU, Dr. Subbalakhsmi, TNAU, Dr. Ramesh, ICRISAT, Bhasker Raj, ICRISAT, Panduranga Rao, ICRISAT, Dr. L. Krishnamurthy, ICRISAT who extended all possible help and moral support during the research period

Seetha Kannan, Narsi Reddy, Om Praksh, Ganapathi, Mahaeshwara rao, Katyayani, Dharani, Anjaiah, Pantaiah, Bhasker, Somaraju, Bryan, Eshwar, Lucas, Ramadoss, Malla Reddy, Bukkamma, Ramakrishna, Gautam, Mani, Marimuthu, Vijaya amma for their help in lab and field works

Akshay, Arun Sharma, Aruna, Azhaguvel, Devvart, Firoz, Giri, Gulia, Kishore, Nedumaran, Nepolean, Prasant, Rizvi, Rupa, Santhosh, Sarvamangala Devi, Senthil vel, Shivaram, Stanley all for their pleasant stay and company at ICRISAT

Mohanraj, Mothilal, Punitha, Ravi, Sundar, Thangaraj, Thiruvengadam who carried out all my official work during my absence

[P. Sathish Kumar]

ABSTRACT

MARKER-ASSISTED SELECTION FOR TERMINAL DROUGHT TOLERANCE IN PEARL MILLET [*Pennisetum glaucum* (L.) R. Br.]

By

P. SATHISH KUMAR

Degree : **Doctor of Philosophy**
(Plant Breeding and Genetics)

Chairman : **Dr. V. Muralidharan**
Professor
Department of Oilseeds
Centre for Plant Breeding and Genetics
Coimbatore - 641 003

2004

Drought at the crop's reproductive stage is one of the most important environmental factors limiting pearl millet productivity; improved adaptation to such drought stress is an important breeding objective. DNA-based marker tools facilitated better understanding of the inheritance and expression of grain and stover yield-related traits in three moisture regimes differing in the intensity and duration of late reproductive-stage stress with different tester backgrounds. In the present study, an attempt was made to transfer consistent drought-tolerance associated major QTLs on LG2 from 863B derived from (the *Iniadi* landrace material from Togo) to the cultivated elite recurrent parent ICMB 841, which is the maintainer of the female parent of several high yielding hybrids that are widely grown in India. Previously a linkage map of loci detected with 28 polymorphic SSR primer pairs and 23 RFLP probe-enzyme

combinations was used in a mapping population based on these parental lines. Here these markers were used to for background selection in the initial stages of the backcrossing programmes. Easily scorable morphological markers and SSR markers (for foreground selection) helped to select 13 segmental introgression homozygotes involving various sections of the LG2 donor genome to study this genomic region responsible for drought tolerance contributing characters. Production of testcross hybrids from these homozygotes with relatively different testers for drought tolerance was followed by their screening in three moisture regimes. To study marker-phenotype associations, the parents were crossed with these testers and evaluated for grain and stover yield-related characters *viz.*, flowering time (FT), plant height (PH), panicle length (PL), panicle diameter (PD), plant count (PC), head count (HC), effective tiller (ET), panicle yield (PY), grain yield (GY), stover yield (SY), hundred-grain mass (HGM), harvest index (HI), and biomass yield (BY). The field evaluation revealed that testers H 77/833-2 and PPMI 301 were the best testers respectively for stover and grain yield-related characters suitable for late-onset terminal drought stress conditions. Association of genomic regions with drought tolerance characters confirmed a role of the genomic regions between SSR markers *Xpsmp*2066 and *Xpsmp*2255 on pearl millet LG2 for genomic performance under relatively mild late-onset terminal drought stress conditions. Similarly, different genomic regions associated with superior performance with testers such as PPMI 301, H 77/833-2 were between SSR markers *Xpsmp*2072 to *Xpsmp*2231; whereas for RIB 335/74 genomic regions between *Xpsmp*2066 to *Xpsmp*2059 (lower arm of LG2). Association of similar genomic regions for grain and stover yield-related characters revealed that simultaneous improvement of grain and stover yield could be possible.

CONTENTS

LIST OF TABLES

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

CHAPTER I

INTRODUCTION

Pearl millet is an important cereal of subsistence farming systems in the dry areas of the semi-arid tropics. The crop is grown as a source of staple food grain and crop residues on over 26 m ha in arid and semi-arid and sub-humid sub-Saharan African and South Asia (Anand Kumar, 1989; FAO and ICRISAT, 1996; FAO, 2000). It is grown primarily for its ability to produce grain under hot, dry conditions on infertile soils of low water-holding capacity where other crops generally fail completely. Per caput food consumption of pearl millet varies greatly between countries. It is highest in West Africa, where pearl millet is a key food staple in the drier regions. Most farmers who rely on this crop are quite poor and frequently experience food shortfalls. Little of the pearl millet production enters the commercial market; most never leaves the village farm in which it is grown. The combination of poverty and severe environmental conditions makes it difficult to improve and productivity in pearl millet; however for most areas where it is grown there is no alternative cereal crop. In sum, pearl millet will remain largely associated with the food security of drought-prone human populations (FAO and ICRISAT, 1996).

Crop improvement is generally more difficult in millets than in most other crops, largely because of the nature of the environments in which they are grown. Drought provides one of the major limitations to food production worldwide. In some parts of the world, particularly the semi-arid tropics and other locations where most of the world's poor people reside, drought is endemic. Moreover, many parts of the Earth's surface are not arable primarily because of severe water limitations, and the amount of land with

these problems is growing every year. Pearl millet is grown primarily as a rainfed crop in the regions where mean annual rainfall ranges from 200 to 800 mm.

Despite being the crop species of choice in some of the most arid dryland agricultural environments in the tropics, pearl millet is not particularly drought tolerant. In the stressful environments where it is most commonly cultivated, pearl millet performs well relative to other crop species on the strengths of its short crop life cycle, developmental plasticity, very rapid growth rate when conditions are favorable, high optimum growth temperature, high temperature tolerance, and deep vigorous root system that is exceptionally tolerant of soil acidity and low inherent soil fertility.

Although higher yielding and more reliable than other cereal crops under these stressful conditions, pearl millet yields are rather low, averaging 500 to 1000 kg ha^{-1} in South Asia and 700-900 kg ha^{-1} in sub-Saharan Africa (FAO and ICRISAT, 1996; FAO, 2000). Therefore breeding for yield and yield stability under water-limiting conditions is, or should be, an important component of most applied pearl millet breeding programs (Mahalakhsmi *et al.* 1997; Hash *et al.* 1999; Yadav and Weltzien, 1999; Bidinger and Hash, 2003). Yield under stress conditions can be thought of as a function of three factors: grain yield potential, growth duration, and inherent stress tolerance *per se* (Bidinger *et al.*, 1987a,b; Mahalakhsmi *et al.*, 1987). Prediction of the effects of stresses on grain yields requires estimates of the relative sensitivity of different stages of crop growth to periods of stress. In pearl millet, for example, reports indicate that drought stress occurring early in crop growth has little effect on grain yields (Lahiri and Kharabanda, 1965) and that sensitivity to stress increases at and after flowering

(Mahalakhsmi and Bidinger, 1985a). In terminal drought stress conditions, the combined effects of phenology and yield potential can account for as much as 50% of the variation in pearl millet grain yield (Bidinger *et al.* 1987a). Because of these effects, the most effective means of improving pearl millet's grain yield in terminal stress environments should be to incorporate specific traits (or responses to stress) that improve the tolerance of terminal stress into otherwise high yielding genotypes of appropriate crop duration (Bidinger *et al.* 1987a; Fussell *et al.* 1991; Bidinger and Hash, 2003).

With recent advances in molecular biology, research for tackling these issues has been accelerated. It is expected that finding unknown genes and gene combinations controlling complex traits like drought will speed up the process of evolving new crop varieties by using the information as a passport to better grain yield. Among the molecular tools available, molecular marker technology is a potent tool to dissect complex traits such as crop response to drought stress into sub traits for further manipulations. Yadav *et al.*, 2002 identified genomic regions that were associated with drought tolerance and yield of pearl millet in one or the other stress environments. In particular, the Quantitative Trait Locus (QTL) on LG2 is of most interest as this is consistently associated with terminal drought tolerance and yield under stress conditions across pearl millet mapping populations, stress environments and tester backgrounds and explained up to 25% of variation in grain yield variation under terminal drought stress conditions.

The large and consistent effect of this genomic region over environments makes it a good candidate for molecular marker-assisted selection (MMAS). For difficult to

evaluate traits such as stress tolerance, MMAS has the potential to be more effective than traditional conventional selection. In the present study, an attempt has been made to assess the effectiveness of MMAS in the breeding of more drought tolerant versions of elite pearl millet seed parent backcross-derived maintainer line using 863B as the donor. Targeting of regions of the donor genome for introgression was based on prior assessment of testcrosses of a mapping population based on the cross ICMB 841 x 863B. The objectives of the study were:

- Complete transfer of one to three drought tolerance QTLs from donor parent 863B to recurrent parent ICMB 841.

- Evaluate the hybrid performance of the improved version(s) of ICMB 841, relative to the original recurrent parent under fully-irrigated and managed terminal drought stress conditions.

REVIEW OF LITERATURE

CHAPTER II

REVIEW OF LITERATURE

2.1. Pearl millet and it's importance

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is an important coarse-grain cereal adapted to arid and semi-arid regions of India and Africa where it is primarily grown as a rainfed crop. Its main areas of cultivation are on low fertility, light-textured soils, receiving less than 500-600 mm of rainfall, where sorghum and (especially) maize are subject to frequent crop failures (Harinarayana *et al.*, 1999). It is primarily a crop of subsistence agriculture, because of both the limited resources and significant environmental constraints of the environments in which it is grown. As a result, its evolution has necessarily favored adaptation and survival over a high level of grain productivity.

On one hand it has been termed "a cereal of the Sahel" (de Wet *et al.*, 1992), because of its origin and evolution and its suite of physiological and developmental traits that provide specific adaptation to marginal and arid environments. These include rapid germination, short duration of key developmental periods and non-synchronous development of tillers. Its moderate haploid DNA content and relatively low recombination rates, its high degree of polymorphism at both phenotypic and molecular levels, plus the ease with which both self and cross-pollinated progenies can be generated due to the ability to cross-pollinate the crop without emasculation by exploiting protogyny, diploid nature and large chromosomes make pearl millet an ideal model organism for genetic research.

A brief review of previous work done in pearl millet with relation to the objectives of the current research programme is made under the following aspects:

1. Importance of RFLP and its application
2. Importance of SSR and its application
3. Genetic linkage and QTL mapping
4. Marker Assisted Selection (MAS) for drought tolerance
5. Integration of MAS into applied plant breeding programmes
6. Inheritance of downy mildew incidence
7. Inheritance of drought tolerance

2.1.1. Origin, evolution and ecology of the crop

Brunken *et al.* (1977) reported that pearl millet was domesticated somewhere along the southern fringes of the Sahara desert, at least 3000 years ago, when then current drying period in this area necessitated a change from Mediterranean cereals to other species better adapted to changing rainfall patterns and increasing aridity. Its progenitor was almost certainly the wild *Pennisetum fallax – P. violaceum* (Stapf and Hubbard, 1934) complex that is widely distributed in both the desert margins and the highland areas within the desert itself (de Wet *et al.*, 1992). Brunken *et al.* (1977) reclassified both progenitors in the (wild) subspecies *monodii* of what is now referred to as *P. glaucum* (de Wet, 1987), based on the fact that both of these species cross readily with the cultivated subspecies.

The major differences between the cultivated and wild subspecies reflect the domestication process: the loss of the abscission layer at the base of the spikelet that results in shattering in the wild subspecies, a significant increase in both inflorescence and seed sizes, supported by a greater plant size, and a concomitant reduction in productive tiller numbers (Brunken *et al.*, 1977; Poncet *et al.*, 2000).

The cross fertility between the cultivated and wild subspecies of *P. glaucum* has also produced a stable, intermediate subspecies – *stenostachyum* – that has the cultivated plant type, but retains the shattering character of its wild progenitor and thus self-seeds in farmers' fields (Brunken *et al.*, 1977). These weedy intermediates or "shibras," which exist as stable populations, cannot be distinguished from the cultivated type in the vegetative stage and thus escape from being removed during the weeding of fields, unlike the wild subspecies.

Shibra × cultivated crosses appear to have lower rates of seed set than either shibra × shibra or cultivated × cultivated crosses (Amoukou, 1993), helping to preserve both as distinct subspecies. However, shibras still function as a constant bridge for the flow of genes from the wild to the cultivated subspecies, because of their effective mimicry of the cultivated type. This opportunity for continuing gene flow from wild progenitors is unique phenomenon among major cereals. Research has indicated the potential value of genes in the *monodii* (Hanna *et al.*, 1985) and *stenostachyum* (Bramel-Cox *et al.*, 1986) genepools.

2.2. Importance of RFLP and its applications

The potential usefulness of genetic markers as an instrument for the plant breeder was recognized more than 80 years ago (Sax, 1923). Until the past 20 years, however, its application was largely hindered by the lack of suitable markers. Advances in molecular biology during the last two decades have provided a new class of genetic markers at the level of DNA. The first of these DNA-based molecular genetic markers to be exploited for studies of crop inheritance and improvement were Restriction Fragment Length Polymorphisms (RFLPs). Investigations in maize (Helentjaris *et al.* 1986, Burr *et al.*

1988), rice (Mc Couch *et al.* 1988), soybeans (Apuya *et al.* 1988), tomato (Bernatzky and Tanksley, 1986), potato (Bonierbale *et al.* 1988), and brassicas (Figdore *et al.* 1988) have demonstrated that a potentially unlimited number of RFLPs exist, which should enable plant geneticists to establish well-saturated genetic maps for any species. This development has stimulated new interest in exploring the applications of genetic markers in plant breeding.

RFLP analysis employs cloned DNA sequences to probe specific regions of the genome for variations that are seen as changes in the length of DNA fragments produced by digestion with restriction endonucleases (Landry *et al.*, 1987). The four primary advantages of RFLP markers over morphological markers are co-dominance, frequent polymorphism, absence or limited influence of the environment, and absence of pleiotropic effects (Botstein *et al.*, 1980; Beckmann and Soller, 1983).

RFLP and morphological markers have been used in practical plant breeding programs to map quantitative trait loci (QTLs) (Tanksley *et al.*, 1982; Edwards *et al.*, 1987; Stuber *et al.*, 1987; Weller *et al.*, 1988; Mohan *et al.*, 1997), assess genetic diversity (Bhattacharjee *et al.*, 2002) and to monitor response to recurrent selection (Stuber *et al.*, 1980, 1982).

One of the foremost attributes of RFLPs compared to isozymes is the substantially greater number of polymorphic markers found within breeding materials (Beckmann and Soller, 1986). However, RFLP assays require more expensive laboratory supplies and are rather time consuming compared to isozyme analyses.

Costs of applying RFLPs to genetic improvement were assessed by Beckmann and Soller (1983) in terms of individuals and number of polymorphisms per individual

that are scored for various applications including varietal identification, identification and mapping of quantitative trait loci and their marker-assisted introgression from resource strain to commercial variety. Hash (1991), Gale and Witcombe (1992), Hash *et al.* (1997, 1999), Hash and Bramel-Cox (2000), and Hash and Witcombe (2002) emphasized the opportunities for potential use of RFLPs in plant breeding with particular reference to downy mildew resistance in pearl millet. A number of recent papers suggest that the use of RFLPs, and other DNA-based molecular markers, can offer a clear advantage in breeding for important qualitative and quantitative traits (Edwards *et al.*, 1987; Melchinger, 1990; Paterson *et al.*, 1991; Arunachalam and Chandrashekaran, 1993; Mohan *et al.*, 1997; Young, 1999; Ribaut *et al.*, 2002).

A number of recent papers on pearl millet suggest that the use of RFLPs and other DNA-based molecular markers offers a clear advantage in breeding for drought tolerance (Yadav *et al.*, 1999; Hash *et al.*, 2000; Yadav *et al.*, 2002) for diversity analysis (Bhattacharjee *et al.*, 2002), for downy mildew resistance (Jones *et al.*, 1995, 2002; Witcombe and Hash, 2000; Hash and Witcombe, 2002).

2.3. Importance of SSR markers and their application

RFLPs markers have limitations in many situations; however, the development of the Polymerase Chain Reaction (PCR) (Saiki *et al.*, 1988) has facilitated the generation of a whole new class of DNA markers.

Microsatellite (or) Simple Sequence Repeat (SSR) length polymorphisms at individual loci are detected by PCR using locus-specific flanking region primers (Weber and May, 1989). These assays typically carry high information content (Cregan *et al.*, 1999) and have been extremely useful for mapping and gene discovery efforts

(Beckmann and Weber, 1992). Comparative advantages of SSR markers over RFLPs include: SSRs relatively simple and can be automated, a high number of public SSR primer pairs are available for genomes of humans and several important crop and livestock species, and less cost per genotype data point.

Microsatellite markers based on SSRs have been developed in many crops including rice (Panaud *et al.*, 1996; Akaji *et al.*, 1996). The ubiquity of SSR and their usefulness as genetic markers in rice have been well established (Mc Couch *et al.*, 1997). The usefulness of SSR has also been demonstrated for a variety of other plant species and this has prompted the initiation of SSR discovery programmes for the majority of agronomically important crops. These markers detect Simple Sequence Length Polymorphism (SSLP) and are rapidly displacing RFLP markers in most genetic analyses, largely because of their technical simplicity, rapid run time and high power genetic resolution.

2.4. Linkage Mapping

Mapping is putting marker loci (and QTLs) in order, indicating the relative distances among them, and assigning them to their linkage group on the basis of their recombination values from all pair-wise and three-point combinations.

A primary genetic linkage map, consisting of easily scored polymorphic marker loci uniformly distributed throughout a genome, is an essential prerequisite to detailed genetic studies and marker-facilitated breeding approaches in any crop plant. Until recently, it has been possible to construct such complete linkage maps only in intensively studied organisms such as bacteria, yeast or fruit flies, in which many visible mutations are available as genetic markers (Lander *et al.*, 1987). The first map of the human

genome based on molecular markers (Botstein *et al.*, 1980) fuelled the development of molecular marker-based genome maps in other organisms.

The theory of linkage mapping is same for DNA markers as in classical genetic mapping; however, several new considerations must be kept in mind. This is primarily a result of the fact that potentially unlimited numbers of DNA markers can be analyzed in a single mapping population. DNA-based maps can be related to existing cytogenetic maps through the use of aneuploid or substitution lines (Minocha and Sidhu, 1981; Helentjaris *et al.*, 1986; Sharp *et al.*, 1989; Young *et al.*, 1987) or *in situ* hybridization (ISH) (Zhang *et al.*, 2000).

2.5. Computer software packages for constructing genetic linkage maps

Advances in computer technology have been essential to progress in DNA marker-based genetic linkage maps. The theory behind linkage mapping with DNA markers is identical to mapping with classical genetic markers, but the complexity of the problem has dramatically increased because of the larger numbers of markers that are available to be used. This increase in numbers of segregating loci (and in some cases the number of progenies in which they are segregating) relative to studies of classical genetic markers has necessitated the development of complex computer algorithms and software packages specifically for this purpose.

Construction of a genetic linkage map from a DNA marker data set requires computer software packages capable of running χ^2 contingency table analyses. The program, LINKAGE-1 (Suiter *et al.*, 1983) carries out this type of analysis automatically and also compares the observed allelic distributions to expected distributions. In a different strategy for optimizing the use of DNA marker information, the computer

program "HyperGene" converts genotypic data into a "graphical genotype" (Young and Tanksley, 1989b,c), in which a complete genome of an individual from the mapping population is displayed.

MAPMAKER/EXP is a linkage analysis software package for constructing primary linkage maps of markers segregating in experimental crosses. It performs full multipoint linkage analysis for dominant, recessive and co-dominant (*eg.*, RFLP-like) markers in BC_1 backcrosses, F_2 and F_3 (self) intercrosses and recombinant inbred lines (Lander *et al.*, 1987; Lincoln *et al.*, 1992a, b).

The software package Joinmap (Stam 1993; Stam and Van Ooijen, 1995) analyses all types of mapping populations, and can combine maps of different mapping populations provided there are common markers. Another software for linkage mapping is Gmendel from Oregon State University, USA (Holloway and Knapp, 1994). The package Mapmanager, with different versions such as QTX, QTXP and QTX-Classic for Macintosh- and IBM compatible computers (Manly, 1993; Manly and Olsen, 1999), can be used to analyze the results of genetic mapping experiments using backcrosses or recombinant inbred lines.

2.6. Pearl millet genetic map

The first detailed molecular marker-based genetic linkage map of pearl millet was published in 1994, and was comprised primarily of RFLP markers (Liu *et al.*, 1994). They placed 181 loci on a linkage map by studying segregation in two F_2 populations. Two crosses (LGD × ICMP 85410 and Tift $23D_2B_1$ × IP 18292) were employed. The total length of this map, which comprised seven linkage groups, was 303 cM and the average distance between loci was about 2 cM. The individual linkage groups (LG)

varied from 90 cM for LG1 to only 30 cM for LG6 (Devos *et al.*, 1995). This pearl millet genetic linkage map was unusual among grass genomes in that it was particularly short, but this difference is expected to reduce with time. Subsequent studies have extended the length of the pearl millet genetic linkage map to circa 700 Haldane cM, but to date no significant linkage has been detected between the marker loci in these seven linkage groups and telomeric sequences that are expected to cap the ends of each (Katrien M. Devos, pers. comm.). This suggests that the pearl millet genetic linkage map will eventually extend to at least 1400 cM (Haldane).

Genetic maps produced using four different crosses [LG1-B-10 × ICMP 85410 (original mapping population), 81B × ICMP 451 (world reference pearl millet mapping population), ICMB 841 × 863B and PT 732B × P 1449-2 segregating for drought tolerance and downy mildew resistance] have been integrated to develop a consensus map of 335 RFLP and 65 SSR markers (Qi *et al.*, in press). An interesting feature of the map is the extreme localization of recombination towards the chromosome ends. Physical mapping of one such region on pearl millet linkage group 1 revealed a physical to genetic distance ratio of <12 kb/cM. This unequal distribution of recombination appears to be largely cross independent, and will have consequences for the transfer of traits from donor to elite pearl millet germplasm.

2.7. Quantitative Trait Loci (QTLs)

A "QTL", the acronym for Quantitative Trait Locus, is one of the genes or gene blocks that underlie quantitative traits (Gelderman, 1975). Before the discovery of molecular markers, QTLs were referred to as polygenes (Mather, 1949). QTL analysis is predicated on associations between phenotypic values for the quantitative trait and the marker alleles

segregating in the mapping population. It has two essential stages; the mapping of markers and the association of the trait phenotype values with the marker genotypes. The basic theory underlying marker mapping has been available since 1920.

Sax (1923) first reported association of simply inherited genetic markers with a quantitative trait in plants when he observed segregation for seed size associated with segregation for a seed coat color marker in beans (*Phaseolus vulgaris* L.). Rasmusson (1935) demonstrated linkage of flowering time (a quantitative trait) in peas (*Pisum sativum* L.) with a simply inherited gene for flower color. Everson and Schaller (1955) found morphological markers that flanked a chromosomal region affecting yield in barley (*Hordeum vulgare* L.).

Extensive work in *Drosophila melanogaster* (Mather and Harrison, 1949) demonstrated the effects of individual chromosomes on quantitative traits. Cavalli (1952) crossed lines of *D. melanogaster* selected for high and low abdominal bristle number, and found evidence of linkage between polygenes. Harrison and Mather (1950) and Gibson and Thoday (1962) by selection experiments in *D. melanogaster*, were able to locate polygenes for bristle number on a particular chromosome. Thoday (1961) developed methods for detecting linkage of polygenes with marker loci. In domesticated animals, associations of quantitative traits with segregation for blood group markers have been reported (Niemann-Sorenson and Robertson, 1961). In wheat (*Triticum aestivum* L.) monosomics have been used to identify association of quantitative traits with individual chromosomes (Law, 1967). These earlier studies provided a background of theory and observation for more recent work with molecular markers (Dudley, 1993).

The first use of a reasonably complete crop genetic linkage map based on RFLP markers was reported in tomato by Paterson *et al.* (1988). They resolved quantitative traits to discrete Mendelian factors in an inter-specific backcross of tomato, mapping at least six QTLs controlling fruit mass and four QTLs for soluble solids. At the same time Rodney Mauricio, 2001 discussed the limits of QTL detection. QTL mapping is determined by several factors, including recombination, the number of progeny in the mapping population and the number of markers. He also reported that the QTL mapping always underestimates the number of genes that are involved in controlling a trait.

2.7.1. QTL mapping and drought tolerance

Drought tolerance is a highly complex character. Unpredictable environmental conditions and the time consuming and expensive nature of assessing component traits confound its precise evaluation. In addition, the efficiency of selection is lower under drought conditions than well-watered conditions, due to a decrease in the heritability of grain yield under stress. Nevertheless, molecular markers have been used to map several QTLs for components of drought tolerance in various crops (overviewed by Nguyen, 2001).

The creation and genotyping of a mapping population is often the more expensive part of the overall effort, but its ultimate success depends much more on the effectiveness of the phenotyping procedure in detecting repeatable, highly heritable differences among recombinant lines, that permit the identification of robust quantitative trait loci (QTLs).

Hash and Witcombe, 1994 and Yadav *et al.*, 2002 developed several pearl millet mapping populations for trait QTL mapping for terminal drought tolerance. Testcrosses of mapping population progenies, derived from inbred pollinators and from seed parents differing in their response to terminal drought, were evaluated in a range of managed

terminal drought stress environments to identify individual QTL associated with drought tolerance. A number of QTLs associated with drought tolerance of grain yield and its agronomic and physiological components have been reported (Yadav *et al.*, 2002).

In rice, QTL mapping for traits conferring drought tolerance have been reported by Champoux *et al.* (1995) for root related characters, Lilley *et al.* (1996) for osmotic adjustment, Ray *et al.* (1996) for root penetration ability, and both Ali *et al.*, (2000) and Shashidhar *et al.*, (2000) for root traits.

Ribaut *et al.* (1996) mapped several putative QTLs in maize for drought conditions. They also discussed whether those QTLs could be used in marker-assisted selection for the improvement of drought tolerance.

For the stay-green component of terminal drought tolerance in sorghum, various QTLs have been mapped by Tunistra *et al.* (1996, 1997); Crasta *et al.* (1999); Tao *et al.* 2000); Xu *et* al., (2000); Subudhi *et al.* (2000); Kebede *et al.* (2001); Cha *et al.* (2002); Haussman *et al.* (2003).

Schneider *et al.* (1997) identified significant QTLs for drought tolerance in common bean using Recombinant Inbred Lines (RILs). Similarly, significant QTL associations for yield and yield components have been reported in barley under low rainfall environments using 254 molecular markers (Eglinton *et al.*, 2001). Foolad (1999) elaborately discussed the QTL mapping approach for salt and cold tolerance in tomato. In this study comparison of salt tolerance during germination and vegetative growth indicated mostly different QTLs contributed to tolerance at these two developmental stages.

In pearl millet, a number of genomic regions for grain yield *per se* and for the drought tolerance of grain yield mapped on LG2 and explained up to 23% of the phenotypic variation. Some of these QTLs were common across stress environments (Yadav *et al.*, 2002).

2.8. QTL analysis: Statistical methods

Jayakar (1970) suggested mathematical-statistical methods for the detection and estimation of linkage between a qualitative marker gene and a locus influencing a quantitative character. Since then, experimental designs for determination of linkage between marker loci and QTLs have been widely described (Elston and Stewart, 1971; Geldermann, 1975; Hill, 1975; Jensen, 1989; Knapp *et al.*, 1990; Lander and Bostein, 1989; Soller and Beckmann, 1983, 1990).

Prioul *et al.*, 1997 used two classical approaches for QTL detection are marker-by-marker ANOVA and multiple marker methods. The principle of the ANOVA is to test whether there are significant differences between the phenotypic means of the genotype classes at a particular marker locus.

Marker-QTL association detection can be conducted through t-tests based on single markers (Soller *et al.*, 1976) or by means of likelihood ratio tests that involve that use of a pair markers bracketing a QTL, a procedure termed 'Interval Mapping' (Jensen, 1989; Knapp *et al.*, 1990; Lander and Botstein, 1989; Weller, 1987), although simpler approaches are also possible (Thoday, 1961; Weller, 1987; Haley and Knott, 1992).

Lander and Botstein (1989) described a set of analytical methods that modify and extend the classical theory for mapping QTLs and that are implemented in the computer software package MAPMAKER/QTL. Estimating the location and the size of the effects

of QTLs using flanking markers was discussed by Martinez and Curnow (1992) in the framework of a backcross using a regression model as the analytical tool.

Composite Interval Mapping evaluates the possibility of a target QTL at multiple analysis points across each intermarker interval. However, at each point it also includes the effect of one or more background markers, as defined as Simple interval Mapping (SIM). The inclusion of a background marker may help to separate target QTL from other linked QTL on the far side of the background marker (Zheng, 1993 and 1994).

Van Ooijen (1999) presented methods that provide reasonably accurate approximations to LOD significance thresholds for QTL analysis, which were obtained by large-scale simulations. Churchill and Doerge (1994) described an empirical method, based on the concept of permutation tests, for estimating threshold values for declaring significant QTL effects.

2.9. QTL mapping software

Normally all QTL mapping software require input of the data for

1. The quantitative trait value(s) for each progeny
2. The genotype (molecular markers) for each progeny

There are over one hundred genetic analysis software packages available. Here is the brief list of some commonly used software packages:

MapMaker/QTL *(ftp://genome.wi.mit.edu/pub/mapmaker3/)* is the original QTL mapping software for Macintosh and IBM computers (Lincoln *et al.*, 1992b). It is user-friendly, freely distributed, and runs on almost all platforms. It will analyze F_2 or backcross data using standard interval mapping procedures.

MQTL is an IBM-compatible computer program for composite interval mapping in multiple environments (Van Ooijen and Maliepaard, 1996). It can also perform simple interval mapping. Currently, MQTL is restricted to the analysis of data from homozygous progeny (doubled haploids, or recombinant inbred lines). Progeny types with more than two marker classes (*e.g.*, F_2) are not handled.

PLABQTL *(http://www.uni-hohenheim.de/~ipspwww/soft.html)* is a freely distributed IBM-compatible computer program for composite interval mapping and simple interval mapping of QTLs (Utz and Melchinger, 1995; Utz *et al.*, 2000). Its main purpose is to localize and characterize QTLs in mapping populations derived from a biparental cross by selfing or production of double haploids. Currently, this program is the easiest software to use for composite interval mapping.

QTL Cartographer *(http://statgen.ncsu.edu/qtlcart/cartographer.html)* is a QTL-mapping software written for UNIX, Macintosh, or Windows computer operating systems. It performs single-marker regression, interval mapping, and composite interval mapping. It permits analysis of F_2 or backcross populations. It displays map positions of QTLs using the GNUPLOT software. QTL Cartographer was developed by the group of Zeng in USA (Zeng, 1993, 1994; Basten *et al.*, 1994, 1997). It allows markers to be chosen as cofactors to reduce the background genetic noise and increase the resolution of QTL detection. This is an effective strategy for improving the ability to detect QTLs of small effect provided that the number of progenies in the mapping population is reasonably large.

SAS is a general statistical analysis software package. It can detect QTL by identifying associations between marker genotype and quantitative trait phenotype by

single-marker analysis approaches such as ANOVA, t-test, and regression (*e.g.*, PROC ANOVA, PROC GLM or PROC REG).

2.10. Reliability of QTL mapping

Kearsey and Farquhar (1998) reported that the available analytical methods locate QTLs with poor precision unless the heritability of a particular trait is high. Also the estimates of the QTL effects, particularly the dominance effects, tend to be inflated because only large estimates are detected as being statistically significant. This is especially problematic where mapping population size is less than optimal (as it usually is).

Darvasi *et al.* (1993) showed that the power of detecting a QTL was virtually the same for a marker spacing of 10 cM as for an infinite number of markers and was only slightly decreased for marker spacings of 20 cM or 50 cM. However, a very important consideration is the confidence interval for the QTL position on the linkage group. Effective utilization of molecular marker technology to manipulate loci controlling quantitative traits is considered to be dependent on tight linkage between the marker (s) and the QTL (Dudley, 1993), but in fact, even loose linkages can be exploited in an applied breeding program (Sharma, 2001).

In most published QTL studies, the number of QTLs is considerably under estimated and the percentage of genetic variation explained by markers is highly erratic and often over estimated (Lynch and Walsh, 1998). These problems can be overcome by backcross transfer of putative QTLs to near-isogenic backgrounds and/or QTL mapping in independent (and large) samples of the mapping population for verification studies of any putative QTLs detected. An additional need is to verify estimated QTL effects and

the possible epistatic interactions of QTL alleles with the genetic background of the material to be improved (Phillips, 1999; Kerns *et al.*, 1999).

Hackett (1997) described diagnostic tools based on residuals, likelihood profiles and regression coefficients for fitting QTL models. These are used to assess the agreement between linkage data and fitted normal mixture models for interval mapping.

Nearly every agronomic trait imaginable has been subjected to DNA marker mapping and QTL analyses *e.g.*, drought tolerance (Martin *et al.*, 1989), seed hardness (Keim *et al.*, 1990), seed size (Fatokun *et al.*, 1992), maturity and plant height (Lin *et al.*, 1995), disease resistance (reviewed by Young, 1996), oil and protein content (Diers *et al.*, 1992), soluble solids content (Paterson *et al.*, 1988), and, of course, yield (Stuber *et al.*, 1987; Yadav *et al.*, 2003). Even when a well performed mapping experiment indicates promising QTLs, there is often much more that needs to be done to make the mapping results ready for application in marker-assisted selection (MAS). Repetition over several years and several locations, repetition in genetically unrelated populations, and detailed analysis in marker-generated populations that isolate the effects of individual QTLs, are factors to increase the efficiency and reliability of use of QTLs in applied plant breeding programs (Young, 1999). However, delay in use of QTLs can be as costly as using them too soon, so several alternative strategies for application of marker-assisted selection to backcross improvement of elite inbred lines have been described by Hash *et al.* (2000) and Hash (2000) to speed up adoption of this technology while minimizing cost and risk.

2.11. Marker-Assisted Selection (MAS)

An important area in which molecular biology is being applied to plant disease resistance is that of marker-assisted selection (MAS) (Dudley, 1993; Jones *et al.*, 1997; Lee, 1995; Malyshev and Kartel, 1997; Michelmore, 1995; Mohan *et al.*, 1997; Young, 1996, 1999).

MAS have been advocated as a useful tool for rapid genetic advance in case of quantitative traits (Lande and Thompson, 1990; Knapp, 1994, 1998). Gimelfarb and Lande (1995) presented detailed analysis of the relationships between genetic markers and QTLs in the process of MAS. Mohan *et al.* (1997) concluded that MAS could be used to pyramid major genes including disease and insect resistance genes, with the ultimate goal of producing crop cultivars with more desirable traits. Thus with MAS it is now possible for plant breeders to conduct several rounds of selection in a year. A study conducted by Eathington *et al.* (1997) assessed the usefulness of marker-associated effects estimated from early generation testcross data for predicting later generation testcross performance.

Hash *et al.* (1997, 1999), Witcombe and Hash (2000), and Hash and Witcombe (2002) have described how multiple resistance gene pyramids can be used practically to strategically deploy resistance genes in a potentially more durable manner than has been previously practiced. The frequency of genotypes having resistance alleles at several loci increases greatly in both seed parent and hybrid when the overall frequency of resistance alleles in maintainer lines increases.

Han *et al.* (1997b) determined the efficiency and effectiveness of molecular marker-assisted selection for the two major malting quality QTL regions on

chromosomes 1 and 4 in barley. In 1998, Lawson *et al.* transferred SCAR markers linked to two genes conferring resistance to rust in sunflower.

Shen *et al.* (2001) utilized a marker-assisted backcross program to transfer the Azucena allele at four QTLs for deeper roots from selected double haploid (DH) lines into IR 64. They also reported that a deep root system contributes efficiently to maintaining the water status of the crop through a stress period in rice.

Dolstra *et al.* (2003) reported QTLs for Nitrogen Use Efficiency (NUE) in perennial rye grass and at the same time used these QTLs as criterion to transfer into recipient genome. Cotton fiber quality is complex trait, found to be influenced by more than 27 QTLs. Lacape *et al.* 2003 decided to use the Advance Backcross-QTL (AB-QTL) strategy to introgress the favorable alleles in an adequate recipient genetic background. Zhou *et al.* (2003) improved the eating and cooking quality of rice through a marker-assisted backcross-breeding programme.

2.12. Theoretical studies on the efficiency of MAS

While most researchers involved in QTL mapping are optimistic about the usefulness of MAS, little research has been done to evaluate its practical effectiveness. MAS for QTL have the potential to make traditional breeding strategies for variety improvement more efficient. The effectiveness and efficiency, and strategies of MAS for QTL have been evaluated and proposed with both experimental and actual breeding populations (Gimelfarb and Lande, 1995; Lindhout *et al.*, 1994; Monforte *et al.*, 1996; Ribaut *et al.*, 1997b; Van Berloo and Stam, 1998).

Results from a few studies have suggested that MAS is at least as effective in identifying superior genotypes as phenotype selection, and is more predictable across

years and locations (Stuber, 1992, 1994, 1995). Schneider *et al.* (1997) have reported that MAS improved drought tolerance performance by 11% under stress and 8% under non-stress in common bean (*Phaseolus vulgaris*).

Using the models, Tanksley and Rick (1980) predicted that the proportion of recurrent parent genome expected in the first backcross generation after selection for twelve markers (one per chromosome in tomato) was nearly same as in the third backcross without selection for recurrent parent phenotype.

Lande and Thompson (1990) studied the efficiency of MAS in the improvement of quantitative traits and concluded that molecular genetics can be integrated with traditional methods of artificial selection on phenotypes by applying MAS. The increase in selection efficiency from the use of marker loci, and sample size necessary to achieve them, depends on the genetic parameters and the selection scheme.

While investigating the use of markers to hasten recovery of the elite parent genome during an introgression-breeding program, Hospital *et al.* (1992) showed that MAS may lead to a gain in time of about two generations.

Computer simulations were used to evaluate responses to MAS by Edwards and Page (1994). They compared MAS responses with those typical of phenotypic recurrent selection in an allogamous annual crop species, such as maize or pearl millet, and concluded that MAS may offer a primary advantage of enabling two selection cycles per year versus the 2 years per cycle.

That the higher efficiency of MAS on QTLs with large effects in early generation is balanced by a higher rate of fixation of unfavorable alleles at QTLs with small effects in later generations was reported by Hospital and Charcosset (1997). This explains why

MAS may become less efficient than phenotypic selection in the long term. MAS efficiency therefore depends on genetic determinism.

Knapp (1998) presented estimates of the probability of selecting one or more superior genotypes by MAS to estimate its cost-efficiency relative to phenotypic selection. The frequency of superior genotypes among selected progeny increases as selection intensity increases. Effectiveness of MAS compared to phenotypic selection was assessed by Van Berloo and Stam (1998) showing that MAS appears particularly promising when dominant alleles are present at QTLs and linked in coupling phase. Uncertainty in estimated QTL map positions reduces the benefits of MAS.

Based on his studies Young (1999) indicated that despite innovations like better marker systems and improved genetic mapping strategies, most marker associations are not sufficiently robust for successful MAS. Romagosa *et al.* (1999) verified the value of four QTLs for selection and compared the efficiency of alternative MAS strategies using these QTLs vs. conventional phenotypic selection for grain yield. Genotypic (MAS) and tandem genotypic and phenotypic selections were at least as good as phenotypic selection. Studies of Charmet *et al.* (1999) showed that the accuracy of QTL location determination greatly affects selection efficiency.

In rice, several authors have demonstrated the efficiency of MAS for the successful transfer of major genes for blast resistance (Inukai *et al.*, 1996; Hittalmani *et al.*, 2000) and for bacterial blight resistance (Huang *et al.*, 1997). MAS for QTLs have recently started to be applied to the genetic improvement of quantitative characters in several crops such as tomato (Lawson *et al.*, 1997; Bernacchi *et al.*, 1998), maize (Graham *et al.*, 1997) and barley (Han *et al.*, 1997b; Toojinda *et al.*, 1998). Useful

guidelines have been provided for methodological choices (Visscher *et al.*, 1996a; Hospital and Charcosset, 1997), and overall breeding strategies have been proposed (Tanksley and Nelson, 1995; Tuinstra *et al.*, 1997).

Moreau *et al.* 1998 studied the efficiency of marker-assisted selection (MAS) based on an index incorporating both phenotypic and molecular information which is evaluated with an analytical approach that takes into account the size of the experiment. Moreau *et al.* (2000) evaluated the relative efficiency of MAS in the first cycle of selection through an analytical approach taking into account the effect of experimental design (population size, number of trials and replication/trial) on QTL detection. They concluded that expected economic returns of MAS compared to the phenotypic selection decreases with the cost of genotyping.

At CIMMYT, (Dreher *et al.*, 2003; Morris *et al.*, 2003) compared the cost involved with the use of conventional breeding methods and MAS for Quality Protein Maize (QPM) line conversion. They concluded that conventional breeding is more expensive and time consuming than MAS.

2.13. Integration of MAS into breeding program

As genomic molecular markers become available in certain species, questions are being raised about the practicality and economic efficiency of their use in breeding programs. In case of selection for a quantitative trait, marker-assisted selection programs can be undertaken (Lande and Thompson 1990).

For the introgression of qualitative traits such as pathotype-specific disease resistances, which are typically controlled by single, dominant genes, backcross breeding has been used for a long time (Allard, 1960). It allows the transfer of one or a few genes

from a – often agronomically inferior – donor genotype into an elite recipient genotype, the recurrent parent.

Stam and Zeven (1981) estimated the length of chromosome segment with the desired marker gene introgressed from a donor by backcrossing into recurrent parent and found that, for instance, for a chromosome with length of 100 cM the length of the introgressed segment will average 32 cM in the BC_6 generation. MAS has the potential to considerably reduce the linkage drag that is associated with conventional backcross breeding programmes. Young and Tanksley (1989a) estimated that, to transfer a gene with only 5 cM of donor DNA into the recipient parent, the number of backcross generations could be reduced from 100 to 2 using MAS. At the same time the heterozygotes at each resistance locus could be eliminated so that the plant breeder could rapidly select for genes in the homozygous state.

Lee (1995) suggested the utility of MAS for achieving and improving genetic gain through backcross breeding depends upon the current and potential role of that breeding method. Backcross breeding has been widely used for introducing monogenic characters and less so for polygenic traits. Perhaps the utility of this method could be made more broadly applicable through QTL mapping.

Markers were efficient in introgression backcross programs for simultaneously introgressing an allele and selecting for the desired genomic background Visscher *et al.*, 1996. Using a marker spacing of 10-20 cM gave an advantage of one to two backcross generations selection relative to random or phenotypic selection for recurrent parent phenotype controlled by alleles in non-target areas of the genome. When the position of

the gene to be introgressed is uncertain, a chromosome segment should be introgressed that is likely to include the allele of interest.

Hospital and Charcosset (1997) demonstrated that using at least three markers per target QTL allows a good control over several generations and background selection is even more efficient in a pyramidal backcrossing program where QTLs are first monitored one by one.

Frisch *et al.* (1999) conducted computer simulations to compare selection strategies with regard to (i) proportion of recurrent parent genome recovered and (ii) the number of marker data points required in a backcross program designed for introgression of one target allele from a donor line into a recipient line. Again Frisch *et al.* (1999) reported that molecular markers can accelerate recovery of recurrent parent genome when (i) the distance between the flanking markers and target locus is optimized and (ii) the minimum number of individuals required to obtain individuals that carry the donor allele at the target locus and have minimum proportion of donor genome on the carrier chromosome are taken into consideration.

Ribaut and Betran (1999) suggested conducting a single large-scale marker-assisted selection (SLA-MAS) to select plants at an early generation with a fixed, favorable genetic background at specific loci, while maintaining as much as possible the allelic segregation in the rest of the genome.

Hash *et al.* (2000) described several alternative marker-assisted backcrossing (MABC) procedures that can be used for transferring QTL from a donor to an elite recurrent parent when these two lines have been used in forming the base mapping

population. Charmet *et al.* (1999) advocated that a recurrent selection scheme is highly preferable for pyramiding many QTLs.

2.14. Importance of downy mildew incidence

The millet downy mildew pathogen was first described as *Protomyces graminicola* on *Setaria verticillata* by Saccardo in 1876. Schröter in 1879 renamed it as *Sclerospora graminicola* (Ullstrup, 1973). This disease is of great economic importance in India but also causes yield losses in many countries in Africa, including Burkina-Faso, Chad, Eritrea, Ghana, Mali, Mozambique, Niger, Nigeria, Senegal, Sudan, Togo, Tanzania and Zambia. This pathogen has been reported in more than 20 countries around the world (Singh *et al.*, 1993).

Over the past 25 years, pearl millet production area in India has come down for many reasons. One of the major causes of this reduction has been the disease downy mildew, caused by an oomycetic pseudo-fungus. Downy mildew is the most devastating disease of pearl millet in India and a major epidemic occurred there in the early 1970s, closely following the release and widespread adoption of several closely related, genetically uniform pearl millet single-cross hybrids (Dave, 1987; Singh *et al.*, 1987; Hash, 1997).

2.14.1. Downy mildew – Screening techniques

The life cycle of *Sclerospora graminicola* (Sacc.) J. Schröt. is comprised of both sexual and asexual phases. The sexual stage produces oospores, which are soil or seed borne and provide the primary source of inoculum each season (Shetty, 1987). The sexual sporangia are produced at night under conditions of moderate temperatures and high relative humidity. Maximum sporangia production occurs at 20°C. No sporulation is recorded at

relative humidity levels below 70%. Sporangia germinate via a germ tube and generally do not remain viable for very long after daybreak. Sexual oospores are thick-walled, spherical brownish yellow, and 22 to 35 µm in diameter. Oospores form following sexual recombination in colonized tissue and can survive from 8 months to 13 years under laboratory conditions (Wilson, 1999).

Early attempts to screen for sources of resistance to pearl millet downy mildew depended on "sick plots" i.e., plots into which infected, oospore-bearing pearl millet plants had been ploughed for several years (Nene and Singh, 1976). The test materials were sown in these plots and infection was initiated by the oospores in the soil. Large-scale field screening techniques have been developed, based on pre-sown infector rows that provide sporangial inoculum (Williams *et al.*, 1981). This technique involves the sowing of infector rows (every fifth or ninth row) with a mixture of susceptible cultivars three weeks before sowing test material.

Singh and Gopinath (1985) described a laboratory downy mildew screening technique using a micro-syringe that is more effective than field screening in producing downy mildew infection in susceptible genotypes. The procedure resembles natural infection but provides greater inoculum uniformity, and does not affect normal host activity. A modified greenhouse method for assessing resistance to downy mildew given by Weltzien and King (1995) is more rapid and is suitable for use throughout the year, independent of season. In this method, instead of inoculating plants individually, seedlings at the coleoptile to one-leaf stage were spray-inoculated with an aqueous suspension of freshly prepared sporangia (about 10^5 sporangia mL^{-1}).

Singh *et al.* (1997) explained all screening techniques available for this disease including dip inoculation, spray inoculation, drop inoculation, injection inoculation, settling tower inoculation and field screening infector-row techniques. Jones *et al.* (2001) discussed effective ways to maintain infection potential of inoculum by spraying a chilled suspension of sporangia. Spraying seedlings with a suspension of sporangia that had been chilled before zoospore release gave uniform and adequately high disease pressure over many hours. Thus there has been tremendous improvement over the past 30 years in the screening methods available to detect the genetic differences in host plant resistance to pearl millet downy mildew (Singh *et al.*, 1997; Hash, 1997).

2.14.2. QTL for downy mildew resistance in pearl millet

The first fairly detailed molecular marker map for pearl millet was constructed by Liu *et al.* (1994) so that QTL analysis is now possible. QTLs for host-plant resistance to downy mildew caused by *S. graminicola* pathogen populations from India, Nigeria, Niger, and Senegal were mapped using the susceptible × resistant cross (LGD-1-B-10 × ICMP 85410) (Jones *et al.*, 1995). Host-plant resistance QTLs were detected that were effective against each of the four pathogen populations. To locate genes in mapping populations other than those for which RFLP maps exist, a skeleton map needs to be transferred. In pearl millet less than 40 single-copy probe-enzyme combinations will produce such a map, with an average map distance of less than 15 cM between marker loci (Liu *et al.*, 1994).

Howarth *et al.* (pers.comm.) identified QTLs for downy mildew resistance and seedling heat tolerance from pearl millet mapping populations produced from crosses ICMP 451 × H77/833-2 and H 77/833-2 × PRLT 2/89-33. Hash *et al.* (pers.comm.)

worked with mapping populations from crosses PT 732B × P 1449-2, 81B × ICMP 451 and ICMB 841 × 863B to locate QTLs for resistance to pearl millet downy mildew QTLs for host-plant resistance effective against downy mildew African and Indian pathogen populations were identified in a new mapping population based on cross W 504 × P 310 (Kolesnikova M A , 2000) The most recent works on QTL mapping for downy mildew were carried out in ICRISAT (Azhaguvel, 2001, Nepolean, 2002) including marker-assisted selection (Sharma, 2001)

2.15. Inheritance of drought tolerance

Genetic variation in crop yield response to drought stress is a "complex trait" This observation has been found in many cases when measurements were made in terms of (i) yield under stress, (ii) the ratio of yield under stress to yield under non stress conditions, (iii) stress/non-stress yield normalized for phenology, and/or (iv) a stress index (Blum, 1988b) Genetic variation in yield response to drought stress as represented by stability analysis is expressed in a more consistent manner, as it accounts for some of the interactions and represents more yield tests in both stress and non-stress environments

The inheritance of yield under drought stress is subject to other environmental interactions and intraplant competition as well as the effect of genetic yield potential The identification of such specific factors is important for understanding the nature of yield stability and it may open the way for the development of selection criteria supplemental to yield. Undoubtedly, some of those factors are associated with specific stress-tolerance mechanisms

As yield performance under stress is affected by both potential yield and stability of yield, functional knowledge of the physiological basis of crop adaptation to stress is

often considered a prerequisite for exploiting specific adaptation to stress in crop breeding programs (Blum, 1988b).

2.15.1. The physiological basis of adaptation

Kowal and Kassam (1978) classified the major areas of pearl millet cultivation as arid to semi-arid: the Sahelian and northern Sudanian zones of Africa south of the Sahara desert, stretching from Senegal in the west to Eritrea in the Horn of Africa, and the northwestern states of India. Both of these areas are on the edges of the major circulation systems that bring rain to much of sub-Saharan Africa (inter-tropical convergence zone) and south Asia (the southwest monsoon). As a result rainy seasons in the major pearl millet growing areas are short (70 to 120 days), with low to moderate (250 to 700 mm) mean total rainfall, and highly variable inter- and intra-annual rainfall.

Water balance simulations in both India (*e.g.*, van Oosterom *et al.*, 1996a) and West Africa (*e.g.*, Eldin, 1983) indicate that periods of low soil moisture availability, which limit potential growth, are the norm rather than the exception in most pearl millet growing environments.

Despite the above emphasis on water, poor soil fertility is the major limitation to productivity in much of the area in which pearl millet is grown (Charreau, 1972; Fussell *et al.*, 1987) resulting frequently in incomplete use of soil water (Payne *et al.*, 1990). Kowal and Kassam (1978) reported that the soils of much of the drier part of the main growing areas for this crop are eolian deposits from adjacent deserts, with a very large proportion of fine sand, and with low inherent fertility and a low cation exchange capacity to retain added nutrients.

In addition in West Africa, many of the sandy soils are highly leached (in previous geologic times) and have a low pH and attendant aluminum toxicity problems, as well as very low available phosphorous levels, all of which directly affect crop growth (Chase *et al.*, 1989; Payne *et al.*, 1991).

2.15.2.1. Adaptation to growing season length

Pearl millet is primarily a quantitative or facultative short-day plant (Belliard and Pernes, 1984), but qualitative or absolute short-day types also exist, in which floral initiation occurs under natural conditions only when the plant experiences its threshold daylength. Kouressy *et al.* (1998) observed that traditional cultivars rely on sensitivity to daylength to adapt their growth cycle to the mean growing season length of their area of origin, which can vary from as little as 60 days in desert margin areas in northwestern India to as long as 180 days in the northern Guinea zone of West Africa.

Kouressey *et al.*, 1998 revealed that the adaptation to season length is critical as potential evaporation rates are high (6-9 mm d^{-1}) and soil moisture storage often limited, meaning that flowering too late involves a serious risk of severe drought stress during grain filling. Flowering too early, however, also has various risks, including poor seed set if flowering occurs during the heaviest part of the rainy season (due a combination of failure of anther dehiscence under highly humid conditions and physical damage to receptive stigmas and/or grounding of the pollen cloud by falling rain drops), and insect, disease and bird damage if grain filling occurs before the end of the rains.

2.15.2.2. Adaptation to variable moisture environments

As much or more than adaptation to overall season length, pearl millet needs adaptation to periods of inadequate soil moisture at almost any time during the growing season. The

crop appears to depend upon a largely opportunistic strategy to reproduce, which is consistent with its evolution in a highly unpredictable environment This strategy combines: (i) short critical growth stages with a high photosynthetic and a high growth rate, to maximize growth during periods of favorable soil moisture with (ii) a surprising degree of developmental plasticity for a cereal, to allow it to rapidly compensate for periods of lost development/growth due to drought stress, and with (iii) a reasonable ability to avoid/tolerate high canopy temperatures resulting from reduced transpiration

2.15.2.2.1. Length of critical growth phases

The growth cycle of the pearl millet is conveniently divided into three growth stages (GS) (Maiti and Bidinger, 1981) The vegetative stage (GS 1) varies from as little as 25% to as much as 65% of the total crop cycle, depending upon the time to floral induction, whereas both the floral morphogenesis (GS 2) and grain filling stages (GS 3) are of fixed duration and are relatively short Bellhard and Pernes (1984) observed that GS 1 is technically composed of a juvenile phase from germination to the point at which the plant is capable of undergoing floral initiation if environmental conditions are inductive and a latency phase between the end of the juvenile phase and actual floral initiation

Dancette (1983) studied that the floral morphogenesis stage (GS 2) between floral initiation and actual flowering, during which apical primordia develop reproductive structures, and existing vegetative primordia complete development The short duration of GS 2 allows the plant to complete this critical growth stage on a relatively small amount of available moisture

The length of GS 3 is from flowering until physiological maturity of the grain Stress during grain filling GS 3 is likely if the rains terminate earlier than the normal date

and the rains during the main part of the season have been insufficient to recharge the soil profile. The combination of a short GS 3 with an appropriate time of flowering for the local conditions provides a reasonable level of adaptation to the effects of stress during grain filling (Craufurd and Bidinger, 1988b; Huda, 1987; Ong, 1983a).

2.15.2.2.1.1. Drought escape

Because of the short length of its GS 2 and GS 3 growth stages, drought escape is a major factor determining relative pearl millet cultivar performance in individual stress environments (Bidinger *et al.*, 1987a), and is often a major cause of G × E interaction in multi-environment trials (van Oosterom *et al.*, 1996b). Bidinger *et al.* (1987b) found that the assessment of true field drought tolerance or susceptibility in pearl millet (as distinct from drought escape) requires that the effects of differential drought escape among cultivars be considered, as these often account for a greater fraction of the observed genotype performance than do differences in tolerance itself.

Mahalakshmi *et al.* (1987) studied that the general effects of the timing of single periods of stress, both before and after flowering in pearl millet. They reported that early genotypes that flowered 20 days before the onset of a terminal (unrelieved, end-of-season) drought stress had four-fold lower yield reduction (12% *vs.*51%) than later flowering genotypes that flowered only 10 days before the onset of the same stress.

2.15.2.2.2. Developmental asynchrony and plasticity

Pearl millet effectively utilizes its developmental asynchrony, almost certainly inherited from its wild progenitors, to adjust to periods of moisture stress prior to flowering that affect normal development and growth. Primary tillers in pearl millet appear at approximately 45-50 degree day intervals (Craufurd and Bidinger, 1988b; Ong, 1984), or

approximately every 3 days at a mean temperature of 25°C Secondary tillers are produced from primaries at similar rates, resulting in a potentially very large number of tillers, all at different stages of development (*e g*, leaf number), in a very short period (Lambert, 1983, Ramond, 1968)

Craufurd and Bidinger (1989) observed that floral initiation among these tillers is not synchronous, although the interval between tiller appearance and floral initiation (GS 1) does decline somewhat in higher order tillers, compared to lower order ones In contrast, the length of the period between floral initiation and flowering (GS 2) is similar for all tillers, which results in tillers that are at different stages of apical development at any given time in GS 2 (Craufurd and Bidinger, 1988b)

Mahalakshmi *et al* (1987) found that there is considerable circumstantial evidence that the sensitivity to drought stress prior to flowering (in terms of subsequent yield loss) increases in more advanced stages of apical development Shoots with a vegetative apex appear to have the ability to arrest development during a period of severe stress and resume development upon the relief of the stress with little effect on overall productivity, if there is sufficient moisture to complete subsequent development (Mahalakshmi and Bidinger, 1985a) Similarly, shoots whose apices are in early stages of panicle development appear to be less affected by stress than those in later stages (Mahalakshmi and Bidinger, 1985b) This probably occurs because floral primordia are in developmental, rather than growth stages (Craufurd and Bidinger, 1988b) and are less ected by the reduction in assimilate supplies as a consequence of stress

Therefore later-developing tillers are likely to be less affected by stress prior to wering than are main shoots and early tillers In addition, later tillers will have a longer

period of recovery, if the stress terminates before flowering, to expand new leaves and produce sufficient assimilate to support full panicle growth.

In addition to direct effects of stress on shoot growth, reduced internode and leaf area expansion, failure of spikelets and florets to complete development, etc., pre-flowering stress appears to alter the normal hierarchy among shoots. In the absence of stress, the main shoot itself (in longer duration, African cultivars) or the main shoot plus the primary tillers (in shorter duration, Indian cultivars) dominates the later developing tillers, resulting in the latter failing to continue growth and to produce a panicle (Craufurd and Bidinger, 1988a; Ong, 1984).

This response provides the opportunity for replacing grain yield lost to the stress on the more advanced main shoot (and first tillers) that have been seriously affected by stress, with an increased yield from less advanced, later-flowering tillers, which have been less affected by the stress (Mahalakshmi and Bidinger, 1986). As a consequence, grain yield in pearl millet is often little affected by a mid-season stress, provided that there is sufficient time and moisture, after the end of the stress period, for later developing tillers (including those which arrested development in a vegetative stage) to reach maturity (Mahalakshmi and Bidinger, 1985b; van Oosterom *et al.*, 2002).

2.15.2.2.3. Drought avoidance, tolerance and water use efficiency

2.15.2.2.3.1. Water uptake

Gregory (1986) observed that pearl millet is capable of producing a very extensive root system under favorable conditions, due to relatively rapid root extension rates driven by the favorable temperatures in tropical soils. Mean root penetration rates of 3.5 cm d^{-1} (Chopart, 1883) to 4.5 cm d^{-1} (Azam Ali *et al.*, 1984) have been measured in sandy soils

under field conditions, with maximum rates approaching 7 cm d^{-1} (Azam Ali *et al.*, 1984).

Active root growth continues to at least flowering in short duration Indian cultivars (Gregory and Squire, 1979) and through grain filling in longer duration West African cultivars, although at reduced rates (Chopart, 1983; Winkel and Do, 1992). In addition, (Squire *et al.*, 1987) there is evidence that there is considerable plasticity in the ratio of root growth to shoot growth in response to increasing aridity of the above ground environment, to support continued water uptake from the soil.

2.15.2.2.3.2. Control of water loss

Stomatal conductance in well-watered pearl millet appears to respond to variation in potential evaporation in such a way as to keep canopy transpiration at as high a level as possible, consistent with maintaining leaf water potentials at favorable levels (Squire, 1979; Henson and Mahalakshmi, 1985). When soil water becomes seriously limiting to transpiration, stomatal opening in response to irradiance is only partial, and closure occurs progressively earlier in the day (Azam Ali, 1983; Do *et al.*, 1996; Henson *et al.*, 1982a), associated with loss of leaf turgor (Henson *et al.*, 1982a). Senescence of older, lower leaves in the canopy and later-developing tillers begins in these conditions, reducing the total crop transpiration, and helping to maintain the water status of the younger, more photosynthetically efficient leaves in the upper canopy (Do *et al.*, 1996; Wallace *et al.*, 1993).

Henson *et al.* (1983) reported the differential sensitivity of pearl millet stomata to water stress before and after flowering, at similar water potentials. Differences in conductance pre- and post-flowering were not explained by differences in turgor, but

were related to lower levels of abscisic acid (ABA) in the leaves of post-flowering plants. This is possibly due to enhanced ABA export associated with enhanced carbon export from the leaves to the developing grain in post-flowering plants (Henson and Mahalakshmi, 1985). This response is consistent with the perception of pearl millet as pursuing a strategy to maximize assimilation, particularly in its most critical growth stage (grain filling).

2.15.2.2.3.3. Water use efficiency

Estimation of water use efficiency (WUE) for pearl millet under typical growing conditions is complicated by two factors: the weak relationship between dry matter and evapotranspiration (ET) in sparse canopies with low percentage ground cover (Payne, 2000), and by the effects of high vapor pressure deficits (VPD) on WUE (Squire *et al.*, 1987). Payne (2000) reported that there are major opportunities to enhance field water use efficiency in such sparse canopy crops by increasing crop growth by improving nutrient supply and increasing plant population. The other factor that reduces WUE of pearl millet in arid environments is a high ambient VPD, which can have a significant effect on WUE (Squire *et al.*, 1987).

2.15.2.2.3.4. Drought and high temperature tolerance

Osmotic adjustment has been shown to occur in pearl millet, but actual changes in osmotic potential under field conditions in several breeding lines were too small to significantly lower the water potential at which turgor became negligible (Do *et al.*, 1996; Henson, 1982; Henson *et al.*, 1982b).

Pearl millet is known to have high optimum (30-35°C) and high maximum (>40°C) temperatures for various physiological processes, including germination (Garcia-

Huidobro *et al.*, 1982), leaf extension (Ong, 1983c), stem elongation (Squire, 1989), photosynthesis (McPherson and Slatyer, 1979). This would be expected from its arid zone origins, and would provide adaptation to the maximum temperatures common it the areas in which it is grown. Genetic differences in optimum/maximum temperatures for germination and vegetative growth have been reported (Mohammed *et al.*, 1988a,b), and suggested useful physiological mechanisms of adaptation or tolerance to high temperature.

2.15.3. The physiological basis of yield determination

2.15.3.1. Biomass productivity

Total biomass productivity in pearl millet, as in any crop, is a product of growth rate and growth duration. Under favorable environmental conditions, the crop has very high potential growth rates (Begg 1965) as it is a C4 cereal, with relatively erect canopy, a potentially high leaf area index (LAI) due to its tillering habit (Begg 1965; Craufurd and Bidinger, 1989), a good radiation use efficiency (Squire *et al.*, 1986), plus a high temperature optimum for assimilation (McPherson and Slatyer, 1979).

These characteristics make it well able to use the high levels of incoming solar radiation characteristic of arid and semi-arid tropical environments. As a consequence, crop duration (combined with environmental/management factors) is more likely to be the major determinant of total biomass productivity than are genetic differences in radiation interception or radiation use efficiency.

2.15.3.1.1. Early canopy development

Early establishment of a leaf area sufficient to intercept a majority of the incoming radiation is essential for producing a large crop biomass (Garcia-Huidobro *et al.*, 1982).

The individual component processes of establishment of an early crop canopy (germination, leaf emergence and leaf extension) have relatively high rates in pearl millet. For example, germination requires a thermal time of less than 20°C days over a relatively wide range of temperatures in pearl millet, from a minimum of about 12°C to a maximum of 48°C, Seedling emergence is equally quick, requiring as little as 30°C days over the estimated base temperature of 10°C (Ong and Monteith, 1985), or approximately 3 calendar days at optimal soil temperatures. Individual leaves are produced at 30-35°C day intervals (Craufurd and Bidinger, 1988b; Ong, 1984), and leaf growth rates are in the range of 7-10 mm per hour at optimum temperatures (Ong, 1983c).

This strategy has a significant cost in terms of early canopy development–LAI and fractional radiation interception in the crop are very small until about 20 days after emergence when individual main shoot leaf size begins to increase and tiller leaf area begins to develop (Craufurd and Bidinger, 1989).

There is genetic variation in early leaf area development (Mohammed *et al.*, 1988b), possibly based on genetic differences in base temperature for this process, but this has not been intentionally exploited. In favorable environments, increasing plant populations provides an effective adjustment mechanism to compensate for slow individual plant leaf area development (Carberry *et al.*, 1985; Craufurd and Bidinger, 1989), but this strategy is less applicable in low fertility, moisture deficit environments.

2.15.3.1.2. Vegetative growth

Pearl millet's major means of developing a full plant canopy is through its tillering ability. The first tiller generally appears in the axial of the third leaf, at approximately 200°C days after emergence, with subsequent primary tillers appearing at 45 to 50°C day

intervals (Craufurd and Bidinger, 1988b; Ong, 1984). Secondary tillers are produced from primaries at similar rates, resulting in a total tillering capacity that can reach 50 per plant, given adequate water, nutrients, and space (Craufurd and Bidinger, 1989; Ramond, 1968).

2.15.3.2. Biomass partitioning

Harvest index (HI) in pearl millet tends to vary inversely with total biomass production, and hence also to vary inversely with season length. HI can exceed 0.40 in short duration cultivars and drop to as low as 0.15 in traditional, long duration, photoperiod-sensitive West African cultivars. This is because daylength-mediated increases in crop duration occur almost entirely in the vegetative period, prior to floral initiation (Carberry and Campbell, 1985; Craufurd and Bidinger, 1988b). Increases in the duration of vegetative growth stages result in the formation of additional vegetative sinks, mainly additional stem internodes, and additional secondary and tertiary tillers (Carberry and Campbell, 1985; Craufurd and Bidinger, 1988b). The increases in biomass productivity are therefore largely in the form of additional vegetative biomass rather than reproductive biomass, with limited effect on grain yield potential, and consequently with a negative effect on harvest index. In addition, in most quantitative daylength-sensitive genotypes, an increase in the vegetative period enhances main shoot advantage over tillers, probably due to a combination of the increased sink size of the main shoot, and the fact that stem internode growth begins earlier in the main shoot than in the tillers (Craufurd and Bidinger, 1988b). As a result, increases in main stem biomass (and in grain number in the main stem panicle) are largely offset by decreases in productive tiller number, total tiller biomass and tiller grain number (Carberry and Campbell, 1985; Craufurd and Bidinger, 1988b).

2.15.3.3. Grain yield

Grain yield in pearl millet is primarily a function of grain number per unit area (Bidinger *et al.*, 2001; Craufurd and Bidinger, 1989), as in other cereals. Grain numbers produced are related to crop growth, and ultimately to radiation interception, during GS2–the period between floral initiation and flowering (Craufurd and Bidinger, 1989; Ong and Squire, 1984). Potential crop growth during this period is a function of the length of the period, in thermal time (Ong, 1983b), and the amount of radiation intercepted per unit thermal time (Squire *et al.*, 1986). There are therefore opportunities for increasing grain numbers (and potentially grain yield) though increasing the leaf area index and the fractional radiation interception at floral initiation, and by increasing the duration of GS 2. Ong and Monteith (1985) observed that the temperature during GS 2 also affects the numbers of calendar days required to complete the growth stage, and hence in radiation intercepted during the stage.

Less is known about the genetic opportunities to extend the length of the period between floral initiation and flowering itself. There is limited genetic variation for this (Bidinger, pers.comm.) and divergent selection for differences in the length of this period was effective in increasing grain numbers in an exploratory experiment (Bidinger pers.comm.). However increases in grain yields resulting from increasing grain numbers by various manipulations have not been proportional to the increase in grain numbers, as individual grain mass is commonly reduced in response to an increase in grain numbers (Alagarswamy and Bidinger 1985; Bidinger *et al.*, 2001; Craufurd and Bidinger, 1989).

In practice, however, grain and biomass yields of pearl millet are much more likely to be limited by low plant population densities (McIntire and Fussell, 1989; Payne,

1997), which limit radiation interception, and by nutrient and water stress, which limit radiation and water use efficiencies (Payne, 2000), than by a limited genetic yield potential.

2.15.3.4. Terminal drought tolerance

Pearl millet is grown almost entirely as a rainfed crop in areas where inter- and intra-seasonal variation in rainfall is the single most important factor that limits its productivity. Although drought stress can occur any time during the crop cycle, terminal stress (flowering through grain filling) is more damaging to the productivity of the crop than stress at the vegetative or pre-flowering reproductive stages (Mahalakhsmi *et* al., 1987). Post-flowering drought stress is one of the most common and serious environmental constraints in these regions (van Oosterom *et al.*, 1996a), reducing mean yields and increasing the magnitude of the annual variation in harvests and the incidence of crop failure (Ceccarelli and Grando, 1996). In general the early stages of plant development of pearl millet are less sensitive to drought because the crop has the ability to recover quickly and fully when water becomes available (Bidinger *et al.*, 1987a, Mahalakhsmi *et al.*, 1987).

Improving the adaptation of pearl millet to terminal drought stress environments is therefore a major objective in ICRISAT's breeding programme aimed at improving the crop's productivity and yield stability.

MATERIALS AND METHODS

CHAPTER III

MATERIALS AND METHODS

3.1. Marker-Assisted Selection (MAS)

3.1.1. Mapping population

Two agronomically elite inbred seed parents ICMB 841 and 863B were crossed to develop a segregating population for genetic linkage map construction and trait analysis. The two parents are known to produce hybrids that distinctly differ in their response to post-flowering stress (F.R. Bidinger, pers. comm.). Parent 863B (Andrews and Anand kumar, 1996) was bred from *Iniadi* landrace material from Togo and was selected for this study based on its combination of agronomic eliteness and superior combining ability for grain filling under terminal drought stress conditions. Parent ICMB 841 (Singh *et al.*, 1990) is the maintainer of the female parent of several high yielding hybrids that are widely grown in India, but lack tolerance to terminal drought stress.

The $F_{2:3}$ segregating population was developed from the cross between ICMB 841 and 863B at ICRISAT, Patancheru, India and the Institute of Grassland and Environmental Research (IGER), UK contributed to genotyping the F_2 population, phenotyping its testcross hybrids, and QTL mapping with the combined data set to tag genes that control terminal drought tolerance (Yadav *et al.*, 2004).

Single plants of the two parental lines were crossed to produce a single F_1 plant that was self-pollinated to produce a large number of F_2 seeds. One hundred and fifty one of these were picked at random to produce the genetic linkage map necessary for QTL analysis (Fig. 1). A random subset of 79 F_2-derived F_3 progenies was testcrossed to two

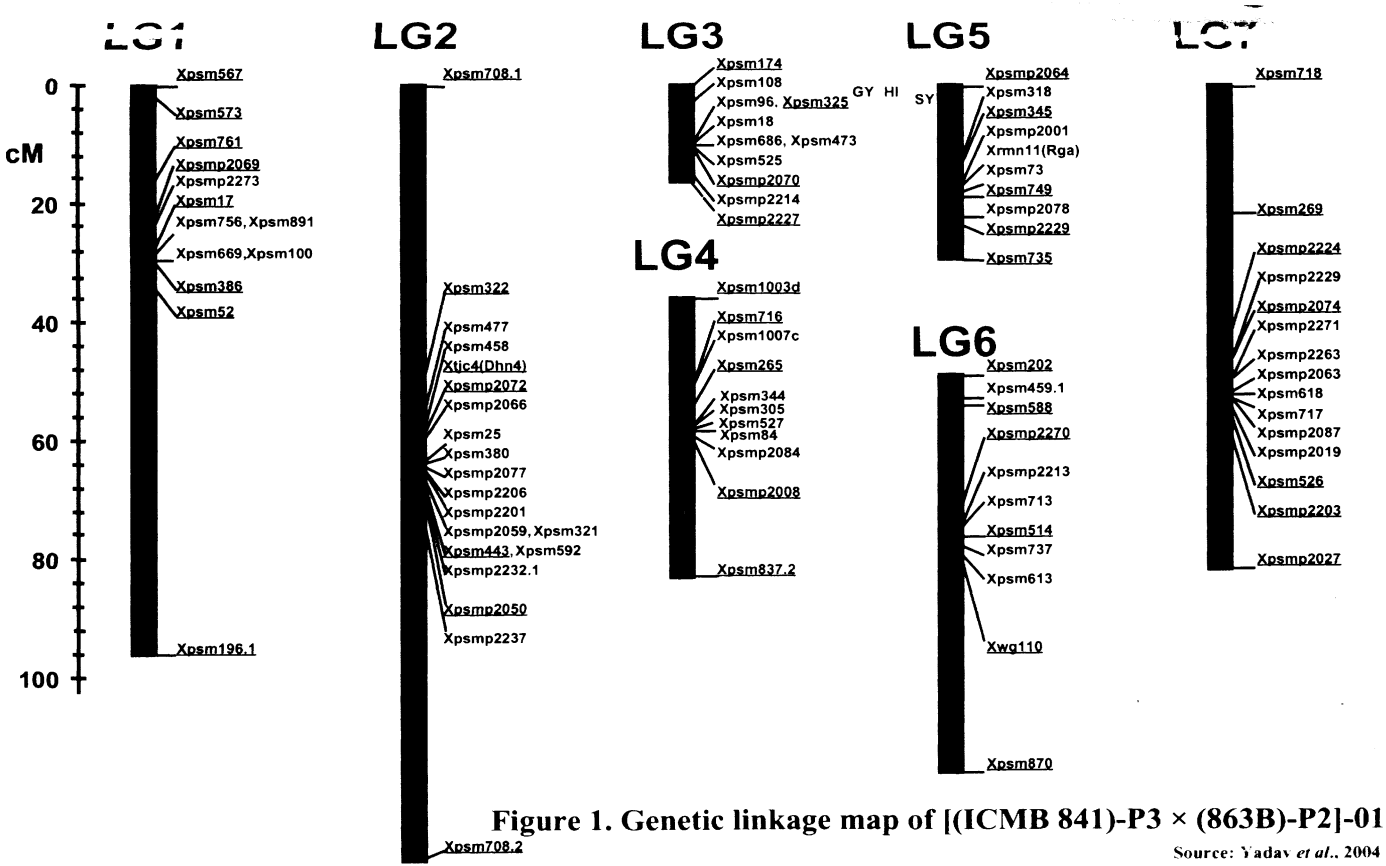


Figure 1. Genetic linkage map of [(ICMB 841)-P3 × (863B)-P2]-01

Source: Yadav *et al.*, 2004

unrelated elite testers H 77/833-2 and PPMI 301 to produce two paired sets of mapping population testcrosses that were used for phenotyping (Fig. 2).

Several mapping population progenies were selected as donors based on their homozygous donor allele marker genotypes in genomic regions identified from preliminary QTL mapping results and immediately backcrossed to ICMB 841 (recurrent parent) to produce the BC_1F_1 generation. In each of these mapping population progeny backcrosses donor parent 863B marker alleles were expected to be heterozygous so that backcrossing the BC_1F_1 plants directly to produce BC_2F_1 progenies expected to segregate 1:1 for 863B alleles in a small number of the target region. Hence around 15-20 BC_1F_1 plants were genotyped in each of two progenies the segregation pattern for each donor parent. Based on the marker data segregate 1:1 for 863B alleles a small number of selected progenies were advanced to the BC_2F_1 generation and then to BC_3F_1 generation. The present study was initiated with, genotyping of BC_3F_1 individuals using RFLP and microsatellite markers.

3.1.2. Molecular marker analysis

3.1.2.1. RFLP analysis

3.1.2.1.1. DNA extraction

Dark-grown, young seedlings (etiolated) or soft, non-green, stem internode tissues are generally used to isolate genomic DNA as they yield DNA with better restriction enzymes digestibility because of lower concentrations of phenolics and other adhering compounds than do green tissues. Several procedures for genomic DNA isolation have been reported, but results obtained by the protocol given by Sharp *et al.* (1988) were most

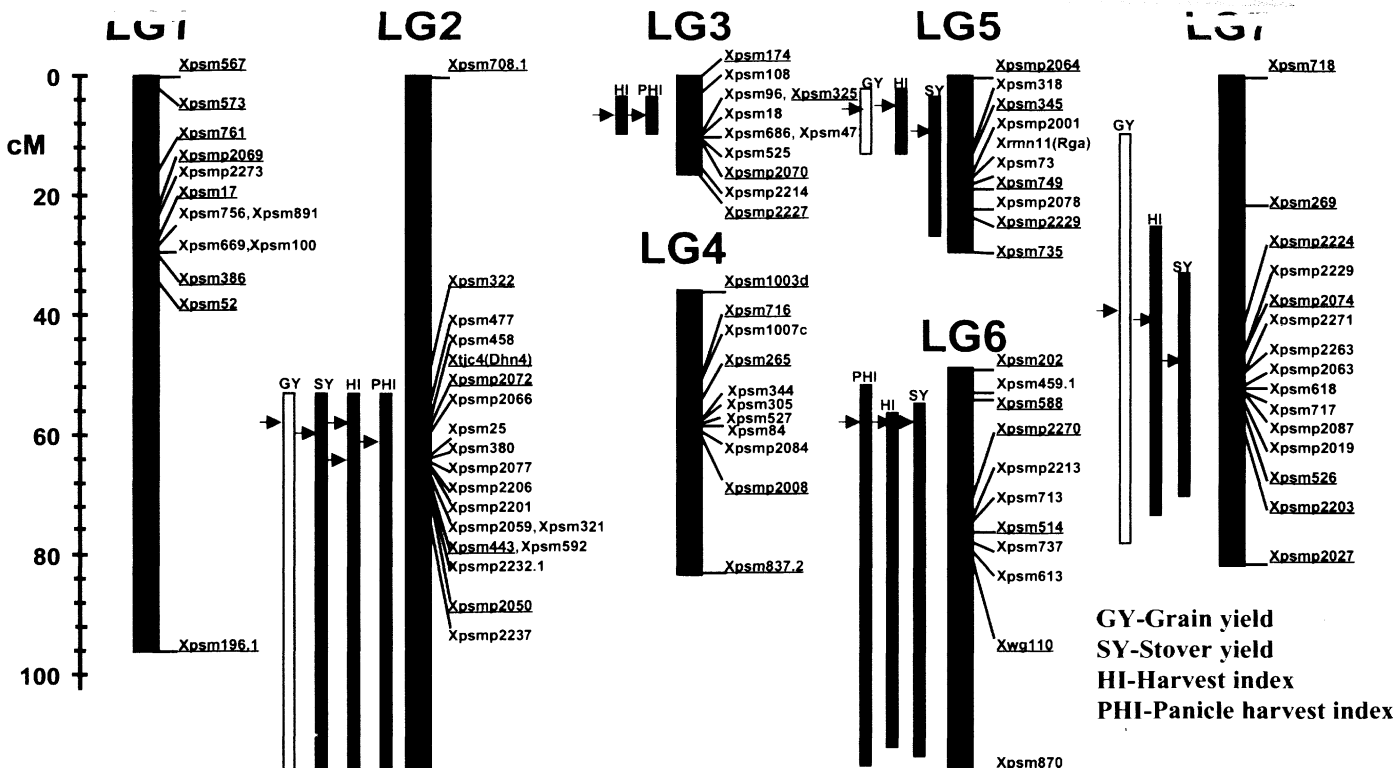


Figure 2. QTLs associated with morphological characters [(ICMB 841)-P3 × (863B)-P2]-01

Source: Yadav *et al.*, 2004

satisfactory. The quality and quantity of DNA were checked by agarose gel electrophoresis. The final DNA concentration was adjusted to 1 $\mu g/\mu l$.

3.1.2.1.2. Restriction enzyme digestion

Twenty μg of DNA with sterile distilled water was digested with *Dra*I, *Eco*RI, *Eco*RV and *Hind*III restriction endonucleases following the endonucleases supplier's instructions (Amersham Pharmacia Biotech, Ltd.). The digestion was performed in a total volume of 30 μl and the reaction was terminated by addition of 3 μl of loading buffer (25% sucrose, 0.1% bromophenol-blue and 20 mM EDTA) to each 30 μl sample.

3.1.2.1.3. Electrophoresis

Fragments of digested DNA obtained after enzyme digestions were separated by electrophoresis unit (Owl Separation Systems Model No. A-1) for 16 h at 38 V/cm in TAE (0.04 M Tris-acetate, 0.001 M EDTA, pH 7.8) buffer. Gels were prepared in the same buffer that was used for electrophoresis. *Hind*III digested Lambda DNA (λ DNA) was used as molecular size markers. Gels were stained in 0.5 μg/ml ethidum bromide for 15 min, destained for 30 min in distilled water, viewed on a UV-transilluminator and photographed to assess the quality of digestion.

3.1.2.1.4. Southern blot hybridization

3.1.2.1.4.1. Preparation of southern blots

DNA fragments obtained after digestion were transferred from agarose gels onto nucleic acid transfer membranes (Hybond-N^+, Amersham Pharmacia Biotech, Ltd.) following the procedure of Reed and Mann (1985). Transferred membranes were soaked in 2xSSC for 2 min to neutralize the alkali, air dried and wrapped with cling film and stored at −20°C for future use.

3.1.2.1.4.2. Labeling of probes

The random-primed method of Feinberg and Vogelstein (1983) was used for labeling DNA with α-^{32}P. Purified insert DNA was denatured by heating at 95°C for 10 min. quenched on ice for 5 min before the labeling reaction mixture was added and incubated at 37°C for 3 hours. The reaction was terminated by adding 2.5 μl of 3 M NaOH to use in hybridization step.

Labeling reaction mixture: 5 μl of oligo-labeling buffer (Amersham Pharmacia Biotech, Ltd:), 2 μl equimolar concentrations of dCTP, dGTP, dTTP, 2 μl (10 mg/ml) acetylated BSA, 5 μl of 50 μCi ^{32}P-dCTP and 2 units of Klenow enzyme.

3.1.2.1.4.3. Hybridization to labeled probes

3.1.2.1.4.3.1. Prehybridization

Southern blots were prehybridized at 65°C with 5 ml of prehybridization solution (3 ml of 5xHSB, 1.5 ml of denatured salmon sperm DNA and 1.5 ml of Denhardt's solution and sterile distilled water to 15 ml) for six hours in case of new blots and one hour for stripped blots. Prehybridization was performed in a Techne Hybridizer (HB-1D).

3.1.2.1.4.3.2. Hybridization

Labeled probe was added to the prehybridization mixture and incubated at 65°C in a hybridization oven for at least 16 hours. Care was taken to remove air bubbles present between the blot and the hybridization bottle.

3.1.2.1.4.3.3. Washing of blots

Following hybridization, the blots were washed following four changes of 50 ml each of ^{32}P wash solutions. Each wash was conducted for 15 min at 65°C in hybridization bottles using hybridization oven. The first two washes were done using wash 1 solution (100 ml

20xSSC, 25 ml 20% SDS and distilled water to 1lit). The second two washes were done using wash 2 solution (10 ml 20xSSC, 25 ml 20% SDS and distilled water to 1 lit). Membranes were air dried and enclosed in cling films.

3.1.2.1.4.3.4. Autoradiography

Autoradiography was conducted at –70°C by exposing the membrane to photographic film (Kodak, X-OMAT™, XK-5) using Kodak intensifying screens in a cassette for various exposure times depending on counts. The X-ray films were developed by a stop bath (1% acetic acid) treatment for 1 min fixed with Kodak fixer for 2 min, washed in running tap water and air-dried. The autoradiograms were photographed using Kodak 100 ASA color films.

3.1.2.1.4.3.5. Scoring RFLP bands

The co-dominantly inherited bands in the autorads were scored as A, B, H, and "—" based on their pattern compared with those of the parents. "A" was defined as the presence of homozygous alleles from the donor parent (863B), "B" was defined as the presence of homozygous alleles from ICMB 841, "H" was defined as the heterozygote (presence of both recurrent and donor parent alleles) shown in Plate 1 and "—" was a missing sample.

3.1.2.2. SSR analysis

3.1.2.2.1. DNA isolation

Based on Mace *et al.* (2004) a 96–well plate mini DNA extraction protocol was employed. For this, DNA was extracted from one-week-old seedlings using a modified CTAB method. DNA was further purified by RNase digestion followed by extraction with phenol/chloroform/iso-amyl alcohol and ethanol precipitation.

3.1.2.2.1.1. Preparation

Pre-chilled steel balls (2 per extraction tube), kept at –20°C for about 30 minutes, were added to the extraction tubes which were held on ice. Before the start of tissue sample collection 3% CTAB buffer (3%w/v CTAB, 1.4 M NaCl, 20mM EDTA, 100mM Tris-Hcl, pH 8.0, 0.17% β-mercaptoethonol) was pre-heated in 65°C water bath. Six-inch long leaf strips were collected (final weight 30 mg) from one-week-old seedlings cut into pieces (1 mm in length). These strips were transferred to the extraction tubes.

3.1.2.2.1.2. Grinding and extraction

Pre-heated 3% CTAB buffer (450 µl) was added to each extraction tube containing leaf tissue samples. Tissue sample grinding was performed on paired 96–well boxes of extraction tubes using the Sigma GenoGrinder at 500 strokes/min for 2 min. Positions of the boxes were then swapped and grinding repeated for another 2 minutes. Grinding was repeated until the color of solution in all tubes was pale green and leaf strips were sufficiently macerated to permit release of DNA into the extraction buffer. After grinding, the tube box was fixed in a locking device and incubated at 65°C in a water bath for 10 min with occasional manual shaking.

3.1.2.2.1.3. Solvent extraction

450 µl of Chloroform:Iso-amyl alcohol (C:IAA=24:1) mixture was added to each tube and the samples were centrifuged at 6200 rpm for 10 min. After centrifugation approximately 300 µl of the aqueous layer was transferred to a fresh tube.

3.1.2.2.1.4. Initial DNA precipitation

To the aqueous layer in each fresh tube, approximately 210 µl of cold (–20°C) isopropanol was added, then the solution was carefully mixed and the tubes were kept at

–20°C for 10 min. The samples were centrifuged at 6200 rpm for 15 minutes. The supernatant was decanted under a fume-hood and the pellets were allowed to air dry for at least 20 minutes.

3.1.2.2.1.5. RNase treatment

To remove RNA, 200 µl of low salt TE buffer and 30 mg of RNase (stock 10 mg/µl) were added to the dry pellet in each tube and mixed properly. The solution was incubated at 37°C for 30 minutes.

3.1.2.2.1.6. Solvent extraction

After incubation, 200 µl of Phenol–Chloroform–IAA (25:24:1) mixture was added to each tube, carefully mixed, and centrifuged at 5000 rpm for 10 minutes. The aqueous layers were transferred to fresh tubes and the step was repeated with the chloroform:IAA (24:1) mixture.

3.1.2.2.1.7. DNA precipitation

To the tubes containing aqueous layer 15 µl (approximately $1/10^{th}$ volume) 3 M sodium acetate and 300 µl (2 vol) 100% ethanol was added and subsequently placed in freezer for 5 minutes. Following incubation, box was centrifuged at 6200 rpm for 15 minutes.

3.1.2.2.1.8. Ethanol wash

After centrifugation supernatant was carefully decanted and to the pellets 200 µl of 70% ethanol was added and centrifuged at 5000 rpm for 5 minutes.

3.1.2.2.1.9. Final re-suspension

Pellets were obtained by carefully decanting off the supernatant and allowed to air dry for an hour. Completely dried pellets were resuspended in 100 µl of $T_{10}E_1$ buffer and kept at room temperature to dissolve completely. Dissolved DNA samples were stored at 4°C.

3.1.2.2.2. Checking DNA quality and DNA concentration

The quality and quantity of DNA isolated from each tissue sample were checked using agarose gel electrophoresis. The final DNA concentration was adjusted to 5 ng/μl by dilution of each sample with an appropriate volume of $T_{10}E_1$ buffer.

3.1.2.2.3. Amplification of SSR markers

A set of 78 pearl millet SSR primer pairs received from John Innes Centre, UK (Table 1) was used for PCR amplification using DNA from the parents as template in order to identify polymorphic SSR markers that could be used for marker assisted selection in this study. The PCR reactions were performed in volumes of 20 μl containing 15 ng genomic DNA, 30 ng/μl each of forward and reverse primers, 2 mM dNTPs, 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 50 mM $MgCl_2$, and 0.5 unit of *Taq* DNA polymerase. The annealing temperature for PCR amplification was maintained based on the specificity of the primer pair used.

PCR reactions were conducted in 96-well plates in a DYAD-Peltier DNA thermocycler (MJ Research) with a PCR profile of 94°C for 3 min followed by 34 cycles of 1 min for denaturation at 94°C, 1 min for annealing at 55°C to 67°C (specific to the primer pairs used), and 1.5 min for extension at 72°C followed by final extension for 4 min at 72°C.

If the parental polymorphism detected was more than 50 bp, then PCR products for the segregating backcross progenies were separated on 6% non-denaturing PAGE (Poly Acrylamide Gel Electrophoresis) gels and silver stained using the procedure of Panaud *et al.* (1996). If the polymorphism between the parents is less than 50 bp, then

PCR products were separated using 4% denaturing PAGE gels, and banding patterns of PCR products were once again visualized by silver staining.

3.1.2.2.4. Choice of the markers analyzed

Based on prior QTL mapping results, all available markers detecting polymorphism between the parents (863B and ICMB 841) were used for marker-assisted selection (Table 1). The polymorphic markers in linkage group 2 were used for foreground selection for the putative drought tolerance QTL allele from donor parent 863B.

3.1.2.2.5. Non-denaturing PAGE (Poly Acrylamide Gel Electrophoresis)

The total PCR product was mixed with 5 µl of loading dye (orange red + EDTA + NaCl + glycerol). About 2 µl of PCR product was loaded into each well of the 6% non-denaturing PAGE gel. The various components of the gel include 52.5 ml of doubled distilled water, 7.5 ml of 10xTBE buffer, 15 ml of acrylamide:bis-acrylamide (29:1) solution, 450 µl of ammonium per sulphate (APS), 100 µl of TEMED and final volume will be around 75 ml.

Along with samples, 100 bp marker (50 ng/µl) was also loaded in the first and last lanes of the gel to ensure proper sizing of amplified PCR fragments. Most of the markers used allowed clear differentiation of donor and recurrent parent alleles. The gel was run at 550 V of constant power in 0.5xTBE buffer for 3 hours using a BioRad gel sequencing apparatus.

3.1.2.2.6. Denaturing gel electrophoresis

PCR products having less than 50 bp difference between the polymorphic alleles can be differentiated using 4% PAGE gels. The various components of the gel include 60 ml of 4% PAGE (210 g of urea, 25 ml of 10% TBE, 50 ml of acrylamide:bisacrylamide (19:1)

Table 1. RFLP and SSR marker loci detecting polymorphism between ICMB 841 and 863B on seven pearl millet linkage groups.

Linkage group (LG)	LG1	LG2	LG3	LG4	LG5	LG6	LG7
	*Xpsm*573	***Xpsmp*2072**	*Xpsm*174	*Xpsmp*2081	*Xpsmp*2202	*Xpsm*202	*Xpsm*718
	*Xpsm*761	***Xpsmp*2088**	*Xpsmp*2249	*Xpsm*716	*Xpsmp*2078	*Xpsm*508	*Xpsmp*2013
	*Xpsmp*2069	***Xpsmp*2066**	*Xpsmp*2267	*Xpsm*265	*Xpsm*318	*Xpsmp*2213	*Xpsm*269
	*Xpsmp*2273	***Xpsmp*2077**	*Xpsmp*2214	*Xpsmp*2076	*Xpsmp*2229	*Xpsm*713	*Xpsmp*2040
	*Xpsm*891	***Xpsmp*2255**		*Xpsmp*2084		*Xpsm*737	*Xpsmp*2063
	*Xpsm*100	***Xpsmp*2201**		*Xpsm*527.1		*Xpsm*613.2	*Xpsm*618
	*Xpsmp*2006	***Xpsmp*2059**		*Xpsmp*837.2		*Xpsm*870	*Xpsmp*2043
	*Xpsm*196.1	***Xpsm*592**					*Xpsmp*2087
		***Xpsm*708.2**					*Xpsmp*2019
							*Xpsm*526
							*Xpsmp*2203
							*Xpsmp*2027
Total RFLP loci	5	**2**	1	4	1	6	4
Total SSR loci	3	**7**	3	3	3	1	8
Total markers	8	**9**	4	7	4	7	12

Details of SSR primer sequence information, repeat type and annealing temperature, and RFLP probe restriction enzyme and the level of polymorphism between the parents are available at the MilletGenes website: http://jic-bioinfo.bbsrc.ac.uk/cereals/millets.html

***Xpsm* = RFLP loci; *Xpsmp* = SSR loci**

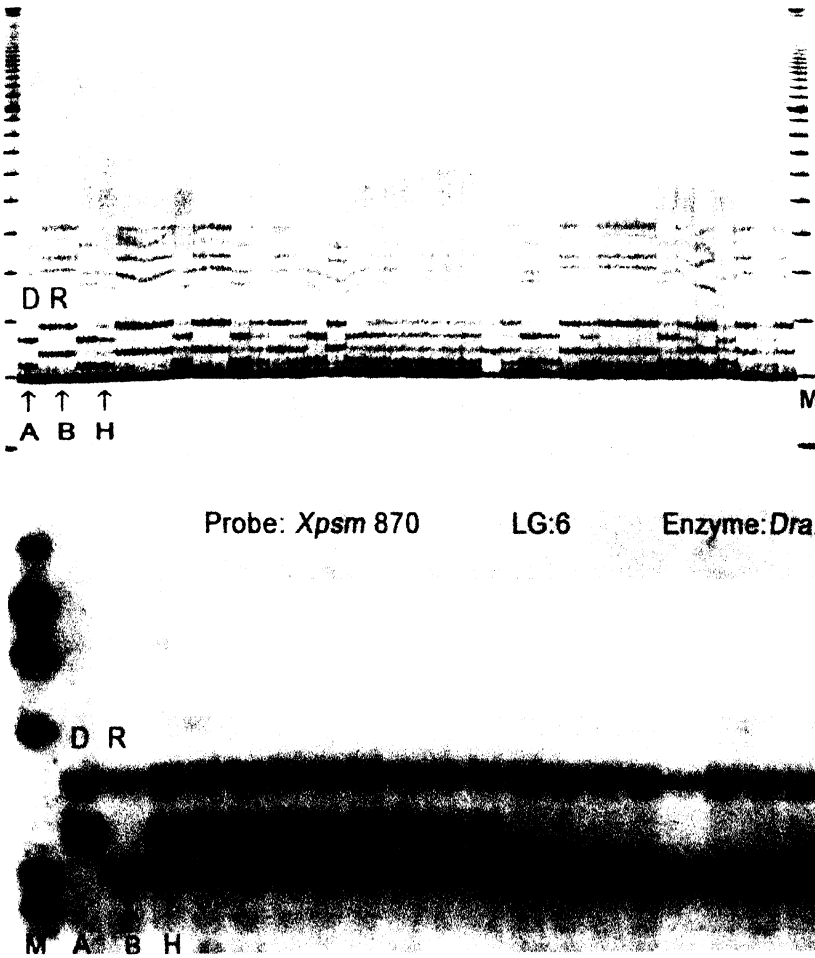
and final volume made up to 500 ml), 450 µl of APS and 45 µl of TEMED. The SSR amplified products were mixed with a loading buffer (98% formamide, 10 mM EDTA, 0.005% each of xylene cyanole and bromophenol blue as tracking dyes), denatured at 94°C for 5 min and run on 4% denaturing polyacrylamide gels containing 7 M urea at a constant current of 100W.

3.1.2.2.7. Silver staining

After running the PAGE gels for the required time, gels were developed by silver staining. Sequential steps involved in silver staining include washing in water for 5 min followed by washing with 0.1% CTAB solution for 20 min (2 g in 2 lit of water). The next step is washing with 0.3% ammonia solution for 15 min (26 ml of 25% ammonia solution in 2 lit of water) and this is followed by staining with 0.1% silver nitrate solution for 15 min (2 g of silver nitrate + 8 ml of 1 M NaOH in 2 lit of water and add ammonia solution until the solution becomes colorless). Developing was done with a developer solution (30 g of sodium carbonate + 400 µl of formaldehyde in 2 lit of water). After developing, the gels were rinsed in water for 1 min and placed for a few seconds in fixer solution (30 ml glycerol in 2 lit of water).

3.1.2.2.8. Scoring the gels

The bands in the gels were scored as A, B, H, and "—" based on their pattern compared with those of the parents. "A" was defined as the presence of homozygous alleles from the donor parent (863B), "B" was defined as the presence of homozygous alleles from recurrent parent ICMB 841, "H" was defined as the heterozygote (presence of both recurrent and donor parent alleles), shown in Plate 1 and "—" was a missing sample.



D = Donor parent = 863B
R = Recurrent parent = ICMB 841
H = Heterozygote
A = Homozygous for donor parent allele
B = Homozygous for recurrent parent allele
M = Marker

Plate 1. Segregation of polymorphic markers for *Xpsmp*2018 and *Xpsm*870 in the BC_3F_1 generation

3.2. Marker-Assisted Selection of backcross progenies

The sequence of MAS operations is presented in Table 2. The parent 863B was the donor of alleles increasing drought tolerance; ICMB 841 was the more elite recurrent parent. Selfed seed from all the backcross generations were used for tissue sampling for DNA isolation and marker analysis. The crossed seeds from selected individuals were advanced for further backcrossing. Full Marker-Assisted Selection (MAS) was used to select plants carrying ICMB 841 alleles and 863B alleles at markers flanking the non-target and target regions in the BC_3F_1, BC_4F_1 and BC_5F_1 generations. Partial MAS (foreground selection only) was used to select plants carrying the 863B alleles at markers flanking the target regions (LG2) in the BC_5F_2 and BC_6F_1 generations as background selection for ICMB 841 alleles in non-target regions of the remaining six pearl millet linkage groups has been completed in the BC_5F_1 generation.

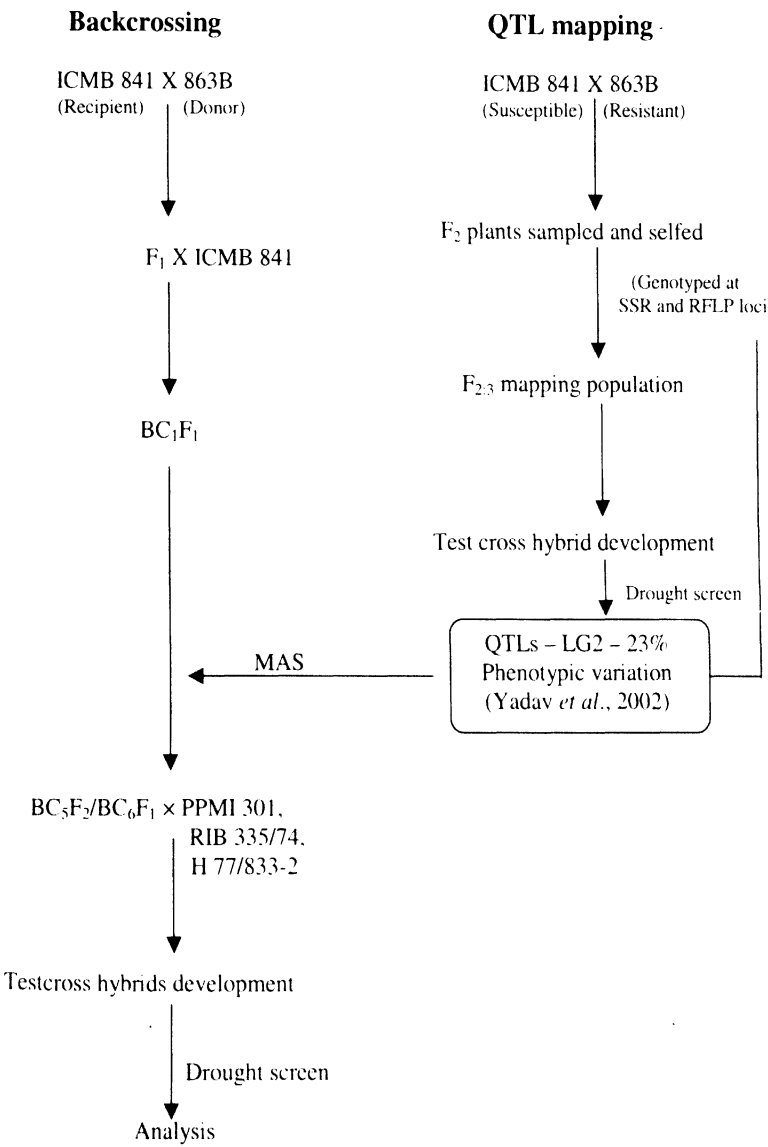
The schematic representation of the development of both BC_5F_2 and BC_5F_3 Near Isogenic Lines (NILs) using MAS at different generations is presented in Figure 3. In each generation up to BC_5F_1, progenies with the heterozygous condition in the target region of linkage group 2 and homozygous for ICMB 841 alleles in the remaining linkage groups (non-target regions) were selected. The BC_5F_2 plants were selfed and BC_6F_1 plants were backcrossed and screened for plants homozygous for the 863B allele at the target regions. In the BC_5F_2 and BC_6F_1 generation plants were selected if they fit one of three categories: 1) Homozygous for 863B alleles in the entire linkage group (LG2) 2) Homozygous for 863B alleles in the either on top or bottom of the LG2. 3) Homozygous for 863B alleles in the middle or based on the number of homozygous allele on the LG2.

Table 2. MAS operations in each generation.

Backcross Generation	Season	Type of MAS	Type of plants selected	No. of plants genotyped	No. of plants selected for further backcrossing
BC_3F_1	Kharif - 2002	*Full	Heterozygous	38	1
BC_4F_1	Rabi - 2002	Full	Heterozygous	202	2
BC_5F_1	Summer - 2003	Full	Heterozygous	36	11
BC_5F_2	Kharif - 2003	*Partial	Homozygous	218	4
BC_6F_1	Kharif - 2003	Partial	Homozygous	237	9
Hybrid development	Rabi - 2003	-	-	-	-
Drought nursery	Summer - 2004	-	-	-	-

* Full MAS = Selection for both foreground and background selection
* Partial MAS = Selection for foreground (LG2)

Figure 3. Schematic procedure for transfer of terminal drought tolerance QTLs by marker-assisted backcrossing



Based on these criteria, BC_5F_3 and BC_6F_2 progenies derived from BC_5F_2 and BC_6F_1 parents respectively, homozygous for donor marker genotype in genomic regions covering the linkage group 2 were selected (Fig 4).

3.3. Conventional backcross introgression

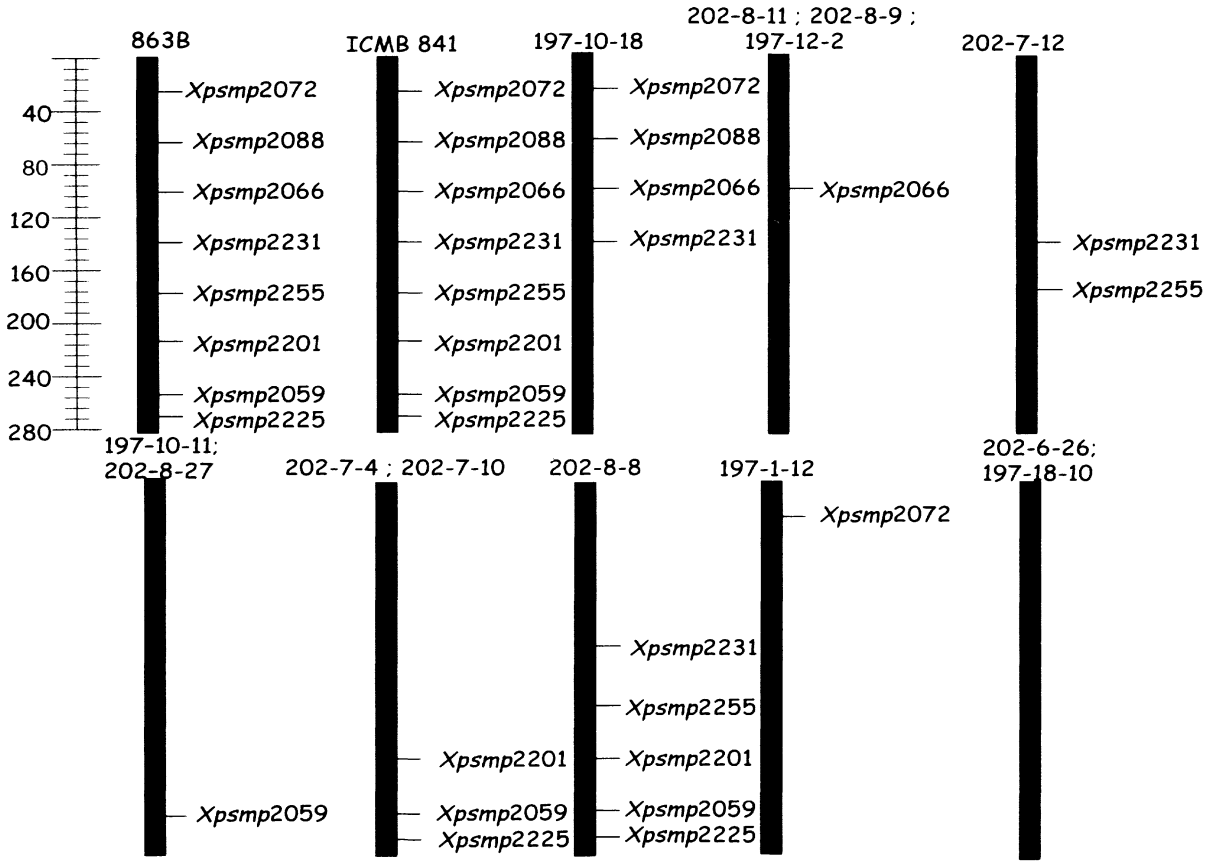
Conventional morphological marker-assisted selection also helped to transfer the genomic regions of interest to the desired recipient genome. In this method, the recurrent parent ICMB 841 was backcrossed to the selected progenies. The easily scorable morphological markers of the recurrent parent genome like hairiness of nodal ring (*Hn/hn*), leaf sheath and leaf blade (*Hl/hl*); green color of node (*Rn/gn*); and yellow color of anthers were used to select the progenies with the background genotype most similar to that of the recurrent parent. These characters helped to reduce the number of plants for backcrossing as well as for genotyping. In that way, the reduced number of each backcross generations was forwarded from BC_3F_1 to BC_6F_1 generation (Table 2).

3.4. Testcross hybrid development

The selected mapped progenies used for drought tolerance QTL mapping were phenotyped as testcross hybrids, rather than using their derived inbred progenies (Yadav *et al.* 2002, 2003, 2004) for several reasons:

1. To restore heterotic vigour to advanced generation backcross derived progenies that might otherwise be too weak for effective screening under stress conditions (pearl millet is highly cross-pollinated in nature and suffers considerably from inbreeding depression);
2. To use the dominantly inherited early flowering of the tester to reduce variation in flowering time among the testunits, in order to focus the marker-

Figure 4. Graphical representation of pearl millet linkage group 2 (LG2) for the selected 13 inbreds along with their donor parent 863B and recipient parent ICMB 841.



assisted selection on specific drought-tolerance traits rather than traits or responses associated with drought escape; and finally;

3. To have testunits that approximate the genetic structure of the F_1 hybrids grown by farmers rather than agriculturally irrelevant F_3 or F_4 inbred lines.

The selected BC_5F_2 progenies (and their donor and recurrent parents) were dusted with bulk pollen from each of the following three testers. Characters of these testers (and their released hybrids) helped to distinguish the reasons for their selection. The first tester RIB 335/74 is highly sensitive to drought. It is the male parent of released early-maturing hybrid RHB 30 (843A × RIB 335/74) developed at RAU, Durgapura. The second tester PPMI 301 is also sensitive to terminal drought stress. It is the male parent of released full-season hybrid Pusa 301 (841A × PPMI 301) developed at IARI, New Delhi. The third tester used for testcross hybrid development H 77/833-2 is the male parent of a number of thermo-tolerant, extra-early, high tillering and high-yielding pearl millet hybrids, including HHB 67 (843A × H 77/833-2; Kapoor *et al.*, 1989) developed at HAU, Hisar. HHB 67, which is widely cultivated in Haryana and the Thar desert margins of Rajasthan in northwestern India. These testcross hybrid seeds were harvested and sown for evaluation in the summer drought nursery at ICRISAT-Patancheru (Jan-April 2004).

3.5. Downy mildew screening

3.5.1. Inoculum

All experiments were carried out using an asexually-maintained pathogen population derived from plants infected with oospores from the ICRISAT field downy mildew nursery at Patancheru, India. The population was collected and maintained as described by Jones (1994) and Jones *et al.* (1995).

Infected leaves from mature plants of well known susceptible genotype 7042(S) were detached, wiped clean of any sporangiophores already present and incubated in darkness in plastic boxes for 8 hr at 20°C and 100% RH. The resulting sporangia were harvested by spraying leaves by de-ionized water and collecting the run-off. The sporangia produced from the leaves were harvested into chilled de-ionized water at approximately 1°C. Suspension was then adjusted to $1x10^5$ sporangia ml^{-1} with water at appropriate temperature. Spraying was carried out using the spray head of a hand-pumped 500 ml sprayer.

3.5.2. Disease incidence determination

40 seeds of all the entries along with parental lines in three replicates and standard checks including susceptible pearl millet genotype 7042(S) (Hash and Witcombe, 1994) were sown in 11.5 cm diameter plastic pots. Each pot was a replicate and there were two pot-replicates for each treatment. Pots were placed on flood benching in a completely randomized block under glasshouse conditions as described by Jones *et al.* (1995). Each pot of seedlings was sprayed at the coleoptile-to-one-leaf stage with approximately 4 ml of inoculum.

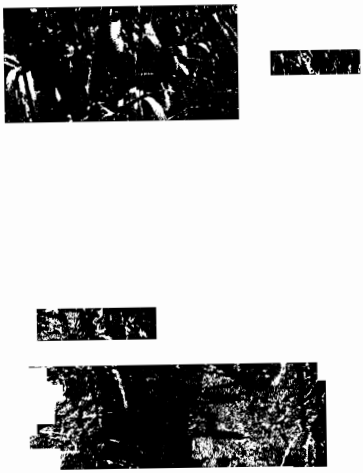
Following inoculation, the glasshouse bench was covered with polythene sheeting for 16-18 hr to maintain high humidity. Disease incidence (% of plants showing chlorotic symptom per pot) was assessed two weeks after inoculation based on number of diseased plants out of total number of plants in a pot.

3.6. Agronomic performance in Drought Nursery

For pearl miller drought tolerance field screening at ICRISAT-Patancheru, only a single designated six hectare field with a shallow and relatively uniform soil profile is used

Control

Late stress



Early stress

Plate 2. Field evaluation of testcross hybrids under drought nursery

(Plate 2). When at field capacity, the profile of this field contains enough plant-available water for about 6 days of full evapotranspiration (ET) during April, when pan evaporation rates average 8-10 mm day^{-1}. As a part of the development of this field for surface irrigation, the A and B horizons of the original soil (50-75 cm depth) were removed, the gravelly subsoil material graded to a uniform slope of 1.5% and the surface soil spread evenly over the graded subsoil. Thus the major source of heterogeneity in the original field – the variable depth of soil to the gravelly C-horizon, and the consequent variable amount of plant-available water – has been largely removed.

Sprinkler irrigation is used to supply water to the crop before flowering, adjusting the amounts of water applied to meet increases in transpiration demand as the season progresses, as pearl millet is sensitive to low soil oxygen tensions that occur following surface (furrow) irrigation during cooler times of the year. Sprinkler lines are placed 14.4 m (24 crop rows) apart, with each sprinkler line in the center of four border rows, so that leakage from the sprinkler lines does not affect test plots.

At the time of initiation of the stress, furrow irrigation is used to be sure that the full soil profile is wetted. The furrows are filled rapidly, one twenty-row strip at a time, to have a sufficient head of water for this purpose. Water is held in the furrows for 4 hours and then drained rapidly to prevent water logging. All irrigation operations are managed by the researchers themselves to assure that irrigation is done as precisely and uniformly as possible (Bidinger, 2002).

The time of sowing of trials in the summer drought nursery is standardized to have the crop flower and fill grain during the period of maximum evaporation demand, and irrigation is managed to achieve a 50-60% reduction in yield for a severe stress and a

30-40% reduction for a moderate stress. Standard crop management procedures (described below) are followed to obtain uniform preflowering crop growth and initiate the stress(es) at fixed crop developmental stage(s). This latter is necessary as differences in temperatures during the earlier, cooler part of the growing season can affect time to flowering, even though a common sowing time across years assures a similar daylength environment each year.

3.6.1. Field/Crop Management

A number of ways to improve the uniformity of the pearl millet crop growth in the ICRISAT Patancheru drought nursery prior to the initiation of the stress treatments have been learned by experience. 1) The field is land planed every 2 to 3 years to remove local surface irregularities that result in collection of excess irrigation water and reduced crop growth. 2) Fertilizer is banded into the ridges with a precision applicator, rather than broadcasting it, to assure that all seedlings have equal access to nutrients. 3) Light sprinkler irrigation is provided prior to sowing, to moisten the surface soil and improve control over the depth of seed placement. 4) Over sowing is done with a precision planter and seedlings thinned about 10 days after emergence to achieve uniform plant stands. 5) Sprinkler irrigation is used in the early crop growth stages, rather that furrow irrigation, to prevent excess water application and reduced crop growth. 6) Sprinkler irrigation is provided at the time of secondary root initiation to assure that these roots penetrate the soil rapidly and completely. 7) Weed management is practiced during the entire year in the screening field to prevent the buildup of weed seed, and cultivation is done early and as often as necessary to remove weed seedlings in early stages before they

can establish. 8) Prophylactic pest and disease control is applied whenever a problem is suspected.

3.6.2. Statistical Design

Incomplete block or alpha designs are generally used in the majority of screening experiments, to provide for as much adjustment capability to local variation in stress intensity as possible. Small blocks of between 6 and 9 plots are used (18-27 m^2/block), with the total number of blocks variable, depending upon the numbers of entries in the trail. It is generally found that the effect of such blocking is statistically significant, despite the general precautions taken in managing these experimental crops.

3.7. Traits evaluated

The observations and measurements taken during the trial were as follows:

1. Flowering time (FT): Time of flowering was recorded as days from seedling emergence to stigma emergence in 50% of the main shoots in a plot.
2. Plant height (PH): Plant height (cm) was measured from the base of the stem to the tip of the main culm panicle at maturity. Data was recorded on three random plants from the middle of each row.
3. Panicle length (PL): Length of the panicle (cm) was measured for main culms of sample plants considered for plant height in each plot.
4. Panicle diameter (PD): Panicle diameter (mm) was measured using Vernier calipers on all those panicles for which panicle length was recorded.

At the time of harvest:

5. Plant count (PC): Number of plants in the middle 4 m of two rows of each plot was counted for all the entries.

6. Head count (HC): Panicles from middle 4 m of two rows of each plot were harvested and counted for all the entries.
7. Effective tillers (ET): Number of productive tillers per plant was calculated by dividing PC by HC.
8. Panicle yield (PY): After harvesting was completed, panicles were put in an oven for 24 hours and dried at a temperature of 60°C. The dry weight of the panicles was then recorded before threshing.
9. Grain yield (GY): Panicles were threshed and their grain cleaned. The weight of the grains from each plot was recorded.
10. Fresh stover yield (FSY): After panicles were harvested, the stem and the tillers were cut for biomass analyses from the middle 4 m length of two rows for all entries.
11. Subsample fresh stover weight (SWS): Samples of fresh stover were then collected from each entry and chopped and fresh weights of these samples were taken.
12. Subsample dry weight (SDS): The chopped samples were kept in a drier for two days at a temperature of 60°C and their dry weights were then recorded.
13. 100-grain mass (HGM): One hundred grains (g) were counted and their weight was recorded for each entry.
14. Number of grains per panicle (PGN): Number of grains per panicle was derived from these primary data [=(100*GY)/(PN*HGM)].
15. Biomass yield (BMY): Above-ground biomass yield was calculated for each plot as the sum of PY and the product of FSY*(SDS/SWS).

16. Harvest Index (HI): Harvest index was calculated for each plot as the ratio of GY and BMY.
17. Drought tolerance indices were calculated for traits 2-9 and 13-16 for each of the two stress treatments by removing linear effects of flowering time in the stress treatment plot and entry mean values for the particular trait in the fully-irrigated control on performance of a particular entry for that trait in the stress environments.

3.8. Statistical analysis

The statistical analyses were done using the program, GENSTAT 6th edition (2002). Analysis of variance, F-ratio and heritability (mean and plot basis) were calculated for each observed or calculated trait for different stress treatments and for different testers. Line × Tester analysis was performed to estimate *gca* of each BC_5F_2 line (and their donor and recurrent parents 863B and ICMB 841 respectively) and the three testers for each trait in each environment (early-onset stress, late-onset stress, and fully irrigated non-stress control). Genotype × environment interactions were assessed by in combined analysis across the three stress and non-stress control treatments.

EXPERIMENTAL RESULTS

CHAPTER IV

EXPERIMENTAL RESULTS

4.1. Marker–Assisted Selection (MAS)

4.1.1. Polymorphism between parents

4.1.1.1. SSR marker

A total of 78 SSR primer pairs were surveyed on the parents ICMB 841 and 863B to identity polymorphic markers between them. Out of 78 SSR primer pairs, 28 detect polymorphism (35.9%) between the parents that can be scored on silver-stained polyacrylamide gels. The size of the amplified fragments ranged from 100 to 420 bp. The linkage group-wise SSR primer pairs detecting polymorphic markers are listed in Table 1. The primer pairs detecting polymorphic markers ranged from three in linkage groups (LG) 3 and 5 to eight in LG7.

4.1.1.2. RFLP markers

In the present study, previously mapped loci detected by RFLP probe-enzyme combinations were utilized for tracking segregation in genomic regions wherever polymorphic SSR loci were found to be less in numbers (especially on LG1, LG4, LG6 and LG7). These RFLP probe-enzyme combinations were thus primarily used for screening the progenies for background selection (recovery of recurrent parent alleles in genomic regions away from the LG2 target of foreground selection). In the initial stages of screening, both foreground and background selection were carried out to cover the entire genome. For this, 23 polymorphic RFLP probe-enzyme combinations were used. The chromosome-wise list of polymorphic RFLP loci used are listed in Table 1.

4.1.2. Genotyping of the BC_3F_1 generation

In this generation 38 backcross families were genotyped. This was the first generation for genotyping in this Ph.D. thesis research program; hence, both RFLP and SSR markers were used to cover the entire set of seven pearl millet linkage groups. In this genotyping all of the polymorphic SSR and RFLP loci listed in Table 1 were used.

Examples of segregation patterns of the progenies for polymorphic RFLP and SSR markers, such as *Xpsm*870 and *Xpsmp*2018, are shown in Plate 1. The genotypic data for the 38 BC_3F_1 individuals are presented in Table 3. Considering the comparison between plant numbers 23 and 30: the total number of loci scored "B" (homozygous for recurrent parent alleles) and "H" (heterozygous for alleles of both parents) are the same; but, the heterozygous loci of plant number 23 were distributed mainly in LG6 and in a few places in LG1 and LG5. For plant number 30, the H loci were distributed mostly in LG2 and in a few places in LG1, LG6 and LG7. This explained that the heterozygosity was maintained in LG2. The B loci (homozygous recurrent parent alleles) were uniformly recovered in other linkage groups.

Since the basic objective of this study was to transfer the entire length of LG2 from the donor parent 863B to ICMB 841, BC_3F_1 plant number 30 was forwarded to the next generation by backcrossing it with ICMB 841.

4.1.3. Genotyping of the BC_4F_1 generation

Seedlings of the one selected backcross family (produced by backcrossing BC_3F_1 plant 30 to ICMB 841) were transplanted in the field for backcrossing. The useful morphological characters like presence of hairiness on nodal ring, leaf sheath, and leaf blade, green color of node, and yellow anther for the recurrent parent ICMB 841 were used as criteria to

Table 3. Genotype data for 38 BC_3F_1 generation individuals.

LG	Locus	P1	P2	1	3	5	7	9	11	13	15	17	19	21	23	26	27	30	31	34	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75
1	*Xpsmp*2069	A	B	B	B	B	B	B	B	B	B	B	B	H	H	B	B	H	B	B	B	B	B	B	B	H	B	B	B	H	B	B	H	B	B	H	B	H	B	B	H
1	*Xpsm*573	A	B	H	H	H	H	H	H	H	H	H	H	H	H	H	A	H	B	B	-	H	H	H	B	B	B	H	H	H	H	H	H	B	H	-	B	B	H	B	B
1	*Xpsm*761	A	B	H	H	H	H	H	H	H	H	H	B	B	B	H	B	B	H	H	-	H	B	H	H	H	H	B	H	B	H	H	B	H	H	B	H	H	H	H	B
1	*Xpsmp*2273	A	B	H	H	H	H	H	B	H	H	H	H	B	B	H	H	B	H	H	H	H	H	H	H	B	H	H	H	B	H	H	B	H	H	B	H	B	H	H	B
1	*Xpsm*891	A	B	H	H	H	H	H	H	H	H	H	H	H	B	B	H	B	H	H	H	H	H	H	H	B	H	H	H	B	H	H	B	H	H	B	H	B	H	H	B
1	*Xpsm*100	A	B	H	H	H	H	H	H	H	H	H	H	H	B	B	A	B	-	H	H	H	H	H	H	H	H	H	H	B	H	H	B	H	H	-	H	B	B	B	B
1	*Xpsmp*2006	A	B	B	-	H	H	H	H	H	-	H	H	-	B	B	-	B	H?	B	B	H?	H?	-	B	B	H	H	H	B	H	B	B	B	B	B	H	B	B	H	B
1	*Xpsm*196.1	A	B	B	H	H	B	B	B	H	B	B	H	H	B	H	H	B	H	H	-	H	H	H	H	B	H	H	H	B	H	B	B	B	H	H	B	H	B	H	B
2	*Xpsmp*2072	A	B	H	H	B	H	B	B	H	B	H	B	B	B	B	A	H	B	H	H	H	H	B	B	B	H	B	H	B	B	B	B	B	B	H	B	B	H	B	B
2	*Xpsmp*2088	A	B	H	B	B	H	B	B	H	B	H	B	B	B	H	A	H	B	B	B	H	H	B	B	H	H	B	H	B	B	B	B	B	B	H	B	B	H	B	B
2	*Xpsmp*2066	A	B	H	H	B	H	B	B	H	B	H	B	B	B	H	A	B	B	B	B	H	B	B	B	B	H	B	H	B	B	B	B	B	B	H	B	B	H	B	B
2	*Xpsmp*2077	A	B	H	H	B	H	B	B	H	B	H	B	B	B	B	H	H	B	H	B	H	H	B	B	B	H	B	B	B	B	B	B	B	B	H	B?	B	H	B	B
2	*Xpsmp*2255	A	B	H	H?	B	H	B	B	B	H	B	H	B	B	B	H?	B	B	B	B	H?	-	B	B	B?	B?	B?	B?	B?	B?	B?	B?	-	H	-	H	B	B?	B?	B?	B?
2	*Xpsmp*2201	A	B	H	H	B	H	B	B	H	B	H	H	B	B	H	H	H	B	B?	B	H	-	-	B	B	H	B	B	B	B	B	B	B	B	H	B	B	H	B	B
2	*Xpsmp*2059	A	B	B	H	B	H	B	B	H	B	H	H?	B	B	B	H?	H?	B	H?	B	H	-	B	-	B	H	B	B	B	B	B	B	B	B	H?	B	B	H?	B	B
2	*Xpsm*592	A	B	H	H	B	H	B	B	H	B	H	B	B	B	H	H	H	B	H	-	H	H	B	B	B	H	B	B	B	B	B	B	B	B	H	B	B	H	B	B
2	*Xpsm*708.2	A	B	H	H	B	B	H	-	-	-	H	H	H	B	H	H	H	B	H	-	H	B	H	H	H	H	H	H	B	H	B	B	H	H	-	B	B	H	H	B
3	*Xpsm*174	A	B	H	H	B	H	B	H	H	B	B	B	B	B	B	B	B	B	B	-	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
3	*Xpsmp*2249	A	B	H	H	B	H	B	H	H	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
3	*Xpsmp*2267	A	B	-	H	B	H	B	H	H	B	B	B	B	B	B	B	B	-	B	B	-	-	-	-	B?	B	B	B	B	B	B	B	B	B	B	-	-	-		
3	*Xpsmp*2214	A	B	H	H	B	H	B	H	H	B	B	B	B	B	B	B	B	-	B	B	-	-	-	-	B	B	B	B	-	B	B	B	B	B	B	B	-	B		
4	*Xpsm*716	A	B	H	B	B	B	H	B	H	B	H	B	B	B	B	B	B	B	B	-	H	H	H	H	H	B	B	B	H	B	B	H	B	B	B	B	B	B	B	H
4	*Xpsmp*2081	A	B	H	B	B	B	H	B	H	B	H	B	B	B	B	B	B	B	B	B	B	H	-	-	H	B	B	B	H	B	B	H	B	B	B	B	B	B	B	H
4	*Xpsmp*2076	A	B	H	B	B	B	H	B	H	B	H	B	B	B	B	-	B	B	-	B	H	-	-	-	H	-	B	B	H	B	B	-	B	B	-	B	B	B	-	H
4	*Xpsm*265	A	B	H	B	B	B	H	B	H	B	H	B	B	B	B	B	B	B	B	-	H	H	H	H	H	B	B	B	H	B	B	H	H	B	B	H	B	B	B	B
4	*Xpsmp*2084	A	B	B	B	B	B	H	B	H	B	H	B	B	B	B	B	B	B	B	B	B	B?	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B?	B	B	B
4	*Xpsm*527.1	A	B	B	B	B	B	H	B	H	B	H	B	B	B	B	B	B	B	B	-	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
4	*Xpsm*837.2	A	B	B	B	B	B	H	H	H	H	H	B	B	B	B	B	B	B	B	-	B	H	H	H	H	H	B	H	B	B	H	H	H	B	H	B	B	B	B	B

Table 3. Genotype data for 38 BC_3F_1 generation individuals (Cont...).

LG	Locus	P1	P2	1	3	5	7	9	11	13	15	17	19	21	23	26	27	30	31	34	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75
5	*Xpsmp*2202	A	B	B	B	B	B	B	B	B	B	B	B	B	H	H	A	B	H	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
5	*Xpsmp*2078	A	B	B	B	B	B	B	B	B	B	B	B	B	H	B	A	B	H	B	B	B	B	B	H	B	B	B	B	B	B	H	B	B	B	B	B	B	B	B	B
5	Xpsm318	A	B	H	H	H	H	H	H	H	H	H	H	H	B	B	A	B	H	H	H	H	H	B	H	B	H	H	H	B	H	H	B	B	H	B	H	H	H	H	B
5	*Xpsmp*2229	A	B	B	H	H	B	B	B	H	B	H	H	H	B	H	-	B	H	-	B	B	-	-	-	B	H	H	H	B	H	B	B	B	H	H	B	B	B	H	B
6	*Xpsm*202	A	B	H	H	-	-	H	-	H	H	H	-	H	H	H	-	B	H	H	-	B	H	H	H	H	H	H	-	H	H	B	B	B	B	-	B	B	-	B	B
6	*Xpsm*588	A	B	B	H	B	B	B	B	B	B	B	B	B	B	B	B	B	H	B	H	H	H	H	H	H	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
6	*Xpsmp*2213	A	B	H	B	H	B	B	H	B	B	H	H	B	H	-	H	B	H	H	B	B	H	H	H	H	H	H	B	B	H	B	H	B	B	H	B	B	H	B	H
6	*Xpsm*713	A	B	-	B	-	-	-	-	-	-	-	H	H	H	H	H	B	H	B	-	B	H	H	H	H	H	H	B	B	H	B	H	B	B	-	B	B	-	B	H
6	*Xpsm*737	A	B	B	B	H	B	H	H	B	H	H	H	H	H	H	H	H	H	H	-	H	H	H	H	H	H	H	B	B	H	H	H	B	B	-	B	B	H	B	H
6	*Xpsm*613.2	A	B	B	B	H	B	H	H	B	H	H	H	H	H	H	H	B	H	H	H	B	H	H	H	H	H	H	B	B	B	H	H	B	H	B	B	B	H	H	B
6	*Xpsm*870	A	B	H	H	H	H	H	H	H	H	H	B	B	B	B	B	B	B	B	-	B	H	B	H	H	H	H	B	H	H	H	H	B	H	H	B	B	B	H	H
7	*Xpsm*718	A	B	H	B	B	B	H	H	B	B	H	H	H/?	H	B	H	H	H	B	B	B	B	B	H	H	H	H	B	B	H	B	H	B	B	H	B	B	H	B	B
7	*Xpsmp*2013	A	B	H	B	B	B	B	B	B	H	H	H	H	B	H	A	B	H	B	H	H	-	H	H	B	B	H	H	B	B	B	B	B	H	H	H	B	B	B	B
7	*Xpsm*269	A	B	B	B	B	B	B	B	B	H	H	H	H	B	H	A	B	H	B	-	H	H	H	H	B	H	H	H	B	B	B	B	B	H	H	H	B	B	H	H
7	*Xpsmp*2040	A	B	B	H	B	B	B	B	B?	H	B	B	H	B	B	A	B	H?	B	B	H	B	B	B	B	H?	H	H	B	B	B	B	B	B	H?	H?	B?	B	H	B
7	*Xpsmp*2063	A	B	H	H	B	H	B	B	H?	B	H	B	B	B	H	A	B	B	H	B	H	B	B	B	B	H	B	H	B	B	B	B	B	B	A	B	B	H	B	B
7	*Xpsm*618	A	B	B	H	H	B	B	B	H	B	B	H	H	B	H	A	B	H	H	-	H	H	H	H	B	H	H	H	B	H	B	B	B	H	H	B	B	B	H	B
7	*Xpsmp*2043	A	B	H	H	H	B	B	B	H	B	B	H	H	B	-	H	B	H	B	H	H	B	H	H	B	H	H	H	B	H	B	B	B	H	H	B	-	B	H	H
7	*Xpsmp*2087	A	B	H	H	B	B	B	B	H	B	B	H	H	B	H	H	B	H	B	H	H	-	-	-	H	H	H	B	H	B	B	B	H	H	B	H	H	B	H	B
7	*Xpsmp*2019	A	B	B	A	H	B	B	B	A	B	B	A	H	B	H	A	B	A	H	H	H	H	H	H	B	H	A	A	B	H	B	B	B	H	H	B	H	B	H	B
7	*Xpsm*526	A	B	H	H	H	B	B	B	H	B	B	H	H	B	H	H	B	H	H	H	H	H	H	H	B	H	H	H	B	H	B	B	B	H	H	B	H	B	H	B
7	*Xpsmp*2203	A	B	H	H	B	B	B	B	H	B	B	H	H	B	B	A	B	H	B	H	H	H	H	H	-	H	H	H	B	B	B	B	B	H	H	B	H	B	B	B
7	*Xpsmp*2027	A	B	B	H	B	B	B	H	-	B	B	H	H	H	H	H?	B	H	B	H?	H?	B	B	B	B	B	B	B	B	B?	B	H	B	B	-	B	B	B	B	B
Total B alleles				18	18	32	28	30	31	12	33	18	24	27	40	26	14	40	23	29	21	17	15	19	19	30	17	26	27	42	29	40	36	43	31	18	41	43	30	31	40
Total H alleles				31	31	17	21	20	17	35	15	31	25	23	11	23	18	11	25	19	14	33	27	24	25	19	33	24	22	9	21	11	13	8	19	24	10	7	18	17	10

P1 = 863B; P2 = ICMB 841

A = Homozygous for donor parent allele

B = Homozygous for recurrent parent allele

H = Heterozygote

select among the progenies. These morphological characters of the recurrent parent helped to reduce the number of plants for SSR and RFLP marker genotyping. For the initial screening of BC_4F_1 individuals, only LG2 markers were used. From the LG2 genotypic data for foreground selection, eight progenies were selected. In these eight progenies, a minimum number of markers to cover all the linkage groups were used to conduct background selection (Table 4).

From Table 4, it was clear that BC_4F_1 plant numbers 197 and 202 shown in bold, are clearly different from the other six plants for which background genotyping was conducted. BC_4F_1 plant numbers 197 and 202 retained heterozygosity in the central portion of LG2 and homozygous recurrent parent ICMB 841 alleles were covered throughout the other six linkage groups. Segregation patterns of the BC_4F_1 progenies for polymorphic markers such as *Xpsm*837.2 and *Xpsmp*2088 are shown in Plate 3.

The other BC_4F_1 plant like 51 and 58 still maintained marker heterozygosity on LG1 and LG6. Hence these individuals were rejected. Finally BC_4F_1 plant numbers 197 and 202 were selected and their backcross progeny forwarded for the next generation of marker-assisted selection.

4.1.4. Genotyping of the BC_5F_1 generation

In each of these two selected BC_5F_1 families, 18 progenies were taken up for marker genotyping. The morphological characters of hairiness and color of node and anther for the recurrent genome was again studied to select these 18 progenies from the individual backcross families. In this generation also both foreground and background selection were applied to select the most appropriate individuals heterozygous for LG2. The eleven

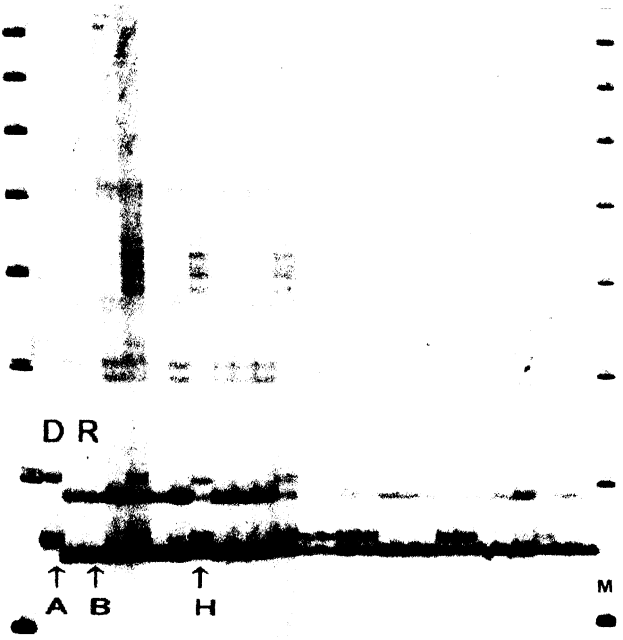
Table 4. Genotype data for eight BC_4F_1 generation individuals.

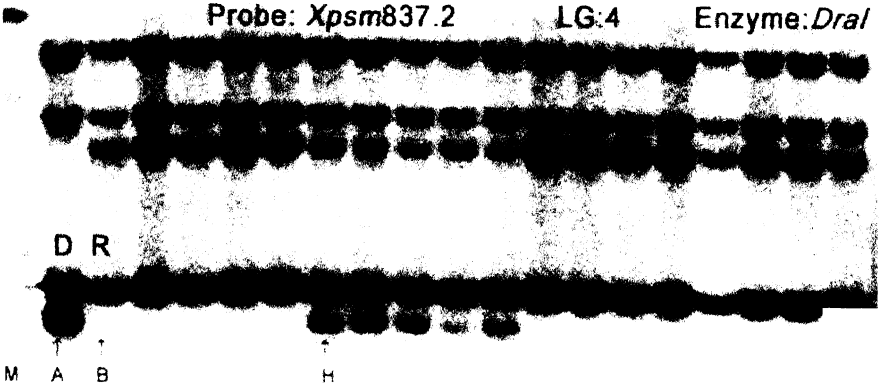
LG	Locus	863B	ICMB 841	51	58	190	191	192	197	198	202
1	*Xpsm*573	A	B	H	H	-	-	-	-	-	-
1	*Xpsmp*2273	A	B	B	B	B	B	B	**B**	B	**B**
2	*Xpsmp*2072	A	B	B	B	B	B	B	**B**	B	**B**
2	*Xpsmp*2088	A	B	H	H	H	H	H	**H**	H	**H**
2	*Xpsmp*2066	A	B	H	H	H	H	H	**H**	H	**H**
2	*Xpsmp*2255	A	B	H	H	H	H	H	**H**	H	**H**
2	*Xpsmp*2201	A	B	H	H	H	H	H	**H**	H	**H**
2	*Xpsmp*2059	A	B	H	H	H	H	H	**H**	H	**H**
2	*Xpsm*708.2	A	B	H	H	B	B	B	**B**	H?	**B**
3	*Xpsmp*2267	A	B	B	B	B	B	B	**B**	-	-
4	*Xpsmp*2084	A	B	B	B	B	B	B	**B**	-	-
5	*Xpsmp*2202	A	B	B	B	B	B	B	**B**	B	**B**
5	*Xpsmp*2229	A	B	B	B	B	B	B	**B**	B	**B**
6	*Xpsmp*2213	A	B	B?	B	B	B	H	**B**	B	-
6	*Xpsm*737	A	B	H	H	H	H	B	**B**	H	**B**
7	*Xpsmp*2019	A	B	B	B	B	B	B	**B**	B	**B**
7	*Xpsmp*2203	A	B	B	B	B	B	B	**B**	B	**B**

A = Homozygous for donor parent allele

B = Homozygous for recurrent parent allele

H = Heterozygote





D = Donor parent = 863B
R = Recurrent parent = ICMB 841
H = Heterozygote
A = Homozygous for donor parent allele
B = Homozygous for recurrent parent allele
M = Marker

Plate 3. Segregation of polymorphic markers for *Xpsmp*2088

BC_5F_1 individuals marked in bold in Table 5 were selected for further selfing and backcrossing.

Two BC_5F_1 plant numbers for which selfed and backcrossed seed was produced, 197-18 and 202-6, retained full heterozygosity in the central portion of LG2 and in all remaining linkage groups the recurrent parent genome was fully recovered. Hence, selfed progenies these two BC_5F_1 individuals were selected to detect introgression homozygotes for the entire length of LG2 in the next generation.

Some of the lines having either one H allele at the bottom of LG2 (*e.g.*, 202-1) or with one B allele at the bottom of LG2 (*e.g.*, 197-10 and 197-12) were selected to generate introgression homozygotes for different portions of the LG2 target region in order to more precisely identify the genomic locations of the DM resistance and drought tolerance QTL that had previously been mapped to this region. For the same purpose several of the remaining lines such as 197-1, 197-3, 197-5, 197-16, 202-4, 202-6, 202-7 and 202-8 were selected for further selfing and backcrossing. Keeping in mind the cost and labor required, and availability of self and backcross seeds, remaining plants such as 202-10, 202-11, 202-12, 202-14, 202-15 and 202-16 were rejected.

4.1.5. Genotyping of the BC_5F_2 generation

Among the selected 12 BC_5F_1 plants, five selfed progenies from (197-18, 202-6, 197-12, 202-8 and 197-1) were selected for advance to generate homozygotes for various portions of LG2 introgressed from 863B. Initial screening was done with two SSR loci, namely *Xpsmp*2072 and *Xpsmp*2225, mapping to the top and bottom of the targeted portion of LG2 in order to reduce the population size.

Table 5. Genotype data for 36 BC_5F_1 generation individuals.

LG	Locus	863B	ICMB 841	197-1	197-2	197-3	197-4	197-5	197-6	197-7	197-8	197-9	197-10	197-11	197-12	197-13	197-14	197-15	197-16	197-17	197-18	202-1	202-2	202-3	202-4	202-5	202-6	202-7	202-8	202-9	202-10	202-11	202-12	202-13	202-14	202-15	202-16	202-17	202-18
1	*Xpsmp*2069	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	-	-	-	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B
1	*Xpsmp*2273	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	B	-	-	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B
2	*Xpsm*458	A	B	**B**	H	**B**	B	**B**	B	B	B	B	**H**	B	**H**	B	B	-	-	-	**H**	**B**	A	H	**H**	H	**H**	**B**	**B**	H	H	H	H	B	H	H	H	B	B
2	*Xpsmp*2072	A	B	**B**	H	**B**	B	**B**	B	B	B	B	**H**	B	**H**	B	B	B	**H**	B	**H**	**B**	-	H	-	H	**H**	**B**	**B**	H	H	H	H	B	H	H	H	B	B
2	*Xpsmp*2088	A	B	**H**	H	**B**	B	**B**	B	B	B	B	**H**	H	**H**	B	B	B	**H**	-	**H**	**B**	B	H	**H**	H	**H**	**B**	**B**	H	H	H	H	B	H	H	H	B	B
2	*Xpsmp*2066	A	B	**H**	H	**B**	B	**B**	B	B	B	B	**H**	B	**H**	B	B	B	**B**	-	**H**	**B**	H	-	-	H	**H**	**B**	**H**	H	H	H	H	B	H	H	H	B	B
2	*Xpsmp*2255	A	B	**H**	H	**H**	B	**B**	B	B	B	B	**H**	H	**H**	B	B	B	-	B	**H**	**B**	H	H	**B**	H	**H**	**B**	**H**	H	H	H	H	H	H	H	H	**B**	B
2	*Xpsmp*2077	A	B	**H**	H	**H**	B	**B**	B	B	B	B	**H**	B	**H**	B	B	B	**B**	B	**H**	**B**	H	H	**B**	H	**H**	**B**	**H**	H	H	H	H	H	H	H	H	B	B
2	*Xpsmp*2201	A	B	**H**	H	**H**	B	**H**	B	B	B	B	**H**	B	**H**	B	B	B	**H**	B	**H**	**B**	-	H	-	H	**H**	**H**	**H**	H	H	H	H	H	H	H	H	B	B
2	*Xpsmp*2059	A	B	**H**	H	**H**	B	**H**	B	B	B	B	**H**	B	**H**	B	B	B	**H**	B	**H**	**H**	H	-	-	H	**H**	**H**	**H**	B	H	H	H	H	H	H	H	B	B
2	*Xpsmp*2231	A	B	**H**	H	**H**	B	**H**	B	B	B	B	**H**	B	**H**	B	B	B	**H**	B	**H**	**B**	H	H	**B**	H	**H**	**H**	**H**	H	H	H	H	H	H	H	H	B	B
2	*Xpsmp*2225	A	B	**H**	H	**H**	B	**B**	B	B	B	B	**H**	B	**H**	B	B	B	**H**	B	**H**	**B**	-	H	**B**	H	**H**	**H**	**H**	H	H	H	H	H	H	H	H	B	B
2	*Xpsm*592	A	B	**H**	H	**B**	B	**B**	B	B	-	H	**B**	H	**B**	B	B	-	-	H	**H**	**H**	B	H	**H**	H	**H**	**H**	**H**	H	H	H	H	H	H	H	H	B	B
3	*Xpsmp*2267	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	B	B	**B**	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B
3	*Xpsmp*2214	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	B	B	**B**	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B
4	*Xpsmp*2081	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	B	-	**B**	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B
5	*Xpsmp*2202	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	-	B	**B**	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B
6	*Xpsmp*2213	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	B	B	-	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B
6	*Xpsm*737	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	B	B	**B**	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B
7	*Xpsmp*2013	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	-	B	**B**	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B
7	*Xpsmp*2019	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	B	B	-	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B
7	*Xpsmp*2203	A	B	**B**	B	**B**	B	**B**	B	B	B	B	**B**	B	**B**	B	B	B	**B**	B	**B**	**B**	B	-	-	B	**B**	**B**	**B**	B	B	B	B	B	B	B	B	B	B

A = Homozygous for donor parent allele

B = Homozygous for recurrent parent allele

H = Heterozygote

Formula reported by Sedcole (1977) helped to calculate the number of plants needed to have a 95% chance of getting at least one plant of the desired genotype based on Mendelian ratios. Based on these calculations and the number of H-scored and B-scored loci in the LG2 in Table 4, the number of individuals to be genotyped in each of the selfed progenies was determined. In this generation only foreground selection was applied to select the individuals homozygous for the alleles of donor parent (863B). In this way 4 individuals were selected (shown in bold) based on their level of homozygosity in LG2 (Table 6).

4.1.6. Genotyping of the BC_6F_1 generation

Out of 12 BC_5F_1 plants selected based on marker genotype (Table 5), 11 were advanced by backcrossing with pollen from recurrent parent ICMB 841. As suggested by Sedcole (1977), the number of progenies to be genotyped in the BC_6F_1 generation was calculated based on the number of heterozygous loci in the target region of LG2. Plant numbers 197-18 and 202-6 were selected, which fully maintained heterozygous condition in the LG2 target region. The other sources for near-isogenic lines (NILs) were chosen based on the number and location of LG2 loci scored B: three B loci at the top of LG2 (202-8), one B locus at the bottom (197-12 and 197-10), two B loci in the middle (197-16), six H loci in the middle (197-3), five H loci at the bottom (202-7), three H loci at the middle (197-5), and two H loci at the bottom (202-1) to get the most appropriate range of genotypes.

Eight SSR primer pairs detecting loci previously mapped to LG2 were taken for genotyping to characterize the amount of the 863B donor genome introgressed in the ICMB 841 recipient genome. To reduce the number of progenies to be genotyped, it was suggested to first screen the progenies with one marker on either end of the LG2

Table 6. LG2 SSR marker genotype data for 55 BC_5F_2 generation individuals.

Marker locus	863B	JCMB 841	**197-18(S)-1**	197-18(S)-2	197-18(S)-3	197-18(S)-4	197-18(S)-5	197-18(S)-6	202-6(S)-2	202-6(S)-12	202-6(S)-19	**202-6(S)-26**	202-6(S)-38	202-6(S)-52	197-12(S)-1	197-12(S)-5	197-12(S)-20	197-12(S)-25	197-12(S)-37	197-12(S)-47	202-8(S)-1	202-8(S)-2	202-8(S)-3	202-8(S)-4	202-8(S)-5	202-8(S)-6	202-8(S)-7	202-8(S)-8	202-8(S)-9	202-8(S)-10	202-8(S)-11	202-8(S)-12	202-8(S)-13	202-8(S)-14	202-8(S)-15	202-8(S)-16	202-8(S)-17	202-8(S)-18	202-8(S)-19	202-8(S)-20	202-8(S)-21	202-8(S)-22	202-8(S)-23	202-8(S)-24	202-8(S)-25	202-8(S)-26	**202-8(S)-27**	202-8(S)-28	202-8(S)-29	202-8(S)-30	202-8(S)-31	202-8(S)-32	202-8(S)-33	202-8(S)-34	197-1(S)-3	197-1(S)-7	**197-1(S)-12**
*Xpsmp*2072	A	B	**A**	H	A	H	H	H?	A	A	H	**A**	H	A	B	H	A	B	A	H	**B**	B	B	B	B	B	B	B	B	B	**B**	B	B	B	**B**	B	B	B	B	B	B	B	**B**	B	B	**B**	B?	**B**	B	**B**	B	B	B	**B**	B	**B?**
*Xpsmp*2088	A	B	**A**	H	A	H	H	B	A	A	H	**A**	H	A	H	H	A	B	A	H	B	B	B	B	B	B	B	B	B	B	**B**	B	B	B	**B**	B	B	B	B	B	B	B	**B**	B	B	**B**	B	B	B	**B**	B	B	B	H	B	**A**
*Xpsmp*2066	A	B	**A**	H	H	H	H	B	A	A	A	**A**	-	A	H	H	B	A	A	B	-	-	H	H	B	H	H	H	B	H	**H**	B	H	A	H	A	H	A	B	H	B	A	H	A	H	**B**	H	-	A	H	H	B	B	A	B	**A**
*Xpsmp*2231	A	B	**A**	B	H	H	H	H	H	H	A	**A**	H	B	A	A	A	B	H	H	H	-	B	H	B	H	B	B	B	A	H	**B**	H	H	H	H	H	H	A	B	H	H	H	H	H	H	**B**	A	B	B	H	H	B	B	A	A	-
*Xpsmp*2255	A	B	**A**	B	H	H	H	H	H	H	A	**A**	A	A	A	H	H	A	B	H	A	H	-	H	H	H	B	-	H	B	H	**H**	H	H	H	H	H	B	H	H	A	B	H	H	H	H	A	H	**B**	A	-	H	H	H	H	B	H	H	**A**
*Xpsmp*2201	A	B	**A**	B	H	H	H	H	H	H	A	**A**	A	A	A	H	A	B	H	H	H	H	B	H	H	B	H	B	B	H	A	H	H	H	H	H	B	H	H	A	B	H	H	H	H	A	H	**B**	A	-	B	H	H	B	B	H	A	**A**
*Xpsmp*2059	A	B	**A**	B	A	B	H	H	H	H	A	**A**	A	A	A	A	H	A	A	H	A	H	H	B	H	B	-	-	B	H	A	H	H	H	H	H	B	H	B	H	A	B	H	H	H	H	A	B	H	H	H	H	A	A	**A**
*Xpsmp*2225	A	B	**A**	B	H	H	H	H	H	H	H	A	H	H	H	H	H	B	H	H	-	-	B	H	B	H	B	B	H	H	H	H	H	H	H	H	H	B	H	H	H	B	H	H	H	H	B	H	H	B	H	H	B	B	H	H	**A**

A = Homozygous for donor parent allele

B = Homozygous for recurrent parent allele

H = Heterozygote

introgression target region. The marker genotypes of the reduced set of progenies that were screened with the remaining markers are presented in Tables 7a,b,c. Out of the 220 "BC_6F_1" plants genotyped at these LG2 SSR loci, at least 33 individuals appeared to have been produced as a result of selfing, rather than backcrossing, of their BC_5F_1 female parent, as they were unexpectedly homozygous for the 863B donor parent allele at one or more of the SSR loci genotyped. Hence selection among these additional BC_5F_2 individuals for introgression homozygotes was also possible.

Those BC_5F_2 plants homozygous for donor alleles on either side of the linkage group were noted for their morphological characters like hairiness on the nodal ring, leaf blade, and leaf sheath, and color of the nodes (green *vs* pigmented). Otherwise, only foreground selection was applied because in the BC_4F_1 and BC_5F_1 generations both types of selections were applied so it was not necessary to perform further background selection as recurrent parent genotype recovery on LG1, LG3, LG4, LG5, LG6 and LG7 was assumed to be complete. Segregation pattern of the progenies for polymorphic marker *Xpsmp*2072 is shown in Plate 4.

The desired BC_5F_2 genotypes were selected based on the level of homozygosity for the donor alleles (Table 8). Individuals were selected based on their number of five A loci at bottom of the linkage group 2 (202-8-8); two A loci at the lower bottom (202-7-4; 202-7-10); three A loci at the top (197-10-16); one A locus at the bottom (197-10-11) and one A locus top middle (202-8-9; 202-8-11; 197-12-2). These segmental introgression homozygotes were selected to study which part of the donor genome in LG2 is responsible for drought-tolerance contributing characters.

Table 7a. Genotype data for 66 BC_6F_1 generation individuals derived from BC_5F_1 plant 197-18

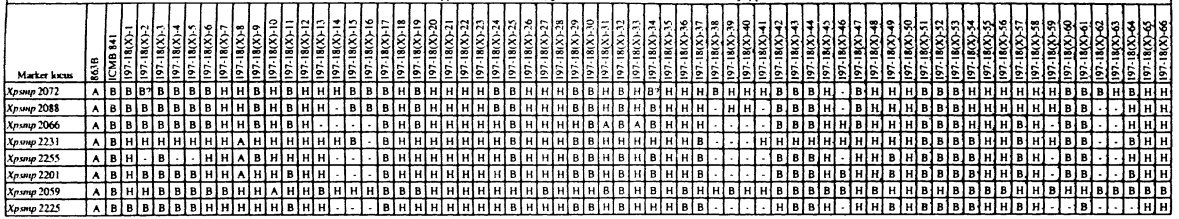


Table 7b. Genotype data for BC_6F_1 generation individuals derived from BC_5F_1 plants 202-6, 197-12, 202-4 and 197-3

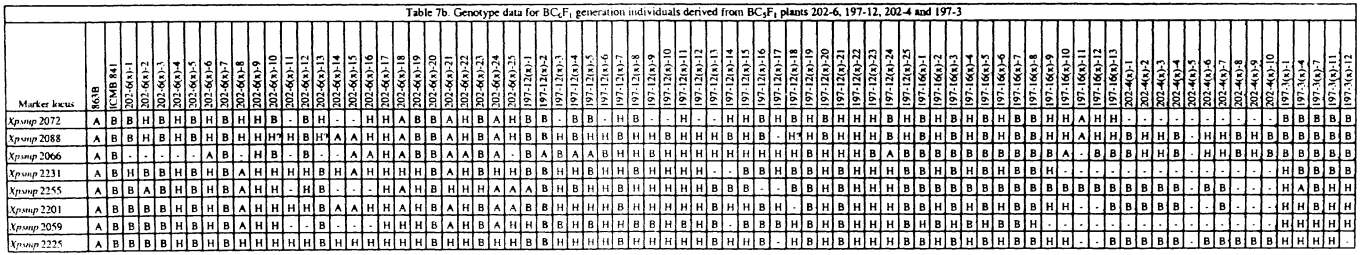
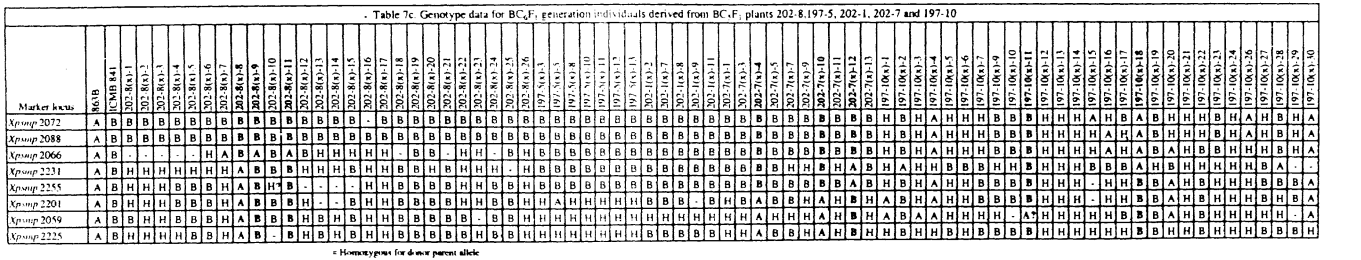


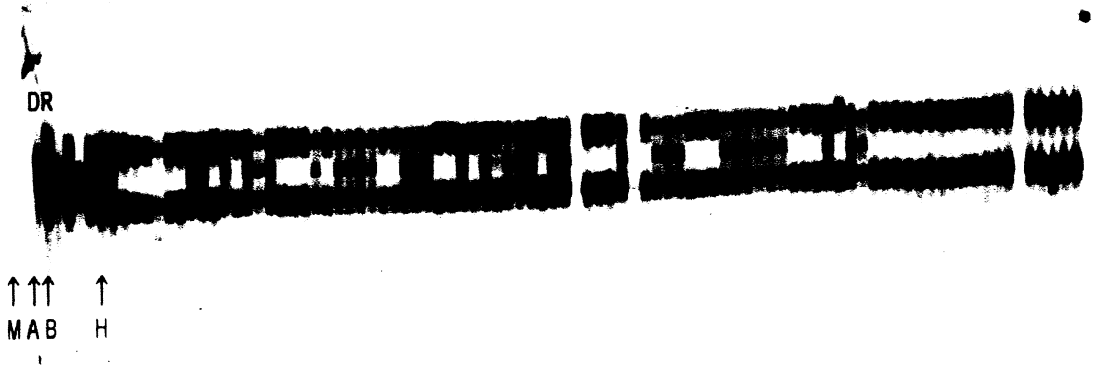
Table 7c. Genotype data for BC_6F_1 generation individuals derived from BC_5F_1 plants 202-8,197-5, 202-1, 202-7 and 197-10



= Homozygous for donor parent allele

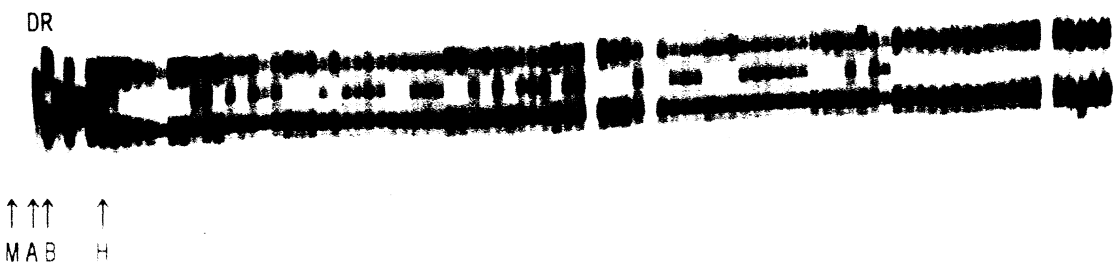
Homozygous for recurrent parent allele

H = Heterozygote



D = Donor parent = 863B
R = Recurrent parent = ICMB 841
H = Heterozygote
A = Homozygous for donor parent allele
B = Homozygous for recurrent parent allele
M = Marker

Plate 4. Segregation of polymorphic marker *Xpsmp*2072 in the BC_5F_2 and BC_6F_1 generations



D = Donor parent = 863B
R = Recurrent parent = ICMB 841
H = Heterozygote
A = Homozygous for donor parent allele
B = Homozygous for recurrent parent allele
M = Marker

Plate 4. Segregation of polymorphic marker *Xpsmp*2072 in the BC_5F_2 and BC_6F_1 generations

Table 8. Marker genotypes of selected plants from BC_5F_2 and BC_6F_1 generations.

Marker locus	863B	ICMB 841	197-10(x)-18	202-8(x)-11	197-12(x)-2	202-8(x)-9	202-7(x)-12	202-8(S)-27	197-10(x)-11	202-7(x)-4	202-7(x)-10	202-8(x)-8	197-1(S)-12	202-6(S)-26	197-18(S)-1
*Xpsmp*2072	A	B	A	B	B	B	B	B	B	B	B	B	B?	A	A
*Xpsmp*2088	A	B	A	B	B	B	B	B	B	B	B	B	A	A	A
*Xpsmp*2066	A	B	A	A	A	A	B	B	B	B	B	B	A	A	A
*Xpsmp*2231	A	B	A	B	B	B	A	B	B	B	B	A	-	A	A
*Xpsmp*2255	A	B	B	B	B	B	A	B	B	B	B	A	A	A	A
*Xpsmp*2201	A	B	B	B	B	B	B	B	B	A	A	A	A	A	A
*Xpsmp*2059	A	B	B	B	B	B	B	A	A?	A	A	A	A	A	A
*Xpsmp*2225	A	B	B	B	B	B	B	B	B	A	A	A	A	A	A

A = Homozygous for donor 863B parent allele

B = Homozygous for recurrent ICMB 841 parent allele

H = Heterozygote

4.1.7. Hybrid seed production

Selfed progenies from segmental introgression homozygotes identified among the segregating BC_5F_2 generation were selected for the development of testcross hybrids. The selected BC_5F_3 progenies were phenotyped as testcross hybrids rather than using their derived inbred lines for several reasons (Yadav *et al.*, 2002).

These selfed progenies were crossed with three pollinators, namely PPMI 301, RIB 335/74 and H 77/833-2. These three pollinators are male parents of released hybrids Pusa 301, RHB 30 and HHB 67, respectively. All three produce hybrids that are relatively sensitive to terminal drought stress. The thirteen improved, segmentally introgressed versions of ICMB 841 along with their donor and recurrent parents, were used as females and the pollen from the three testers were dusted onto receptive stigmas on pre-anthesis panicles protected by selfing bags to produce seeds of 45 testcross hybrids.

4.1.8. Evaluation in Drought Nursery

Evaluation of 45 testcross hybrids in the 2004 summer season Drought Nursery in field RP11A at ICRISAT-Patancheru to assess the following inferences:

1. to identify the most appropriate tester for use in comparing agronomic performance of the introgression lines with their recurrent parent ICMB 841, under both stress and non-stress conditions,
2. to assess drought tolerance of testcross hybrids relative to those of recurrent parent ICMB 841, and
3. to more closely identify the position of the LG2 drought tolerance QTL of donor parent 863B.

4.2. Downy mildew screening

Simultaneously, 13 MAS-derived versions of ICMB 841 introgressed with overlapping segments of LG2 from 863B (Table 8) with their two parents along with three tester pollinators and two control entries were screened against three different pearl millet downy mildew (DM) isolates [Patancheru isolate (Sg153), Durgapura isolate (Sg151) and Jamnagar isolate (Sg140)] in three replicates under greenhouse conditions at ICRISAT-Patancheru. Similarly, 45 testcross hybrids derived from crosses of these 13 MAS-derived inbred lines and their two parents with the three pollinators were screened against the same three isolates under greenhouse conditions. Since most of the testcross hybrids seeds were taken for field trials, the small number of remnant testcross seeds available were used for screening against these pathogens in a single replications only.

In individual treatments, the total number of plants (TPC) before inoculation and the number of plants infected with downy mildew (DMC) were counted. Disease reaction for each entry in each replicate was expressed as the percentage of inoculated seedlings that were infected (downy mildew incidence, DMI%) and as the arcsine-transformation of this value. Entry means for DMI%, arcsine-transformed DMI, TPC and DMC are presented in Table 9 for each of the three-pathogen isolates.

Among the testers, H 77/833-2 was found to be highly susceptible to all isolates. Pollinator PPMI 301 exhibited variable levels of resistance to the three isolates. Pollinator RIB 335/74 was consistently resistant to all three pathogen isolates. Susceptible control entries 7042(S) and 843B were consistently highly susceptible to all three pathogen isolates indicating that the level of disease pressure provided in the screens was adequate to detect susceptibility.

Table 9. **Performance summary for downy mildew incidence for the inbreds when screened under greenhouse conditions against three pathogen isolates.**

	DM Patancheru Isolate (Sg153)				DM Durgapura Isolate (Sg151)				DM Jamnagar Isolate (Sg140)			
Pedigree	**DMI %**	**Asin DMI**	**TPC**	**DMC**	**DMI %**	**Asin DMI**	**TPC**	**DMC**	**DMI %**	**Asin DMI**	**TPC**	**DMC**
197-10-18	65 3	0 731	22	13	63 2	0 707	25	15	17 2	0 173	28	5
202-8-11	39 1	0 403	29	11	28 6	0 294	37	11	9 7	0 097	38	4
197-12-2	18 8	0 189	30	6	12 8	0 129	35	4	6 3	0 063	31	2
202-8-9	7 7	0 077	35	3	7 5	0 075	30	2	2 5	0 025	27	1
202-7-12	62 3	0 685	31	19	17 8	0 179	37	7	2 8	0 028	36	1
202-8-27	0 9	0 009	37	0	11 3	0 113	39	4	0 0	0 000	38	0
197-10-11	23 0	0 234	37	8	23 8	0 242	38	9	0 9	0 009	37	0
202-7-4	56 8	0 629	29	17	64 9	0 730	32	21	1 6	0 016	24	0
202-7-10	52 9	0 576	28	14	92 1	1 243	28	26	20 5	0 208	25	4
202-8-8	57 3	0 638	31	18	24 8	0 256	28	7	4 1	0 041	38	2
197-1-12	23 3	0 238	41	9	14 7	0 148	38	6	6 6	0 066	35	2
202-6-26	23 2	0 234	23	5	25 9	0 263	21	5	9 0	0 090	27	2
197-18-1	21 4	0 221	26	6	18 7	0 189	27	5	4 8	0 048	31	2
863B	6 3	0 063	20	1	0 0	0 000	12	0	4 6	0 046	28	1
ICMB 841	28 8	0 295	25	7	29 9	0 307	29	8	7 5	0 076	27	2
H 77/833-2	95 2	1 391	29	27	100 0	1 571	23	23	100 0	1 571	32	32
PPMI 301	8 2	0 082	13	1	36 1	0 380	16	6	1 4	0 014	17	0
RIB 335/74	13 7	0 139	31	4	12 7	0 127	35	5	8 7	0 087	38	3
7042(S)	97 9	1 452	33	32	94 6	1 245	31	30	99 0	1 491	36	36
843B	100 0	1 571	13	13	90 9	1 150	13	12	96 6	1 418	27	26
SE (±)	8 9	0 110	3 54	3 27	7 7	0 100	2 27	2 54	3 1	0 050	2 97	1 37
Mean	40 1	0 490	28 1	10 82	38 5	0 470	28 73	10 35	20 2	0 280	30 88	6 28
CV (%)	38 4	39 98	21 79	52 4	34 8	35 77	13 66	42 52	26 7	31 08	16 66	37 68
F-ratio	12 70**	17 60**	4 38**	7 00**	18 00**	23 76**	13 39**	10 79**	120 90**	111 29**	3 83**	64 24**
h^2(plot basis)	0 80	0 85	0 53	0 67	0 90	0 88	0 81	0 77	1 00	0 97	0 49	0 95
h^2(mean basis)	0 90	0 94	0 77	0 86	0 90	0 96	0 93	0 91	1 00	0 99	0 74	0 98

** Significant at 0 01 level of probability
DMI-Downy Mildew Incidence
TPC-Total Plant Count
DMC-Downy mildew count
Asin Arc sine transformation

4.2.1. Analysis of variance for experimental inbreds and their parents

A performance summary output from the analysis of variance for each of the three DM screens for the 13 experimental inbreds and their two parents is presented in Table 10. The mean downy mildew incidence was high for both the Patancheru (32.5%) and Durgapura (29.1%) isolates. For the Jamnagar isolate, the mean value of downy mildew incidence (6.5%) was low but differences between the 15 inbreds were significant none-the-less. The operational heritabilities of all three isolates were high on the mean basis, but substantially less on the plot basis.

4.2.2. Interaction analysis

Genotype × isolate interaction analysis of variance is presented in Table 11. From this pooled analysis, it was inferred that isolate, genotype and genotype × isolate interaction variances were highly significant, so comparisons of genotype means for screens against individual pathogen isolates is more appropriate than comparison of genotype means across the three pathogen isolates.

4.2.3. Mean performance of downy mildew incidence of parents and experimental inbreds

Mean disease incidence values for individual inbred lines for screens against each of the three pathogen isolates are presented graphically in Figure 5. Among the parents, 863B was highly resistant to all three pathogen isolates and ICMB 841 was moderately susceptible to two of the three isolates. Among the experimental inbreds, 202-8-9 and 202-8-27 were the most consistently resistant to all three pathogen isolates. From Table 8, Table 9 and Figure 5 it was inferred that the introgressed segments along LG2 for these highly resistant individuals are not the same. An experimental introgression line (197-12-

Table 10. Performance summary for 13 inbreds and their two parents for downy mildew incidence.

Traits	DM Patancheru Isolate (Sg153)				DM Durgapura Isolate (Sg151)				DM Jamnagar Isolate (Sg140)			
	DMI %	Asin DMI	TPC	DMC	DMI %	Asin DMI	TPC	DMC	DMI %	Asin DMI	TPC	DMC
SE (±)	9.81	0.21	3.64	3.28	7.90	0.10	1.92	2.33	3.10	0.03	3.13	0.90
Mean	32.47	0.35	29.56	9.27	29.07	0.33	30.44	8.76	6.53	0.07	31.18	1.89
CV (%)	52.35	57.97	21.36	61.24	47.06	53.75	10.95	46.08	82.30	83.06	17.39	82.15
F-ratio	4.83**	4.37**	2.80**	3.45**	10.08**	10.47**	14.88**	9.12**	3.47**	3.45**	2.67**	2.68**
h^2(plot basis)	0.56	0.53	0.37	0.45	0.75	0.76	0.82	0.73	0.45	0.45	0.36	0.36
h^2(mean basis)	0.79	0.77	0.64	0.71	0.90	0.90	0.93	0.89	0.71	0.71	0.63	0.63

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

Figure 5. Distribution of MAS-derived inbreds, their parents (863B and ICMB 841) and testcross pollinators (H 77/833-2, PPMI 301, RIB 335/74), and susceptible controls [7042 (S) and 843B] for disease incidence (DMI%) in screens conducted under greenhouse conditions at ICRISAT-Patancheru with three different downy mildew isolates (Patancheru, Durgapura and Jamnagar)

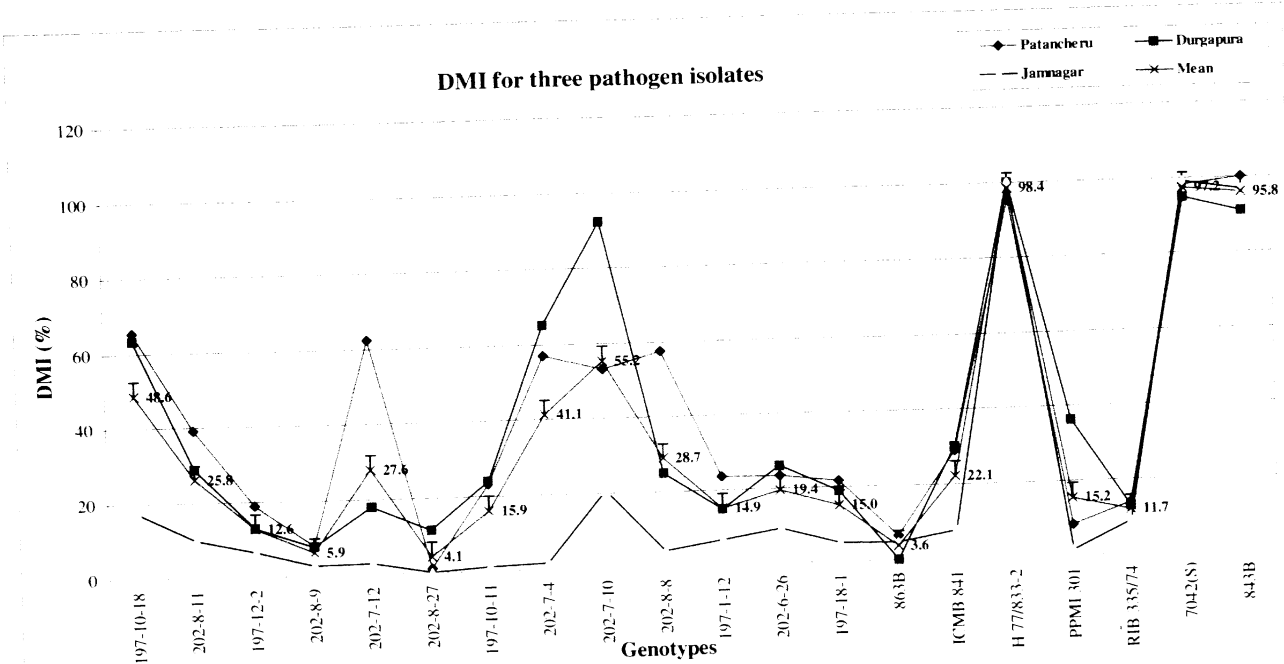


Table 11. Analyses of variance for the pooled analysis of downy mildew incidence.

Source of variation	Degrees of freedom	Mean squares
Isolates	2	7350.7**
Genotype	19	8580.1**
Genotype × Isolate	38	583.2**
Error	120	148.4
Total	179	

** Significant at 0.01 level of probability

2) having a similar introgression line to that of resistant line 202-8-9 (197-12-2), was significantly more susceptible to the pathogen isolates from Patancheru and Jamnagar. Further experimental inbred 202-8-11 (which has a marker genotype identical to those of 197-12-2 and 202-8-9) (Table 7) appeared to be as susceptible as recurrent parent ICMB 841 to all three pathogens isolates.

The mean of disease incidence was highest for test inbreds 197-10-18 and 202-7-10 against all three pathogen isolates. The total number of A loci on LG2 (Table 8) for inbred 202-7-10 was three, with these located at the lower arm of the linkage group. But for the inbred 197-10-18, the four introgressed A loci were on the upper portion of LG2. These two inbreds do not appear to share overlapping introgressed segments from 863B.

The inbreds carrying introgression of the donor genome across the full length of the central portion of LG2, namely 202-6-26 and 197-18-1, showed levels of susceptibility to downy mildew that were comparable to recurrent parent ICMB 841. The individuals with only one A allele or one B allele, namely 197-1-12 and 197-10-11, showed this same level of susceptibility to all the three pathogen isolates.

From this it was inferred that at least one genomic region from 863B that is not associated with LG2 plays a major role in the variation level of resistance expressed in seedling screens against these three different pathogen isolates.

Mean disease incidence for screens against the Patancheru (40.1%) and Durgapura (38.5%) isolates were almost equal, while that for the screen against the isolate Jamnagar (20.2%) was significantly lower indicating that this latter isolate was less virulent than the first two against the range of host genotypes included in these screens. By comparing the observed differences between the backcross progenies and

their parents, 202-8-27 was identified as significantly more resistant than ICMB 841 in screens against the Patancheru and Jamnagar isolates. But for the Durgapura isolate, only backcross progeny 202-8-9 showed significantly better disease incidence than recurrent parent. The operational heritabilities of screens for all three isolates were high on both plot and mean bases shown in Tables 4, 9, and 10.

4.2.4. Combining Ability Estimates

Estimates of *gca* and *sca* effects for downy mildew reactions against the three pathogen isolates are furnished in Table 12. Due to paucity of seeds, only one replication was available to study the *gca* and *sca* effects of the testcross hybrids, so statistical analysis of variance of this data set required for estimation of experimental errors for these *gca* and *sca* estimates was not possible. This data set gives an extremely preliminary overall idea on the performance of the individual hybrids with regard to downy mildew incidence.

The mean disease incidence performance of testcross hybrids of introgression lines 197-1-12, 197-10-11 and 202-8-27 were low resulting in negative *gca* estimates for these lines. Among the testers, testcross hybrids both PPMI 301 and RIB 335/74 showed low mean disease incidence values, so they too had negative *gca* estimates for this trait. Among the introgression lines, 197-10-11, 197-1-12 and 202-8-27 had the most negative *gca* effects estimates and among the testers PPMI 301 and RIB 335/74 recorded negative *gca* effects estimates consistently across the three pathogen isolates. The experimental inbred lines with consistently negative *gca* estimates (197-10-11, 197-1-12, and 202-8-27) produced DM resistant hybrids with resistant testers PPMI 301 and RIB 335/74 (not shown).

Table 12. Estimates of *gca* and *sca* effects of testcross hybrids for downy mildew incidence.

Lines& Testers	DM Patancheru isolate (Sg153)				DM Durgapura isolate (Sg151)				DM Jamnagar isolate (Sg140)			
	PPMI 301	RIB 335/74	H 77/833-2	*gca* lines	PPMI 301	RIB 335/74	H 77/833-2	*gca* lines	PPMI 301	RIB 335/74	H 77/833-2	*gca* lines
197-10-18	-1.2	-2.4	3.6	2.1	5.5	3.0	-8.6	-3.3	-1.7	-4.2	5.9	1.4
202-8-11	0.2	5.2	-5.4	-4.7	1.3	2.8	-4.1	0.5	9.7	3.7	-13.3	-6.5
197-12-2	0.4	4.5	-5.0	-4.9	-6.9	-3.5	10.4	0.6	3.8	9.5	-13.4	-6.8
202-8-9	5.6	0.8	-6.5	4.6	16.1	6.2	-22.4	0.8	3.8	10.0	-13.7	-4.0
202-7-12	-0.5	-1.4	1.9	-1.3	1.2	4.6	-5.8	-7.5	14.4	2.7	-17.2	-5.6
202-8-27	4.6	11.9	-16.5	-9.1	9.7	2.6	-12.4	-5.6	5.5	5.6	-11.2	-8.5
197-10-11	6.5	8.1	-14.7	-11.0	1.3	4.7	-6.0	-7.6	3.1	3.2	-6.2	-6.0
202-7-4	-8.0	-14.1	22.1	22.3	-21.8	-22.2	43.9	19.2	-26.8	-13.8	40.5	29.4
202-7-10	-20.2	-18.5	38.7	15.7	-14.0	-26.2	40.2	23.3	-22.5	-19.7	42.2	26.4
202-8-8	8.6	1.4	-10.0	-6.8	9.0	3.0	-12.0	-5.9	5.9	3.1	-9.1	-6.0
197-1-12	8.0	7.5	-15.5	-10.1	3.9	12.4	-16.3	-10.2	10.2	4.9	-15.0	-7.7
202-6-26	-4.6	-8.4	13.0	8.7	-16.5	-7.8	24.2	19.5	-23.3	-23.2	46.4	20.3
197-18-1	-6.4	2.3	4.1	1.9	3.2	6.0	-9.2	-3.4	5.6	5.7	-11.3	-8.5
863B	3.2	2.3	-5.5	-7.7	5.6	9.0	-14.6	-11.9	6.6	6.7	-13.2	-9.5
ICMB 841	3.6	0.7	-4.3	0.2	2.1	5.5	-7.6	-8.4	5.6	5.7	-11.3	-8.5
***gca* testers**	-7.4	-6.5	13.8		-5.6	-9.0	14.6		-6.6	-6.7	13.2	

Inbreds 202-7-4 and 202-7-10, which had among the highest positive *gca* effects for screens against all three pathogen isolates (indicating that they conferred susceptibility to their hybrids), also recorded highly positive *sca* effects in combination with susceptible tester H 77/833-2 across all three pathogen isolates. From Table 8 and Figure 5 it was clearly observed that these two susceptible inbreds shared similar introgressed genomic regions from 863B at the lower end of linkage group 2. However, since inbreds 202-8-8, 197-1-12, 202-6-26 and 197-18-1 share this introgressed region and had numerically lower disease incidence values resulting in near-zero *gca* estimates it is unlikely that the 863B introgressions responsible for the apparent increased susceptibility of hybrids of 202-7-4 and 202-7-10 is not located on LG2.

With *per se* performance and *gca* of introgression lines and testers Durgapura isolate exhibited positive and significant association value (Table 13) followed by Patancheru isolate however, Jamnagar isolate exhibited non-significant correlation value. As these correlations are based on single-replication screens of the hybrids against each of the three pathogen isolates. They must be considered extremely preliminary. Further screening to confirm these results will be necessary once seed is available for this.

4.3. Screening for drought tolerance

The resultant testcross hybrids were evaluated for drought tolerance in the summer-2004 drought nursery at ICRISAT-Patancheru. The results of analyses of variances, summaries of testcross mean performance and combining abilities for the grain and stove yield-related characters, for each of the three moisture regimes are presented below.

Table 13. Correlation coefficients between testcross hybrids *gca* and *per se* performance of downy mildew incidence for three pathogen isolates.

Pathogen isolate	Correlation values
Patancheru isolate (Sg153)	0.563*
Durgapura isolate (Sg151)	0.708**
Jamnagar isolate (Sg140)	0.340

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

4.3.1. Fully irrigated non-stress control treatment

4.3.1.1 Analysis of variance

The analyses of variance for testcross hybrids and their different agronomic characters are presented in Table 14. Hybrids were highly significantly different for all of the 17 observed characters. Effects of lines were highly significant for all agronomic characters observed except for panicle yield per plot, panicle length and grain number per plot. Effects of testers were also highly significant for all observed agronomic characters except for plant number per plot and plant height. For line × tester effects, flowering time, plant number per plot, stover yield per plot, biomass yield per plot plant height, panicle length, panicle diameter and hundred grain mass were found to be significant.

4.3.1.2. Performance summary

The mean values and their respective operational heritabilities of all the characters for each of the 45 testcross hybrids and control entries are presented in Table 15. Trait means, their respective F-ratios and operational heritabilities of the complete data set (including control entries) are presented separately in the same table.

4.3.1.2.1. Flowering time

Among the 45 testcross hybrids, the mean values for flowering time ranged from 42 to 47 days, and the trial mean value for flowering time was 44 days. The cross 202-7-10 × H 77/833-2 was later flowering while drought tolerant donor line 863B exhibited early flowering time in its hybrids with all three testers. Among the testers, H 77/833-2 hybrids showed later flowering times and RIB 335/74 hybrids showed comparatively early flowering times.

Table 14. Analyses of variance for testcross hybrids in fully irrigated non-stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

SV	DF	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
Replication	2	3.05**	15.83	1383.54	0.15	94853.54*	24202.08	2.71	104.88**	544657.53**	936846.90**	114.83**	1068.50**	2.51	4.31**	0.002	22816.96	1.37E+09
Hybrids	44	5.85**	33.14**	3089.75**	1030.61**	129944.68**	223487.28**	74520.94**	24986.38**	263718.64**	795633.37**	265258.67**	88587.67**	29541.72**	9872.87**	3291.98**	232165071.07**	3.18E+09**
Lines (L)	14	3.82**	46.36**	3291.47**	0.65**	34683.64	76179.59**	30.42**	86.80**	85555.45*	193522.71*	25.94**	310.91**	1.49	36.18**	0.02**	264413.81**	8.05E+08
Testers (T)	2	81.45**	2.72	31967.94**	6.86**	1600665.64**	1968610.51**	258.25**	591.65**	3769159.05**	9701014.83**	222.44**	0.36	237.54**	276.36**	0.29**	1203426.35**	2.98E+10**
L × T	28	1.46**	25.64*	624.72	0.21	36920.16	27860.33	2.53	10.55	89323.53*	186480.57**	8.25	108.70*	1.92*	2.45**	0.01**	70355.81	7.07E+08
Error	88	0.49	14.99	513.73	0.13	24131.39	19925.16	3.45	10.65	47178.12	88179.15	5.85	56.08	1.05	0.82	0.002	72484.78	4.97E+08

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

SV-Sources of variation
DF-Degrees of freedom
FT-Flowering time (days after emergence)
ET-Effective tiller number per plant
H.I-Harvest index

Table 15. Performance summary under fully irrigated non-stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	42	67	110	1.68	2683.1	2047.4	18.79	76.3	2213.8	4900.4	41.8	168	23.7	32.6	0.874	2149	235300
ICMB 841 × PPMI 301	45	72	164	2.29	2742.3	1890.7	11.61	68.8	2154.9	4882.0	38.5	148	24.3	23.9	0.757	1535	252100
197-10-18 × PPMI 301	45	72	140	1.94	2699.8	1905.7	13.71	70.4	2167.7	4853.4	39.5	146	24.2	24.0	0.800	1707	238500
202-8-11 × PPMI 301	44	71	158	2.25	2702.9	1849.0	11.84	68.5	2062.8	4771.5	38.7	143	24.9	23.2	0.770	1540	238900
197-12-2 × PPMI 301	45	67	155	2.31	2616.2	1994.2	13.24	76.4	2124.1	4744.7	42.2	151	25.1	24.6	0.819	1626	243500
202-8-9 × PPMI 301	44	70	181	2.68	2790.0	1877.5	10.37	67.1	2119.2	4968.6	37.1	152	24.1	23.2	0.712	1433	262700
202-7-12 × PPMI 301	46	67	144	2.16	2700.7	1956.5	13.59	72.4	2237.4	4931.5	39.7	171	24.8	23.7	0.770	1762	256000
202-8-27 × PPMI 301	44	72	173	2.39	2702.8	1794.1	10.45	66.4	1919.6	4628.0	38.8	134	23.9	23.4	0.742	1406	241200
197-10-11 × PPMI 301	45	75	140	1.86	2494.3	1720.1	13.18	68.1	2412.5	4912.3	34.4	154	24.1	24.3	0.723	1797	232900
202-7-4 × PPMI 301	44	68	158	2.33	2530.0	1772.0	11.35	70.0	1801.9	4326.0	41.2	148	24.0	24.3	0.724	1565	244800
202-7-10 × PPMI 301	45	66	178	2.73	2700.0	2002.7	11.34	74.3	2179.8	4882.9	41.3	159	24.0	24.6	0.748	1507	269300
202-8-8 × PPMI 301	44	70	152	2.16	2477.8	1766.7	12.04	71.4	2136.2	4606.3	38.6	149	26.2	24.9	0.720	1704	248100
197-1-12 × PPMI 301	44	68	150	2.17	2657.7	1895.6	12.84	71.6	2336.5	5013.7	38.3	146	24.5	24.3	0.760	1701	246000
202-6-26 × PPMI 301	45	68	156	2.30	2822.5	2092.7	13.43	74.3	2225.3	5064.6	41.4	153	24.5	23.8	0.732	1834	281900
197-18-1 × PPMI 301	45	70	137	1.95	2686.0	1998.1	15.24	74.5	2308.6	5001.0	40.1	148	25.5	24.4	0.774	1968	256200
863B × RIB 335/74	42	65	133	2.06	2482.2	1860.0	14.36	74.9	2227.8	4701.8	40.0	177	25.7	30.5	0.900	1590	207500
ICMB 841 × RIB 335/74	44	68	208	3.11	2326.4	1470.7	7.29	63.4	1838.6	4164.3	35.6	158	23.5	20.0	0.592	1191	248700
197-10-18 × RIB 335/74	43	69	207	3.02	2319.0	1527.5	7.28	65.7	1835.5	4169.3	36.6	148	23.7	22.1	0.617	1185	245100
202-8-11 × RIB 335/74	42	67	203	3.07	2131.4	1303.6	6.73	59.2	1531.6	3661.6	33.0	146	23.4	19.9	0.554	1174	234100
197-12-2 × RIB 335/74	44	70	158	2.25	2167.5	1483.6	9.36	68.3	1758.6	3919.6	37.9	155	24.6	21.7	0.631	1457	235700
202-8-9 × RIB 335/74	43	70	204	2.91	2366.9	1479.0	7.22	62.4	1827.9	4195.3	35.3	148	24.1	21.3	0.610	1177	241900
202-7-12 × RIB 335/74	43	69	190	2.79	2351.1	1545.7	8.22	65.7	1802.4	4146.5	37.5	151	23.4	21.6	0.607	1343	256600
202-8-27 × RIB 335/74	42	69	201	2.91	2172.5	1263.9	6.34	58.2	1709.3	3872.7	32.4	143	24.9	21.5	0.590	1107	220000
197-10-11 × RIB 335/74	44	76	182	2.40	2439.9	1530.8	8.44	63.0	1882.8	4329.6	35.8	155	23.2	21.2	0.620	1390	247300
202-7-4 × RIB 335/74	42	70	192	2.76	2230.7	1406.6	7.43	62.9	1742.7	3968.7	34.6	150	24.1	21.4	0.694	1094	211100
202-7-10 × RIB 335/74	42	65	153	2.34	2167.9	1370.5	10.24	63.3	1807.0	3977.3	34.8	145	24.3	21.3	0.578	1773	238600
202-8-8 × RIB 335/74	43	72	164	2.29	2319.3	1506.1	9.25	65.0	1757.4	4076.9	37.3	149	24.2	21.7	0.614	1523	246200
197-1-12 × RIB 335/74	42	75	175	2.32	2208.1	1398.5	8.15	63.5	1587.8	3800.6	37.3	140	23.0	20.6	0.533	1567	262000
202-6-26 × RIB 335/74	42	70	169	2.42	2340.2	1507.7	8.83	64.3	1616.8	3965.5	38.1	153	23.3	21.9	0.617	1431	241400
197-18-1 × RIB 335/74	42	68	163	2.39	2524.3	1693.6	10.65	67.3	1988.7	4531.5	37.5	153	24.0	21.3	0.600	1759	278500
863B × H 77/833-2	43	69	153	2.21	2750.0	2086.1	13.76	75.9	2292.6	5046.0	41.4	166	20.0	26.7	0.758	1814	275000
ICMB 841 × H 77/833-2	46	72	217	3.01	2643.1	1773.1	8.19	67.2	2566.1	5227.8	34.3	155	19.2	19.3	0.599	1322	290900
197-10-18 × H 77/833-2	46	65	195	3.01	2721.3	1868.8	9.68	68.6	2506.7	5227.9	35.6	154	20.0	19.9	0.580	1655	320800
202-8-11 × H 77/833-2	45	70	239	3.40	2806.3	1872.4	7.91	66.7	2758.9	5567.4	33.5	154	20.7	19.8	0.610	1285	308200

Table 15. Performance summary under fully irrigated non-stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004 (Cont...).

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-Grain mass (g)	Grain No./panicle	Grain No./plot
197-12-2 × H 77/833-2	45	73	174	2.39	2552.8	1730.0	10.09	67.6	2362.4	4909.1	34.9	147	20.2	19.0	0.612	1652	284800
202-8-9 × H 77/833-2	45	73	221	3.03	2658.0	1785.7	8.03	67.4	2324.2	5003.8	35.6	142	20.1	18.8	0.599	1345	292500
202-7-12 × H 77/833-2	46	72	212	2.95	2610.5	1680.1	7.97	64.5	2512.2	5124.0	33.0	155	19.9	19.0	0.592	1331	283500
202-8-27 × H 77/833-2	45	76	213	2.82	2630.7	1685.3	8.08	64.0	2131.6	4763.3	35.7	141	18.8	18.1	0.617	1306	271600
197-10-11 × H 77/833-2	46	70	228	3.26	2668.2	1828.9	8.02	68.3	2539.6	5203.5	35.4	153	21.5	20.3	0.587	1357	310100
202-7-4 × H 77/833-2	46	67	224	3.35	2614.8	1735.5	7.80	66.3	2329.7	4933.6	35.3	147	20.2	18.8	0.591	1310	294600
202-7-10 × H 77/833-2	47	62	187	3.01	2318.7	1634.2	8.89	70.7	2035.1	4365.2	37.9	149	20.0	19.1	0.603	1459	270500
202-8-8 × H 77/833-2	45	68	209	3.06	2565.8	1710.7	8.19	66.6	2267.3	4824.4	35.2	148	20.8	19.1	0.610	1352	281700
197-1-12 × H 77/833-2	45	67	185	2.77	2528.8	1725.2	9.52	68.1	2217.3	4721.3	36.7	156	20.2	19.3	0.604	1610	291200
202-6-26 × H 77/833-2	45	62	212	3.45	2462.3	1669.9	7.85	67.9	2321.2	4775.9	34.9	156	21.5	20.0	0.611	1292	275000
197-18-1 × H 77/833-2	45	73	212	2.89	2621.0	1831.9	8.72	70.0	2550.7	5173.8	35.6	152	20.5	19.4	0.632	1391	289600
Minimum	**42**	**62**	**133**	**1.68**	**2131.4**	**1263.9**	**6.34**	**58.2**	**1531.6**	**3661.6**	**32.4**	**134**	**18.8**	**18.1**	**0.533**	**1094**	**207500**
Maximum	**47**	**76**	**239**	**3.45**	**2822.5**	**2092.7**	**15.24**	**75.9**	**2758.9**	**5567.4**	**41.4**	**177**	**26.2**	**30.5**	**0.900**	**1968**	**320800**
Mean	**44**	**69**	**184**	**2.60**	**2493.9**	**1688.7**	**9.62**	**67.5**	**2112.3**	**4607.5**	**36.7**	**152**	**22.7**	**21.60**	**0.645**	**1476**	**262900**
SE (±)	**0.4**	**2.24**	**13.09**	**0.21**	**89.69**	**81.5**	**1.07**	**1.88**	**125.4**	**171.44**	**1.4**	**4.33**	**0.59**	**0.52**	**0.02**	**155.42**	**12877.01**
CV (%)	**1.59**	**5.57**	**12.62**	**13.92**	**6.17**	**8.21**	**18.38**	**4.79**	**10.35**	**6.43**	**6.50**	**4.96**	**4.49**	**4.09**	**6.07**	**17.92**	**8.57**
F-ratio	**11.90****	**2.08**	**5.58****	**4.98****	**4.45****	**6.60****	**6.67****	**5.75****	**5.41****	**7.04****	**4.04****	**3.03****	**11.86****	**31.25****	**14.32****	**2.53**	**4.15****
h^2 (plot basis)	**0.78**	**0.26**	**0.60**	**0.57**	**0.53**	**0.65**	**0.65**	**0.61**	**0.60**	**0.67**	**0.50**	**0.40**	**0.78**	**0.91**	**0.82**	**0.34**	**0.51**
h^2 (mean basis)	**0.92**	**0.52**	**0.82**	**0.80**	**0.78**	**0.85**	**0.85**	**0.83**	**0.82**	**0.86**	**0.75**	**0.67**	**0.92**	**0.97**	**0.93**	**0.61**	**0.76**
ICMB 93333 × PPMI 301	47	73	126	1.68	2833.1	2230.4	18.09	78.7	2454.4	5281.1	42.6	178	23.0	28.9	0.772	2349	290400
ICMB 94111 × PPMI 301	43	68	134	1.99	2771.8	2113.8	16.15	76.4	2464.2	5235.7	40.4	165	26.9	33.4	0.898	1807	235300
ICMB 97111 × PPMI 301	43	70	136	1.95	2668.1	2022.7	14.92	75.7	1943.4	4605.7	43.5	161	22.4	28.8	0.818	1846	250500
ICMB 98222 × PPMI 301	45	70	115	1.62	2889.9	2182.3	19.57	75.6	2427.1	5318.4	41.5	161	21.8	32.6	0.874	2270	249600
ICMB 99111 × PPMI 301	45	67	152	2.26	2693.6	2035.8	13.48	75.5	2312.7	4996.7	40.5	151	22.6	27.3	0.769	1761	267500
ICMB 99222 × PPMI 301	44	70	114	1.64	2931.9	2320.8	20.48	79.1	2479.5	5408.0	43.2	178	23.0	31.2	0.889	2297	261800
ICMB 841 × PPMI 301	42	69	154	2.27	2641.7	1968.9	12.93	74.4	2108.7	4741.7	41.0	154	20.7	30.6	0.741	1750	267500
863B × PPMI 301	43	69	103	1.50	2620.4	2044.8	19.66	78.1	2095.9	4723.7	43.3	164	23.4	30.6	0.906	2164	225300
ICMH 451	51	74	136	1.85	2363.6	1804.5	13.64	76.3	2414.5	4774.7	37.6	187	24.8	25.1	0.901	1511	202400
Minimum	**42**	**62**	**103**	**1.50**	**2131.4**	**1263.9**	**6.34**	**58.2**	**1531.6**	**3661.6**	**32.4**	**134**	**18.8**	**18.1**	**0.533**	**1094**	**202400**
Maximum	**51**	**76**	**239**	**3.45**	**2931.9**	**2320.8**	**20.48**	**79.1**	**2758.9**	**5567.4**	**43.5**	**187**	**26.9**	**33.4**	**0.906**	**2349**	**320800**
Mean	**44**	**69**	**174**	**2.47**	**2532.6**	**1758.8**	**10.91**	**69.1**	**2147.4**	**4680.2**	**37.5**	**155**	**22.7**	**23.2**	**0.683**	**1567**	**260600**
SE (±)	**0.40**	**2.31**	**13.00**	**0.21**	**98.01**	**85.35**	**1.11**	**1.78**	**132.56**	**188.33**	**1.36**	**4.38**	**0.68**	**0.55**	**0.020**	**157.34**	**13280.5**
CV (%)	**1.71**	**5.76**	**13.15**	**14.94**	**6.64**	**8.30**	**17.21**	**4.44**	**10.71**	**6.94**	**6.23**	**4.92**	**5.11**	**4.06**	**5.86**	**17.26**	**8.90**
F-ratio	**14.73****	**1.80**	**6.90****	**5.66****	**4.27****	**8.13****	**10.80****	**8.56****	**4.62****	**5.87****	**4.80****	**5.54****	**8.72****	**56.22****	**21.09****	**3.68****	**3.90****
h^2 (plot basis)	**0.82**	**0.21**	**0.66**	**0.61**	**0.52**	**0.70**	**0.77**	**0.72**	**0.55**	**0.62**	**0.56**	**0.60**	**0.72**	**0.95**	**0.87**	**0.47**	**0.49**
h^2 (mean basis)	**0.93**	**0.44**	**0.86**	**0.82**	**0.77**	**0.88**	**0.91**	**0.88**	**0.78**	**0.83**	**0.79**	**0.82**	**0.89**	**0.98**	**0.95**	**0.73**	**0.74**

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

Among control entries, ICMH 451 recorded the latest flowering time (51 days). The heritabilities of this trait, with and without control hybrids included in the analysis, were very high (≥0.92). The high F-ratio for this trait indicated the statistical significance of differences among the testcross hybrids and controls.

4.3.1.2.2. Plant number per plot

The non-significance of variation in plant numbers per plot was used as an indicator for other observations. The mean value for plant number per plot ranged from 62 to 76. The mean value was 69 plants per plot. As the plots for this experiment were over sown and thinned to a uniform stand, no differences in entry means were expected for this trait.

4.3.1.2.3. Panicle number per plot

The mean value for panicle number per plot ranged from 133 to 239. Between the testcross hybrids of the two parental lines of the drought tolerance introgression lines, those of donor parent 863B produced lower numbers of panicles than did those of recurrent parent ICMB 841. Most of the introgression line testcross hybrids produced panicle numbers equal to or greater than those of the recurrent parent across all three testers. Across testers hybrids of introgression lines 202-8-11, 197-10-18, 197-12-2, 202-8-9 and 202-8-27 produced larger numbers of panicles than did hybrids of ICMB 841. Testcrosses of introgression lines 202-6-26 and 197-18-1 produced comparatively lower numbers of panicles than did hybrids of the other backcross progenies. The overall number of panicles produced was highest with hybrids of tester H 77/833-2 followed by those of RIB 335/74, and lowest with the hybrids of tester PPMI 301. The operational heritabilities of this trait were high (0.82).

Most of the control entries were PPMI 301 hybrids and hence the trial mean value for panicle number per plot reduced to 174 from 184 when these control entries were included in the analysis. Among these control entries, ICMB 99111 × PPMI 301 produced the highest number of panicles (152). The F-ratio statistics indicated that the control and testcross hybrids differed significantly in panicle numbers per plot.

4.3.1.2.4. Effective tiller number per plant

For introgression line testcross hybrids, entry mean value of effective tiller number per plant ranged from 1.68 to 3.45, with a trial mean value of 2.60. The overall effective tiller number was higher for hybrids of recurrent parent ICMB 841 than for those of donor parent 863B. The testcrosses of introgression lines 202-6-26 and 197-18-1 produced more tillers per plant with testers RIB 335/74 and H 77/833-2. Among control entries, ICMB 99111 × PPMI 301 and ICMB 841 × PPMI 301 produced larger numbers of effective tillers (2.26) per plot. Heritability on mean basis was high (≥0.80) for this trait.

4.3.1.2.5. Panicle yield per plot

Among introgression line testcross hybrids, the entry mean values for panicle yield ranged from 2131 g (202-8-11 × RIB 335/74) to 2822 g (202-6-26 × PPMI 301) per plot, and a trial mean value of 2493 g. Among the testers, hybrids of PPMI 301 and H 77/833-2 produced greater panicle yields than those of RIB 335/74. Among the controls, ICMB 99222 × PPMI 301 produced the highest panicle yield (2932 g) followed by ICMB 93333 × PPMI 301 (2833 g). The operational heritabilities of panicle yield was high, (≥0.77) both whether the controls were included in the analysis or not.

4.3.1.2.6. Grain yield per plot

The range among introgression line hybrids for grain yield was from 1263 g (202-8-27 × RIB 335/74) to 2093 g (202-6-26 × PPMI 301) in this fully-irrigated control environment, and the trial mean value was 1689 g. Most of the hybrids of testers PPMI 301 and H 77/833-2 surpassed the trial mean value.

ICMB 99222 × PPMI 301 yielded more grain per plot (2321 g) than other control entries. Among control entries, the lowest grain yield per plot was recorded in ICMH 451 (1805 g). The operational heritabilities of this trait were high (≥0.85), and the F-ratio statistics showed that the testcross hybrids were significantly different from each other in mean grain yield per plot in this fully irrigated control environment.

4.3.1.2.7. Grain yield per panicle

Per panicle grain yield ranged from 6.34 g (202-8-27 × RIB 335/74) to 15.24 g (197-18-1 × PPMI 301) among the 45 experimental testcross hybrids. Among testers, PPMI 301 hybrids produced higher grain yield per panicle than did those of the other two testers. Heritability on mean basis was high (≥0.85). Across the control hybrids, ICMB 99222 × PPMI 301 recorded the highest grain yield per panicle (20.48 g) followed by 863B × PPMI 301 (19.66 g). Late-maturing ICMH 451 exhibited the lowest grain yield per panicle (13.64 g) among control entries.

4.3.1.2.8. Panicle harvest index

Among introgression line testcross hybrids, the entry mean values for panicle harvest index ranged from 58.2% (202-8-27 × RIB 335/74) to 75.9% (863B × H 77/833-2). Differences in panicle harvest index of hybrids of the parental entries were high across testers. The mean panicle harvest index of PPMI 301 hybrids crossed the overall trial

mean value (67.5%) while the mean for hybrids of tester RIB 335/74 was lower. ICMB 99222 × PPMI 301 had the highest panicle harvest index value among the control testcross hybrids.

4.3.1.2.9. Stover yield per plot

Testcross hybrids of donor parent 863B outyielded those of the recurrent parent ICMB 841 for stover in combinations with testers PPMI 301 and RIB 335/74, but stover yield of the testcross hybrid of ICMB 841 with tester H 77/833-2 outyielded that of donor parent 863B. Introgression line testcross hybrid entry mean values ranged from 1532 g (202-8-11 × RIB 335/74) to 2759 g (202-8-11 × H 77/833-2). Among the testers, hybrids of H 77/833-2 produced higher stover yields. The larger numbers of panicles produced by hybrids of H 77/833-2 contributed to these higher stover yields.

Significant differences were observed in treatment means of stover yield whether the control testcross hybrids were included in the analysis or not. The operational heritabilities on mean basis were high (≥0.78) for this trait. Among the controls, ICMH 451 produced high stover yield (2415 g), comparable to that of the higher yielding experimental and control entries (including ICMB 99222 × PPMI 301, ICMB 93333 × PPMI 301 and ICMB 94111 × PPMI 301).

4.3.1.2.10. Biomass yield per plot

Biomass yields of testcross hybrids of 197-10-11, 197-18-1, 202-7-12, and 202-8-9 with testers PPMI 301 and H 77/833-2 were higher than those of the recurrent parent ICMB 841 and donor parent 863B with testers PPMI 301 and RIB 335/74. But recurrent parent ICMB 841 outyielded the donor parent for biomass when crossed with tester H 77/833-2. Among the introgression line testcross hybrids, average biomass yield ranged between

202-8-11 × RIB 335/74 (3662 g) and 202-8-11 × H 77/833-2 (5567 g). Except 202-7-10 × H 77/833-2, testcross hybrids of H 77/833-2 outyielded the overall mean biomass yield (4608 g). The heritability of biomass yield was high (≥0.83).

The overall mean biomass yield for the trial increased to 4680 g per plot from 4608 g per plot when the control entries were included in the analysis as these generally had higher biomass yield. Among these control entries, ICMB 99222 × PPMI 301 produced the highest biomass yield per plot (5408 g).

4.3.1.2.11. Harvest index

Among introgression line testcross hybrids, the average value of harvest index was 36.7%. The mean values of individual testcross hybrids ranged from 32.4% (202-8-27 × RIB 335/74) to 42.2% (197-12-2 × PPMI 301). Among the testers, hybrids of PPMI 301 showed higher harvest index followed by those of RIB 335/74 and H 77/833-2. Among the control testcrosses, ICMB 97111 × PPMI 301 had the highest harvest index value (43.5%) and ICMH 451 had lowest harvest index value (37.6%); otherwise the differences among control entries for this trait were meager. This trait had high heritability values (≥0.75).

4.3.1.2.12. Plant height

Among introgression line testcross hybrids, the range for plant height was from 134 cm (202-8-27 × PPMI 301) to 177 cm (863B × RIB 335/74) and the mean was 152 cm. There was a large margin of difference in plant height between testcross hybrids of the two parents of these introgression lines, ICMB 841 and 863B. No testcross hybrids crossed the height of the donor parent 863B across the three testers. Among controls, ICMH 451 was the tallest hybrid (187 cm) followed by ICMB 99222 × PPMI 301 and

ICMB 93333 x PPMI 301 (178 cm). Because of ICMH 451, the trial mean when the controls were analysed along with testcross hybrids increased by 3 cm and the heritability of plant height increased from 0.67 to 0.82.

4.3.1.2.13. Panicle length

The mean value of introgression line testcross hybrids for panicle length was 22.7 cm, and the observed range was from 18.8 cm (202-8-27 x H 77/833-2) to 26.2 cm (202-8-8 x PPMI 301). Statistically significant differences in panicle lengths were observed between these testcross hybrids. Panicle lengths of the controls were similar those of testcross hybrids except that ICMB 94111 x PPMI 301 had the lengthiest panicles (26.9 cm). The heritability on mean basis for this trait was high (≥0.89).

4.3.1.2.14. Panicle diameter

Among introgression line testcross hybrids the mean value for panicle diameter ranged from 18.1 cm (202-8-27 x H 77/833-2) to 32.6 cm (863B x PPMI 301). As for plant height, there was a substantial difference in panicle diameter of hybrids of the donor and recurrent parents, and the panicle diameters of the introgression line hybrids were similar to the hybrids of the recurrent parent. Among controls, highest panicle diameter was observed in ICMB 94111 x PPMI 301 (33.4 cm). As most of the control entries had means on the higher side for panicle diameter, the trial mean has increased from 21.6 cm to 23.2 cm when the controls were included. Heritability of this trait was very high (≥0.97).

4.3.1.2.15. Hundred-grain mass

Among parental testcross hybrids, except for the tester PPMI 301, the marginal difference for hundred grain mass was high between the parents (863B x RIB 335/74 – 0.900 g),

(841B x RIB 335/74 – 0.592 g) and (863B x H 77/833-2 – 0.758 g), (841B x H 77/833-2 – 0.599 g). The mean value of hundred-grain mass for introgression line testcrosses was high (0.645 g). Among controls, the mean value of 863B x PPMI 301 was the highest 0.906 g, marginally exceeding the hundred-grain mass of other control hybrids included in the experiment. The operational heritabilities of hundred-grain mass were high (0.93).

4.3.1.2.16. Grain number per panicle

Among testcrosses of the introgression lines and their parents the range for number of grains per panicle was from 1094 (202-7-4 x RIB 335/74) to 2149 (863B x PPMI 301). Grain number per panicle was high among the testcross hybrids of tester PPMI 301, with 197-18-1 x PPMI 301 (1968) and 202-6-26 x PPMI 301 (1834) having the highest numbers of grains per panicle. Testcross 202-7-10 x RIB 335/74 produced the highest number of grains per panicle (1773) among hybrids of tester RIB 335/74.

Among control entries, ICMB 93333 x PPMI 301 had the highest number of grains per panicle. By inclusion of controls in the analysis, heritability of 100-grain mass, was increased from 0.61 to 0.73.

4.3.1.2.17. Grain number per plot

Number of grains per plot varied from 207500 (863B x RIB 335/74) to 320800 (197-10-18 x H 77/833-2), with an introgression line testcross hybrid mean for this trait of 262900. Among the testers, hybrids of H 77/833-2 produced larger numbers of grains per plot followed by those of testers PPMI 301 and RIB 335/74. Among control testcrosses, the highest number of grains per plot was produced by ICMB 93333 x PPMI 301; however, when compared to the mean of the trial as a whole, the controls were not superior to the introgression line testcross hybrids. Hence the heritability of grain number

per plot was marginally reduced from 0.76 to 0.74 when these control entries were included in the analysis.

4.3.1.3. Estimates of components of genetic variation

The magnitudes of genetic components of variance are presented in Table 16. The significance of lines and testers as sources of variation (Table 14) contributed to the high degree of additive genetic variation (σ^2A) for most observed traits. Highly significant σ^2A of flowering time, panicle number per plot, grain yield per plot, grain yield per panicle, panicle harvest index, stover yield, harvest index, plant height, panicle diameter, hundred grain mass and grain number per panicle indicated that the parents (both lines and testers) exhibit heritable variation for all of these characters, and that this variation could be exploited in both OPVs and hybrids. The dominance component of genetic variation is indicative mainly of line × tester interaction that can only be exploited in hybrids.

Dominant genetic variance (σ^2D) was significant for flowering time, stover yield per plot, harvest index, plant height, panicle length, panicle diameter, hundred-grain mass and grain number per plot. The ratio of additive and dominance variance was large for flowering time, panicle number per plot, panicle yield per plot, grain yield per plot, stover yield per plot, biomass yield per plot, harvest index, panicle length, panicle diameter, hundred-grain mass and grain number per plot. Only in case of plant height was σ^2D greater than σ^2A. Since the effect of allelic interactions were less, parental performance itself can be used as the criteria for choosing among the lines and testers for further breeding programmes.

Table 16. Estimates of additive and dominant components of genetic variation in among testcross hybrids of introgression lines and their parents in fully irrigated non-stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Genetic comp.	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
σ^2A	3.0**	0.0	1255.9**	0.3**	57833.7**	73669.2**	10.5**	24.4**	136150.6**	352650.1	8.6**	3.5**	8.7**	11.4**	0.01**	49152.9**	1.0E+09
σ^2D	0.3**	3.5*	37.0	0.0	4262.9	2645.1	-0.3	0.0	14048.5*	32767.1	0.8**	17.5*	0.3*	0.5**	0.001**	0.0	6.9E+08 **
σ^2A: σ^2D	9.4	0.0	33.9	∞	13.6	27.9	∞	∞	9.7	10.8	10.7	0.2	30.1	21.0	10.4	∞	15.5

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

4.3.1.4. Contributions of lines and testers

The relative contributions of lines and testers and their interaction to variation in performance of the testcross hybrids is tabulated in Table 17. Under fully irrigated non-stress conditions the introgression lines and their parents, lines contributed more to testcross hybrid variation for plant height (58.9%) and grain number per panicle (45.8%). Testers contributed more to testcross hybrids variation for flowering time, panicle number per plot, effective tiller number per plant, panicle yield per plot, grain yield per plot, stover yield per plot, biomass yield per plot, panicle length, hundred-grain mass and grain number per plot. For testcross hybrid performance, there was equal contribution observed from lines and testers for grain yield per panicle, panicle harvest index, harvest index and panicle diameter. Only for plant height was the line × tester interaction component a major contributor to variation among the testcross hybrids.

4.3.1.5. Combining Ability

The results of the combining ability analysis, in the form of tabulated *gca* effects the lines and testers, are presented in Table 18.

4.3.1.5.1. General Combining Ability

For flowering time, the best negative combiners, which contribute earliness to their hybrids among lines, were 202-8-27 and 863B. Among testers, RIB 335/74 was the negative combiner. Tester RIB 335/74 thus conferred early flowering and is suitable to produce hybrids to escape from terminal drought stress.

For grain yield related characters like panicle numbers, effective tiller numbers, panicle yield, grain yield per plot and panicle harvest index, positive combing ability is considered favourable. Introgression lines 202-8-11 and 202-8-9, the recurrent parent

Table 17. Relative contributions (%) of introgression lines and testers, parents and their interaction towards variation in testcross hybrids in fully irrigated non-stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Genetic comp.	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	Plant H.I. (%)	height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
Lines	20.78	47.29	35.43	31.98	10.29	18.44	42.03	45.11	10.66	9.91	34.95	58.85	3.80	44.91	29.24	45.82	12.42
Testers	63.33	0.40	50.70	47.91	67.82	68.07	50.98	43.92	67.08	70.98	42.82	0.01	86.41	49.01	57.69	29.79	65.76
Lines × Testers	15.89	52.31	13.87	20.11	21.90	13.49	6.99	10.96	22.26	19.10	22.23	41.15	9.79	6.07	13.07	24.38	21.81

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

Table 18. Estimates of gca effects of introgression lines and testers under fully irrigated non-stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Lines & Testers	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H. I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B	-1.66**	-1.16	-49.76**	-0.69**	81.01	262.30**	5.76**	8.21**	24.01	103.10	4.85**	14.59**	-0.03	7.11**	0.17**	405.50**	-20555.00**
ICMB 841	0.34	0.50	23.68**	0.32**	-20.01	-12.58	-1.50*	0.22	33.21	11.30	-0.18	1.70	-0.85*	0.14	-0.01	-180.50*	5279.00
197-10-18	0.34	-0.94	2.02	0.07	58.68	39.21	0.08	-0.06	54.92	111.70	-0.02	-1.42	-0.27	-0.09	0.01	13.80	8043.00
202-8-11	-0.33	-0.16	20.46**	0.31**	30.68	-49.67	-1.33*	-3.31**	58.47	87.20	-2.29**	-3.19	0.16	-1.18**	-0.02	-164.60	-354.00
197-12-2	0.45	0.50	-15.21*	-0.26*	-62.88	19.10	0.73	2.61*	0.89	-63.90	1.06	0.36	0.43	-0.38	0.03	76.50	-5369.00
202-8-9	-0.10	1.62	22.23**	0.27*	70.96	-23.67	-1.60**	-2.71*	17.85	115.60	-1.43	-3.53	-0.11	-1.02**	-0.10**	-179.50*	4943.00
202-7-12	0.67**	-0.05	4.46	0.05	45.68	16.43	-0.24	-0.49	77.99	121.80	-0.44	7.70**	-0.17	-0.71*	0.00	-23.40	5315.00
202-8-27	-0.66**	2.95	15.02*	0.10	-12.99	-134.79**	-1.79**	-5.10**	-178.25*	-193.20	-1.57	-11.86**	-0.34	-1.12**	-0.01	-228.70*	-15820.00*
197-10-11	1.12**	4.06**	2.35	-0.11	8.68	-35.24	-0.19	-1.75	130.49	137.30	-1.99*	2.47	0.08	-0.17	-0.02	12.50	3351.00
202-7-4	0.01	-1.05	12.46	0.23	-38.99	-74.90	-1.28*	-1.87	-125.39	-166.30	-0.25	-2.42	-0.09	-0.65*	0.01	-179.00*	-9931.00
202-7-10	0.56*	-5.50**	-6.54	0.11	-135.77**	-48.46	-0.01	1.71	-111.93	-249.60*	0.90	-1.53	-0.09	-0.45	-0.02	77.70	-598.00
202-8-8	-0.10	0.62	-6.10	-0.12	-49.54	-48.90	-0.19	-0.40	-36.62	-88.10	-0.20	-1.86	0.87*	-0.21	-0.01	24.50	-1396.00
197-1-12	-0.21	0.84	-13.10	-0.21	-58.99	-44.46	0.22	-0.16	-87.59	-148.50	0.30	-3.97	-0.30	-0.68*	-0.03	124.00	6327.00
202-6-26	-0.33	-2.94	-0.98	0.12	10.79	26.54	-0.07	0.62	-34.92	-26.00	0.79	3.14	0.23	-0.21	-0.01	17.30	6048.00
197-18-1	-0.10	0.73	-10.98	-0.20	72.68	109.10*	1.42*	2.50*	176.87*	247.60*	0.46	-0.19	0.48	-0.39	0.01	203.90*	14716.00*
PPMI 301	0.21*	0.26	-27.03**	-0.39**	124.10*	177.90**	2.76**	3.72**	32.50	160.50**	2.55**	-0.08	1.53**	2.59**	0.08**	186.90**	-10018.00**
RIB 335/74	-1.44**	-0.03	0.77	0.01	-217.00**	-230.40**	-1.47**	-3.53**	-304.30**	-523.30**	-0.98**	-0.01	1.11**	-0.25	-0.04**	-117.00**	-19233.00**
H 77/833-2	1.23**	-0.23	26.26**	0.39**	92.90**	52.50*	-1.30**	-0.19	271.80**	362.80**	-1.57**	0.10	-2.64**	-2.35**	-0.05**	-69.80	29252.00**

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

ICMB 841, and tester H 77/833-2 showed positive *gca* for effective tiller number per plant and panicle number per plot. Introgression line 202-8-9 and testers PPMI 301 and H 77/833-2 exhibited positive *gca* for panicle yield per plot. For grain yield per plot and grain yield per panicle, the donor parent 863B and introgression line 197-18-1 were the positive combiners and among testers both PPMI 301 and H 77/833-2 showed positive *gca* effects, but tester H 77/833-2 exhibited negative *gca* for grain yield per panicle. Similarly, for panicle harvest index the best positive combiners among introgression lines and testers were the donor parent 863B, 197-12-2 and 197-18-1 and tester PPMI 301. The significantly negative combiners for panicle harvest index were 202-8-11, 202-8-9 and 202-8-27 among introgression lines and tester RIB 335/74.

For stover yield per plot only introgression line 197-18-1 and tester H 77/833-2 showed positive *gca*. Introgression line 202-8-27 was the only negative combiners for stover yield per plot and for biomass yield per plot the negative combiners were line 202-7-10 and tester RIB 335/74. For harvest index, except the donor parent 863B and tester PPMI 301, none of the lines and testers showed positive *gca* effects, but introgression lines 202-8-11 and 197-10-11 and tester H 77/833-2 showed negative *gca* effects.

Donor parent 863B and introgression line 202-7-12 had positive *gca* effects for plant height. For panicle length, introgression 202-8-8 and testers PPMI 301 and RIB 335/74 showed long panicles with positive *gca* effects while the recurrent parent ICMB 841 and tester H 77/833-2 had negative *gca* effects for this trait. Six of the introgression lines and tester H 77/833-2 showed negative *gca* effects for panicle diameter while the donor parent 863B and tester PPMI 301 showed significantly positive *gca* effects for this

trait. For grain number per panicle, donor parent 863B, introgression line 197-18-1 and tester PPMI 301 exhibited positive *gca* effects.

The prominent negative combiners for grain number per panicle among introgression lines and testers were recurrent parent ICMB 841, introgression lines 202-8-27, 202-8-9 and 202-7-4, and testers RIB 335/74. For grain number per plot, introgression line 197-18-1 and tester H 77/833-2 showed significantly positive *gca* effects.

4.3.1.5.2. Specific Combining Ability

The *sca* effects of testcross hybrids of the introgression lines and their recurrent and donor parents are presented in Table 19. Among testcross hybrids, very few showed significant *sca* effects. For example, 202-7-10 × RIB 335/74 and 202-7-4 × RIB 335/74 were early flowering while hybrids of the same introgression lines crossed with H 77/833-2, flowered very late; 202-7-10 × PPMI 301 showed positive ability for panicle number per plot; for panicle yield per plot 202-7-10 × PPMI 301 showed positive *sca*, and hybrids 202-8-11 × RIB 335/74 and 202-7-10 × H 77/833-2 showed significantly negative *sca* effects. The hybrids 863B × RIB 335/74 and 202-8-11 × H 77/833-2 had high positive *sca* effects for both stover yield and biomass yield per plot.

Introgression lines testcross hybrids, 202-7-12 × PPMI 301 and 197-1-12 × H 77/833-2 exhibited positive *sca* effects for plant height. The donor parent exhibited positive *sca* for panicle length, panicle diameter and 100-grain mass with tester RIB 335/74, but showed negative *sca* effects with tester PPMI 301. The positive combiners for 100-grain mass were 863B × RIB 335/74, 202-8-9 × RIB 335/74 and 202-8-9 × H 77/833-2. The testcross hybrids, 202-7-10 × PPMI 301 showed positive *sca* for grain

Table 19. Estimates of sca effects of testcross hybrids under fully irrigated non-stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H. I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	0.35	2.74	-0.75	-0.08	-158.11	-162.16*	0.98	-2.10	-231.60	-393.50*	-0.01	-8.36**	-1.57**	-1.36**	-0.07	223.71	6597.00
ICMB 841 × PPMI 301	-0.99*	-0.26	0.81	0.02	-52.82	27.09	-0.56	2.49	-95.60	-152.30	1.71	-3.47	-0.21	2.64**	0.02	-57.29	1156.00
197-10-18 × PPMI 301	0.01	3.19	-14.19	-0.33	18.89	-25.34	0.74	-1.53	-64.00	-48.90	-0.18	-3.03	0.03	-0.59	0.05	4.04	-19591.00
202-8-11 × PPMI 301	0.35	1.41	-16.64	-0.28	18.22	-7.46	0.32	-0.05	-110.00	-95.60	1.09	-3.25	0.41	-0.34	0.04	15.81	-10766.00
197-12-2 × PPMI 301	-0.10	-3.26	16.36	0.33	24.78	76.11	-0.28	2.14	-13.50	7.50	1.38	-1.81	0.23	0.23	0.05	-138.96	-1151.00
202-8-9 × PPMI 301	-0.54	-1.37	6.58	0.21	78.79	-11.10	-0.95	-2.46	52.50	184.90	-1.66	6.42	-0.19	-0.46	-0.17**	-63.53	5680.00
202-7-12 × PPMI 301	0.68	-2.37	-11.30	-0.08	29.56	58.11	0.93	1.27	57.40	83.10	0.38	14.86**	0.57	-0.34	0.03	96.26	659.00
202-8-27 × PPMI 301	0.01	-0.37	4.14	0.08	59.89	27.66	-0.65	-0.08	-15.80	40.30	0.60	-4.25	-0.19	-0.23	0.01	-53.74	6956.00
197-10-11 × PPMI 301	-0.43	1.19	-16.19	-0.25	-170.78	-159.56*	0.51	-2.27	90.70	-84.00	-3.35*	0.08	-0.41	-0.21	0.00	95.71	-20486.00
202-7-4 × PPMI 301	0.01	-0.70	-7.30	-0.11	-58.78	-47.23	-0.26	-0.22	-223.70	-286.30	1.59	-0.70	-0.28	0.20	-0.03	55.15	4667.00
202-7-10 × PPMI 301	-0.21	1.41	33.03*	0.43*	187.00*	157.00	-1.63	1.11	144.20	327.40	0.77	7.08	-0.28	0.36	0.02	-259.85	19884.00
202-8-8 × PPMI 301	-0.21	-0.04	4.25	0.05	-93.89	-64.89	-0.50	0.15	43.10	-54.60	-0.90	1.08	0.93	0.40	-0.01	-9.63	-516.00
197-1-12 × PPMI 301	0.24	-2.26	5.25	0.12	24.22	13.33	-0.17	-0.06	236.90	257.30	-1.83	-1.47	0.40	0.30	0.04	-111.52	-10362.00
202-6-26 × PPMI 301	0.35	0.85	2.48	-0.04	137.45	140.00	0.61	1.56	148.70	282.30	0.58	0.08	-0.10	-0.70	0.00	128.59	25836.00*
197-18-1 × PPMI 301	0.46	-0.15	-6.53	-0.08	-44.44	-21.56	0.94	0.05	-19.20	-67.50	-0.16	-3.25	0.65	0.11	0.02	75.26	-8562.00
863B × RIB 335/74	0.66	-3.30	4.45	0.16	101.70	118.55	-0.10	2.52	346.50**	450.10**	-0.82	8.24	1.79**	1.55**	0.10*	-200.40	-12832.00
ICMB 841 × RIB 335/74	0.66	-2.30	8.67	0.23	48.72	-9.24	-0.04	-1.46	-5.50	45.10	-0.50	3.79	0.38	-1.95**	-0.02	-13.40	2583.00
197-10-18 × RIB 335/74	-0.01	0.14	23.67	0.34	-72.30	-26.70	-1.43	1.02	-18.40	-88.80	0.25	-1.10	-0.04	0.31	-0.01	-213.06	-3830.00
202-8-11 × RIB 335/74	-0.67	-2.64	2.90	0.15	-187.97*	-145.80	-0.66	-2.11	-253.90*	-439.90*	-1.22	-1.99	-0.73	-0.83	-0.05	-33.93	-8412.00
197-12-2 × RIB 335/74	0.55	0.36	-2.10	-0.03	-52.41	-22.92	-0.21	0.85	-40.60	-91.10	0.57	4.79	0.23	0.17	-0.02	-4.73	270.00
202-8-9 × RIB 335/74	0.77	-0.75	3.12	0.05	-0.25	7.18	0.12	0.30	-9.90	-37.00	0.49	-1.65	0.27	0.45	0.09*	-28.45	-3928.00
202-7-12 × RIB 335/74	-0.34	-0.42	7.56	0.14	19.37	51.08	-0.24	1.72	-85.70	-64.40	1.77	-9.21*	-0.44	0.40	-0.01	-18.84	10482.00
202-8-27 × RIB 335/74	-0.01	-3.08	5.01	0.20	-86.63	-64.37	-0.38	-0.91	150.10	65.30	-2.28	4.02	1.27*	0.75	-0.02	-49.18	-5038.00
197-10-11 × RIB 335/74	0.55	2.14	-4.33	-0.14	110.70	78.08	0.17	0.61	-71.00	41.70	1.65	0.35	-0.82	-0.47	0.01	-7.73	3088.00
202-7-4 × RIB 335/74	-1.01*	1.59	0.23	-0.05	-7.63	3.41	0.04	0.16	190.90	185.10	-1.62	4.57	0.25	0.14	0.06	-111.62	-19842.00
202-7-10 × RIB 335/74	-1.23**	0.70	-20.44	-0.36	0.48	-59.03	1.61	-2.55	121.10	123.50	-2.18	-5.99	0.45	-0.10	-0.03	310.38*	-1608.00
202-8-8 × RIB 335/74	0.77	1.59	-12.88	-0.23	66.25	67.08	0.88	0.93	-28.30	39.90	1.33	-0.65	-0.61	0.07	0.00	114.27	6793.00
197-1-12 × RIB 335/74	-0.12	5.03*	3.12	-0.11	-48.63	-46.37	-0.52	-0.58	-159.10	-205.80	0.89	-8.21*	-0.64	-0.56	-0.06	57.71	14785.00
202-6-26 × RIB 335/74	-0.34	3.47	-10.66	-0.31	4.59	-23.70	0.25	-0.90	-158.20	-151.70	1.00	0.35	-0.94	0.27	0.00	28.82	-5492.00
197-18-1 × RIB 335/74	-0.23	-2.53	-8.33	-0.03	104.03	72.75	0.50	0.43	22.00	127.90	0.67	2.68	-0.42	-0.19	-0.03	170.16	22981.00
863B × H 77/833-2	-1.01*	0.56	-3.70	-0.07	56.41	43.61	-0.88	-0.42	-114.90	-56.60	0.83	0.13	-0.23	-0.19	-0.03	-23.31	6234.00
ICMB 841 × H 77/833-2	0.33	2.56	-9.48	-0.25	4.10	-17.84	0.60	-1.03	101.10	107.20	-1.21	-0.32	-0.17	-0.69	0.00	70.69	-3739.00
197-10-18 × H 77/833-2	-0.01	-3.33	-9.48	-0.01	53.41	52.04	0.69	0.51	82.40	137.70	-0.07	4.13	0.01	0.28	-0.04	209.03	23421.00
202-8-11 × H 77/833-2	0.33	1.23	13.74	0.13	169.74	153.25	0.35	2.16	363.90**	535.60**	0.13	5.24	0.32	1.17*	0.01	18.13	19178.00
197-12-2 × H 77/833-2	-0.45	2.90	-14.26	-0.30	27.63	-53.19	0.50	-2.99	54.00	83.60	-1.95	-2.99	-0.46	-0.40	-0.03	143.69	882.00
202-8-9 × H 77/833-2	-0.23	2.12	-9.70	-0.26	-78.54	3.92	0.83	2.16	-42.50	-147.90	1.17	-4.76	-0.08	0.01	0.08*	91.98	-1752.00
202-7-12 × H 77/833-2	-0.34	2.79	3.74	-0.06	-48.92	-109.19	-0.69	-2.99	28.30	-18.70	-2.15	-5.65	-0.13	-0.07	-0.02	-77.42	-11140.00
202-8-27 × H 77/833-2	-0.01	3.45	-9.15	-0.28	26.74	36.70	1.03	0.99	-134.30	-105.60	1.68	0.24	-1.08	-0.52	0.01	102.92	-1918.00
197-10-11 × H 77/833-2	-0.12	-3.33	20.52	0.39	60.08	81.48	-0.68	1.67	-19.70	42.30	1.70	-0.43	1.23*	0.69	-0.01	-87.97	17398.00
202-7-4 × H 77/833-2	0.99*	-0.88	7.07	0.16	66.41	43.81	0.22	0.06	32.90	101.20	0.03	-3.87	0.03	-0.33	-0.03	56.47	15175.00
202-7-10 × H 77/833-2	1.44**	-2.10	-12.59	-0.07	-187.48*	-97.96	0.02	1.45	-265.30*	-450.90**	1.41	-1.10	-0.17	-0.27	0.01	-50.53	-18275.00
202-8-8 × H 77/833-2	-0.56*	-1.55	8.63	0.18	27.63	-2.19	-0.38	-1.08	-14.80	14.80	-0.42	-0.43	-0.33	-0.47	0.01	-164.64	-6277.00
197-1-12 × H 77/833-2	-0.12	-2.77	-8.37	-0.01	24.41	33.04	0.69	0.65	-77.90	-51.50	0.94	9.68*	0.24	0.27	0.02	53.80	-4423.00
202-6-26 × H 77/833-2	-0.01	-4.33	8.19	0.35	-142.03	-116.30	-0.86	-0.67	9.60	-130.50	-1.58	-0.43	1.04	0.43	0.00	-157.42	-20344.00
197-18-1 × H 77/833-2	-0.23	2.67	14.85	0.11	-59.59	-51.19	-1.45	-0.48	-2.80	-60.40	-0.51	0.57	-0.24	0.08	0.01	-245.42	-14419.00

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

number per panicle and 202-6-26 × PPMI 301 exhibited positive *sca* for grain number per plot.

4.3.2. Late stress treatment

4.3.2.1.Analysis of variances

The analyses of variances for testcross hybrids and their different characters in the late-onset terminal drought stress environment are presented in Table 20. Hybrids were significantly different for all the observed agronomic characters except plant number per plot. Lines were highly significant as sources of variation among the hybrids for flowering time, panicle number per plot, effective tiller number per plant, panicle harvest index, grain yield per panicle, stover yield per plot, biomass yield per plot, harvest index, plant height, panicle length, panicle diameter, 100-grain mass, grain number per panicle and grain number per plot. Testers were highly significant as sources of variation for all observed characters except plant number per plot and plant height. For line × tester interaction, flowering time, grain yield per panicle, plant height, panicle length and panicle diameter were found to be significant.

4.3.2.2. Performance summary

The mean values and their respective heritabilities of seventeen characters for each of the 45-testcross hybrids without controls are presented in Table 21. Similarly, the mean values and heritabilities of the full set of trial entries including the controls, are tabulated separately in the same table.

4.3.2.2.1. Flowering time

Among 45 testcross hybrids, mean values for flowering time ranged from 41 to 46 days, with a trial environment mean value for flowering time of 44 days. The average

Table 20. Analyses of variance for testcross hybrids in late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

SV	DF	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
Replications	2	0.67	32.81	1546.80*	0.14	261859.55**	107541.63*	1.45	7.30	1511729.55**	3003110.20**	58.41	568.45**	0.19	0.86	0.01	148728.45*	1.66E+09
Hybrids	44	6.97**	22.05	3339.80**	1113.89**	97864.82**	184794.55**	61617.61**	20734.12**	290058.35**	678439.34**	226247.35**	75557.02**	25196.24**	8431.54**	2810.53**	257200.32**	2.68E+09**
Lines (L)	14	5.61**	25.83	3800.07**	0.76**	60946.22	160430.61**	34.42**	175.92**	176366.71*	331578.31*	89.28**	215.86**	2.94**	51.89**	0.04**	263283.93**	1.09E+09
Testers (T)	2	97.87**	41.36	32763.52**	5.69**	966655.55**	1439670.19**	202.01**	939.98**	4084160.44**	6493681.83**	834.06**	152.32	180.74**	312.04**	0.19**	2293444.61**	4.59E+09**
L x T	28	1.15**	15.13	270.89	0.06	28208.84	21652.53	2.16*	16.37	65036.14	97292.52	15.48	103.14*	2.22**	3.31**	0.01	51309.20	9.45E+08
Error	88	0.48	15.47	409.73	0.09	34397.01	29208.63	1.14	16.49	81693.32	178959.47	9.72	55.06	0.84	1.00	0.01	38143.35	9.30E+08

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

SV-Sources of variation
DF-Degrees of freedom
FT-Flowering time (days after emergence)
ET-Effective tiller number per plant
H.I-Harvest index

Table 21. Performance summary under late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot),	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	42	70	106	1.55	2242.0	1615.2	15.93	72.5	1702.6	4249.1	38.4	161	22.4	31.0	0.881	1831	190100
ICMB 841 × PPMI 301	45	70	153	2.19	2281.3	1446.9	9.75	63.4	1622.5	3894.8	37.5	154	23.0	23.1	0.604	1623	246300
197-10-18 × PPMI 301	44	66	161	2.43	2402.9	1569.6	9.79	65.1	1589.9	3995.7	39.2	156	23.6	23.5	0.625	1593	255000
202-8-11 × PPMI 301	43	73	179	2.45	2311.3	1453.0	8.29	62.9	1662.7	3971.4	36.8	145	22.6	23.2	0.603	1367	243600
197-12-2 × PPMI 301	45	75	125	1.66	2242.3	1552.2	12.55	69.0	1564.7	3807.6	41.0	155	23.9	24.2	0.657	1894	236000
202-8-9 × PPMI 301	44	70	174	2.46	2185.1	1361.5	7.97	62.6	1958.6	4165.9	33.0	159	23.7	22.3	0.569	1395	241700
202-7-12 × PPMI 301	45	73	168	2.28	2150.4	1292.5	7.67	59.4	1846.5	3983.0	32.2	159	24.7	23.2	0.589	1288	214600
202-8-27 × PPMI 301	44	72	171	2.37	2404.7	1523.3	8.83	62.6	1480.3	3895.6	38.7	154	23.1	21.6	0.617	1423	246200
197-10-11 × PPMI 301	46	70	180	2.57	2233.7	1401.9	7.63	62.0	1681.5	3902.7	33.9	160	23.3	22.7	0.560	1363	250000
202-7-4 × PPMI 301	44	68	170	2.49	2240.8	1413.7	8.38	63.2	1687.8	3922.5	36.1	147	23.0	23.0	0.548	1542	260700
202-7-10 × PPMI 301	44	65	146	2.25	2068.3	1294.6	9.01	62.2	1508.9	3546.8	36.1	146	22.4	23.9	0.591	1524	221000
202-8-8 × PPMI 301	45	70	146	2.08	2274.4	1511.8	10.36	65.9	1727.8	3995.3	37.3	149	23.1	22.0	0.653	1579	228600
197-1-12 × PPMI 301	44	72	150	2.08	2289.9	1515.4	10.03	65.7	1759.7	4041.7	37.4	159	24.1	23.8	0.645	1546	231100
202-6-26 × PPMI 301	45	66	144	2.18	2114.1	1416.6	10.02	66.9	1384.7	3471.2	41.1	148	23.4	22.7	0.599	1711	239900
197-18-1 × PPMI 301	44	71	169	2.44	2238.4	1532.0	9.34	68.2	2023.0	4261.9	35.9	155	25.3	26.0	0.583	1679	263500
863B × RIB 335/74	41	68	110	1.63	2107.4	1541.8	14.18	73.1	1433.7	3539.7	43.7	179	25.1	29.9	0.851	1664	181500
ICMB 841 × RIB 335/74	43	71	190	2.68	1887.6	1038.4	5.57	55.3	1198.4	3100.0	35.1	153	22.5	19.4	0.464	1183	223900
197-10-18 × RIB 335/74	42	69	194	2.81	1992.7	1145.9	6.06	58.3	1444.5	3450.5	33.8	151	24.6	19.0	0.535	1178	227800
202-8-11 × RIB 335/74	42	71	202	2.86	1949.1	1021.0	5.01	52.4	1325.2	3296.9	31.1	159	24.8	19.3	0.467	1106	219000
197-12-2 × RIB 335/74	43	72	163	2.27	1935.5	1238.1	7.57	64.2	1613.0	3568.4	35.3	158	24.9	21.2	0.548	1377	225200
202-8-9 × RIB 335/74	42	73	210	2.89	1982.2	1112.6	5.37	56.2	1628.1	3609.5	31.1	149	22.8	20.1	0.492	1099	228900
202-7-12 × RIB 335/74	43	72	192	2.67	1877.3	992.5	5.25	52.5	1533.4	3411.9	28.7	157	22.9	18.9	0.443	1161	223600
202-8-27 × RIB 335/74	42	69	208	3.03	1815.9	1006.3	4.72	54.1	1421.6	3223.9	30.5	149	23.0	19.0	0.450	1008	210200
197-10-11 × RIB 335/74	43	67	199	2.99	2054.4	1165.8	5.92	56.7	1545.6	3602.5	32.4	155	22.7	19.1	0.455	1289	256900
202-7-4 × RIB 335/74	41	70	193	2.75	1941.2	1126.1	5.85	58.0	1333.6	3249.1	34.4	151	23.1	19.8	0.541	1097	210700
202-7-10 × RIB 335/74	42	70	181	2.57	1898.7	1064.8	5.96	55.9	1067.6	2969.5	36.4	155	23.6	20.0	0.479	1220	221100
202-8-8 × RIB 335/74	43	71	174	2.49	2057.9	1211.1	7.00	59.2	1524.7	3591.3	34.0	154	22.8	20.4	0.513	1376	238800
197-1-12 × RIB 335/74	42	71	198	2.81	1897.6	1013.9	5.12	53.2	1408.7	3306.6	30.5	146	22.0	19.4	0.461	1106	219700
202-6-26 × RIB 335/74	42	70	184	2.61	1993.0	1124.9	6.16	56.2	1336.1	3336.6	33.6	141	21.7	20.7	0.516	1170	214100
197-18-1 × RIB 335/74	43	67	190	2.85	2088.7	1237.7	6.58	59.3	1598.7	3704.8	33.3	158	23.8	21.5	0.481	1334	254400
863B × H 77/833-2	42	72	148	2.08	2369.2	1739.9	11.83	73.2	2072.0	4456.7	39.1	163	19.4	26.7	0.660	1836	269100
ICMB 841 × H 77/833-2	46	75	219	2.91	2051.8	1073.0	4.75	51.2	2160.9	4204.6	25.0	153	19.2	18.0	0.454	1113	243700
197-10-18 × H 77/833-2	46	68	209	3.05	2028.1	1083.5	5.25	53.3	2131.9	4159.1	26.4	149	20.0	17.9	0.496	1049	218000
202-8-11 × H 77/833-2	46	72	228	3.15	2122.9	1128.6	5.06	53.3	1999.3	4127.3	27.5	147	19.8	17.9	0.477	1044	236600

Table 21. Performance summary under late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004 (Cont...).

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H. I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
197-12-2 × H 77/833-2	46	72	192	2.65	2168.7	1319.0	7.00	60.9	2049.3	4210.7	31.5	149	20.5	19.6	0.488	1441	275300
202-8-9 × H 77/833-2	46	75	231	3.09	2242.2	1265.8	5.69	56.5	2130.2	4362.0	29.0	140	19.8	18.2	0.500	1155	258200
202-7-12 × H 77/833-2	45	67	206	3.07	1970.2	1053.9	5.13	53.4	1895.5	3891.3	27.5	148	20.0	18.4	0.484	1064	218800
202-8-27 × H 77/833-2	44	72	220	3.07	2087.5	1136.5	5.29	54.8	1963.0	4066.6	28.1	139	19.6	18.3	0.481	1109	241200
197-10-11 × H 77/833-2	46	74	212	2.86	1968.6	1074.2	5.13	54.4	1917.9	3872.0	27.9	152	19.7	18.1	0.491	1036	217600
202-7-4 × H 77/833-2	46	70	225	3.20	2002.7	1120.8	4.85	53.8	1832.3	3830.4	27.0	151	19.4	18.2	0.467	1003	234700
202-7-10 × H 77/833-2	46	70	202	2.89	1867.0	1075.3	5.17	56.9	1775.9	3643.8	30.3	150	19.3	18.0	0.476	1089	222300
202-8-8 × H 77/833-2	45	74	202	2.74	2039.5	1213.4	6.04	59.4	2013.8	4050.2	30.0	151	20.0	18.6	0.505	1201	243600
197-1-12 × H 77/833-2	45	74	217	2.94	2147.9	1243.2	5.75	57.8	2021.1	4166.5	30.1	158	20.0	18.5	0.504	1150	248200
202-6-26 × H 77/833-2	45	68	203	3.02	1985.5	1126.1	5.46	56.8	1925.9	3906.4	29.0	147	20.8	19.2	0.503	1125	225600
197-18-1 × H 77/833-2	46	72	215	2.98	2193.4	1288.9	6.14	58.6	2185.6	4370.6	29.3	148	20.4	18.6	0.492	1244	264600
Minimum	**41**	**65**	**106**	**1.63**	**1815.9**	**992.5**	**4.72**	**51.2**	**1067.6**	**2969.5**	**25.0**	**139**	**19.2**	**17.9**	**0.443**	**1003**	**181500**
Maximum	**46**	**75**	**231**	**3.20**	**2404.7**	**1739.9**	**15.93**	**73.2**	**2185.6**	**4456.7**	**43.7**	**179**	**25.3**	**31.0**	**0.881**	**1894**	**275300**
Mean	**44**	**71**	**184**	**2.74**	**2097.9**	**1264.1**	**7.34**	**59.8**	**1704.2**	**3808.5**	**33.2**	**153**	**22.2**	**21.1**	**0.545**	**1320**	**234300**
SE (±)	**0.4**	**2.27**	**11.69**	**0.17**	**107.08**	**98.67**	**0.62**	**2.34**	**165.02**	**244.24**	**1.8**	**4.26**	**0.53**	**0.58**	**0.03**	**112.76**	**17604.45**
CV (%)	**1.57**	**5.57**	**11.06**	**11.48**	**8.83**	**13.45**	**14.47**	**6.77**	**16.92**	**11.15**	**9.28**	**4.85**	**4.14**	**4.70**	**8.62**	**14.67**	**12.97**
F-ratio	**14.60****	**1.27**	**7.01****	**6.04****	**2.36**	**4.46****	**18.84****	**6.62****	**3.47****	**2.58**	**7.84****	**2.58**	**12.54****	**32.97****	**11.14****	**5.79****	**1.24**
h^2 (plot basis)	**0.82**	**0.08**	**0.67**	**0.63**	**0.31**	**0.54**	**0.86**	**0.65**	**0.45**	**0.35**	**0.70**	**0.34**	**0.79**	**0.91**	**0.77**	**0.61**	**0.08**
h^2 (mean basis)	**0.93**	**0.22**	**0.86**	**0.83**	**0.58**	**0.78**	**0.95**	**0.85**	**0.71**	**0.61**	**0.87**	**0.61**	**0.92**	**0.97**	**0.91**	**0.83**	**0.20**
ICMB 93333 × PPMI 301	47	72	106	1.47	2218.9	1665.0	15.45	74.7	2363.2	4732.5	37.5	188	23.0	27.3	0.639	2444	257500
ICMB 94111 × PPMI 301	44	72	131	1.82	2252.2	1614.0	12.65	71.8	1978.3	4236.8	38.3	158	24.3	28.5	0.737	1691	212800
ICMB 97111 × PPMI 301	43	72	160	2.22	2177.2	1605.0	10.51	73.6	1487.7	3661.5	44.1	162	20.5	26.9	0.760	1386	206400
ICMB 98222 × PPMI 301	46	67	113	1.70	2199.4	1620.9	14.28	74.1	1863.0	4075.7	40.4	170	21.8	31.6	0.718	1969	224200
ICMB 99111 × PPMI 301	44	72	151	2.10	2002.1	1428.6	9.34	70.7	1699.1	3696.0	38.4	162	20.4	27.9	0.591	1567	235800
ICMB 99222 × PPMI 301	44	67	153	2.27	2453.6	1881.5	12.71	76.6	1759.9	4207.1	45.0	169	23.9	31.1	0.690	1850	269700
ICMB 841 × PPMI 301	43	70	145	2.06	2281.7	1663.8	11.73	72.8	1727.4	4003.0	41.9	149	19.9	30.0	0.577	2036	288100
863B × PPMI 301	42	68	104	1.47	2340.9	1671.9	16.10	71.6	1556.7	3767.6	44.9	166	22.3	30.5	0.796	2046	211300
ICMH 451	51	72	116	1.61	1823.8	1273.0	10.84	69.5	2426.0	4234.0	29.8	195	25.6	23.5	0.724	1509	174400
Minimum	**41**	**65**	**104**	**1.47**	**1815.9**	**992.5**	**4.72**	**51.2**	**1067.6**	**2969.5**	**25.0**	**139**	**19.2**	**17.9**	**0.443**	**1003**	**174400**
Maximum	**51**	**75**	**231**	**3.20**	**2453.6**	**1881.5**	**16.10**	**76.6**	**2426.0**	**4732.5**	**45.0**	**195**	**25.6**	**31.6**	**0.851**	**2444**	**288100**
Mean	**44**	**71**	**176**	**2.56**	**2111.2**	**1315.7**	**8.11**	**61.7**	**1728.7**	**3838.8**	**34.3**	**155**	**22.2**	**22.2**	**0.566**	**1398**	**2334400**
SE (±)	**0.42**	**2.25**	**12.9**	**0.18**	**109.05**	**100.58**	**0.84**	**2.24**	**175.58**	**244.45**	**1.84**	**4.46**	**0.57**	**0.67**	**0.03**	**130.81**	**16642.57**
CV (%)	**1.63**	**5.52**	**12.79**	**12.90**	**8.93**	**13.19**	**17.75**	**6.25**	**17.55**	**10.99**	**9.28**	**4.97**	**4.42**	**5.23**	**9.12**	**16.12**	**12.33**
F-ratio	**18.14****	**1.24**	**7.39****	**6.89****	**2.45**	**5.30****	**14.99****	**10.52****	**3.02****	**2.62**	**7.82****	**5.50****	**10.81****	**37.06****	**12.64****	**6.13****	**1.91**
h^2 (plot basis)	**0.85**	**0.08**	**0.68**	**0.66**	**0.33**	**0.59**	**0.82**	**0.76**	**0.40**	**0.35**	**0.69**	**0.60**	**0.77**	**0.92**	**0.80**	**0.63**	**0.23**
h^2 (mean basis)	**0.94**	**0.20**	**0.86**	**0.85**	**0.59**	**0.81**	**0.93**	**0.90**	**0.67**	**0.62**	**0.87**	**0.82**	**0.91**	**0.97**	**0.92**	**0.84**	**0.48**

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

Table 21. Performance summary under late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004 (Cont...).

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H. I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
197-12-2 × H 77/833-2	46	72	192	2.65	2168.7	1319.0	7.00	60.9	2049.3	4210.7	31.5	149	20.5	19.6	0.488	1441	275300
202-8-9 × H 77/833-2	46	75	231	3.09	2242.2	1265.8	5.69	56.5	2130.2	4362.0	29.0	140	19.8	18.2	0.500	1155	258200
202-7-12 × H 77/833-2	45	67	206	3.07	1970.2	1053.9	5.13	53.4	1895.5	3891.3	27.5	148	20.0	18.4	0.484	1064	218800
202-8-27 × H 77/833-2	44	72	220	3.07	2087.5	1136.5	5.29	54.8	1963.0	4066.6	28.1	139	19.6	18.3	0.481	1109	241200
197-10-11 × H 77/833-2	46	74	212	2.86	1968.6	1074.2	5.13	54.4	1917.9	3872.0	27.9	152	19.7	18.1	0.491	1036	217600
202-7-4 × H 77/833-2	46	70	225	3.20	2002.7	1120.8	4.85	53.8	1832.3	3830.4	27.0	151	19.4	18.2	0.467	1003	234700
202-7-10 × H 77/833-2	46	70	202	2.89	1867.0	1075.3	5.17	56.9	1775.9	3643.8	30.3	150	19.3	18.0	0.476	1089	222300
202-8-8 × H 77/833-2	45	74	202	2.74	2039.5	1213.4	6.04	59.4	2013.8	4050.2	30.0	151	20.0	18.6	0.505	1201	243600
197-1-12 × H 77/833-2	45	74	217	2.94	2147.9	1243.2	5.75	57.8	2021.1	4166.5	30.1	158	20.0	18.5	0.504	1150	248200
202-6-26 × H 77/833-2	45	68	203	3.02	1985.5	1126.1	5.46	56.8	1925.9	3906.4	29.0	147	20.8	19.2	0.503	1125	225600
197-18-1 × H 77/833-2	46	72	215	2.98	2193.4	1288.9	6.14	58.6	2185.6	4370.6	29.3	148	20.4	18.6	0.492	1244	264600
Minimum	**41**	**65**	**106**	**1.63**	**1815.9**	**992.5**	**4.72**	**51.2**	**1067.6**	**2969.5**	**25.0**	**139**	**19.2**	**17.9**	**0.443**	**1003**	**181500**
Maximum	**46**	**75**	**231**	**3.20**	**2404.7**	**1739.9**	**15.93**	**73.2**	**2185.6**	**4456.7**	**43.7**	**179**	**25.3**	**31.0**	**0.881**	**1894**	**275300**
Mean	**44**	**71**	**184**	**2.74**	**2097.9**	**1264.1**	**7.34**	**59.8**	**1704.2**	**3808.5**	**33.2**	**153**	**22.2**	**21.1**	**0.545**	**1320**	**234300**
SE (±)	**0.4**	**2.27**	**11.69**	**0.17**	**107.08**	**98.67**	**0.62**	**2.34**	**165.02**	**244.24**	**1.8**	**4.26**	**0.53**	**0.58**	**0.03**	**112.76**	**17604.45**
CV (%)	**1.57**	**5.57**	**11.06**	**11.48**	**8.83**	**13.45**	**14.47**	**6.77**	**16.92**	**11.15**	**9.28**	**4.85**	**4.14**	**4.70**	**8.62**	**14.67**	**12.97**
F-ratio	**14.60****	**1.27**	**7.01****	**6.04****	**2.36**	**4.46****	**18.84****	**6.62****	**3.47****	**2.58**	**7.84****	**2.58**	**12.54****	**32.97****	**11.14****	**5.79****	**1.24**
h^2 (plot basis)	**0.82**	**0.08**	**0.67**	**0.63**	**0.31**	**0.54**	**0.86**	**0.65**	**0.45**	**0.35**	**0.70**	**0.34**	**0.79**	**0.91**	**0.77**	**0.61**	**0.08**
h^2 (mean basis)	**0.93**	**0.22**	**0.86**	**0.83**	**0.58**	**0.78**	**0.95**	**0.85**	**0.71**	**0.61**	**0.87**	**0.61**	**0.92**	**0.97**	**0.91**	**0.83**	**0.20**
ICMB 93333 × PPMI 301	47	72	106	1.47	2218.9	1665.0	15.45	74.7	2363.2	4732.5	37.5	188	23.0	27.3	0.639	2444	257500
ICMB 94111 × PPMI 301	44	72	131	1.82	2252.2	1614.0	12.65	71.8	1978.3	4236.8	38.3	158	24.3	28.5	0.737	1691	212800
ICMB 97111 × PPMI 301	43	72	160	2.22	2177.2	1605.0	10.51	73.6	1487.7	3661.5	44.1	162	20.5	26.9	0.760	1386	206400
ICMB 98222 × PPMI 301	46	67	113	1.70	2199.4	1620.9	14.28	74.1	1863.0	4075.7	40.4	170	21.8	31.6	0.718	1969	224200
ICMB 99111 × PPMI 301	44	72	151	2.10	2002.1	1428.6	9.54	70.7	1699.1	3696.0	38.4	162	20.4	27.9	0.591	1567	235800
ICMB 99222 × PPMI 301	44	67	153	2.27	2453.6	1881.5	12.71	76.6	1759.9	4207.1	45.0	169	23.9	31.1	0.690	1850	269700
ICMB 841 × PPMI 301	43	70	145	2.06	2281.7	1663.8	11.73	72.8	1727.4	4003.0	41.9	149	19.9	30.0	0.577	2036	288100
863B × PPMI 301	42	68	104	1.47	2340.9	1671.9	16.19	71.6	1556.7	3767.6	44.9	166	22.3	30.5	0.796	2046	211300
ICMH 451	51	72	116	1.61	1823.8	1273.0	10.84	69.5	2426.0	4234.0	29.8	195	25.6	23.5	0.724	1509	174400
Minimum	**41**	**65**	**104**	**1.47**	**1815.9**	**992.5**	**4.72**	**51.2**	**1067.6**	**2969.5**	**25.0**	**139**	**19.2**	**17.9**	**0.443**	**1003**	**174400**
Maximum	**51**	**75**	**231**	**3.20**	**2453.6**	**1881.5**	**16.10**	**76.6**	**2426.0**	**4732.5**	**45.0**	**195**	**25.6**	**31.6**	**0.851**	**2444**	**288100**
Mean	**44**	**71**	**176**	**2.56**	**2111.2**	**1315.7**	**8.11**	**61.7**	**1728.7**	**3838.8**	**34.3**	**155**	**22.2**	**22.2**	**0.566**	**1398**	**2334400**
SE (±)	**0.42**	**2.25**	**12.9**	**0.18**	**109.05**	**100.58**	**0.84**	**2.24**	**175.58**	**244.45**	**1.84**	**4.46**	**0.57**	**0.67**	**0.03**	**130.81**	**16642.57**
CV (%)	**1.63**	**5.52**	**12.79**	**12.90**	**8.93**	**13.19**	**17.75**	**6.25**	**17.55**	**10.99**	**9.28**	**4.97**	**4.42**	**5.23**	**9.12**	**16.12**	**12.33**
F-ratio	**18.14****	**1.24**	**7.39****	**6.89****	**2.45**	**5.30****	**14.99****	**10.52****	**3.02****	**2.62**	**7.82****	**5.50****	**10.81****	**37.06****	**12.64****	**6.13****	**1.91**
h^2 (plot basis)	**0.85**	**0.08**	**0.68**	**0.66**	**0.33**	**0.59**	**0.82**	**0.76**	**0.40**	**0.35**	**0.69**	**0.60**	**0.77**	**0.92**	**0.80**	**0.63**	**0.23**
h^2 (mean basis)	**0.94**	**0.20**	**0.86**	**0.85**	**0.59**	**0.81**	**0.93**	**0.90**	**0.67**	**0.62**	**0.87**	**0.82**	**0.91**	**0.97**	**0.92**	**0.84**	**0.48**

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

flowering time of hybrids of tester H 77/833-2 was late, and preceded by hybrids of PPMI 301 and RIB 335/74. The earliest flowering times were recorded in 863B × RIB 335/74 and 202-7-4 × RIB 335/74. Among controls, ICMH 451 recorded the latest flowering time (51 days). The heritabilities of this trait for testcross hybrids, both without and with controls, were very high (0.93 and 0.94). The high F-ratios for this trait indicated statistical significance of differences between experimental and the control testcross hybrid entries.

4.3.2.2.2. Plant number per plot

The range of plant number per plot was from 65 to 75 in this moisture regime, with a mean value of 71. Non-significance of plant number per plot was used as an indicator for other plot-basis observations and suggests that plant stands were sufficiently uniform across genotypes tested to not adversely affect estimates of other yield components in this environment.

4.3.2.2.3. Panicle number per plot

The mean value for panicle number per plot was ranged from 106 (863B × PPMI 301) to 231 (202-8-9 × H 77/833-2). Hybrids of donor parent 863B produced lower numbers of panicles than those of recurrent ICMB 841. Among introgression line testcrosses, those of 197-12-2, 202-7-10, 202-8-8 and 202-6-26 produced lower numbers of panicles than did testcrosses of recurrent parent ICMB 841. H 77/833-2 hybrids gave higher numbers of panicles than did those of the other two testers, RIB 335/74 and PPMI 301. The operational heritability (entry mean basis) of this trait was high (0.86).

Trial mean value of number of panicles per plot reduced to 176 when controls were analyzed along with the introgression line testcross hybrids. The lowest number of

panicles per plot was recorded for the testcrosses of donor parent 863B and ICMB 93333 with tester PPMI 301. Statistical significance of the F-ratios for this trait indicated clear differences among testcross and control hybrids for plot panicle number.

4.3.2.2.4. Effective tiller number per plant

For testcross hybrids of the introgression lines and their parents, the mean value of effective tiller per plant varied from 1.63 (863B × RIB 335/74) to 3.2 (202-8-9 × H 77/833-2) with a trial mean value of 2.74. Hybrids of H 77/833-2 produced larger numbers of effective tillers than did hybrids of the other two testers. Among control entries, ICMB 99222 × PPMI 301 gave the highest effective tiller numbers per plant. Most of the control entries had limited tillering ability and hence the trial mean value including controls was reduced to 2.56 effective tillers per plant.

4.3.2.2.5. Panicle yield per plot

The range for panicle yield among testcrosses of the introgression lines and their parents was from 1816 g (202-8-27 × RIB 335/74) to 2405 g (202-8-27 × PPMI 301) with a trial environmental mean value of 2098 g. Most of the testcross hybrids involving testers PPMI 301 and H 77/833-2 surpassed this environment mean panicle yield. Non-significance of the F-ratios for this trait indicates testcross hybrids were not different from each other in panicle yields in this moderately stressful moisture regime.

4.3.2.2.6. Grain yield per plot

Among testcross hybrids the mean plot grain yield value ranged from 993 g (202-7-12 × RIB 335/74) to 1740 g (863B × H 77/833-2) in this moisture regime. Among the testers, hybrids of RIB 335/74 produced lower grain yields than those of H 77/833-2 and PPMI 301. H 77/833-2 provided a high-yielding hybrid only with donor parent 863B, but gave

much lower yielding hybrids in combination with ICMB 841 and most of the backcross-derived introgression lines.

Most of the control hybrids yielded higher than the environmental mean value of the experimental testcross hybrids and hence, the overall mean value for grain yield per plot increased from 1264 g to 1316 g when these controls were included in the analysis. ICMB 99222 × PPMI 301 produced the high mean plot grain yield (1882 g) among these control entries. The heritability of grain yield per plot was reasonably high (≥0.78) in this environment.

4.3.2.2.7. Grain yield per panicle

Grain yield per panicle ranged from 4.72 g (202-8-27 × RIB 335/74) to 15.93 g (863B × PPMI 301) in this late-onset terminal drought stress environment. PPMI 301-derived hybrids exhibited greater grain yields per panicle than did hybrids of the other two testers. The heritabilities calculated on entry mean basis were very high (≥0.93) for this trait.

Among control hybrids, ICMB 93333 × PPMI 301 yielded highest (15.45 g), but this was marginally less than donor parent hybrid 863B × PPMI 301 (16.10 g). Most of the control hybrids showed higher single-panicle grain yields than the mean of the experimental testcross hybrids in this environment.

4.3.2.2.8. Panicle harvest index

Testcross entry mean values for panicle harvest index ranged from 51.2% (841B × H 77/833-2) to 73.2% (863B × H 77/833-2) with a trial mean panicle harvest index of value of 59.8% under this late-onset drought stress moisture regime. PPMI 301 produced hybrids with higher mean panicle harvest index values than did the other two testers.

4.3.2.2.9. Stover yield per plot

As in the control treatment, hybrids of the donor parent 863B outyielded those of the recurrent parent ICMB 841 for stover yield with two testers, namely PPMI 301 and RIB 335/74. The mean value of introgression line testcross hybrids ranged from 1068 g (202-7-10 × RIB 335/74) to 2186 g (197-18-1 × H 77/833-2) in this late-onset terminal drought stress environment. Across testers, hybrids of introgression line 197-18-1 ranked first for stover yield in this environment followed by those of 202-8-9. Among control hybrids, ICMH 451 (2426 g) gave the highest stover yield. In comparison with the fully irrigated control moisture regime, the entry mean-basis heritability values for stover yield in this late-onset stress treatment were reduced to 0.71 from 0.82 when control entries were excluded from the data analyses.

4.3.2.2.10. Biomass yield per plot

Biomass yields of hybrids for donor parent 863B were higher across testers than were those of the recurrent parent ICMB 841. As in case of stover yield, biomass yields of the testcrosses of introgression line 197-18-1 ranked first across the three testers. The average biomass yield ranged from 2970 g (202-7-10 × RIB 335/74) to 4457 g (863B × H 77/833-2). H 77/833-2 hybrids gave comparatively higher biomass yields than those of the other two testers. The entry mean-basis heritability value for biomass yield was reduced to 0.61 in this late-onset terminal drought stress treatment from 0.86 in the fully irrigated non-stress moisture regime control.

4.3.2.2.11. Harvest index

The average value of harvest index across testcrosses of the introgression lines and their parents was 33.2% in this late-onset terminal drought stress environment. The mean values of testcross hybrids ranged from 25% (841B × H 77/833-2) to 43.7% (863B × RIB 335/74). PPMI 301 hybrids showed higher harvest index values than did those of the other tester parents. Among PPMI 301 hybrids, those of introgression lines 202-26 (41.1%) and 197-12-2 (41%) ranked higher for harvest index values. The heritability value (entry mean basis) of this trait was high (0.87).

Parental testcross hybrid 863B × PPMI 301 produced a high harvest index value (44.9%) comparable with ICMB 99222 × PPMI 301, which had the highest harvest index value (45%) among control entries. The late-maturing dual-purpose hybrid ICMH 451 showed a very poor grain harvest index value of 29.8% in this terminal drought stress environment.

4.3.2.2.12. Plant height

The range for plant height was from 139 cm (202-8-27 × H 77/833-2) to 179 cm (863B × RIB 335/74) in this environment with an introgression line testcross hybrid mean of 153 cm. Among PPMI 301 testcross hybrids, that involving introgression line 197-10-11 (160 cm) was the tallest. The heritability (entry mean basis) of this trait was low among experimental testcross hybrids in this environment (≥0.61), but improved when control hybrids were included in the analysis (≥0.82).

Among controls, ICMH 451 was the tallest hybrid (195 cm) followed by ICMB 93333 × PPMI 301 (188 cm). Since most of the controls were taller than the experimental testcross hybrids, the trial mean value for this environment increased by 3 cm when the

controls were included in the analysis. For the trial as a whole, the heritability of plant height for this environment increased from 0.61 to 0.82 when the controls were included in the analysis.

4.3.2.2.13. Panicle length

The environmental mean value of testcross hybrids for panicle length was 22.2 cm. Among testcross hybrids, the observed range for panicle length in this moisture regime from 19.2 cm (841B × H 77/833-2) to 25.3 cm (197-18-1 × PPMI 301). Among control entries, ICMH 451 had the lengthiest panicles (25.6 cm). The F-ratio statistics indicated that significant differences were observed among the testcross hybrids and control entries. The operational heritability of this trait remained high for testcross hybrids in this moisture regime, whether controls were included in the data analysis or not (≥0.91).

4.3.2.2.14. Panicle diameter

Among testcross hybrids, the mean value for panicle diameter in this moisture regime ranged from 17.9 cm (197-10-18 × H 77/833-2 and 202-8-11 × H 77/833-2) to 31cm (863B × PPMI 301). The line 197-18-1 produced testcrosses with large panicle diameter across PPMI 301 and RIB 335/74 and even achieved fairly high levels for this trait in combination with H 77/833-2. In contrast, hybrids of introgression line 197-10-18 had small panicle diameters, almost equal to those of hybrids of recurrent parent ICMB 841, across all three testers.

Among controls, panicle diameter differences were high in this moisture regime with entry means ranging from 31.6 cm (ICMB 98222 × PPMI 301) to 23.5 cm (ICMH 451). The operational heritability of this trait was very high ≥0.97 in this moderately stressful moisture regime.

4.3.2.2.15. Hundred-grain mass

The range for hundred-grain mass in this environment was from 0.443 g (202-7-12 × RIB 335/74) to 0.881 g (863B × PPMI 301). The mean value of testcross hybrids for hundred-grain mass was 0.545 g. Most of the testcross hybrids gave similar hundred-grain mass values as the counterpart testcrosses of ICMB 841. Among testers, PPMI 301 hybrids exhibited overall higher hundred-grain mass. Among controls, the donor parent hybrid (863B × PPMI 301) was having the highest hundred-grain mass (0.796 g) followed by ICMB 97111 × PPMI 301. The heritability of this trait was high (≥0.91).

4.3.2.2.16. Grain number per panicle

The mean number of grains per panicle in this late-onset terminal drought stress moisture regime ranged between 1003 (202-7-4 × H 77/833-2) and 1894 (197-12-2 × PPMI 301), with an environmental mean grain number per panicle of 1320. Across testers, hybrids of introgression line 197-12-2 produced high grain numbers per panicle. Similar to the fully irrigated control treatment, 863B × PPMI 301 produced large grain numbers per panicle (2046).

4.3.2.2.17. Grain number per plot

The range of number of grains per plot was from 1815660 (863B × RIB 335/74) to 275336 (197-12-2 × H 77/833-2) in this moisture regime. The mean grain number per plot was 234312. Among controls, 841B × PPMI 301 (288156) and ICMH 451 (174452) produced the highest and lowest grain numbers per plot. The entry mean heritability of this trait was low (≥0.48) when controls were included and very low (≥0.20) for testcross hybrids analysed separately from the controls.

4.3.2.3. Estimates of components of variation

The genetic components of variance for observed agronomic traits among the experimental testcross hybrids in this late-onset terminal drought stress environment are presented in Table 22. Both lines and testers contributed to the additive genetic variation (σ^2A). For flowering time, panicle number per plot, effective tiller per plant, grain yield per plot, grain yield per panicle, panicle harvest index, stover yield per plot, biomass yield per plot, harvest index, plant height, panicle length, panicle diameter and grain number per panicle, additive genetic variation was highly significant, demonstrating the heritable genetic contributions of the hybrid parents to hybrid performance in this environment.

The characters that showed significance for dominance genetic variation in this environment were flowering time, grain yield per panicle, plant height, panicle length and panicle diameter. The ratio of additive to dominance variance was large for flowering time, panicle number per plot, effective panicles per plant, panicle yield per plot, grain yield per plot, grain yield per panicle, panicle harvest index, stover yield per plot, biomass yield per plot, harvest index, panicle length, panicle diameter, hundred-grain mass, grain number per panicle and grain number per plot. Only in case of plant height was σ^2D greater than σ^2A.

The relative importance of dominance genetic variance was low for most traits observed in this trial, suggesting that parental performance under conditions of terminal drought stress could be used as criteria for selecting parents for further use in pearl millet hybrid breeding programmes.

Table 22. Estimates of additive and dominance components of genetic variation among testcross hybrids of introgression lines and their parents in late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Genetic comp.	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
σ^2A	3.7**	1.4	1334.1**	0.3**	35969.7	57659.18**	8.6**	40.2**	152979.8*	245580.6*	33.1**	6.0**	6.6**	13.2**	0.0	90892.9**	1.4E+08
σ^2D	0.2**	∞	∞	0.0	∞	∞	0.3*	0.0	∞	∞	1.9	16.0*	0.5**	0.8**	0.0	4388.6	5.1E+08
σ^2A: σ^2D	16.7	∞	∞	∞	∞	∞	25.4	∞	∞	∞	17.2	0.4	14.5	17.2	∞	20.7	27.48

** Significant at 0.01 level of probability; * Significant at 0.05 level probability

4.3.2.4. Contributions of lines and testers

The relative contributions of lines and testers and their interaction to variation in testcross hybrids of the introgression lines and their parents are tabulated in Table 23. Under late-onset terminal drought stress conditions, the introgression lines and their parents contributed more to testcross hybrid variation for panicle harvest index (51.3%), plant height (48.63%) and hundred-grain mass (55.2%).

Testers contributions to variation were greater for flowering time (63.9%), panicle yield per plot (54.1%), grain yield per plot (50.2%), stover yield per plot (65.6%), biomass yield per plot (63.8%), harvest index (59.8%) and panicle length (77.8%). Similar contributions of both lines and testers were observed for panicle number per plot, effective tiller number per plant, grain yield per panicle, panicle diameter and grain number per panicle. Only for plant height and grain number per plot were the involvement of line × tester interaction components a major contributor to variation among the testcross hybrids.

4.3.2.5. Combining Ability

The results of the combining ability analysis for this late-onset drought stress environment, in the form of tabulated *gca* effects of the lines and testers, are presented in Table 24.

4.3.2.5.1. General Combining Ability (gca)

The best combiners for early flowering among lines were the donor parent 863B and introgression line 202-8-27. Similarly among testers RIB 335/74 showed negative *gca* effects for flowering time. Only introgression line 197-10-18 showed negative *gca* effects for plant number per plot. For panicle number per plot, and effective tiller number per

Table 23. **Relative contributions (%) of lines and tester parents and their interaction to variations in testcross hybrids in late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.**

Lines/Testers	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
Lines	25.62	41.67	42.12	45.03	23.86	39.19	50.92	51.30	19.82	22.81	37.30	48.63	8.85	50.34	55.20	37.96	30.03
Testers	63.86	9.53	51.88	48.27	54.06	50.24	42.70	39.16	65.56	63.81	49.77	4.90	77.79	43.25	34.84	47.24	18.01
Lines × Testers	10.52	48.80	6.00	6.70	22.08	10.58	6.38	9.55	14.62	13.38	12.93	46.47	13.37	6.42	9.96	14.80	51.96

Table 24. Estimates of gca effects of introgression lines and testers under late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Lines & Testers	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H. I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B	-2.30**	-0.53	-59.15**	-0.82**	188.41**	409.38**	6.44**	13.41**	-90.20	133.00	9.61**	13.21**	0.20	8.28**	0.237**	449.00**	-14448.00
ICMB 841	0.36	1.47	-5.30	-0.14	-58.82	-62.49	0.22	-1.40	-140.30	-201.60	1.11	-1.02	-1.34**	0.65*	-0.043**	140.20*	6876.00
197-10-18	0.03	-2.75*	4.92	0.17	73.26	23.77	-0.29	-0.93	58.90	129.70	-0.39	-0.02	0.53	-1.07**	0.010	-57.50	-255.00
202-8-11	-0.08	1.47	19.81**	0.22*	42.48	-58.90	-1.24**	-3.87**	-9.90	30.10	-1.93	-1.24	0.27	-1.06**	-0.027	-158.70*	-1821.00
197-12-2	0.70**	2.47	-23.19**	-0.40**	26.04	103.55	1.64**	4.56**	45.80	69.30	2.29*	1.65	0.90**	0.52	0.022	239.30**	10270.00
202-8-9	-0.19	2.03	21.92**	0.22*	53.48	-3.34	-1.01*	-1.22	235.80*	286.80*	-2.33*	-2.46	-0.02	-1.00**	-0.022	-114.80	8491.00
202-7-12	0.36	0.03	5.48	0.08	-110.07	-168.45**	-1.42**	-5.07**	78.00	-34.60	-4.38**	2.99	0.36	-1.05**	-0.037*	-160.30*	-16428.00
202-8-27	-0.64**	0.25	16.81*	0.23*	-28.63	-71.79	-1.21**	-2.83*	-101.50	-132.60	-0.87	-5.24*	-0.27	-1.55**	-0.027	-151.40*	-3737.00
197-10-11	1.25**	-0.30	14.03*	0.21*	-9.52	-48.90	-1.16**	-2.09	55.70	43.70	-2.44*	3.10	-0.28	-1.24**	-0.041**	-100.60	7373.00
202-7-4	-0.41	-0.97	13.03	0.22*	-36.85	-44.55	-1.02**	-1.53	-98.70	-138.00	-0.78	-3.68	-0.34	-0.92**	-0.024	-114.20	977.00
202-7-10	0.25	-2.42	-6.97	-0.02	-154.63*	-126.45	-0.70*	-1.64	-249.10**	-406.20**	0.66	-1.90	-0.40	-0.54	-0.027	-53.50	-14023.00
202-8-8	0.25	0.92	-9.08	-0.16	13.26	44.43	0.43	1.96	59.10	69.90	0.54	-0.35	-0.21	-0.86**	0.015	54.30	1365.00
197-1-12	-0.08	1.70	5.48	0.01	13.60	-19.23	-0.42	-1.37	67.90	79.00	-1.43	2.10	-0.14	-0.64	-0.007	-63.60	-2011.00
202-6-26	-0.08	-2.53	-6.19	0.01	-62.63	-46.79	-0.15	-0.15	-158.20	-223.30	1.04	-8.90**	-0.21	-0.35	-0.004	4.00	-8191.00
197-18-1	0.59**	-0.86	8.37	0.17	50.60	69.77	-0.12	2.19	246.60**	294.70*	-0.70	1.76	0.95**	0.84*	-0.025	87.90	25562.00*
PPMI 301	0.27**	-0.41	-28.27**	-0.38**	149.28**	202.20**	2.43**	5.26**	-44.60	109.60	4.21**	0.50	1.14**	2.92**	0.074**	259.30**	5060.00
RIB 335/74	-1.59**	-0.68	2.79	0.07	-143.69**	-137.70**	-0.99**	-2.25**	-276.40**	-422.60**	0.18	1.54	1.18**	-0.72**	-0.030**	-106.50**	-11626.00*
H 77/833-2	1.32**	1.10	25.48**	0.32**	-5.58	-64.50*	-1.44**	-3.01**	321.10**	313.00**	-4.39**	-2.04	-2.31**	-2.20**	-0.044**	-152.80**	6556.00

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

plant, introgression lines 202-8-11, 202-8-9, 202-8-27 and 197-10-11, and tester H 77/833-2 exhibited positive *gca* effects. For both of these characters, the negative combiners were donor parent 863B, introgression line 197-12-2 and tester PPMI 301.

Among introgression lines and testers, the donor parent for drought tolerance 863B and tester PPMI 301 showed positive *gca* effects, and tester RIB 335/74 and introgression lines 202-7-10 and 202-7-12 were negative combiners for panicle yield per plot and grain yield per plot. For grain yield per panicle and panicle harvest index the best positive combiners were the donor parent 863B, introgression line 197-12-2 and testers PPMI 301. Similarly, tester RIB 335/74 and introgression line 202-8-27 exhibited negative *gca* effects for both of these characters.

The best positive combiners for stover yield per plot and biomass yield per plot among introgression lines were 202-8-9 and 197-18-1, and among testers was H 77/833-2. The negative combiners for both of the above characters were 202-7-10 and RIB 335/74. For harvest index, among introgression lines and testers the donor parent 863B, introgression line 197-12-2, and tester PPMI 301 showed positive *gca* effects. The donor parent 863B also exhibited positive *gca* effects for plant height, panicle diameter, hundred-grain mass and grain number per panicle. The introgression lines 197-12-2 and 197-18-1 showed positive *gca* effects for lengthier panicles, as did tester PPMI 301. For panicle diameter, recurrent parent ICMB 841, introgression line 197-18-1 and tester PPMI 301 showed positive *gca* effects. Only two introgression lines (202-7-12 and 197-10-11) and recurrent parent ICMB 841, along with testers RIB 335/74 and H 77/833-2, showed significant negative *gca* effects for hundred-grain mass.

For grain number per panicle and grain number per plot, tester RIB 335/74 showed negative *gca* effects, while introgression line 197-12-2 and 863B were positive combiners for grain number per panicle in this moisture regime. The only significantly positive and negative combiners for grain number per plot in this environment were introgression line 197-18-1 and tester RIB 335/74 respectively.

4.3.2.5.2. Specific Combining Ability (sca)

The *sca* effects of testcross hybrids of the introgression lines and their recurrent and donor parents are presented in Table 25. ICMB 841 × PPMI 301, 202-8-11 × PPMI 301 and 863B × H 77/833-2 showed *sca* for early flowering and 202-7-10 × H 77/833-2, 863B × RIB 335/74 and 202-6-26 × PPMI 301 showed *sca* for late flowering time. Testcross hybrids of donor parent 863B with tester PPMI 301 exhibited negative sca effects for both panicle harvest and plant height. The recurrent parent ICMB 841 showed positive *sca* effects in combination with tester PPMI 301 for grain yield per panicle, panicle harvest index, harvest index panicle diameter and grain number per panicle.

Another parental testcross hybrid 863B × RIB 335/74 showed positive *sca* effects grain yield per panicle, plant height, panicle length, panicle diameter and hundred-grain mass. Only testcross hybrid ICMB 841 × PPMI 301 showed significantly positive *sca* effects for both panicle harvest index, and harvest index in this moisture regime. Testcross hybrids with significantly positive *sca* effects for plant height were 202-8-9 × PPMI 301and 863B × RIB 335/74 and in contrast the ones with negative *sca* effects for plant height were 197-1-12 × RIB 335/74 and 202-6-26 × RIB 335/74. Similarly, most three testcross hybrids showed negative *sca* effects for panicle length including ICMB 841 × PPMI 301, 197-1-12 × RIB 335/74 and 202-6-26 × RIB 335/74. For hundred-grain

Table 25. Estimates of sca effects of testcross hybrids under late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H. I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	0.39	1.30	18.11	0.24	-93.53	-158.62	-1.01	-4.92*	-245.15	-269.20	-1.27	-12.05**	-0.92	-0.71	-0.025	-199.00	-16747.00
ICMB 841 × PPMI 301	-0.94*	-1.70	-25.18*	-0.29	-3.99	97.92	2.31**	4.97*	-249.59	-258.60	4.93**	-3.16	-1.17*	3.23**	0.009	378.33**	11085.00
197-10-18 × PPMI 301	0.06	-1.14	1.60	0.05	115.17	98.83	0.34	1.03	-70.12	40.10	1.93	3.50	-0.25	0.55	-0.001	60.36	16437.00
202-8-11 × PPMI 301	-0.83*	1.64	4.71	0.02	59.61	65.83	-0.32	1.47	61.49	116.10	0.77	-5.94	-0.95	0.14	0.013	-64.75	6739.00
197-12-2 × PPMI 301	0.06	2.30	-6.95	-0.14	-27.94	-25.61	1.01	-0.89	-132.97	-165.90	0.79	0.17	-0.32	-0.37	0.019	63.58	-14635.00
202-8-9 × PPMI 301	-0.05	-1.92	-3.06	0.04	-123.39	-94.39	-0.85	-0.85	26.21	-102.10	-1.40	8.62*	0.44	-0.90	-0.025	-80.31	-7395.00
202-7-12 × PPMI 301	0.39	3.08	8.05	-0.01	-2.83	-32.28	-0.81	-1.09	200.89	193.10	-2.21	6.17	1.06*	0.16	0.008	-142.20	-8526.00
202-8-27 × PPMI 301	0.06	1.86	-0.29	-0.07	157.72	99.72	0.09	0.10	-64.57	88.20	1.74	5.39	0.05	-1.01	0.027	-16.09	8868.00
197-10-11 × PPMI 301	0.50	0.42	11.49	0.14	23.61	4.16	-0.92	-0.72	50.19	68.80	-1.72	3.06	0.23	-0.05	-0.016	-123.44	4521.00
202-7-4 × PPMI 301	0.17	-0.92	2.49	0.06	40.95	1.81	-0.37	-0.33	169.55	205.50	-0.98	-2.83	0.06	-0.21	-0.045	65.39	20495.00
202-7-10 × PPMI 301	-0.50	-3.14	-2.18	0.07	-7.61	-44.94	-0.15	-1.26	142.15	129.60	-2.52	-5.27	-0.48	0.28	0.001	-12.98	-4394.00
202-8-8 × PPMI 301	-0.16	-1.47	-0.06	0.03	0.83	-18.50	0.04	-1.39	-2.04	-6.20	-0.73	-2.50	0.03	-1.40*	0.022	-65.75	-13853.00
197-1-12 × PPMI 301	0.17	0.42	-10.29	-0.15	8.17	42.17	0.65	1.47	96.69	99.90	0.07	4.06	0.96	0.35	0.034	19.80	-7699.00
202-6-26 × PPMI 301	0.84*	-2.03	-4.62	-0.03	-52.28	7.72	0.40	2.09	-112.65	-169.90	2.40	1.06	0.26	-1.07	-0.013	116.14	8602.00
197-18-1 × PPMI 301	-0.16	1.30	6.16	0.07	-94.50	-43.83	-0.40	0.34	129.92	30.50	-1.79	-0.27	1.01	1.00	-0.010	0.91	-3497.00
863B × RIB 335/74	0.93*	-1.76	-16.38	-0.21	-34.35	0.73	1.34*	1.97	84.58	15.50	0.60	10.90*	1.58**	1.20*	0.101**	-9.29	-27081.00
ICMB 841 × RIB 335/74	0.59	-0.43	9.77	0.16	-30.12	-31.73	-1.10	-0.56	-79.55	-107.20	0.53	0.13	0.46	-1.67**	-0.006	-181.49	-6806.00
197-10-18 × RIB 335/74	-0.74	1.79	3.21	-0.02	15.14	45.34	0.11	2.04	-1.69	15.90	0.90	-1.21	0.68	-0.48	0.014	11.20	6425.00
202-8-11 × RIB 335/74	0.37	-0.76	-4.01	-0.03	-39.08	-44.99	0.00	-1.48	-38.77	-75.40	-0.97	8.02	1.25*	-0.23	-0.020	40.42	-1587.00
197-12-2 × RIB 335/74	-0.07	-0.43	0.32	0.00	-64.97	-18.10	-0.48	1.28	111.14	48.60	-0.98	1.13	0.58	0.13	0.013	-86.58	-10074.00
202-8-9 × RIB 335/74	-0.19	0.68	2.21	0.01	-2.42	6.12	0.00	-0.21	42.55	42.60	-0.80	-3.43	-0.46	0.54	0.001	-11.14	-1520.00
202-7-12 × RIB 335/74	-0.07	1.68	0.32	-0.07	22.80	15.90	0.14	-0.22	26.39	51.70	-0.45	-2.21	-0.81	-0.64	-0.033	96.64	16089.00
202-8-27 × RIB 335/74	0.26	-1.54	5.65	0.15	-191.64	-129.10	-0.67	-1.46	-0.16	-189.30	-2.23	-0.99	-0.05	0.00	-0.037	-65.58	-12476.00
197-10-11 × RIB 335/74	-0.30	-2.99	-0.90	0.12	103.25	80.68	0.62	1.20	38.73	144.50	1.41	-1.99	-0.34	-0.22	-0.017	165.26	25802.00
202-7-4 × RIB 335/74	-0.63	1.35	-5.90	-0.13	49.58	60.32	0.56	2.11	16.38	68.40	1.75	0.13	0.09	0.16	0.052	-13.44	-12625.00
202-7-10 × RIB 335/74	-0.30	2.79	1.77	-0.07	78.36	49.90	0.18	0.02	-147.49	-66.60	2.38	1.68	0.65	0.12	-0.006	48.53	10373.00
202-8-8 × RIB 335/74	0.70	0.13	-2.79	-0.01	64.14	45.01	0.28	0.52	49.79	116.40	0.26	0.46	-0.41	0.81	-0.014	97.42	13351.00
197-1-12 × RIB 335/74	0.04	-0.99	6.99	0.14	-69.53	-104.66	-0.88	-3.35	-53.97	-121.00	-2.04	-10.99*	-1.24*	-0.48	-0.046	-54.69	-2069.00
202-6-26 × RIB 335/74	-0.63	2.90	3.99	-0.06	72.69	10.23	-0.24	-1.87	41.35	116.50	-1.17	-4.99	-1.44**	0.46	0.005	-58.36	-1970.00
197-18-1 × RIB 335/74	0.04	-2.43	-4.24	0.03	26.14	14.34	0.14	0.02	-89.27	-60.70	0.81	3.35	-0.53	0.31	-0.007	21.09	4167.00
863B × H 77/833-2	-1.32**	0.46	-1.73	-0.02	127.88	157.88	-0.33	2.96	160.57	253.70	0.67	1.15	-0.66	-0.49	-0.076**	208.29	43828.00*
ICMB 841 × H 77/833-2	0.35	2.13	15.41	0.13	34.10	-66.19	-1.20*	-4.41	329.14*	365.70	-5.46**	3.04	0.71	-1.56**	-0.003	-196.84	-4279.00
197-10-18 × H 77/833-2	0.68	-0.65	-4.81	-0.03	-130.31	-144.18	-0.44	-3.07	71.81	-56.00	-2.83	-2.30	-0.43	-0.07	-0.013	-71.56	-22862.00
202-8-11 × H 77/833-2	0.46	-0.87	-0.70	0.02	-20.53	-20.84	0.32	0.01	-22.72	-40.80	0.20	-2.07	-0.30	0.09	0.007	24.33	-5152.00
197-12-2 × H 77/833-2	0.01	-1.87	6.63	0.14	92.92	43.71	-0.53	-0.39	21.83	117.20	0.19	-1.30	-0.26	0.24	-0.032	23.00	24709.00
202-8-9 × H 77/833-2	0.24	1.24	0.85	-0.04	125.80	88.27	0.85	1.05	-68.76	59.50	2.20	-5.19	0.03	0.36	0.024	91.44	8915.00
202-7-12× H 77/833-2	-0.32	-4.76*	-8.37	0.07	-19.97	16.38	0.68	1.31	-227.28	-244.80	2.66	-3.96	-0.25	0.48	0.024	45.55	-7564.00
202-8-27 × H 77/833-2	-0.32	-0.32	-5.37	-0.08	33.92	29.38	0.59	1.37	64.73	101.10	0.48	-4.41	0.00	1.01	0.010	81.67	3608.00
197-10-11 × H 77/833-2	-0.21	2.57	-10.59	-0.26	-126.86	-84.84	0.30	-0.48	-88.92	-213.30	0.31	-1.07	0.11	0.27	0.032	-41.82	-30323.00
202-7-4 × H 77/833-2	0.46	-0.43	3.41	0.07	-90.53	-62.14	-0.19	-1.78	-185.93	-274.00	-0.77	2.70	-0.15	0.04	-0.008	-51.95	-7870.00
202-7-10 × H 77/833-2	0.79*	0.35	0.41	0.00	-70.75	-4.95	-0.03	1.24	5.34	-62.90	0.15	3.59	-0.16	-0.40	0.005	-35.56	-5979.00
202-8-8 × H 77/833-2	-0.54	1.35	2.85	-0.02	-64.97	-26.51	-0.32	0.88	-47.75	-110.20	0.47	2.04	0.38	0.59	-0.008	-31.67	502.00
197-1-12 × H 77/833-2	-0.21	0.57	3.30	0.01	61.36	62.49	0.23	1.88	-42.72	21.10	1.97	6.93	0.28	0.13	0.011	34.89	9768.00
202-6-26 × H 77/833-2	-0.21	-0.87	0.63	0.10	-20.42	-17.95	-0.16	-0.21	71.31	53.40	-1.23	3.93	1.18*	0.61	0.007	-57.78	-6632.00
197-18-1 × H 77/833-2	0.13	1.13	-1.92	-0.09	68.36	29.49	0.26	-0.36	-40.65	30.20	0.98	-3.07	-0.47	-1.31*	0.017	-22.00	-670.00

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

mass, donor parental hybrids showed positive and negative *sca* effects respectively, when 863B was crossed with testers RIB 335/74 and H 77/833/2.

4.3.3. Early stress treatment

4.3.3.1. Analyses of variances

The analyses of variances for testcross hybrids of introgression lines and their parents for 17 different agronomic characters in the early-onset terminal drought stress environment are presented in Table 26. Hybrids were significantly different for all the observed agronomic characters in this moisture regime. Effects of lines were highly significant for most observed agronomic characters including flowering time, panicle number per plot, effective tiller number per plant, grain yield per plot, grain yield per panicle, panicle harvest index, stover yield per plot, biomass yield per plot, harvest index, hundred-grain mass and grain number per panicle. Similarly, lines showed significant differences for plant number per plot, panicle yield per plot and plant height.

Effects of testers were highly significant for all characters except plant number per plot and panicle diameter. Line × tester interaction effects were observed to be non-significant for all characters except flowering time, grain yield per panicle, harvest index and grain number per panicle suggesting that genetic variation for most observed traits was controlled by additive effects in this particular environment.

4.3.3.2. Performance summary

The trait mean values and their respective heritabilities of all characters for each of 45 testcross hybrids in this early-onset terminal drought stress environment are presented in Table 27. Trait means, their respective F-ratios and heritabilities of the combined data set for this environment, including control entries, are presented separately in the same table.

Table 26. Analyses of variance for testcross hybrids in early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

		Mean squares																
SV	DF	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
Replications	2	0.9	26.14	3388.90**	0.545	389281.26**	117729.79**	2.68*	14.64	1312576.64**	2825812.56**	26.75	451.47**	3.26	5.52	0.009**	13569.55	1.75E+09
Hybrids	44	7.49**	31.86*	2369.56**	790.301**	45175.74**	97098.45**	32377.87**	10984.20**	262876.71**	591983.89**	194079.98**	64820.53**	21611.10**	7219.90**	2406.65*	298694.84**	1.85E+09**
Lines (L)	14	4.91**	39.15*	3139.45**	0.627**	53070.85*	101393.62**	18.04**	181.23**	220914.25**	422960.03**	61.01**	176.12*	5.55	19.05	0.021**	283620.58**	5.25E+08
Testers (T)	2	105.56**	23.5	23418.59**	4.142**	117981.55**	311021.81**	74.72**	713.32**	1803836.38**	2128453.26**	411.68**	218.87	28.80**	15.14	0.035**	2157395.90**	3.10E+09*
L × T	28	1.77**	24.89	464.43	0.094	35613.79	20595.61	2.01**	25.04	117790.62	176181.64	21.38*	96.20	2.51	14.86	0.004	89031.93**	1.46E+09**
Error	88	0.41	18.18	332.44	0.076	23349.11	14858.79	0.80	19.97	89763.22	141063.84	12.37	89.57	3.97	13.16	0.003	37303.29	6.96E+08

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

SV-Sources of variation
DF-Degrees of freedom
FT-flowering time (days after emergence)
ET-Effective tiller number per plant
HI-Harvest Index

Table 27. Performance summary under early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H. I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	42	70	107	1.54	1647.0	1069.2	9.89	65.1	1279.5	2946.8	36.0	164	23.4	30.6	0.627	1578	169300
ICMB 841 × PPMI 301	46	72	141	1.98	1442.5	757.4	5.36	51.8	1494.9	2956.9	25.4	164	24.1	24.6	0.451	1187	168800
197-10-18 × PPMI 301	45	71	125	1.75	1653.8	910.2	7.54	55.6	1850.6	3493.4	26.9	154	23.2	22.2	0.417	1828	226900
202-8-11 × PPMI 301	44	71	156	2.24	1635.0	840.9	5.46	51.5	1599.4	3210.1	26.0	154	23.4	21.6	0.463	1212	183300
197-12-2 × PPMI 301	46	72	102	1.43	1516.5	932.9	9.14	62.0	1114.7	2637.6	35.6	151	22.0	22.9	0.470	1932	193600
202-8-9 × PPMI 301	44	76	156	2.10	1500.9	744.2	4.61	49.6	1377.9	2881.4	25.2	150	20.8	19.4	0.391	1182	187300
202-7-12 × PPMI 301	46	74	154	2.06	1537.9	881.7	5.74	57.6	1349.5	2896.4	31.7	162	22.8	24.0	0.423	1376	211000
202-8-27 × PPMI 301	44	73	156	2.14	1593.3	875.5	5.73	53.8	1712.0	3324.9	25.8	160	24.2	26.7	0.449	1304	198600
197-10-11 × PPMI 301	46	70	169	2.44	1662.7	901.2	5.17	53.2	1701.2	3362.1	26.3	156	22.2	22.1	0.478	1074	182100
202-7-4 × PPMI 301	45	62	156	2.50	1538.8	886.0	5.66	57.9	1243.9	2828.3	31.6	154	21.4	19.9	0.439	1305	195400
202-7-10 × PPMI 301	45	67	159	2.40	1573.4	912.5	6.20	58.5	1446.9	2971.2	31.1	165	22.3	22.2	0.526	1147	178200
202-8-8 × PPMI 301	44	70	127	1.83	1520.4	887.0	7.01	57.9	1203.4	2726.6	32.2	149	24.3	22.8	0.490	1427	176500
197-1-12 × PPMI 301	44	74	134	1.79	1616.3	943.2	6.99	57.3	1529.5	3157.0	30.0	152	21.9	20.1	0.489	1451	198300
202-6-26 × PPMI 301	45	66	134	2.03	1550.2	869.9	6.24	56.0	1358.6	2915.6	29.0	160	24.5	26.5	0.428	1470	201500
197-18-1 × PPMI 301	45	65	121	1.83	1575.7	992.8	8.14	62.7	1503.2	3068.4	32.3	160	22.2	22.6	0.498	1671	205500
863B × RIB 335/74	42	65	112	1.72	1756.4	1138.6	9.97	64.2	1710.5	3449.8	32.5	159	23.5	24.9	0.662	1512	171200
ICMB 841 × RIB 335/74	43	70	161	2.30	1265.1	584.1	3.41	44.7	1323.6	2592.1	21.6	158	22.4	20.0	0.370	938	154900
197-10-18 × RIB 335/74	42	72	182	2.57	1455.0	653.9	3.49	44.4	1267.5	2710.8	23.4	147	23.0	18.7	0.386	902	165400
202-8-11 × RIB 335/74	43	75	190	2.54	1429.0	662.2	3.65	46.0	1255.8	2657.4	25.9	156	24.4	23.7	0.361	1010	187900
197-12-2 × RIB 335/74	43	74	159	2.12	1381.2	714.6	4.72	52.6	1477.8	2873.7	25.7	158	23.1	24.1	0.431	1104	164200
202-8-9 × RIB 335/74	43	71	185	2.63	1429.4	679.5	3.70	47.9	1770.5	3269.5	21.8	159	24.1	22.5	0.388	940	170100
202-7-12 × RIB 335/74	42	72	185	2.56	1516.0	694.5	3.73	45.7	1383.0	2952.1	23.9	164	23.9	28.5	0.373	1025	186200
202-8-27 × RIB 335/74	42	71	201	2.82	1519.4	681.1	3.41	44.5	1657.6	3196.9	21.6	160	25.5	20.6	0.419	833	169400
197-10-11 × RIB 335/74	43	75	178	2.38	1430.9	652.2	3.62	45.5	1763.4	3206.0	20.3	154	25.2	23.7	0.448	817	150200
202-7-4 × RIB 335/74	42	72	172	2.37	1347.3	697.1	4.38	48.5	1216.0	2568.7	27.1	152	22.6	21.4	0.358	1185	185500
202-7-10 × RIB 335/74	42	72	194	2.69	1489.9	756.5	4.01	49.6	1354.0	2847.6	26.6	154	24.1	20.4	0.358	1150	221600
202-8-8 × RIB 335/74	43	73	183	2.51	1402.0	850.0	4.54	56.3	1342.1	2747.9	28.5	157	24.9	22.2	0.377	1149	219300
197-1-12 × RIB 335/74	42	75	167	2.22	1457.3	704.0	4.26	48.4	1525.7	2957.5	23.6	153	23.1	24.6	0.383	1117	188700
202-6-26 × RIB 335/74	42	65	162	2.54	1565.1	726.4	4.60	46.7	1211.1	2788.5	26.7	158	22.3	25.0	0.418	1098	175500
197-18-1 × RIB 335/74	43	69	161	2.36	1564.3	835.8	5.37	53.9	1582.9	3123.9	27.5	152	22.8	21.1	0.419	1283	201800
863B × H 77/833-2	42	72	136	1.89	1902.7	1286.9	9.57	67.9	2067.4	4006.4	32.8	155	22.7	21.2	0.567	1679	226700
ICMB 841 × H 77/833-2	47	75	185	2.50	1605.7	841.7	4.58	51.5	1910.4	3509.3	23.5	159	22.2	23.4	0.407	1131	205700
197-10-18 × H 77/833-2	45	71	195	2.76	1384.5	757.8	4.18	53.5	2147.0	3569.3	21.5	150	21.9	19.0	0.398	979	175200
202-8-11 × H 77/833-2	46	73	200	2.77	1442.2	736.3	3.73	51.7	1803.4	3188.3	23.3	142	22.5	20.2	0.444	824	162900

Table 27. Performance summary under early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004 (Cont...).

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H. I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
197-12-2 × H 77/833-2	47	43	140	1.92	1517.6	894.0	6.41	59.6	1817.5	3326.1	27.4	162	21.6	23.0	0.474	1342	185900
202-8-9 × H 77/833-2	45	43	198	2.69	1590.4	765.6	4.00	48.6	2187.9	3824.9	20.8	144	22.0	20.2	0.396	1027	195400
202-7-12 × H 77/833-2	46	68	191	2.82	1498.4	853.1	4.43	56.5	1674.9	3134.4	26.7	153	23.6	23.5	0.378	1182	228700
202-8-27 × H 77/833-2	44	70	203	2.89	1526.9	703.8	3.40	46.0	1381.4	2904.7	24.1	161	22.8	23.4	0.377	929	188900
197-10-11 × H 77/833-2	46	71	214	3.03	1650.0	855.7	4.07	51.2	1841.0	3495.5	24.8	152	22.5	22.3	0.380	1070	230200
202-7-4 × H 77/833-2	46	72	189	2.60	1523.0	721.7	3.91	47.3	1673.6	3202.2	24.0	142	21.2	19.2	0.432	914	169300
202-7-10 × H 77/833-2	47	67	170	2.57	1414.2	769.1	4.59	55.3	1502.0	2917.1	27.5	160	19.6	25.9	0.437	1033	170600
202-8-8 × H 77/833-2	46	71	163	2.29	1513.7	748.2	4.53	49.2	1689.8	3185.0	22.8	154	23.4	21.2	0.408	1103	180600
197-1-12 × H 77/833-2	46	69	172	2.50	1562.2	860.8	5.05	55.7	1770.5	3297.1	26.1	154	22.9	22.7	0.428	1179	200900
202-6-26 × H 77/833-2	45	68	192	2.84	1479.0	766.2	3.87	51.6	1749.1	3228.1	23.2	146	20.7	18.6	0.403	984	193100
197-18-1 × H 77/833-2	45	69	191	2.76	1577.4	871.2	4.46	54.9	1754.4	3335.6	25.8	158	21.2	23.6	0.421	1076	207600
Minimum	**42**	**62**	**102**	**1.54**	**1265.1**	**584.1**	**3.40**	**44.4**	**1114.7**	**2568.7**	**20.3**	**142**	**19.6**	**18.6**	**0.358**	**817**	**150200**
Maximum	**47**	**76**	**214**	**3.03**	**1902.7**	**1286.9**	**9.97**	**67.9**	**2187.9**	**4006.4**	**36.0**	**165**	**25.5**	**30.6**	**0.662**	**1932**	**230200**
Mean	**44**	**71**	**165**	**2.44**	**1528.0**	**819.3**	**5.26**	**53.1**	**1568.4**	**3098.7**	**26.6**	**155**	**22.9**	**22.6**	**0.434**	**1192**	**189100**
SE (±)	**0.37**	**2.46**	**10.53**	**0.16**	**88.22**	**70.38**	**0.52**	**2.58**	**172.98**	**216.84**	**2.03**	**5.45**	**1.15**	**2.09**	**0.03**	**112**	**15234.1**
CV (%)	**1.45**	**6.03**	**11.06**	**11.79**	**9.97**	**14.78**	**16.82**	**8.39**	**19.12**	**12.12**	**13.1**	**6.1**	**8.72**	**16.13**	**12.09**	**15.9**	**13.81**
F-ratio	**18.20****	**1.62**	**7.10****	**5.90****	**1.92**	**4.01****	**12.97****	**5.31****	**2.53**	**2.43**	**4.18****	**1.41**	**1.18**	**1.23**	**4.02****	**6.57****	**1.78**
h^2 (plot basis)	**0.85**	**0.17**	**0.67**	**0.62**	**0.24**	**0.50**	**0.80**	**0.59**	**0.34**	**0.32**	**0.51**	**0.12**	**0.06**	**0.07**	**0.50**	**0.65**	**0.21**
h^2 (mean basis)	**0.95**	**0.38**	**0.86**	**0.83**	**0.48**	**0.75**	**0.92**	**0.81**	**0.60**	**0.59**	**0.76**	**0.29**	**0.15**	**0.19**	**0.75**	**0.85**	**0.44**
ICMB 93333 × PPMI 301	47	70	92	1.32	1349.0	888.0	9.75	64.6	1627.3	2954.8	29.7	158	21.9	24.9	0.461	2121	193400
ICMB 94111 × PPMI 301	43	71	115	1.58	1721.0	1121.0	10.07	65.2	1721.8	3428.3	32.8	162	23.5	27.1	0.630	1597	178800
ICMB 97111 × PPMI 301	43	74	122	1.69	1451.9	935.5	7.45	64.4	1763.2	3186.7	28.4	161	22.4	24.3	0.566	1319	165200
ICMB 98222 × PPMI 301	46	73	98	1.37	1596.5	1075.6	11.25	67.3	1765.7	3315.4	31.9	140	24.0	21.4	0.576	1942	184600
ICMB 99111 × PPMI 301	44	75	141	1.85	1393.9	812.5	5.73	58.8	1644.2	3055.6	27.0	164	22.7	24.9	0.454	1271	179000
ICMB 99222 × PPMI 301	43	69	96	1.42	1691.6	1149.0	12.02	67.0	1262.7	2963.5	39.9	149	21.9	24.2	0.560	2130	205800
ICMB 841 × PPMI 301	42	70	125	1.77	1642.8	1076.9	9.20	65.3	1168.1	2839.1	39.1	146	20.6	18.7	0.507	1802	215500
863B × PPMI 301	43	73	132	1.80	1642.5	1009.8	8.46	62.0	1787.6	3391.5	29.8	151	23.1	22.8	0.513	1610	194800
ICMH 451	51	73	125	1.65	1101.9	741.1	6.89	67.5	1621.1	2698.1	27.9	157	26.0	22.2	0.583	1177	130000
Minimum	**42**	**62**	**92**	**1.32**	**1101.9**	**584.1**	**3.40**	**44.4**	**1114.7**	**2568.7**	**20.3**	**140**	**19.6**	**18.6**	**0.358**	**817**	**130000**
Maximum	**51**	**76**	**214**	**3.03**	**1902.7**	**1286.9**	**12.02**	**67.9**	**2187.9**	**4006.4**	**39.9**	**165**	**26.0**	**30.6**	**0.662**	**2130**	**230200**
Mean	**44**	**71**	**157**	**2.22**	**1527.2**	**848.5**	**5.89**	**55.1**	**1575.6**	**3104.4**	**27.5**	**155**	**22.9**	**22.8**	**0.453**	**1273**	**188200**
SE (±)	**0.39**	**2.43**	**11.62**	**0.17**	**93.12**	**77.27**	**0.73**	**2.58**	**175.71**	**225.67**	**2.1**	**5.65**	**1.14**	**2.16**	**0.03**	**131**	**15002.6**
CV (%)	**1.51**	**5.94**	**12.83**	**13.20**	**10.58**	**15.82**	**21.41**	**8.12**	**19.35**	**12.62**	**13.27**	**6.31**	**8.61**	**16.47**	**11.40**	**17.82**	**13.81**
F-ratio	**21.86****	**1.46**	**7.72****	**7.26****	**2.11**	**3.80****	**10.02****	**7.31****	**2.10**	**1.98**	**4.52****	**1.37**	**1.27**	**1.37**	**6.30****	**6.30****	**1.98**
h^2 (plot basis)	**0.87**	**0.13**	**0.69**	**0.68**	**0.27**	**0.48**	**0.75**	**0.68**	**0.27**	**0.25**	**0.54**	**0.11**	**0.08**	**0.11**	**0.64**	**0.64**	**0.25**
h^2 (mean basis)	**0.95**	**0.32**	**0.87**	**0.86**	**0.53**	**0.74**	**0.90**	**0.86**	**0.52**	**0.49**	**0.78**	**0.27**	**0.21**	**0.27**	**0.84**	**0.84**	**0.49**

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

4.3.3.2.1. Flowering time

Among experimental testcross hybrids, the entry mean values for flowering time ranged from 42 to 47 days, with an overall trial mean of 44 days. The hybrids of tester RIB 335/74 were comparatively early flowering. Among RIB 335/74 testcross hybrids, those produced with introgression lines 197-10-18, 202-827, 202-7-12, 202-7-4, 202-7-10, 197-1-12 and 202-6-26, recorded the trial minimum flowering time for this environment (42 days). Among controls, ICMH 451 was the latest flowering, preceded immediately by ICMB 93333 × PPMI 301, at 51 and 47 days respectively. The operational heritability of this trait was extremely high (0.95) in this moisture regime.

4.3.3.2.2. Plant number per plot

The range of plant number per plot was from 62 to 76 plants with a mean value of 71 plants. There was no significant difference between the entries for plant numbers per plot across the testcross hybrids and controls in this environment.

4.3.3.2.3. Panicle number per plot

The entry mean value for panicle number per plot in the early-onset terminal drought stress moisture regime ranged from 102 (197-12-2 × PPMI 301) to 214 (197-10-11 × H 77/833-2) with an overall environment mean of 165. Across experimental entries and controls, introgression lines 202-8-11, 202-8-9, 202-8-27 and 202-7-10 produced hybrids with high numbers of panicles in this environment. Among the testers, hybrids of H 77/833-2 had the highest number of panicles per plot. The heritability on mean basis was ≥0.86 for this trait.

Among control entries, ICMB 99111 × PPMI 301 produced the largest number of panicles per plot (141). The drought tolerance QTL donor parent hybrid (863B × PPMI

301) produced many panicles (132) and was statistically equivalent to the best of the control entries. The F-ratio for this environment indicated the control and testcross hybrids differed significantly in panicle number per plot.

4.3.3.2.4. Effective tiller number per plant

For experimental testcross hybrids, the mean value of effective tiller number per plant in this moisture regime ranged from 1.72 (863B × RIB 335/74) to 3.03 (202-8-11 × H 77/833-2) with an overall trial mean of 2.44. Among testcross hybrids of high-tillering tester H 77/833-2, those involving introgression lines 202-7-4, 202-8-9 and 197-18-1 had the highest effective tiller numbers.

Most of the control entries had lower values of effective tiller number when compared to the experimental testcross hybrids, hence the environmental mean value reduced to 2.22 when control entries were included in the analysis.

4.3.2.2.5. Panicle yield per plot

The range for panicle yield per plot of the testcross hybrids in the early-onset terminal drought stress environment was from 1265 g (841B × RIB 335/74) to 1903 g (863B × H 77/833-2) with an overall mean value of 1528 g. Among hybrids of tester PPMI 301, those of introgression lines 197-10-18, 202-8-11, 197-10-11 and 197-1-12 had panicle yields above the environmental mean value.

With tester RIB 335/74, hybrids of the above-listed introgression lines yielded below the environmental mean value. This is indicative of strong tester effects for this trait, at least in this early-onset drought stress environment. Hybrids of tester H 77/833-2 with several of the above-listed introgression lines also yielded below this environmental

mean value. All three testcross hybrids of donor parent 863B had panicle yields above the environmental mean.

Among control entries, ICMB 94111 × PPMI 301 and ICMH 451 had the highest (1721 g) and lowest (1102 g) panicle yield per plot, respectively. The second highest yielder, ICMB 99222 × PPMI 301, produced panicle yields similar to those of PPMI 301 testcrosses with the introgression line donor and recurrent parents.

4.3.2.2.6. Grain yield per plot

The range among introgression line hybrids for grain yield was from 584 g (ICMB 841 × RIB 335/74) to 1287 g (863B × H 77/833-2). The hybrids of tester RIB 335/74 were below the trial mean value of testcross hybrids except 202-8-8 × RIB 335/74 (850 g) and 197-18-1 × RIB 335/74 (836 g).

Among control entries, ICMB 99222 × PPMI 301 yielded more grain per plot (1149 g) and the lowest grain yield was recorded for late-flowering in ICMH 451 (741 g). The operational heritability of this trait was ≥0.74. The F-ratio statistics showed that the testcross hybrids were significantly different from each other in mean grain yield in this early-onset terminal drought stress environment.

4.3.2.2.7. Grain yield per panicle

Per panicle grain yield ranged from 3.40 g (202-8-27 × H 77/833-2) to 10.0g (863B × RIB 335/74). Across all three testers, the introgression lines 197-12-2 and 197-18-1 maintained higher grain yield per panicle. Heritability of this was high ≥0.92. Among controls, ICMB 99222 × PPMI 301 recorded the highest grain yield per panicle (12.02 g) followed by ICMB 98222 × PPMI 301 (11.25 g) and panicles of ICMB 99111 × PPMI

301 yielded (5.73 g) lower than control mean value of 5.89 g for the combined data set of control and experimental testcross hybrids.

4.3.2.2.8. Panicle harvest index

The mean value for panicle harvest index ranged from 44.4% (197-10-18 × RIB 335/74) to 67.9% (863B × H 77/833-2) with trial mean in this moisture regime of 53.1%. Across testers, the hybrids of introgression lines 197-12-2, 202-8-8 and 197-18-1 maintained higher panicle harvest index values in this more severe drought stress environment.

The mean values of control entries were mostly high hence the combined mean value (55.1%) was higher than the environmental mean for experimental testcross hybrid (53.1%). Among control entries, ICMH 451 (67.5%), ICMB 98222 × PPMI 301 (67.3%) and ICMB 99222 × PPMI 301 (67.0%) had the highest panicle harvest index values.

4.3.2.2.9. Stover yield per plot

Testcrosses of the donor parent 863B maintained numerically higher stover yields than those of recurrent parent ICMB 841. Introgression line testcross hybrid mean stover yields values ranged from 1115 g (197-12-1 × PPMI 301) to 2188 g (202-8-9 × H 77/833-2) per plot with an environmental mean value of 1568 g. Across testers, hybrids of introgression lines 197-10-11 and 197-10-18 yielded numerically more stover. Similarly, hybrids of introgression line 202-8-9 gave high stover yield with testers RIB 335/74 and H 77/833-2, while those of introgression line 202-8-27 gave high stover yields with testers PPMI 301 and RIB 335/74. However, differences observed in treatment means of stover yield among experimental and control testcross hybrids were non-significant due to the relatively low heritability of this trait in this environment ($\leq$0.60).

4.3.2.2.10. Biomass yield per plot

The mean values of introgression line testcross hybrids ranged from 2569 g (202-7-4 × RIB 335/74) to 4006 g (863B × H 77/833-2) in the early-onset terminal drought moisture regime with an environmental mean of 3099 g. Across testers, hybrids of introgression lines 197-10-11 and 197-10-18 yielded more biomass. However, the non-significant F-ratio indicated that the testcross hybrids were not significantly different from each other for this trait in this terminal drought stress environment. Among control entries, ICMB 94111 × PPMI 301 (3428 g) and ICMB 98222 × PPMI 301 (3315 g) had numerically higher biomass yields comparable with that of 863B × PPMI 301 (3392 g). Due to poor biomass yield differentiation of control entries, the mean-basis heritability of this trait reduced to 0.49 when the full data set of controls and experimental testcrosses for this environment was analyzed.

4.3.2.2.11. Harvest index

The average value of harvest index among experimental testcross hybrids in this early onset terminal drought stress environment was 26.6%. The mean values of individual testcross hybrids ranged from 20.3% (197-10-11 × RIB 335/74) to 36.0% (863B × PPMI 301). Across testers, hybrids of 197-12-2 and 197-18-1 showed higher harvest index values, while those of 202-8-8 had high harvest index values with testers PPMI 301 and RIB 335/74, but not with H 77/833-2.

Among controls, ICMB 99222 × PPMI 301 had the highest harvest index value (39.9%) followed by 841B × PPMI 301 (39.1%). Most of the control entries had higher harvest index values than the experimental testcross hybrids and hence the environmental

mean harvest index for this trait increased to 27.5% when the control entries were included in the analysis.

4.3.2.2.12. Plant height

Among the 45-introgression line and parental testcross hybrids, plant height ranged from 142 cm (202-8-11 × H 77/833-2 and 202-7-4 × H 77/833-2) to 165 cm (202-7-10 × PPMI 301) with a trial environmental mean value of 155 cm. There was little difference between testcross hybrids of the two parents ICMB 841 and 863B across the three testers. Among testers, PPMI 301 imparted more height to the testcross hybrids of introgression lines 202-7-12 (162 cm), 202-6-26 and 197-18-1 (160 cm). Introgression line 202-7-12 gave uniformly tall hybrids across testers. Among control entries, ICMB 98222 × PPMI 301 was the shortest hybrid (140 cm), followed by that of recurrent parent ICMB 841 (146 cm). However, the heritability of plant height was relatively low (≥ 0.29) and in this moisture regime its F-ratios were non-significant.

4.3.3.2.13. Panicle length

The environmental mean value of introgression line and parental testcross hybrids for panicle length was 22.9 cm. The observed range of testcross hybrids for panicle length was from 19.6 cm (202-7-10 × H 77/833-2) to 25.5 cm (202-8-27 × RIB 335/74), but no statistically significant difference on panicle length was observed between the testcross hybrids and for control entries in this environment. The heritability of this trait was the lowest among observed characters, indicating that there was little genetic variation detected in this stress environment for a trait that usually has relatively high heritability.

4.3.3.2.14. Panicle diameter

Among introgression line and parental testcross hybrids, the environmental mean value for panicle diameter ranged from 18.6 mm (202-6-26 × H 77/833-2) to 30.6 mm (863B × PPMI 301). The difference in panicle diameter between the parental testcross hybrids of ICMB 841 and 863B was substantially reduced with testers RIB 335/74 and H 77/833-2 but clearly discernable with tester PPMI 301. Among control entries, ICMB 94111 × PPMI 301 had the largest panicle diameter (27.1 mm) followed by ICMB 94111 × PPMI 301 and ICMB 99111 × PPMI 301 (24.9 mm). The heritability of this trait improved to ≤0.27 from ≤0.19 when the larger diameter control entries were included in the analysis of this trait.

4.3.3.2.15. Hundred-grain mass

Among introgression line parental testcross hybrids, the mean value for 100-grain mass ranged from 0.358 g (202-7-4 × RIB 335/74) to 0.662 g (863B × RIB 335/74) with a trial environmental mean value of 0.434 g. The hybrids of tester PPMI 301 had large 100-grain mass values. Among control entries, ICMB 94111 × PPMI 301 had the highest hundred grain mass (0.630 g) and ICMB 93333 × PPMI 301 had the lowest (0.461 g). When the controls were included in this analysis, heritability of this trait increased from ≥0.75 to ≥0.84.

4.3.3.2.16. Grain number per panicle

Among testcross hybrids of the introgression lines and their parents, the range for number of grains per panicle was from 817 (197-10-11 × RIB 335/74) to 1932 (197-12-2 × PPMI 301). Grain number per panicle was highest among hybrids of tester PPMI 301. Hybrids of introgression lines 197-12-2, 197-10-18 and 197-18-1 had numerically higher

grain numbers per panicle than either of their parental lines (863B and 841B) with tester PPMI 301, but none of the 13 introgression lines had hybrids with higher grain numbers per panicle than 863B with either of the other two testers. Among control entries ICMB 99222 × PPMI 301 (2130) and ICMB 93333 × PPMI 301 (2121) had the highest numbers of grains per panicle. Significant F-ratios showed that the testcross hybrids and controls were significantly different from each other for this trait in this environment.

4.3.3.2.17. Grain number per plot

Number of grains per plot varied from 150200 (197-10-11 × RIB 335/74) to 230200 (197-10-11 × H 77/833-2) with a trial environmental mean value of 189100. Among testcrosses, hybrids of high-tillering H 77/833-2 and large-panicled PPMI 301 produced larger numbers of grains per plot. Non-significant differences were observed for this trait whether or not control entries were included in the analysis with testcross hybrids. The heritability of this trait was increased marginally from ≤ 0.44 to ≤ 0.49 when control entries were included in the analysis. Among control entries ICMB 99222 × PPMI 301 (205800) had the largest number of grains per plot but this value was numerically less than that of parental hybrid 841B × PPMI 301 (215500).

4.3.3.3. Estimates of components of genetic variation

The genetic components of variance for observed traits among the testcross hybrids of introgression lines and their parents in this early-onset drought stress environment are presented in Table 28. The significance of both lines and testers as sources of variation (Table 26) contributed to the high degree of additive genetic variation (σ^2A) for most observed traits. Highly significant σ^2A for flowering time, panicle number per plot, effective tiller numbers per plant, panicle yield per plot, grain yield per plot, grain yield

Table 28. Estimates of additive and dominance components of genetic variation among testcross hybrids of introgression lines and their parents in early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Genetic comp.	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
σ^2A	4.0**	0.5*	949.2**	0.2**	3697.2**	13749.0**	3.3**	31.3**	66265.5**	81446.3**	15.9**	7.5*	1.1*	0.2**	0.001**	83813.1**	25896296.3*
σ^2D	0.5**	2.2	44.0	0.0	4088.2	1912.3	0.4**	1.7	9342.5	11705.9	3.0*	2.2	0.0	0.6	0.003	17242.9**	255759081.3*
σ^2A: σ^2D	8.8	0.2	21.6	28.8	0.9	7.2	8.2	18.5	7.1	7.0	5.3	3.4	0.0	0.3	3.33	4.9	0.1

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

per panicle, panicle harvest index, 100-grain mass and grain number per panicle indicated that the testcross parents (both lines and testers) exhibit substantial heritable variation for all of these traits that can be exploited in breeding both open-pollinated varieties and hybrids. Dominance genetic variance (σ^2D), which is best exploited in breeding of hybrids, was highly significant only for flowering time and grain yield per panicle. The ratio of additive to dominance variance was ≥ 1 for all the observed characters except for plant number per plot, panicle yield, panicle diameter, and grain number per plot.

4.3.3.4. Contributions of lines and testers

The relative contributions of lines and testers and their interactions to variation in testcross hybrid performance for the observed agronomic traits in this early-onset terminal drought stress environment are tabulated in Table 29. Under the relatively severe drought stress conditions of this environment, the introgression lines and their parents lines contributed more than the testers to variation in panicle yield per plot, grain yield per plot, grain yield per panicle, harvest index, plant height, panicle diameter and 100-grain mass. Testers contributed more only in case of flowering time (64.09%). For testcross hybrid performance there were approximately equal contributions of lines, testers and interaction components to stover yield per plot, biomass yield per plot, harvest index, panicle length and grain number per panicle. For plant number per plot, panicle yield, panicle diameter, and grain number per plot the interaction component was a major contributor to variation among the testcross hybrids.

Table 29. Relative contributions (%) of lines and testers, parents and their interactions towards variations in hybrids in early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Lines & Testers	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
Lines	20.88	42.43	42.35	44.60	37.60	54.22	55.12	54.39	30.93	39.19	37.53	44.05	37.82	37.41	61.72	36.84	13.48
Testers	64.09	3.64	45.13	42.09	11.94	23.76	32.62	30.58	36.08	28.17	36.17	7.82	28.03	4.25	14.58	40.03	11.38
Lines x Testers	15.04	53.93	12.53	13.31	50.46	22.03	12.25	15.03	32.99	32.64	26.30	48.13	34.14	58.34	23.70	23.13	75.14

4.3.3.5. Combining Ability

The results of the combining ability analyses for the line × testers set grown in the early-onset terminal drought stress environment, in the form of tabulated *gca* effects the lines and testers, are presented in Table 30.

4.3.3.5.1. General Combining Ability (gca)

The best (negative) combiners for early flowering time, which contributed earliness to their hybrids, were 863B, 202-8-11, 202-8-27, and RIB 335/74. For panicle number and effective tiller number per plot, the best combiners were 202-8-27, 197-10-11, 202-8-11, 202-7-4, 202-7-10, 202-7-12, 202-8-9, RIB 335/74 and H 77/833-2. Parental line 863B, introgression lines 197-18-1, and tester PPMI 301 showed positive combining ability for grain yield per plot, grain yield per panicle and panicle harvest index. The other introgression line 197-12-2 showed positive *gca* effects for grain yield per panicle and panicle harvest index.

Among testers, PPMI 301, RIB 335/74 were negative combiners and H 77/833-2 was the positive combiner for stover and biomass yield; while among the lines, the donor parent 863B and introgression line 197-10-11 exhibited significant positive *gca* for these traits in this environment. Introgression line 202-8-9 exhibited positive *gca* only for stover yield per plot. For harvest index, tester PPMI 301 was the best combiner and testers H 77/833-2 and RIB 335/74 were the worst combiners. Among introgression lines, 197-12-2 and the parent 863B showed positive *gca* for harvest index. None of the testers showed significant *gca* for plant height but introgression lines 202-8-27 and 202-7-12 showed positive combining ability for this trait, contributing approximately 7 cm in additional height to their hybrids compared to the trial mean.

Table 30. Estimates of gca effects of introgression lines and testers in early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Lines & Testers	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B	-1.91**	-0.74	-43.59**	-0.59**	237.29**	347.10**	4.38**	12.53**	276.70**	514.70**	5.56**	2.27	0.71	1.88	0.16**	424.60**	7391.00
ICMB 841	0.08	-0.07	-7.70	-0.11	-26.67	-25.12	0.31	-1.46	-167.30	-193.20	1.21	-2.62	-0.31	-0.22	-0.03	112.80	1693.00
197-10-18	-0.03	0.37	2.53	0.02	-8.89	-33.15	-0.21	-2.02	188.20	180.10	-2.87*	-5.62	-0.16	-2.50*	-0.03	30.10	1280.00
202-8-11	-0.25	1.93	16.53**	0.16	-15.45	-67.56	-1.05**	-3.55*	-17.20	-47.10	-1.70	-4.40	0.57	-0.67	-0.01	-183.90**	-9585.00
197-12-2	1.30**	2.48	-31.36**	-0.51**	-63.12	28.66	1.43**	4.76**	-97.10	-159.50	2.77*	2.49	-0.60	0.87	0.03	252.60**	-5371.00
202-8-9	-0.14	2.48	14.08*	0.12	-44.78	-101.12*	-1.23**	-4.57**	213.00*	173.50	-4.22**	-4.84	-0.56	-1.79	-0.04*	-159.10*	-5667.00
202-7-12	0.63**	0.48	12.53*	0.16	-20.67	-19.45	-0.70*	-0.02	-98.20	-118.10	0.65	7.04*	0.59	2.81*	-0.04*	-29.40	15119.00
202-8-27	-0.80**	0.82	23.53**	0.30**	29.88	-73.56	-1.15**	-5.16**	16.50	47.10	-2.93*	7.48*	1.33*	1.05	-0.02	-203.90**	-8458.00
197-10-11	0.85**	1.37	21.30**	0.25**	46.33	-29.12	-1.05**	-3.34*	201.40*	248.40*	-3.02**	-0.62	0.45	0.17	0.00	-219.90**	-5286.00
202-7-4	-0.14	-1.96	8.08	0.18*	-64.78	-51.70	-0.64*	-1.93	-189.80	-253.90*	0.75	-5.84	-1.12	-2.30	-0.02	-73.80	-4767.00
202-7-10	0.52*	-2.30	8.53	0.19*	-42.01	-10.90	-0.44	1.11	-132.20	-173.50	1.65	5.82	-0.86	0.33	0.01	-93.50	321.00
202-8-8	-0.03	0.48	-8.03	-0.14	-66.78	-5.63	-0.01	1.10	-155.30	-221.40	1.11	-1.07	1.35*	-0.42	-0.01	19.80	1848.00
197-1-12	0.08	2.04	-6.59	-0.15	30.33	19.11	0.11	0.51	42.40	73.50	-0.21	-0.29	-0.24	-0.04	0.00	30.50	3511.00
202-6-26	-0.25	-4.29**	-3.36	0.12	-42.12	-58.89	-0.43	-1.84	-128.20	-169.60	-0.48	-1.62	-0.36	0.89	-0.02	-36.30	-6182.00
197-18-1	0.08	-3.07*	-6.47	0.00	51.44	81.33*	0.66*	3.87**	47.10	99.20	1.74	1.82	-0.80	-0.05	0.01	129.60*	14151.00
PPMI 301	0.41**	-0.79	-25.76**	-0.33**	43.14	80.93**	1.48**	3.94**	-119.80**	-76.00	3.49**	0.78	-0.01	0.41	0.03**	252.30**	5053.00
RIB 335/74	-1.69**	0.64	8.13**	0.09*	-56.58*	-85.18**	-0.85**	-4.03**	-111.30*	-169.30**	-1.66**	1.71	0.80**	0.25	-0.02**	-140.10**	-9583.00*
H 77/833-2	1.28**	0.15	17.64**	0.24**	13.44	4.26	-0.60**	0.09	231.10**	245.30**	-1.83**	-2.49	-0.79**	-0.66	-0.01	-112.20**	4530.00

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

For panicle length, the best positive combiner among lines and testers were 202-8-27, 202-8-8 and RIB 335/74. The only significantly positive combiners among introgression lines and testers for both 100-grain mass and grain number per panicle were donor parent 863B and tester PPMI 301. However, introgression lines 197-12-2 and 197-18-1 both had significantly positive *gca* for grain number per panicle in this early-onset terminal drought stress environment.

4.3.3.5.2. Specific Combining Ability (sca)

The *sca* effects of testcross hybrids of the 13-introgression lines and their recurrent and donor parents are tabulated in Table 31. Among these testcross hybrids, very few showed significant favourable *sca* effects in this early-onset terminal drought stress environment: ICMB 841 × PPMI 301, 202-7-10 × RIB 335/74, 863B × H 77/833-2 and 197-10-11 × H 77/833-2 were early flowering; 202-7-4 × PPMI 301 and 863B × RIB 335/74 had significantly negative *sca* for effective tiller number and ICMB 841 × PPMI 301 and 863B × RIB 335/74 showed significantly positive *sca* for grain yield per panicle. In this environment, both 863B × PPMI 301 and ICMB 841 × RIB 335/74 showed significantly negative *sca* effects for panicle yield per plot, grain yield per plot and grain yield per panicle.

Only testcross hybrid 202-8-8 × RIB 335/74 showed positive *sca* for panicle harvest index, which was accompanied by positive *sca* effects for grain number per plot. Introgression lines testcross hybrid 197-10-18 × RIB 335/74 showed significantly negative *sca* effects for stover yield and 202-8-27 × H 77/833-2 exhibited negative *sca* for both biomass and stover yield per plot. The recurrent parent ICMB 841 hybrid with PPMI 301 alone showed positive *sca* whereas with RIB 335/74 showed negative *sca* for

Table 31. Estimates of sca effects of testcross hybrids in early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	0.25	3.12	18.43	0.18	-190.77*	-190.28**	-1.61**	-4.36	29.50	-162.00	-4.14*	-1.78	0.84	2.22	-0.07*	-170.50	-9278.00
ICMB 841 × PPMI 301	-1.74**	-2.55	-5.79	-0.02	129.30	141.30*	1.81**	3.56	-314.40	-185.80	7.49**	-11.89	0.47	0.82	0.01	329.60**	25491.00
197-10-18 × PPMI 301	0.03	0.34	-14.35	-0.21	150.19	81.33	0.95	0.43	216.60	366.00	-0.54	3.78	0.52	1.84	-0.01	325.60**	32336.00*
202-8-11 × PPMI 301	-0.41	-1.22	-1.35	0.05	71.41	3.07	-0.30	-2.18	170.10	256.00	-2.61	5.22	-0.05	-0.63	0.01	-54.10	-946.00
197-12-2 × PPMI 301	0.03	-0.10	-6.13	-0.07	-18.59	-3.82	0.91	0.01	-235.90	-255.10	2.49	-6.33	-0.21	-0.83	-0.02	219.50	6292.00
202-8-9 × PPMI 301	-0.53	3.56	-0.24	-0.10	-120.59	-102.04	-0.98	-3.02	-283.70	-409.60	-0.89	-1.67	-1.48	-1.68	-0.03	-125.20	-10526.00
202-7-12 × PPMI 301	1.02**	3.23	3.99	-0.06	-22.70	-0.70	-0.37	0.39	0.10	-23.30	0.78	1.78	-0.60	-1.71	0.00	-77.90	-2279.00
202-8-27 × PPMI 301	0.14	2.23	-6.68	-0.17	-4.92	28.07	0.07	1.76	247.80	242.20	-1.51	-2.00	0.05	2.75	0.00	32.20	5058.00
197-10-11 × PPMI 301	0.81	-1.66	7.87	0.17	11.63	-5.70	-0.60	-0.72	52.30	63.20	-0.96	3.11	-1.09	-1.00	0.01	-163.80	-8949.00
202-7-4 × PPMI 301	0.14	-5.99*	8.43	0.32*	-25.59	7.55	-0.51	2.63	-15.70	-42.00	0.58	4.67	-0.36	-0.70	0.00	-85.80	5081.00
202-7-10 × PPMI 301	0.14	-0.99	9.32	0.16	46.30	32.08	-0.18	0.13	133.80	179.40	-0.82	1.67	0.35	-1.07	0.05	-209.50*	-18117.00
202-8-8 × PPMI 301	-0.30	-0.77	-5.46	-0.05	22.75	-15.52	0.21	-0.42	-88.50	-66.40	0.82	-3.11	0.13	0.36	0.03	-44.40	-17732.00
197-1-12 × PPMI 301	-0.41	2.01	5.43	0.02	69.30	37.41	0.08	-0.44	40.50	109.10	-0.14	-3.22	-0.73	-2.83	0.02	-64.40	-2801.00
202-6-26 × PPMI 301	0.59	0.67	-3.46	-0.11	-76.92	-25.93	-0.14	0.64	38.00	-39.60	-0.79	4.11	1.99	2.71	-0.02	28.70	2510.00
197-18-1 × PPMI 301	0.25	-1.88	-10.02	-0.11	-40.81	13.18	0.67	1.60	9.60	-32.00	0.25	5.67	0.15	-0.25	0.02	60.10	-6139.00
863B × RIB 335/74	1.02**	-5.30*	-16.46	-0.09	43.06	53.86	1.14*	2.37	-21.30	23.20	1.82	0.96	-0.84	0.25	0.09**	10.20	-18686.00
ICMB 841 × RIB 335/74	0.70	-1.30	-3.68	0.01	-216.64*	-163.60*	-1.35**	-3.07	34.50	-180.70	-4.79*	4.51	-0.92	-2.55	-0.01	-258.70*	-33176.00*
197-10-18 × RIB 335/74	0.14	-0.08	4.10	0.07	-49.42	-71.23	-0.75	-2.88	-376.70*	-424.70	1.15	-4.82	-0.49	-1.54	0.01	-197.30	-19785.00
202-8-11 × RIB 335/74	0.03	1.36	0.76	-0.04	27.81	15.85	0.25	0.35	-194.30	-195.40	2.53	2.62	0.17	1.62	-0.04	132.30	19969.00
197-12-2 × RIB 335/74	-0.53	0.14	17.99	0.24	11.81	-21.04	-1.16*	-1.43	119.40	132.60	-2.19	-0.27	0.07	0.46	-0.01	-210.80	-1634.00
202-8-9 × RIB 335/74	0.59	-3.19	-3.13	0.06	-7.19	42.07	0.48	3.24	107.80	111.10	0.79	7.40	0.97	1.51	0.02	41.90	-329.00
202-7-12 × RIB 335/74	-0.85*	0.14	2.10	0.02	66.03	-26.26	-0.03	3.52	23.90	91.30	-1.90	0.18	-0.38	2.91	0.00	-27.50	-8367.00
202-8-27 × RIB 335/74	0.25	-0.86	7.76	0.13	60.47	29.85	0.11	0.43	185.40	247.30	-0.56	-2.27	0.54	-3.20	0.03	-52.70	-6757.00
197-10-11 × RIB 335/74	-0.08	2.59	-17.35	-0.33*	-116.31	-65.26	0.21	-0.40	105.60	-9.30	-1.87	-2.16	1.06	0.76	0.04	-37.00	-31783.00*
202-7-4 × RIB 335/74	-0.41	2.59	-7.79	-0.20	-52.19	23.90	0.70	1.53	-49.90	-100.70	1.17	0.40	0.06	0.96	-0.03	198.50	13246.00
202-7-10 × RIB 335/74	-1.08**	2.92	13.10	0.08	75.69	23.16	-0.12	-0.96	30.70	107.80	-0.07	-4.60	1.24	-2.71	-0.05*	170.80	39606.00**
202-8-8 × RIB 335/74	0.47	0.81	17.99	0.22	-13.86	111.37	-0.01	5.70*	41.50	29.10	2.42	4.29	-0.12	-0.15	-0.03	52.00	35240.00*
197-1-12 × RIB 335/74	-0.30	1.59	-0.13	-0.06	-43.64	-51.82	-0.30	-1.41	28.50	-13.70	-1.28	0.18	-0.35	1.92	-0.03	10.70	-174.00
202-6-26 × RIB 335/74	0.03	-2.08	-8.68	-0.01	150.47	60.52	0.58	-0.70	-116.50	35.40	2.10	2.51	-0.96	1.37	0.02	67.40	2313.00
197-18-1 × RIB 335/74	0.03	0.70	-6.57	-0.10	63.92	38.63	0.26	0.76	81.40	146.70	0.71	-8.93	-0.06	-1.60	0.00	100.20	10318.00
863B × H 77/833-2	-1.28**	2.19	-1.97	-0.09	147.71	136.42	0.47	1.99	-8.20	138.80	2.32	0.82	-0.01	-2.47	-0.02	160.30	27965.00
ICMB 841 × H 77/833-2	1.05**	3.85	9.47	0.01	87.34	22.30	-0.46	-0.49	279.90	366.50	-2.70	7.38	0.45	1.73	0.01	-70.90	7685.00
197-10-18 × H 77/833-2	-0.17	-0.26	10.25	0.15	-100.77	-10.10	-0.20	2.46	160.20	58.70	-0.61	1.04	-0.03	-0.29	0.01	-128.30	-12551.00
202-8-11 × H 77/833-2	0.39	-0.15	0.59	0.00	-99.22	-18.92	0.05	1.83	24.20	-60.60	0.08	-7.84	-0.13	-0.99	0.03	-78.20	-19023.00
197-12-2 × H 77/833-2	0.50	-0.04	-11.86	-0.16	6.78	24.86	0.25	1.42	116.50	122.60	-0.30	6.60	0.14	0.38	0.03	-8.70	-4658.00
202-8-9 × H 77/833-2	-0.06	-0.37	3.36	0.04	127.78	59.97	0.50	-0.21	175.90	298.50	0.10	-5.73	0.51	0.16	0.01	83.30	10854.00
202-7-12 × H 77/833-2	-0.17	-3.37	-6.08	0.04	-43.33	26.97	0.40	3.13	-24.00	-68.00	1.13	-1.96	0.98	-1.20	0.00	105.30	10646.00
202-8-27 × H 77/833-2	-0.39	-1.37	-1.08	0.03	-55.55	-57.92	-0.18	-2.19	-433.20*	-489.40*	2.07	4.27	-0.59	0.45	-0.03	20.40	1699.00
197-10-11 × H 77/833-2	-0.72*	-0.93	9.47	0.17	104.67	70.97	0.39	1.12	-157.80	-53.90	2.83	-0.96	0.03	0.24	-0.05	200.80	40732.00**
202-7-4 × H 77/833-2	0.27	3.41	-0.64	-0.13	77.78	-31.45	-0.18	-4.16	65.60	142.70	-1.74	-5.07	0.29	-0.26	0.03	-112.60	-18327.00
202-7-10 × H 77/833-2	0.94*	-1.93	-22.41*	-0.24	-121.99	-55.25	0.50	0.84	-164.50	-287.20	0.90	2.93	-1.59	3.78	0.01	38.70	-21490.00
202-8-8 × H 77/833-2	-0.17	-0.04	-12.53	-0.17	-8.88	-95.85	-0.19	-5.28**	47.00	37.40	-3.23	-1.18	-0.02	-0.20	-0.01	-7.60	-17507.00
197-1-12 × H 77/833-2	0.72	-3.59	-5.30	0.04	-25.66	14.41	0.22	1.84	-69.00	-95.40	1.42	3.04	1.08	0.91	0.00	53.80	2975.00
202-6-26 × H 77/833-2	-0.61	1.41	12.14	0.12	-73.55	-34.59	-0.44	0.05	78.40	4.20	-1.31	-6.62	-1.03	-4.08	0.00	-96.10	-4824.00
197-18-1 × H 77/833-2	-0.28	1.19	16.59	0.21	-23.11	-51.81	-0.92	-2.36	-90.90	-114.80	-0.96	3.27	-0.09	1.85	-0.02	-160.30	-4178.00

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

harvest index. Testcross hybrid 863B × RIB 335/74 exhibited positive *sca* for 100-grain mass and testcross hybrid 202-7-10 × RIB 335/74 showed negative *sca* for the same character.

Highly significant positive and negative *sca* effects for grain number per panicle and grain number per plot were observed for hybrids 197-10-18 × PPMI 301 and ICMB 841 × RIB 335/74, respectively, in this environment. Testcross hybrids that showed positive *sca* effects for grain number per plot were 197-10-18 × PPMI 301, 202-7-10 × RIB 335/74, 202-8-8 × RIB 335/74 and 197-10-11 × H 77/833-2.

4.3.4. Genotype × Environment interaction analysis (G × E)

Introgression lines testcross hybrids were evaluated under three moisture regimes namely: non-stress irrigated control, late-onset terminal drought stress and early-onset terminal drought stress conditions. The results of analyses of variances and summaries of testcross combining abilities for the stover and grain-yield related characters for the pooled or G × E interaction analysis are presented and discussed below.

4.3.4.1. Analysis of variance

The pooled analyses of variances for testcross hybrids and their different agronomic characters are presented in Table 32. The three moisture regimes environments varied significantly for panicle numbers per plot, effective tiller numbers, panicle yield per plot, grain yield per plot, grain yield per panicle, panicle harvest index, stover yield per plot, biomass yield per plot, harvest index, panicle length, panicle diameter, 100-grain mass, grain number per panicle and grain number per plot. Hybrids were highly significant for all agronomic characters except plant number per plot.

Table 32. Analyses of variance for testcross hybrids over three moisture regimes, ICRISAT-Patancheru, drought nursery, summer-2004.

		Mean squares															
SV	DF	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
Environments (Env)	2	2.7	64.4	12510.1*	3.0*	33056856.8**	26994932.0**	777.3**	7392.7**	10501054.4*	78259137.7**	3787.8**	440.1	21.0*	59.0**	1.802**	2867628.9**	1.65+11**
Hybrids	44	5.4**	20.8	2239.6**	747.0**	74455.2**	118120.7**	39387.1**	13250.7**	241306.5**	524817.6**	174990.0**	58431.3**	19484.0**	6504.7**	2168.267**	193004.5**	1.84E+09**
Lines (L)	14	13.4**	83.9**	9004.1**	1.7**	105559.0**	295657.2**	77.5*	402.6**	302691.8**	676259.9**	143.9**	392.9**	4.2*	77.3**	0.079**	695104.4**	1.19E+09
Testers (T)	2	283.5**	14.4	86406.0**	16.3**	2133702.9**	3135170.1**	501.5**	2043.7**	8814755.7**	15972512.3**	1287.7**	2636.4*	372.7**	471.1**	0.446**	5491666.8**	2.45E+10**
L × T	28	3.2**	26.5	477.5	0.1	45059.1*	37249.0*	3.2*	27.3*	128496.3*	215136.4*	23.4**	143.1**	2.6	7.0	0.009**	98755.8**	1.21E+09*
Env. × Lines	28	0.5	13.7	563.4	0.1	21570.8	21173.2	2.8*	20.7	90072.7	135901.4	16.1*	155.0**	2.9	14.9**	0.003	58108.5	6.16E+08
Env. × Testers	4	0.7	26.6	872.0	0.2	275799.8**	292068.4**	16.8**	100.2**	421196.9**	1175302.6**	90.2**	67.6	37.2**	66.8**	0.037**	81306.4	6.52E+09**
Env. × L × T	56	0.5	19.6	441.3	0.1	27841.8	16429.7	1.8	12.3	71826.9	122408.8	10.8	82.5	2.0	6.8	0.002	55971.6	9.51E+08
Pooled error	264	0.5	16.2	418.3	0.1	27277.4	21319.8	1.8	15.7	72749.3	136048.3	9.3	66.9	2.0	5.0	0.002	49493.0	7.06E+08

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

SV-Sources of variation
DF-Degrees of freedom
FT-Flowering time (days after emergence)
ET-Effective tiller number per plant
H I-Harvest index

Similarly, contributions of introgression lines and their parents to the observed variation in testcross hybrid performance were significant or highly significant for all observed agronomic characters except for grain number per plot. The three testers used for testcross hybrid development were significantly different for all the characters except for plant number per plot.

Line × tester effects: for flowering time, panicle yield per plot, grain yield per plot, grain yield per panicle, panicle harvest index, stover yield, biomass yield, harvest index, plant height, 100-grain mass, grain number per panicle and grain number per plot were all found to be significant. The significant variance attributable to line × tester interactions suggests the role of specific combining ability in the inheritance of these traits.

The lines × environments interactions were significant for grain yield per panicle, harvest index, plant height and panicle diameter. The variance due to interaction between testers and environments were significant for panicle yield per plot, grain yield per plot, grain yield per panicle, panicle harvest index, stover yield, biomass yield, harvest index, panicle length, panicle diameter, 100-grain mass and grain number per plot. No significant variance was observed for line × tester × environment interaction for any of the observed agronomic characters.

4.3.4.2. Estimates of components of genetic variation

Estimates of the components of genetic variation from the across-environment analysis are presented in Table 33. The significance of lines and testers as sources of variation among the testcrosses (Table 32) contributed to the high degree of additive genetic variation (σ^2A) for most observed traits. Highly significant σ^2A of flowering time, plant

Table 33. Estimates of additive and dominant components of genetic variation in over three moisture regimes, ICRISAT-Patancheru, drought nursery, summer-2004.

Genetic comp.	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No. /panicle	Grain No./plot
σ^2A	10.8**	1.7**	3498.3**	0.7**	79597.9**	124308.5**	21.2**	1158.5**	327948.3**	600685.2**	87.7**	5.8**	14.1*	19.8**	0.0	221824.4**	8.62E+08**
σ^2D	0.3**	1.1	6.6	0.0	1976.0*	1770.0*	0.2*	∞	5771.0*	8788.0*	∞	10.7**	0.0	0.2	0.0	5474.0**	5.61E+07*
σ^2A: σ^2D	34.3	1.5	531.7	∞	40.3	70.2	140.4	∞	56.8	68.4	∞	0.5	∞	92.5	∞	40.5	15.3

** Significant at 0.01 level of probability: * Significant at 0.05 level of probability

number per plot, panicle number per plot, effective tiller number per plant, panicle yield per plot, grain yield per plot and per panicle, panicle harvest index, stover yield, biomass yield, harvest index, plant height, panicle length, grain number per panicle and per plot, and significant σ^2A of panicle diameter indicated that the testcross hybrid parents (both lines and testers) exhibit heritable variation for all of these traits.

Dominant genetic variation (σ^2D) exhibited significance for flowering time, panicle yield per plot, grain yield per plot, grain yield per panicle, stover yield, biomass yield, plant height and grain number per panicle and grain number per plot. The ratio of additive and dominance variance was large for flowering time, panicle number per plot, effective tiller number per plant, panicle yield, grain yield per plot and grain yield per panicle, panicle harvest index, stover yield, biomass yield, harvest index, panicle length, panicle diameter, hundred-grain mass, grain number per panicle and grain number per plot. Only in case of plant height was σ^2D greater than σ^2A.

4.3.4.3. Contributions of lines and testers

The relative contribution of lines and testers and their interaction to variation in the testcross hybrids is tabulated in Table 34. Testers contributed more than the introgression lines and their parents to testcross variation for flowering time (66.98%), panicle yield per plot (60.90%), grain yield per plot (54.75%), stover yield (69.13%), biomass yield (67.34%) and panicle length (84.86%).

For testcross hybrid performance there was nearly equal contribution from lines and testers for panicle number per plot, effective tiller numbers, grain yield per panicle, panicle harvest index, harvest index, panicle diameter, 100-grain mass and grain number per panicle. Both lines and interaction component contributed equally for the plant

Table 34. Relative contributions (%) of introgression lines and testers, parents and their interactions towards observed variation in testcross hybrids across three moisture regimes, ICRISAT-Patancheru, drought nursery, summer-2004.

Lines & Testers	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
Lines	22.16	60.37	40.37	40.45	21.09	36.14	49.78	53.74	16.64	19.96	38.41	55.11	6.70	48.80	49.35	41.45	16.74
Testers	66.98	1.48	55.35	54.19	60.90	54.75	46.14	38.97	69.23	67.34	49.08	4.74	85.05	42.38	39.96	46.78	49.18
Lines × Testers	10.86	38.15	4.28	5.37	18.01	9.11	4.08	7.29	14.13	12.70	12.51	40.15	8.26	8.82	10.69	11.78	34.08

height. Only for plant number per plot, plant height and grain number per plot were line × tester interaction components major contributors to the variation observed among the testcross hybrids across the three moisture regimes of this experiment.

4.3.4.4. Combining ability

The results of the combining ability analysis for mean performance across the three moisture regimes, in the form of tabulated *gca* effects of lines and testers, are presented in Table 35.

4.3.4.4.1. General Combining Ability (*gca*)

For flowering time, the best negative combiners that contributed earliness to their hybrids, among the introgression lines and parents were 863B and 202-8-27. Among testers, RIB 335/74 was the only negative combiner. Tester RIB 335/74 contributed early flowering to its hybrids across moisture regimes and hence could be suitable to produce early-maturing hybrids to escape from terminal drought stress.

Among introgression lines, 197-12-2 and 202-8-9 showed positive *gca* effects, and 202-7-10 and 202-6-26 showed negative *gca* effects for plant number per plot. For panicle number per plot and effective tiller number per plant, introgression lines 202-8-11, 202-8-9, 202-8-27, 197-10-11, 202-7-4 and testers RIB 335/74 and H 77/833-2 exhibited positive *gca* effects. Significant positive *gca* effects were observed among introgression lines and their parents for panicle yield per plot for the drought tolerance donor parent 863B and for testers PPMI 301 and H 77/833-2.

Across three moisture regimes, the donor parent 863B and introgression lines 197-12-2 and 197-18-1 exhibited significant positive *gca* effects for several of the observed grain yield-related agronomic characters. For grain yield per plot, the

Table 35. Estimates of gca effects of introgression lines and testers over three moisture regimes, ICRISAT-Patancheru, drought nursery, summer-2004.

Lines & Testers	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H. I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B	-1.96**	-0.81	-50.83**	-0.70**	168.91**	339.59**	5.52**	11.38**	70.18	250.3**	6.67**	10.02**	0.29	5.76**	0.189**	426.3**	-9204
ICMB 841	0.26*	0.64	3.56	0.02	-35.17	-33.40	-0.32	-0.88	-91.45	-127.9	0.71	-0.65	-0.84**	0.19	-0.029**	24.2	4616
197-10-18	0.11	-1.11	3.15	0.09	41.02	9.94	-0.14	-1.00	100.70	140.5*	-1.09	-2.35	0.04	-1.22**	-0.008	-4.5	3024
202-8-11	-0.22	1.08	18.93**	0.23**	19.24	-58.71*	-1.20**	-3.58**	10.47	23.4	-1.97**	-2.94	0.33	-0.97*	-0.019*	-169.1**	-3920
197-12-2	0.82**	1.82*	-23.25**	-0.39**	-33.32	50.44	1.26**	3.98**	-16.83	-51.4	2.04**	1.50	0.25	0.33	0.023**	189.4**	-156
202-8-9	-0.15	2.04**	19.41**	0.20**	26.55	-42.71	-1.28**	-2.83**	155.55**	192.0**	-2.66**	-3.61*	-0.23	-1.27**	-0.029**	-151.1**	2589
202-7-12	0.56**	0.15	7.49	0.10	-28.35	-57.16*	-0.79**	-1.86*	19.27	-10.3	-1.39*	5.91**	0.26	0.35	-0.029**	-71.0	1335
202-8-27	-0.70**	1.34	18.45**	0.21**	-3.91	-93.38**	-1.39**	-4.37**	-87.74	-92.9	-1.79**	-3.20*	0.24	-0.54	-0.020*	-194.7**	-9338
197-10-11	1.08**	1.71	12.56**	0.12*	15.16	-37.75	-0.80**	-2.39**	129.20*	143.1*	-2.48**	1.65	0.08	-0.41	-0.020*	-102.7*	1813
202-7-4	-0.18	-1.33	11.19**	0.21**	-46.87	-57.05*	-0.98**	-1.78*	-137.98**	-186.1**	-0.10	-3.98*	-0.52*	-1.29**	-0.014	-122.3**	-4573
202-7-10	0.45**	-3.40**	-1.66	0.09	-110.80**	-61.94*	-0.38	0.39	-164.43**	-276.5**	1.07	0.80	-0.45	-0.22	-0.014	-23.1	-4768
202-8-8	0.04	0.67	-7.73*	-0.14*	-34.35	-3.37	0.08	0.88	-44.28	-79.9	0.48	-1.09	0.67*	-0.50	-0.003	32.9	605
197-1-12	-0.07	1.52	-4.73	-0.12	-5.02	-14.86	-0.03	-0.34	7.59	1.3	-0.44	-0.72	-0.23	-0.45	-0.013	30.3	2609
202-6-26	-0.22	-3.25**	-3.51	0.08	-31.32	-26.38	-0.21	-0.46	-107.11*	-139.7*	0.45	-2.46	-0.11	0.11	-0.011	-5.0	-2775
197-18-1	0.19	-1.07	-3.03	-0.01	58.24	86.73**	0.66*	2.85**	156.86**	213.9**	0.50	1.13	0.21	0.13	-0.003	140.5**	18143**
PPMI 301	0.30**	-0.31	-27.02**	-0.37**	105.51**	153.70**	2.23**	4.30**	-44.00	64.7*	3.42**	0.40	0.89**	1.97**	0.070**	232.8**	31
RIB 335/74	-1.58**	-0.02	3.90*	0.06*	-139.10**	-151.10**	-1.11**	-3.27**	-230.70**	-371.7**	-0.82**	1.08	1.03**	-0.24	-0.031**	-121.2**	-13481**
H 77/833-2	1.28**	0.34	23.13**	0.32**	33.59*	-2.60	-1.11**	-1.04**	274.70**	307.0**	-2.60**	-1.48*	-1.92**	-1.74**	-0.040*	-111.6**	13450

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

significant positive combiners were donor parent 863B, introgression line 197-18-1, and tester PPMI 301. Positive *gca* effects for grain yield per panicle and panicle harvest index were exhibited by introgression lines 197-12-2 and 197-18-1 and donor parent 863B. Among testers, PPMI 301 showed positive *gca* effects for both grain yield per panicle and panicle harvest index.

For stover yield per plot, the best combiners among introgression lines were 202-8-9, 197-10-11 and 197-18-1 and the best among testers was H 77/833-2. Similarly, the negative combiners for stover yield per plot were introgression lines 202-7-4, 202-7-10 and 202-6-26 and tester RIB 335/74. Among introgression lines and their parents, the donor parent 863B, 202-8-9, 197-10-11 and 197-18-1 and among testers PPMI 301 and H 77/833-2 exhibited positive *gca* effects for biomass yield per plot.

Positive *gca* effects for harvest index among introgression lines and their parent were noted for the donor parent 863B, introgression line 197-12-2, and tester PPMI 301. For plant height, the donor parent 863B and introgression line 202-7-12 showed positive *gca* effects and introgression lines 202-8-9, 202-8-27 and 202-7-4 and tester H 77/833-2 showed negative *gca* effects. Only one introgression line 202-8-8 and testers PPMI 301 and RIB 335/74 exhibited positive *gca* effects for panicle length.

For panicle diameter, only the donor parent 863B and tester PPMI 301 showed positive *gca* effects. None of the introgression lines showed significant positive gca effects for panicle diameter. For both 100-grain mass and grain number per panicle, the positive combiners were the donor parent 863B, introgression line 197-12-2, and tester PPMI 301. Four introgression lines and the remaining testers, RIB 335/74 and H 77/833-

2 had significantly negative gca effects for both of these traits. Introgression line 197-18-1 showed positive *gca* effects for grain number per panicle and grain number per plot.

4.3.4.4.2. Specific Combining Ability (*sca*)

The *sca* effects of testcross hybrids of the introgression lines and their recurrent and donor parents across three moisture regimes in the summer 2004 drought nursery at ICRISAT-Patancheru are presented in Table 36. Among testcross hybrids ICMB 841 × PPMI 301, 202-7-4 × RIB 335/74, 202-7-10 × RIB 335/74 and 863B × H 77/833-2 showed significant negative *sca* effects for flowering time and in contrast, introgression lines, 202-7-10, 202-7-4 when crossed with H 77/833-2 produced late-flowering hybrids. Across the three moisture regimes, testcross hybrids 863B × RIB 335/74 and ICMB 841 × H 77/833-2 had fewer plant numbers per plot than expected based upon the *gca* values of their parental lines and testers.

For panicle number per plot and effective tiller per plant, only testcross hybrid 202-7-10 × PPMI 301 showed significantly positive *sca* effects. Testcross hybrids, of donor parent 863B showed negative *sca* effects with PPMI 301 and positive *sca* effects with tester H 77/833-2 for panicle yield per plot and grain yield per plot. Testcross hybrid ICMB 841 × PPMI 301 showed positive *sca* effects for both grain yield per panicle and panicle harvest index. For stover yield and biomass yield per plot, the recurrent parent ICMB 841 crossed with H 77/833-2 produced significant and positive *sca* effects.

Among testcross hybrids, ICMB 841 × PPMI 301 exhibited nagative *sca* effects for stover yield and positive *sca* effects for harvest index. For plant height, testcross hybrids 202-7-12 × PPMI 301, 863B × RIB 335/74 and 197-1-12 × H 77/833-2 showed

Table 36. Estimates of *sca* effects of testcross hybrids over three [illegible]

Hybrids	FT	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H. I. (%)	Plant height (cm)	Panicle length (cm)	[illegible] diameter (mm)	grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	0.33	2.39	11.93	0.11	-147.47**	-170.35**	-0.55	-3.79**	-149.09	-274.92*	-1.80	-7.43**	-0.55	0.05	-0.060**	-48.61	-6476
ICMB 841 × PPMI 301	-1.22**	-1.50	-10.05	-0.10	24.16	88.77	1.19**	3.68**	-219.86*	-198.87	4.71**	-6.18*	-0.31	2.23**	0.007	216.87**	12577
197-10-18 × PPMI 301	0.03	0.80	-8.98	-0.16	94.75	51.61	0.68	-0.03	27.48	119.06	0.40	1.42	0.10	0.60	0.008	130.00	9726
202-8-11 × PPMI 301	-0.30	0.61	-4.42	-0.07	49.75	20.48	-0.10	-0.25	40.52	92.16	-0.25	-1.32	-0.20	-0.28	0.018	-34.34	-1657
197-12-2 × PPMI 301	0.00	-0.35	1.10	0.04	-7.25	15.56	0.54	0.42	-127.43	-137.85	1.55	-2.66	-0.10	-0.33	0.012	48.03	-3165
202-8-9 × PPMI 301	-0.37	0.09	1.09	0.05	-55.06	-69.18	-0.92**	-2.11	-68.35	-108.95	-1.32	4.45	-0.41	-1.01	-0.026	-89.68	-4081
202-7-12 × PPMI 301	0.70**	1.31	0.24	-0.05	1.34	8.38	-0.09	0.19	86.12	84.30	-0.35	7.60**	0.34	-0.63	0.010	-41.27	-3382
202-8-27 × PPMI 301	0.07	1.24	-0.94	-0.05	70.90	51.82	-0.17	0.59	55.82	123.56	0.28	-0.29	-0.03	0.50	0.010	-12.53	6960
197-10-11 × PPMI 301	0.29	-0.02	1.06	0.02	-45.18	-53.70	-0.34	-1.24	64.37	16.03	-2.01*	2.08	-0.42	-0.42	-0.006	-63.83	-8305
202-7-4 × PPMI 301	0.11	-2.54	1.21	0.09	-14.47	-12.62	-0.38	0.69	-23.30	-40.94	0.39	0.38	-0.19	-0.24	-0.029	11.57	10080
202-7-10 × PPMI 301	-0.19	-0.91	13.39*	0.22*	75.23	48.05	-0.65	-0.01	140.05	212.12	-0.86	1.16	-0.14	-0.14	0.022	-160.78*	-874
202-8-8 × PPMI 301	-0.22	-0.76	-0.42	0.01	-23.44	-32.97	-0.09	-0.56	-15.81	-42.41	-0.27	-1.51	0.36	-0.21	0.011	-39.94	-10700
197-1-12 × PPMI 301	0.00	0.05	0.13	0.00	33.90	30.97	0.19	0.33	124.70	155.44	-0.63	-0.21	0.21	-0.73	0.031*	-52.05	-6954
202-6-26 × PPMI 301	0.59**	-0.17	-1.87	-0.06	2.75	40.60	0.29	1.43	24.69	24.27	0.73	1.75	0.72	0.31	-0.016	91.14	12316
197-18-1 × PPMI 301	0.18	-0.24	-3.46	-0.04	-59.92	-17.40	0.40	0.66	40.09	-23.00	-0.56	0.71	0.60	0.29	0.008	45.43	-6066
863B × RIB 335/74	0.87**	-3.46*	-9.46	-0.05	36.80	57.71	0.79	2.28	136.62	162.96	0.53	6.70*	0.84	1.00	0.100**	-66.49	-19533*
ICMB 841 × RIB 335/74	0.65**	-1.35	4.92	0.13	-66.01	-68.19	-0.83	-1.70	-16.86	-80.93	-1.59	2.81	-0.03	-2.06**	-0.011	-151.19*	-12466
197-10-18 × RIB 335/74	-0.20	0.62	10.33	0.13	-35.53	-17.53	-0.69	0.06	-132.26	-165.85	0.76	-2.38	0.05	-0.57	0.005	-133.06	-5731
202-8-11 × RIB 335/74	-0.09	-0.68	-0.12	0.03	-66.42	-58.31	-0.14	-1.08	-162.31	-236.90	0.11	2.88	0.23	0.19	-0.036*	46.26	3322
197-12-2 × RIB 335/74	-0.02	0.03	5.40	0.07	-35.19	-20.69	-0.62	0.23	63.32	30.06	-0.87	1.88	0.29	0.25	-0.002	-100.70	-3813
202-8-9 × RIB 335/74	0.39	-1.09	0.74	0.04	-3.29	18.46	0.20	1.11	46.80	38.92	0.16	0.77	0.26	0.83	0.010	0.76	-1925
202-7-12 × RIB 335/74	-0.42	0.47	3.33	0.03	36.07	13.57	-0.04	-0.67	-11.79	26.21	-0.19	3.75	-0.54	0.89	-0.012	16.78	6068
202-8-27 × RIB 335/74	0.17	-1.83	6.14	0.16	-72.60	-54.54	-0.31	-0.65	111.75	41.09	-1.69	0.25	0.59	-0.82	-0.010	-55.81	-8090
197-10-11 × RIB 335/74	0.06	0.58	-7.53	-0.12	32.55	31.17	0.33	0.47	24.44	58.93	0.40	-1.26	-0.03	0.02	0.012	40.17	-964
202-7-4 × RIB 335/74	-0.68**	1.84	-4.49	-0.13	-3.42	29.21	0.43	1.27	52.45	50.97	0.43	1.70	0.13	0.42	0.030	24.47	-6405
202-7-10 × RIB 335/74	-0.87**	2.14	-1.86	-0.12	51.51	4.67	0.56	-1.17	1.43	54.87	0.04	-2.97	0.78	-0.90	-0.030	176.57*	16122
202-8-8 × RIB 335/74	0.65**	0.84	0.77	-0.01	38.84	74.49	0.38	2.38	21.00	61.78	1.34	1.37	-0.38	0.24	-0.011	87.90	18459*
197-1-12 × RIB 335/74	-0.13	1.88	3.33	-0.01	-53.93	-67.61	-0.57	-1.78	-61.50	-113.50	-0.81	-6.34*	-0.74	0.29	-0.044**	4.56	4181
202-6-26 × RIB 335/74	-0.31	1.43	-5.12	-0.13	75.92	15.68	0.20	-1.16	-77.79	0.07	0.64	-0.71	-1.11*	0.70	0.011	12.63	-1716
197-18-1 × RIB 335/74	-0.05	-1.42	-6.38	-0.03	64.70	41.91	0.30	0.40	4.70	71.33	0.73	-0.97	-0.34	-0.49	-0.013	97.15	12489
863B × H 77/833-2	-1.20**	1.07	-2.47	-0.06	110.66*	112.64*	-0.24	1.51	12.47	111.96	1.27	0.70	-0.30	-1.05	-0.040	115.10	26009**
ICMB 841 × H 77/833-2	0.58**	2.85*	5.13	-0.04	41.85	-20.58	-0.35	-1.98	236.72**	279.80*	-3.12**	3.37	0.33	-0.17	0.004	-65.68	-111
197-10-18 × H 77/833-2	0.17	-1.41	-1.35	0.04	-59.22	-34.08	0.01	-0.03	104.78	46.79	-1.17	0.96	-0.15	-0.03	-0.013	3.06	-3995
202-8-11 × H 77/833-2	0.39	0.07	4.54	0.05	16.67	37.83	0.24	1.33	121.79	144.74	0.14	-1.56	-0.04	0.09	0.018	-11.92	-1665
197-12-2 × H 77/833-2	0.02	0.33	-6.50	-0.11	42.44	5.13	0.07	-0.65	64.12	107.79	-0.68	0.77	-0.19	0.07	-0.010	52.67	6977
202-8-9 × H 77/833-2	-0.02	1.00	-1.83	-0.09	58.35	50.72	0.72	1.00	21.55	70.03	1.16	-5.23	0.15	0.18	0.016	88.92	6006
202-7-12 × H 77/833-2	-0.28	-1.78	-3.57	0.02	-37.41	-21.95	0.13	0.49	-74.33	-110.51	0.55	-3.86	0.20	-0.26	0.002	24.49	-2686
202-8-27 × H 77/833-2	-0.24	0.59	-5.20	-0.11	1.70	2.72	0.48	0.06	-167.57	-164.64	1.41	0.03	-0.56	0.31	0.000	68.34	1130
197-10-11 × H 77/833-2	-0.35	-0.56	6.47	0.10	12.63	22.54	0.00	0.77	-88.81	-74.96	1.61	-0.82	0.46	0.40	-0.006	23.66	9269
202-7-4 × H 77/833-2	0.58**	0.70	3.28	0.03	17.89	-16.59	-0.05	-1.96	-29.15	-10.03	-0.83	-2.08	0.06	-0.18	-0.001	-36.04	-3675
202-7-10 × H 77/833-2	1.06**	-1.23	-11.53	-0.10	-126.74*	-52.72	0.09	1.18	-141.48	-266.99*	0.82	1.81	-0.64	1.04	0.008	-15.79	-15247
202-8-8 × H 77/833-2	-0.42	-0.08	-0.35	0.00	-15.41	-41.52	-0.30	-1.83	-5.18	-19.36	-1.06	0.14	0.01	-0.03	-0.001	-47.96	-7760
197-1-12 × H 77/833-2	0.13	-1.93	-3.46	0.01	20.04	36.65	0.38	1.46	-63.20	-41.94	1.44	6.55**	0.54	0.44	0.013	47.49	2773
202-6-26 × H 77/833-2	-0.28	-1.26	6.99	0.19	-78.67	-56.28	-0.48	-0.27	53.10	-24.34	-1.37	-1.04	0.40	-1.01	0.004	-103.77	-10600
197-18-1 × H 77/833-2	-0.13	1.66	9.84	0.07	-4.78	-24.50	-0.70	-1.06	-44.79	-48.34	-0.16	0.25	-0.27	0.21	0.006	-142.58	-6423

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

positive *sca* effects. Testcross hybrids ICMB 841 × PPMI 301 showed positive *sca* effects for panicle diameter and grain number per panicle.

For 100-grain mass, testcross hybrids 197-1-12 × PPMI 301 and 863B x RIB 335/74 showed positive *sca* effects and 863B × PPMI 301, 197-1-12 × RIB 335/74 and 863B × H 77/833-2 showed negative *sca* effects. Testcross hybrids ICMB 841 × PPMI 301, 197-10-11 × PPMI 301, and 202-7-10 × RIB 335/74 showed positive *sca* effects for grain number per panicle. For grain number per plot, 863B × H 77/833-2 showed highly significant positive *sca* effects and 197-10-11 × PPMI 301 and 863B × RIB 335/74 showed significant negative *sca* effects.

4.3.5. Drought Response Index (DRI)

Drought response indices (DRI) were calculated for the late-onset terminal drought stress and early-onset terminal drought stress environments using linear terms for time to flowering and the particular agronomic character for which DRI was being determined. The way in which DRI was determined, its distribution is symmetric with a positive kurtosis and a mean of zero (Bidinger *et al.*, 1987b). Thirty and fifty per cent of the individual genotypes in late-onset and early-onset stress treatments, respectively had DRI values for grain yield that were not significantly different from zero, indicating that their measured grain yield in the particular stress environment was adequately estimated by their grain yield potential (measured in the control environment) and time to flowering (measured in the terminal stress environment). The remaining entries had non-zero (real) values of DRI, indicating that relative to other sources of variation in the trial, they had different responses (i.e., tolerant or sensitive) to the stress environment at the probability level used in the definition of DRI.

The results of analyses of variances, testcross entry mean DRI values and combining abilities for each of the introgression lines, their parents and the testers are described below for the yield-related characters in each of the two terminal drought stress moisture regimes.

4.3.5.1. Late-onset terminal drought stress treatment

4.3.5.1.1. Analysis of variances

The analyses of variances for testcross hybrid DRI values for different agronomic characters are presented in Table 37. DRI values of the testcross hybrids were significantly different for all observed characters except plant number per plot. Effects of lines were highly significant for DRI values of all agronomic characters except plant number per plot, panicle yield per plot, grain yield per plot, panicle harvest index, stover yield per plot, biomass yield per plot, harvest index, panicle length, hundred-grain mass and grain number per plot. Effects of testers were highly significant for DRI values of all observed agronomic characters except plant number per plot, grain yield per panicle, biomass yield per plot, plant height, panicle length, panicle diameter, hundred-grain mass and grain number per plot. Line × tester effects did not contribute significantly to DRI values of any of the observed characters.

4.3.5.1.2. Drought response index (DRI)

Drought response index values of all 16 observed yield-related characters for each of the 45 testcross hybrids in the relatively mild late-onset terminal drought stress moisture regime are presented in Table 38. For number of panicles per plot, testcross hybrids 197-18-1 × H 77/833-2, 202-8-9 × PPMI 301, 202-7-12 × RIB 335/74, 197-18-1 × RIB 335/74, 202-7-4 × RIB 335/74 and 202-7-12 × PPMI 301 exhibited large positive DRI

Table 37. Analyses of variance for testcross hybrids using DRI values in relatively mild late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

		Mean squares															
SV	DF	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
Replications	2	0.202	0.093	0.215	0.001	0.134	0.059	0.125	0.106	0.285	0.530	0.411	0.369	0.305	0.085	0.498	0.044
Hybrids	44	2.028	3.945**	5.410**	4.145**	4.218**	5.209**	4.342**	4.571*	4.388*	4.435**	4.482**	4.044**	4.434**	3.764*	4.817**	4.203*
Lines	14	2.473	4.730**	6.69**	0.985	2.456	6.364**	3.315	3.748	3.425	2.360	5.377**	2.681	4.687*	3.325	4.551**	1.997
Testers	2	1.040	13.670**	14.66**	15.439**	17.749**	4.337	14.404**	14.458**	7.692	19.088**	1.949	5.812	3.282	1.589	30.912**	3.130
Lines × Testers	28	1.876	1.795	2.036	2.087	1.961	2.485	1.407	2.003	2.240	2.127	1.892	2.251	2.271	1.816	1.115	2.860
Error	88	1.812	1.948	2.215	1.785	1.837	2.291	2.035	2.815	2.881	1.512	1.838	2.021	2.289	2.438	1.981	2.557

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

SV-Sources of variation
DF-Degrees of freedom
FT-Flowering time (days after emergence)
ET-Effective tiller number per plant
H.I.-harvest index

...ids under relatively mild late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Hybrids	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	1.04	0.00	0.00	1.64	4.12	-1.22	0.00	-1.58	0.00	0.00	0.00	0.00	2.60	5.55	-1.18	-1.63
ICMB 841 × PPMI 301	0.00	-4.89	0.00	0.00	2.53	6.97	0.00	-3.26	-2.57	2.22	0.00	-4.12	1.64	-1.87	6.61	1.98
197-10-18 × PPMI 301	2.55	-3.59	-3.88	1.36	2.57	4.83	0.00	-1.53	0.00	0.00	1.13	0.00	0.00	0.00	4.22	0.00
202-8-11 × PPMI 301	-3.26	-1.98	-1.98	-1.84	1.34	0.00	0.00	-3.57	-4.44	1.62	-1.16	0.00	0.00	0.00	1.53	0.00
197-12-2 × PPMI 301	1.01	0.00	0.00	2.13	2.22	1.72	2.47	0.00	0.00	1.32	2.54	0.00	-1.67	0.00	1.22	1.15
202-8-9 × PPMI 301	0.00	2.21	0.00	2.61	1.39	-2.61	3.19	-2.32	0.00	3.03	2.31	0.00	-1.92	-1.05	0.00	0.00
202-7-12 × PPMI 301	0.00	1.73	0.00	0.00	2.33	-3.51	0.00	1.65	1.87	0.00	1.39	2.42	3.86	-2.93	0.00	2.17
202-8-27 × PPMI 301	-1.43	0.00	0.00	1.72	1.29	0.00	0.00	1.38	2.33	-1.25	-1.14	0.00	-1.11	-2.52	1.41	2.14
197-10-11 × PPMI 301	1.71	1.29	0.00	0.00	1.55	-1.20	0.00	0.00	0.00	0.00	-1.05	-2.94	1.49	-2.08	0.00	1.03
202-7-4 × PPMI 301	-3.70	-3.24	-1.52	-1.65	0.00	1.30	-2.59	-2.04	-2.99	-1.14	-2.68	-1.38	0.00	-1.21	1.71	-1.29
202-7-10 × PPMI 301	0.00	-1.41	-2.22	2.72	2.22	2.59	1.82	0.00	1.58	1.24	0.00	-3.81	-4.14	3.39	1.03	0.00
202-8-8 × PPMI 301	1.52	1.04	-1.56	0.00	0.00	-3.72	-2.43	0.00	0.00	-1.76	0.00	2.55	0.00	-2.17	-1.61	-1.81
197-1-12 × PPMI 301	-2.80	0.00	0.00	2.37	2.68	0.00	1.78	-1.22	0.00	1.43	1.69	0.00	0.00	-1.99	1.05	1.70
202-6-26 × PPMI 301	0.00	0.00	0.00	-1.13	0.00	0.00	2.38	2.19	1.35	0.00	1.89	1.33	0.00	0.00	0.00	0.00
197-18-1 × PPMI 301	1.03	0.00	-2.11	1.28	2.18	0.00	1.09	0.00	0.00	1.26	2.56	1.57	0.00	0.00	0.00	0.00
863B × RIB 335/74	-1.19	-2.61	-3.00	0.00	2.12	3.74	0.00	-1.52	-1.79	1.72	2.84	0.00	0.00	3.83	1.41	-2.99
ICMB 841 × RIB 335/74	0.00	-1.26	0.00	-1.29	-2.10	0.00	0.00	-2.49	-3.01	1.41	0.00	0.00	1.11	0.00	0.00	0.00
197-10-18 × RIB 335/74	0.00	0.00	-1.10	0.00	0.00	0.00	1.40	1.42	1.61	0.00	0.00	2.72	1.05	1.50	0.00	0.00
202-8-11 × RIB 335/74	0.00	1.17	0.00	0.00	-1.47	-1.54	-1.70	0.00	0.00	-1.67	-4.08	-2.49	0.00	0.00	-1.55	0.00
197-12-2 × RIB 335/74	0.00	0.00	1.99	-1.27	-2.43	0.00	1.77	0.00	0.00	0.00	0.00	-2.28	-2.29	-2.00	0.00	-1.12
202-8-9 × RIB 335/74	-2.55	1.34	1.44	0.00	0.00	0.00	1.26	0.00	0.00	0.00	0.00	0.00	-1.86	-2.62	0.00	1.98
202-7-12 × RIB 335/74	-2.19	2.01	1.13	0.00	0.00	-2.77	0.00	0.00	0.00	0.00	0.00	1.21	2.38	0.00	-1.84	1.70
202-8-27 × RIB 335/74	0.00	0.00	1.10	0.00	-1.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-2.48	0.00	0.00
197-10-11 × RIB 335/74	0.00	0.00	1.26	0.00	-2.28	0.00	0.00	0.00	0.00	0.00	2.09	4.81	1.27	0.00	0.00	0.00
202-7-4 × RIB 335/74	0.00	1.94	0.00	0.00	-1.92	-3.44	0.00	-3.10	-3.06	2.09	0.00	0.00	0.00	0.00	-2.99	0.00
202-7-10 × RIB 335/74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.07	0.00	0.00	-1.38	0.00	0.00	0.00	0.00
202-8-8 × RIB 335/74	0.00	0.00	0.00	-1.74	-2.56	-1.59	-3.94	0.00	0.00	-3.13	0.00	0.00	-2.82	-2.89	0.00	0.00
197-1-12 × RIB 335/74	0.00	0.00	1.22	0.00	-1.26	0.00	-1.21	0.00	0.00	0.00	0.00	3.58	-3.54	1.15	0.00	0.00
202-6-26 × RIB 335/74	1.56	0.00	1.48	0.00	-1.54	0.00	0.00	1.59	0.00	0.00	-1.03	-1.28	0.00	0.00	0.00	0.00
197-18-1 × RIB 335/74	0.00	1.94	1.04	0.00	-2.37	-1.91	-2.31	0.00	0.00	-2.32	0.00	-1.12	0.00	1.43	-2.68	0.00
863B × H 77/833-2	1.03	0.00	-1.52	0.00	3.92	1.11	0.00	3.20	3.49	-1.02	0.00	-1.55	1.21	0.00	1.73	3.13
ICMB 841 × H 77/833-2	2.42	0.00	0.00	0.00	-1.58	0.00	-2.69	0.00	0.00	-1.29	0.00	0.00	0.00	0.00	0.00	0.00
197-10-18 × H 77/833-2	0.00	0.00	0.00	1.40	0.00	0.00	3.03	0.00	1.65	1.61	0.00	1.52	2.93	0.00	0.00	2.40
202-8-11 × H 77/833-2	-1.43	0.00	1.25	0.00	-1.18	0.00	0.00	0.00	0.00	0.00	-1.74	0.00	0.00	0.00	0.00	-1.12
197-12-2 × H 77/833-2	0.00	0.00	1.57	0.00	-1.17	0.00	0.00	2.08	1.48	-1.61	-2.06	1.59	2.66	0.00	0.00	0.00
202-8-9 × H 77/833-2	1.61	-1.25	0.00	-1.96	-1.56	0.00	-1.28	-1.05	-2.20	0.00	0.00	-2.62	-2.37	1.99	0.00	-2.38
202-7-12 × H 77/833-2	0.00	0.00	0.00	1.04	0.00	0.00	0.00	1.29	1.73	0.00	0.00	0.00	0.00	0.00	0.00	1.60
202-8-27 × H 77/833-2	0.00	0.00	1.78	-1.37	-1.19	0.00	0.00	0.00	-1.22	-1.21	0.00	-1.17	0.00	0.00	-1.14	0.00
197-10-11 × H 77/833-2	0.00	0.00	1.58	-1.44	-1.15	0.00	-1.43	-1.13	-1.78	0.00	-1.19	-1.05	-1.56	0.00	0.00	0.00
202-7-4 × H 77/833-2	0.00	0.00	0.00	0.00	-1.48	0.00	-1.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.05	-1.72
202-7-10 × H 77/833-2	1.92	0.00	0.00	0.00	0.00	0.00	1.61	1.60	0.00	0.00	0.00	0.00	1.29	1.00	0.00	0.00
202-8-8 × H 77/833-2	-2.59	0.00	1.29	-1.81	-1.80	0.00	0.00	0.00	-1.57	0.00	-1.33	0.00	0.00	0.00	0.00	-1.81
197-1-12 × H 77/833-2	-1.72	0.00	1.05	-1.73	-1.50	-1.70	-2.29	0.00	0.00	-1.43	0.00	0.00	-1.87	2.49	-2.62	-2.39
202-6-26 × H 77/833-2	2.29	1.07	1.35	1.19	0.00	0.00	0.00	2.05	2.47	0.00	-1.73	0.00	1.03	1.55	0.00	1.17
197-18-1 × H 77/833-2	1.93	2.48	0.00	0.00	0.00	-1.30	0.00	1.85	2.31	0.00	1.30	0.00	0.00	1.29	-1.85	0.00

values. Superior maintenance of numbers of effective tillers per plant under late-onset terminal drought stress, indicated by positive DRI for this trait, was only observed among the hybrids of high-tillering testers H 77/833-2 and RIB 335/74. Many hybrids of tester PPMI 301 had negative DRI values for number of effective tillers per plant, indicating that tillering of these hybrids was reduced in this stress environment relative to the fully-irrigated control environment. Testcross hybrids 197-12-2 × RIB 335/74 (1.99) and 202-8-27 × H 77/833-2 (1.78) had the highest, positive DRI values for effective tiller number per plant in this relatively mild terminal drought stress environment.

For grain yield-related characters, like panicle yield per plot, grain yield per plot, grain yield per panicle, panicle harvest index and grain number per panicle, tester PPMI 301 produced larger numbers of testcross hybrids with large positive DRI values than did the other two testers. Among introgression lines and their parents, testcross hybrids of both the donor parent 863B and recurrent parent ICMB 841 with PPMI 301 exhibited large positive DRI values for grain yield per plot. For the same character, all the hybrid entries of H 77/833-2 and RIB 335/74 except those of the donor parent 863B showed either negative or zero DRI values. Thus donor parent 863B and tester PPMI 301 appear to have conferred some degree of drought tolerance for grain yield to their testcross hybrids in this relatively mild, late-onset terminal drought stress environment. Conversely, recurrent parent ICMB 841, testers RIB 335/74 and H 77/833-2 and introgression lines 202-7-4, 202-8-8 and 202-6-26 appear to have conferred a greater degree of grain yield drought stress sensitivity to their testcrosses, with introgression lines 197-10-18, 202-7-12 and 202-7-10 having conferred an intermediate stress response

(at least when measured in terms of grain yield) DRI to their testcross hybrids in this environment.

In contrast, DRI for grain yield per panicle was negative for the donor parent 863B with tester PPMI 301 (-1.22) but positive with testers RIB 335/74 (3.74) and H 77/833-2 (1.11). Recurrent parent ICMB 841 exhibited a high DRI value for grain yield per panicle with tester PPMI 301 (6.97). More of the testcross hybrids of PPMI 301 showed positive DRI values for grain yield per panicle than did those of the other two testers.

Among the 45 testcross hybrids, those of introgression lines 202-8-9 and 197-12-2 had large positive DRI values for panicle harvest index with testers PPMI 301 and RIB 335/74. Similarly, introgression line 202-7-10 exhibited large positive DRI values for this trait with testers PPMI 301 and H 77/833-2. For stover and biomass yield per plot, the testcross hybrids of H 77/833-2 showed higher frequencies of positive DRI values than did hybrids of the other two testers. Testcross hybrids introgression lines 202-6-26 and 202-7-12 exhibited positive DRI values for stover (and biomass) yields with testers PPMI 301 and H 77/833-2.

For harvest index, tester PPMI 301 produced larger numbers of hybrids with positive DRI values than either RIB 335/74 or H 77/833-2. Testcross hybrid 202-8-9 × PPMI 301 had the highest positive DRI value (3.03). Under these relatively mild late-onset terminal drought stress conditions, the testcross hybrids of PPMI 301 maintained their plant height well, with seven exhibiting positive DRI values. Among all testcross hybrids, the parental hybrid 863B × RIB 335/74 had the highest positive DRI (2.84) for plant height in this environment. For panicle length and panicle diameter, hybrids of

introgression line 197-10-18 had large positive DRI with testers RIB 335/74 and H 77/833-2, while introgression line 202-7-12 had large positive DRI in its hybrids with testers PPMI 301 and RIB 335/74. Similarly, panicle diameter was maintained by the testcross hybrids of donor parent 863B with both PPMI 301 and H 77/833-2.

For hundred-grain mass, donor parent hybrids 863B × PPMI 301 (5.55) and 863B × RIB 335/74 (3.83) had the highest positive DRI values. Across testers RIB 335/74 and H 77/833-2, hybrids of introgression lines 197-1-12 and 197-18-1 maintained high positive DRI values for hundred-grain mass. Similarly, hybrids of 202-7-10 maintained positive DRI for this trait across testers PPMI 301 and H 77/833-2. Among testcross hybrids of introgression lines and their parents, ICMB 841 × PPMI 301 had the highest positive DRI for grain number per panicle followed by several of the introgression line testcross hybrids of PPMI 301. For grain number per plot, 863B × H 77/833-2 had a large positive DRI value (3.13), followed by 197-10-18 × H 77/833-2 (2.40), 202-7-12 x PPMI 301 (2.17), 202-8-27 × PPMI 301 (2.14), ICMB 841 × PPMI 301 (1.98) and 202-8-9 × RIB 335/74 (1.98).

4.3.5.1.3. Combining Ability for DRI for late-onset terminal drought stress

4.3.5.1.3.1. General Combining Ability for DRI

The results of the combining ability analysis for this late-onset terminal drought stress environment, using DRI values of individual replications, are presented in Table 39 in the form of tabulated *gca* effects of the lines and testers.

H 77/833-2 was the only line or tester exhibiting significant positive gca effects for DRI of number of panicles per plot. Only one introgression line, 197-18-1, had significant positive gca effects for DRI of effective tiller number of per plant. In contrast,

Table 39. Estimates of gca effects of introgression lines and testers with DRI values under relatively mild late-onset terminal drought stress conditions, ICRISAT-Patancheru, summer-2004.

Lines & Testers	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B	-0.05	-1.84**	-2.16**	0.14	0.71	2.25**	0.48	0.56	0.83	0.84*	1.64**	-0.40	0.82	1.55**	1.73**	0.04
ICMB 841	0.49	-0.20	-0.27	0.08	-0.03	0.25	0.24	-0.27	-0.25	0.51	-0.18	-0.21	0.30	0.09	0.54	0.29
197-10-18	-0.78	0.09	0.35	0.08	-0.14	-0.55	-0.34	-0.34	0.13	0.10	-0.19	0.65	-1.06*	0.25	-0.36	-0.43
202-8-11	0.56	0.47	0.04	0.10	-0.36	-0.40	-0.35	-0.32	-0.20	-0.27	0.10	0.21	0.11	-0.08	-0.42	-0.27
197-12-2	0.75	-1.04*	-1.33**	0.51	0.60	1.13**	0.62	-0.28	0.04	0.69	0.16	0.96*	0.78	0.11	1.35**	0.67
202-8-9	0.55	0.63	0.46	-0.01	-0.15	0.03	0.28	1.34*	0.86	-0.41	-0.45	-0.16	-0.01	0.02	-0.45	0.31
202-7-12	-0.10	0.25	0.25	-0.74	-1.27**	-0.95	-1.26**	0.21	-0.22	-1.13**	0.08	0.58	-0.42	-0.52	-0.84	-0.91
202-8-27	0.24	0.62	0.93	0.09	0.13	-0.02	0.47	-0.09	0.08	0.09	-0.41	-0.32	-0.47	-0.34	-0.44	0.00
197-10-11	-0.34	0.41	0.77	-0.16	0.29	-0.13	0.49	-0.82	-0.87	0.08	0.44	-0.08	-1.12*	-0.50	-0.28	0.03
202-7-4	-0.23	0.11	0.25	-0.06	0.11	-0.03	0.23	-0.10	-0.10	-0.29	-0.46	-0.42	-0.19	-0.92	-0.05	0.00
202-7-10	-0.83	-0.21	-0.31	-0.43	-0.51	-0.62	-0.88	-1.07*	-1.34*	0.21	-0.06	-0.28	0.18	-0.31	-0.20	-0.44
202-8-8	0.41	-0.16	-0.32	0.27	0.65	0.57	0.88	0.47	0.57	0.31	-0.13	-0.79	-0.67	0.80	0.05	0.06
197-1-12	0.36	0.86	0.61	0.14	0.09	-0.33	-0.37	0.60	0.52	-0.66	1.02*	0.05	0.35	0.41	-0.62	-0.25
202-6-26	-0.71	-0.61	-0.38	-0.43	-0.47	-0.07	-0.60	-0.60	-0.54	-0.01	-1.90**	-0.68	-0.16	-0.02	-0.05	-0.16
197-18-1	-0.33	0.64	1.11*	0.41	0.36	-1.12*	0.12	0.71	0.49	-0.07	0.34	0.88	1.56**	-0.54	0.02	1.05*
PPMI 301	-0.10	-0.62**	-0.66**	0.65**	0.72**	0.36	0.65**	-0.24	0.17	0.73**	0.16	0.20	0.24	0.05	0.95**	0.25
RIB 335/74	-0.07	0.23	0.30	-0.48*	-0.42*	-0.19	-0.29	-0.40*	-0.47*	-0.22	0.07	0.22	-0.29	-0.21	-0.53*	-0.27
H 77/833-2	0.17	0.40*	0.35	-0.17	-0.29	-0.17	-0.36	0.64**	0.30	-0.51**	-0.23	-0.41*	0.06	0.15	-0.41*	0.02

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

for DRI of panicle number per plot and effective tiller number per plant introgression line 197-12-2, donor parent 863B and tester PPMI 301 showed significant negative *gca* effects. For DRI of both panicle yield and grain yield per plot, tester PPMI 301 was the only testcross hybrid parent with significant positive *gca* effects. Tester RIB 335/74 and introgression line 202-7-12 showed negative *gca* effects for DRI of grain yield per plot.

Donor parent 863B and introgression line 197-12-2 had significant positive *gca* effects and introgression line 197-18-1 had significant negative *gca* effects for DRI of grain yield per panicle. For DRI of panicle harvest index, tester PPMI 301 and introgression line 202-7-12 were the only significant positive and negative combiners, respectively.

For DRI of stover yield per plot, introgression line 202-8-9 and tester H 77/833-2 were the significantly positive combiners. For DRI of both stover yield and biomass yield per plot, introgression line 202-7-10 and tester RIB 335/74 were the only negative combiners with significant *gca* effects. For DRI of harvest index donor parent 863B and tester PPMI 301 were the significantly positive combiners while introgression line 202-7-12 and tester H 77/833-2 had significant negative *gca* effects. For DRI of plant height, the significant positive combiners were donor parent 863B and introgression line 197-1-12, while introgression line 202-6-26 showed significant negative *gca* effects. Significant positive *gca* effects for DRI of panicle length were exhibited by introgression line 197-12-2 whereas tester H 77/833-2 showed significant negative *gca* effects for this trait.

Introgression lines 197-10-18 and 197-10-11 both showed significant negative *gca* effects for DRI of panicle diameter, while 197-18-1 showed significantly positive *gca* effects for the same character. Among the introgression lines and testers, only donor parent 863B showed significant positive *gca* effects for DRI of hundred-grain mass. For

DRI of grain number per panicle, the donor parent 863B, introgression line 197-12-2 and tester PPMI 301 showed significant positive *gca* effects, whereas testers RIB 335/74 and H 77/833-2 exhibited significant negative *gca* effects. Among introgression lines and testers only 197-18-1 showed positive *gca* effects for DRI of grain number per plot in this moderately severe late-onset terminal drought stress environment.

4.3.5.1.3.2. Specific Combining Ability for DRI

Estimated *sca* effects of the 45 testcross hybrids of the introgression lines and their recurrent and donor parents for DRI of various yield-related traits in the late-onset terminal drought stress moisture regime are presented in Table 40. Among testcross hybrids, 202-7-12 × H 77/833-2 showed significantly negative gca effects for DRI of plant number per plot and significant positive *sca* effects for DRI of harvest index. Hybrid, 197-10-18 × H 77/833-2 had significantly negative *sca* effects for DRI of grain yield per plot. Testcross hybrid 202-8-11 × RIB 335/74 showed positive *sca* effects for DRI of panicle length. For DRI of grain number per plot, testcross hybrid 863B × H 77/833-2 showed positive *sca* effects and 863B × RIB 335/74 showed negative *sca* effects.

4.3.5.2. Early-onset terminal drought stress treatment

4.3.5.2.1. Analysis of variances for DRI

The analyses of variances for testcross hybrids and DRI values of their different agronomic characters for the relatively severe early-onset terminal drought stress environment are presented in Table 41. Testcross hybrids were highly significant sources of observed variation in DRI of nearly all agronomic characters observed in this study. Effects of lines were significant for DRI of all characters except plant number per plot, panicle yield per plot, panicle harvest index, stover yield per plot, harvest index, panicle

Table 40. Estimates of sca effects of test-cross hybrids with DRI values under relatively mild late-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Hybrids	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	0.15	0.59	0.70	-0.84	-1.04	-0.15	-0.70	-0.56	-0.56	-0.95	-0.67	-0.98	-1.08	-0.52	-0.49	-0.74
ICMB 841 × PPMI 301	-0.38	0.38	0.39	0.37	0.57	-0.25	0.76	1.05	0.81	-0.03	-0.40	0.01	0.05	0.96	0.21	0.70
197-10-18 × PPMI 301	-0.45	0.04	0.33	1.02	0.97	-0.20	0.85	-0.12	0.34	0.83	0.87	-0.06	1.40	-1.13	0.53	1.06
202-8-11 × PPMI 301	0.77	0.64	0.61	0.07	0.16	-0.68	0.22	0.22	0.44	-0.46	-0.86	-1.37	0.72	-0.36	-0.24	0.05
197-12-2 × PPMI 301	0.71	-1.13	-1.60	-0.53	-0.53	1.43	-0.60	-0.43	-0.63	0.07	0.04	-0.69	-0.40	-0.14	0.84	-0.89
202-8-9 × PPMI 301	-0.45	0.05	0.22	-1.32	-0.55	-0.75	-0.12	-0.01	-0.78	-0.32	0.62	0.59	0.15	-0.05	-0.54	-0.34
202-7-12 × PPMI 301	1.29	0.68	-0.02	0.04	-0.61	-1.67	-0.75	1.36	1.02	-0.60	0.09	0.60	0.73	0.02	-0.89	-0.17
202-8-27 × PPMI 301	0.50	-0.38	-0.66	1.13	0.54	1.04	0.39	-0.74	0.25	1.08	0.78	0.11	-0.15	0.66	0.39	1.05
197-10-11 × PPMI 301	-0.19	1.20	0.74	0.46	1.16	0.31	0.35	-0.70	-0.38	0.46	0.66	0.69	0.02	-0.07	-0.38	-0.25
202-7-4 × PPMI 301	-0.26	0.18	0.44	0.59	0.27	-0.42	-0.20	0.80	1.02	-0.89	-0.07	0.22	-0.49	-0.45	0.24	0.71
202-7-10 × PPMI 301	-0.86	-1.53	-0.95	-0.86	-1.46	0.84	-0.89	0.20	-0.24	-0.94	-1.35	-0.29	0.19	-0.17	0.34	-0.40
202-8-8 × PPMI 301	-0.30	-0.27	0.01	0.54	0.59	0.41	-0.39	-0.17	0.35	0.44	-0.63	-0.95	-1.51	1.16	-0.43	-0.71
197-1-12 × PPMI 301	0.08	-1.00	-0.90	0.39	0.41	0.88	0.74	0.04	-0.21	0.69	0.64	0.36	0.19	0.44	0.60	-0.32
202-6-26 × PPMI 301	-0.93	-0.20	0.06	-0.62	-0.24	0.41	0.37	-1.53	-1.59	0.91	0.28	0.79	-0.53	0.33	0.46	0.38
197-18-1 × PPMI 301	0.33	0.76	0.62	-0.43	-0.24	-1.20	-0.03	0.60	0.16	-0.31	-0.01	0.96	0.69	-0.68	-0.64	-0.13
863B × RIB 335/74	-0.78	-0.99	-1.14	-0.24	0.27	0.73	0.35	-0.56	-0.81	1.28	1.14	1.32	0.51	1.57	-0.15	-1.84*
ICMB 841 × RIB 335/74	-0.41	-0.45	-0.43	-0.41	-0.39	0.34	-0.23	-1.41	-1.24	0.51	0.00	-0.63	0.33	-0.37	-0.04	-0.43
197-10-18 × RIB 335/74	0.68	-0.29	-0.63	0.35	0.61	1.13	0.32	0.15	0.23	0.29	-0.41	0.77	-0.98	0.45	0.64	0.46
202-8-11 × RIB 335/74	-0.49	-0.24	-0.67	0.26	0.40	0.60	0.31	0.41	0.71	0.16	1.45	2.02*	0.16	0.40	0.40	0.24
197-12-2 × RIB 335/74	-0.19	0.05	0.16	-0.08	-0.16	-0.37	0.07	0.40	0.02	-0.46	-0.24	0.41	-0.29	0.76	-0.43	-0.43
202-8-9 × RIB 335/74	0.14	-0.17	-0.20	0.07	0.08	0.16	-0.03	0.55	0.18	-0.26	0.00	-0.53	0.28	-0.34	0.19	0.00
202-7-12 × RIB 335/74	0.36	-0.29	-0.52	-0.18	-0.15	0.47	-0.63	-0.17	-0.18	-0.97	0.18	-0.43	-0.92	-0.77	0.56	0.38
202-8-27 × RIB 335/74	-0.15	0.07	0.49	-1.13	-0.73	-0.46	-0.32	-0.10	-0.63	-0.53	-0.38	-0.84	-1.37	-0.87	-0.50	-0.69
197-10-11 × RIB 335/74	-0.68	0.05	0.83	0.71	0.15	-0.04	0.36	0.66	0.85	0.15	-0.43	-0.03	0.67	-0.73	0.77	1.54
202-7-4 × RIB 335/74	0.62	-0.31	-0.52	0.33	0.34	0.22	0.50	0.03	0.14	0.87	-0.24	-0.09	0.03	-0.31	-0.20	-0.25
202-7-10 × RIB 335/74	1.00	1.12	0.64	0.67	0.71	-0.93	0.83	-0.75	-0.47	1.09	0.33	0.06	0.08	-0.02	-0.18	0.38
202-8-8 × RIB 335/74	-0.27	0.47	0.38	0.16	-0.20	-0.01	0.27	0.12	0.37	-0.09	0.29	0.33	0.54	-0.24	0.44	0.58
197-1-12 × RIB 335/74	-0.28	0.34	0.86	-0.61	-0.39	-0.73	-0.97	-0.14	-0.07	-0.78	-1.10	-0.72	-0.09	0.10	-0.75	-0.06
202-6-26 × RIB 335/74	1.27	0.76	0.45	0.45	-0.10	-0.65	-0.58	1.06	0.97	-0.97	-1.16	-1.15	0.45	-0.22	-0.50	0.09
197-18-1 × RIB 335/74	-0.82	-0.11	0.29	-0.33	-0.45	-0.48	-0.26	-0.25	-0.06	-0.28	0.59	-0.49	0.62	0.60	-0.25	0.06
863B × H 77/833-2	0.64	0.40	0.44	1.08	0.77	-0.58	0.36	1.12	1.37	-0.33	-0.47	-0.34	0.58	-1.05	0.64	2.52**
ICMB 841 × H 77/833-2	0.80	0.08	0.04	0.05	-0.18	-0.09	-0.53	0.36	0.43	-0.48	0.40	0.62	-0.38	-0.59	-0.17	-0.27
197-10-18 × H 77/833-2	-0.24	0.24	0.30	-1.36	-1.58*	-0.93	-1.17	-0.03	-0.56	-1.12	-0.47	-0.72	-0.42	0.68	-1.17	-1.51
202-8-11 × H 77/833-2	-0.28	-0.40	0.06	-0.33	-0.56	0.08	-0.53	-0.63	-1.15	0.29	-0.59	-0.65	-0.88	-0.05	-0.16	-0.28
197-12-2 × H 77/833-2	-0.51	1.07	1.44	0.61	0.69	-1.06	0.53	0.03	0.61	0.39	0.20	0.28	0.69	-0.62	-0.41	1.33
202-8-9 × H 77/833-2	0.31	0.12	-0.01	1.25	0.46	0.58	0.14	-0.54	0.61	0.58	-0.62	-0.07	-0.43	0.38	0.36	0.34
202-7-12 × H 77/833-2	-1.64*	-0.38	0.55	0.14	0.76	1.20	1.38	-1.19	-0.84	1.56*	-0.27	-0.17	0.19	0.75	0.33	-0.21
202-8-27 × H 77/833-2	-0.36	0.32	0.17	0.01	0.19	-0.58	-0.07	0.84	0.38	-0.55	-0.41	0.73	1.52	0.21	0.11	-0.36
197-10-11 × H 77/833-2	0.87	-1.25	-1.58	-1.17	-1.31	-0.27	-0.71	0.05	-0.47	-0.61	-0.22	-0.66	-0.69	0.80	-0.39	-1.28
202-7-4 × H 77/833-2	-0.37	0.13	0.08	-0.91	-0.61	0.20	-0.30	-0.83	-1.17	0.02	0.31	-0.13	0.46	0.76	-0.04	-0.46
202-7-10 × H 77/833-2	-0.14	0.41	0.31	0.19	0.75	0.09	0.05	0.55	0.71	-0.15	1.03	0.23	-0.27	0.18	-0.16	0.02
202-8-8 × H 77/833-2	0.58	-0.19	-0.40	-0.70	-0.39	-0.40	0.12	0.05	-0.71	-0.35	0.35	0.62	0.97	-0.92	-0.01	0.13
197-1-12 × H 77/833-2	0.20	0.66	0.04	0.23	-0.02	-0.15	0.24	0.10	0.28	0.10	0.46	0.36	-0.10	-0.53	0.15	0.38
202-6-26 × H 77/833-2	-0.35	-0.56	-0.51	0.17	0.34	0.23	0.21	0.47	0.61	0.06	0.88	0.36	0.08	-0.11	0.04	-0.47
197-18-1 × H 77/833-2	0.49	-0.65	-0.91	0.76	0.69	1.67	0.29	-0.36	-0.10	0.59	-0.58	-0.47	-1.31	0.08	0.90	0.07

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

Table 41. Analyses of variance for testcross hybrids using DRI values for the relatively severe early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

		Mean squares															
SV	DF	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
Replications	2	0.063	0.143	0.011	0.095	0.154	0.095	0.009	0.006	0.107	0.038	0.080	0.413	0.176	0.033	0.029	0.013
Hybrids	44	2.281	3.736**	4.044**	3.507**	4.017**	4.973**	4.062**	4.212**	4.542**	3.951**	4.797**	3.152**	4.025*	5.228**	4.643**	4.134**
Lines	14	2.158	4.312**	4.352**	1.979	4.417**	7.071**	2.815	2.566	3.450**	2.659	5.760**	1.611	3.618	6.444**	2.845*	1.219
Testers	2	1.439	8.644**	8.383**	4.741	3.158	2.550	3.012	17.486	7.629**	11.799**	3.995	1.767	2.373	4.120	13.252**	5.182*
Lines × Testers	44	2.402	1.902	1.623	2.064	2.041	1.993	2.155	1.959	2.661	1.657	2.303	1.509	2.695	2.591	2.189	3.084**
Error	88	1.772	1.676	1.484	1.738	1.898	2.458	1.741	2.009	1.049	1.794	2.520	1.720	2.387	2.104	1.286	1.526

** Significant at 0.001 level of probability; * Significant at 0.05 level of probability

SV-Sources of variation
DF-Degrees of freedom
FT-Flowering time (days after emergence)
ET-Effective tiller number per plant
H.I-Harvest index

length, panicle diameter and grain number per plot. Effects of testers were significant for DRI of panicle number per plot, effective tiller number per plant, biomass yield per plot, harvest index, grain number per panicle and grain number per plot. For line x tester interaction effects, only those for DRI of grain number per plot were found to be significant.

4.3.5.2.2. Drought Response Index (DRI)

Drought response index values for each of the 45 testcross hybrids for observed agronomic characters observed in this early-onset terminal drought stress environment are presented in Table 42. For panicle number per plot and effective tiller number per plant, hybrids of introgression line 202-8-9 had large positive DRI values across testers PPMI 301 and H 77/833-2 in this environment while hybrids of introgression line 197-12-2 had large positive DRI values across testers RIB 335/74 and H 77/833-2.

For panicle yield per plot, grain yield per plot and grain yield per panicle, hybrids of recurrent parent ICMB 841 surprisingly exhibited positive DRI values with testers PPMI 301 and RIB 335/74, as did hybrids of introgression line 197-1-12 with these testers. The only other testcross hybrid combination with positive DRI for these three traits in this relatively severe terminal drought stress environment was that of donor parent 863B crossed with tester PPMI 301. Interestingly hybrids, 202-8-8 × PPMI 301, 202-7-12 × RIB 335/74, 197-10-11 × RIB 335/74, 202-8-8 × RIB 335/74, 202-6-26 × RIB 335/74, 197-10-11 × H 77/833 and 197-1-12 × H 77/833-2 all exhibited negative DRI values for these three traits in this environment indicating that they were relatively sensitive to this severe terminal drought stress regime.

For panicle harvest index, introgression line testcross hybrids 863B x PPMI 301, 197-12-2 × PPMI 301,197-1-12 × PPMI 301, ICMB 841 × RIB 335/74, 202-8-11 × RIB

Table 42. Drought Response Index (DRI) for testcross hybrids under relatively severe early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Hybrids	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	0.00	0.00	0.00	1.48	2.31	1.17	2.21	2.17	2.48	0.00	0.00	1.14	1.00	2.07	1.38	0.00
ICMB 841 × PPMI 301	-1.82	-2.33	-2.68	2.47	2.09	4.81	0.00	-3.60	-2.26	3.75	-4.16	0.00	0.00	0.00	4.90	2.89
197-10-18 × PPMI 301	1.26	-4.24	-4.04	2.01	0.00	1.69	0.00	1.76	2.11	-1.84	0.00	1.01	0.00	-2.14	4.06	2.70
202-8-11 × PPMI 301	-1.80	-1.18	0.00	-1.31	0.00	0.00	0.00	-2.73	-2.79	0.00	-1.48	2.06	0.00	1.04	0.00	-1.09
197-12-2 × PPMI 301	0.00	0.00	0.00	0.00	1.36	5.37	2.86	-2.54	-2.59	3.14	-1.28	-1.33	0.00	0.00	5.24	0.00
202-8-9 × PPMI 301	-1.28	4.11	3.55	1.48	1.00	0.00	0.00	0.00	0.00	0.00	2.00	2.64	2.44	0.00	0.00	0.00
202-7-12 × PPMI 301	-2.87	-1.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.21	-2.24	0.00	0.00	0.00
202-8-27 × PPMI 301	-3.96	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.03	0.00	0.00	0.00	1.01	1.67
197-10-11 × PPMI 301	0.00	0.00	0.00	-2.25	-1.46	0.00	0.00	0.00	0.00	-1.15	2.35	1.17	1.02	0.00	0.00	-1.46
202-7-4 × PPMI 301	-1.30	0.00	0.00	1.78	0.00	0.00	-1.06	0.00	1.27	-1.76	0.00	0.00	0.00	0.00	0.00	0.00
202-7-10 × PPMI 301	0.00	-1.76	-1.26	0.00	0.00	0.00	0.00	-2.16	-1.50	1.53	0.00	-2.15	-2.50	0.00	0.00	0.00
202-8-8 × PPMI 301	1.86	2.10	0.00	-1.07	-1.97	-2.79	-1.87	-1.81	-1.98	-1.67	0.00	-1.92	-2.39	-2.50	0.00	0.00
197-1-12 × PPMI 301	0.00	0.00	0.00	1.46	2.95	4.82	3.10	-2.04	-1.12	3.08	2.54	0.00	5.02	4.69	2.06	-1.55
202-6-26 × PPMI 301	2.44	-1.20	-1.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.04	0.00	0.00	0.00
197-18-1 × PPMI 301	1.77	0.00	-1.57	0.00	0.00	0.00	0.00	-1.14	-1.08	1.43	2.83	0.00	0.00	1.93	0.00	0.00
863B × RIB 335/74	-2.04	-2.42	-1.83	0.00	0.00	-1.04	0.00	0.00	0.00	0.00	1.16	0.00	0.00	-2.23	1.46	1.46
ICMB 841 × RIB 335/74	0.00	-2.98	-2.24	1.72	3.60	5.51	3.57	0.00	0.00	2.93	1.33	-1.37	0.00	2.73	3.95	1.42
197-10-18 × RIB 335/74	1.39	0.00	0.00	0.00	-1.46	-2.39	-2.55	-1.02	-1.15	-1.73	-2.26	0.00	-2.74	-1.13	-2.08	-1.61
202-8-11 × RIB 335/74	-2.96	0.00	1.65	-1.50	1.26	0.00	1.65	0.00	0.00	0.00	0.00	1.59	0.00	-1.20	0.00	2.68
197-12-2 × RIB 335/74	0.00	1.49	1.39	-1.16	0.00	0.00	1.52	0.00	0.00	1.30	0.00	0.00	0.00	0.00	0.00	-1.49
202-8-9 × RIB 335/74	1.19	0.00	0.00	0.00	-1.26	-2.03	-1.69	1.43	1.38	-1.71	1.40	2.85	-1.35	0.00	-2.38	-1.33
202-7-12 × RIB 335/74	0.00	0.00	0.00	-1.28	-1.66	-1.95	-1.19	0.00	0.00	-1.46	0.00	0.00	1.32	0.00	-1.38	0.00
202-8-27 × RIB 335/74	0.00	0.00	0.00	0.00	0.00	-1.10	-1.23	0.00	0.00	0.00	2.23	0.00	3.84	-2.02	0.00	0.00
197-10-11 × RIB 335/74	2.25	0.00	0.00	-3.03	-1.77	-1.18	0.00	0.00	-1.40	0.00	0.00	-1.49	-1.57	0.00	-1.15	-2.30
202-7-4 × RIB 335/74	1.26	4.60	2.78	0.00	-1.09	-2.72	-1.33	2.59	2.16	-1.95	0.00	1.66	0.00	1.41	-3.53	-2.60
202-7-10 × RIB 335/74	0.00	2.84	2.05	-2.35	0.00	-1.03	0.00	-1.33	-2.15	0.00	-1.11	-1.07	0.00	-1.83	0.00	0.00
202-8-8 × RIB 335/74	0.00	0.00	0.00	-1.06	-1.42	-1.54	-1.03	2.59	2.30	-2.26	0.00	0.00	0.00	0.00	-1.57	-1.13
197-1-12 × RIB 335/74	0.00	0.00	0.00	4.93	5.44	8.15	3.73	2.08	3.35	2.68	0.00	0.00	1.28	7.71	2.82	-1.06
202-6-26 × RIB 335/74	0.00	0.00	0.00	-1.10	-1.34	-1.05	-1.13	-1.17	-1.72	0.00	0.00	1.16	0.00	-1.67	0.00	0.00
197-18-1 × RIB 335/74	1.03	0.00	0.00	0.00	0.00	-1.05	0.00	0.00	0.00	0.00	0.00	0.00	-1.45	-1.01	0.00	2.81
863B × H 77/833-2	0.00	-1.33	-1.35	0.00	-3.05	-3.09	-2.94	-2.24	-1.73	-1.55	0.00	-1.43	0.00	-1.25	-1.67	0.00
ICMB 841 × H 77/833-2	1.58	0.00	0.00	0.00	0.00	1.17	0.00	-1.14	0.00	1.30	0.00	1.43	0.00	0.00	1.08	0.00
197-10-18 × H 77/833-2	0.00	-1.43	-1.29	0.00	1.29	1.73	1.67	0.00	0.00	1.03	2.48	0.00	1.16	1.51	0.00	0.00
202-8-11 × H 77/833-2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-2.47	-2.58	-2.31	0.00	-1.02	0.00
197-12-2 × H 77/833-2	-1.18	1.28	2.39	0.00	-1.52	-1.80	-1.49	-1.17	-1.18	0.00	1.74	0.00	1.28	-1.36	-1.46	0.00
202-8-9 × H 77/833-2	0.00	1.61	1.68	1.71	0.00	0.00	0.00	0.00	1.63	0.00	0.00	0.00	0.00	-1.08	0.00	2.88
202-7-12 × H 77/833-2	-1.29	0.00	1.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.15	-1.53	1.28	0.00	0.00	1.25
202-8-27 × H 77/833-2	1.20	0.00	-1.12	0.00	-1.37	0.00	-1.60	0.00	0.00	0.00	-3.24	-1.14	-1.51	0.00	-1.50	-1.79
197-10-11 × H 77/833-2	0.00	0.00	0.00	-2.60	-1.75	-1.15	0.00	0.00	0.00	0.00	-3.41	0.00	-1.11	0.00	-2.07	-2.30
202-7-4 × H 77/833-2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-1.30	0.00	1.88	-2.64	3.08	0.00	0.00	-1.84
202-7-10 × H 77/833-2	0.00	-2.28	-1.82	0.00	0.00	0.00	-1.07	0.00	0.00	-1.02	0.00	1.44	0.00	0.00	0.00	0.00
202-8-8 × H 77/833-2	-1.64	0.00	1.63	0.00	0.00	0.00	1.39	0.00	0.00	1.44	0.00	1.95	1.30	-1.21	0.00	2.80
197-1-12 × H 77/833-2	0.00	2.15	0.00	-3.28	-1.45	-1.42	0.00	3.19	2.16	-1.76	-1.21	0.00	-1.95	0.00	-1.95	-1.31
202-6-26 × H 77/833-2	0.00	0.00	0.00	0.00	0.00	0.00	-1.34	3.86	4.04	-2.05	-2.94	0.00	0.00	0.00	0.00	0.00
197-18-1 × H 77/833-2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.26	0.00	0.00	0.00	0.00

335/74, 197-12-2 × RIB 335/74, 197-1-12 × RIB 335/74, 197-10-18 × H 77/833-2 and 202-8-8 × H 77/833-2 showed positive DRI values under these early-onset terminal drought stress conditions. For stover yield per plot and biomass yield per plot, DRI values of testcross hybrids 863B × PPMI 301, 197-10-18 × PPMI 301, 202-8-9 × RIB 335/74, 202-7-4 × RIB 335/74, 202-8-8 × RIB 335/74, 197-1-12 × RIB 335/74, 197-1-12 × H 77/833-2 and 202-6-26 × H 77/833-2 were positive in this relatively severe drought stress environment, indicative of their relatively better ability than other trial entries to maintain stover and biomass yields under these conditions.

For harvest index, testcross hybrids ICMB 841 × PPMI 301, 197-12-2 × PPMI 301, 202-7-10 × PPMI 301, 197-1-12 × PPMI 301, 197-18-1 × PPMI 301, ICMB 841 × RIB 335/74, 197-12-2 × RIB 335/74, 197-1-12 × RIB 335/74, ICMB 841 × H 77/833-2, 197-10-18 × H 77/833-2 and 197-1-12 × H 77/833-2 showed positive DRI values for this stress treatment.

For plant height, five testcrosses of PPMI 301, and four testcrosses each of RIB 335/74 and H 77/833-2 exhibited positive DRI values in this relatively severe drought stress environment. Large positive DRI values for plant height were observed for testcross hybrids 197-1-12 × PPMI 301, 197-18-1 × PPMI 301, 202-8-27 × RIB 335/74 and 197-10-18 × H 77/833-2.

For panicle length, testcrosses of introgression lines 202-8-9 and 202-8-11 showed positive DRI values with testers PPMI 301 and RIB 335/74. Under these early-onset stress conditions, positive panicle diameter DRI values were observed for testcross hybrids 863B × PPMI 301, 202-8-9 × PPMI 301, 197-10-11 × PPMI 301, 197-1-12 × PPMI 301, 202-8-27 × RIB 335/74, 202-7-12 × RIB 335/74, 197-1-12 × RIB 335/74,

197-10-18 × H 77/833-2, 197-12-2 × H 77/833-2, 202-7-12 × H 77/833-2, 202-7-4 × H 77/833-2 and 202-8-8 × H 77/833-2.

Among introgression lines testcross hybrids, 197-1-12 × RIB 335/74 and 197-1-12 × PPMI 301 had the largest positive DRI values for hundred-grain mass in this environment. In addition, 863B × PPMI 301, 202-8-11 × PPMI 301, 197-18-1 × PPMI 301, 202-7-4 × RIB 335/74 and 197-10-18 × H 77/833-2 had positive DRI values for this trait in this early-onset terminal drought stress treatment. For grain number per panicle, testcrosses of donor parent 863B showed positive DRI with testers PPMI 301 and RIB 335/74 as did testcrosses of recurrent parent ICMB 841 with all three testers. In addition, testcrosses of introgression lines 197-10-18 and 197-1-12 with PPMI 301, 197-12-2 with PPMI 301 and RIB 335/74 and 202-8-27 with PPMI 301 showed positive DRI values for grain number per panicle in this relatively severe drought stress environment.

For grain number per plot, testcrosses of introgression lines 197-10-18 and 202-8-27 and recurrent parent ICMB 841 with tester PPMI 301; donor parent 863B; recurrent parent ICMB 841, and introgression lines 197-18-1 and 202-8-11 with RIB 335/74; and introgression lines 202-8-8, 202-8-9 and 202-7-12 with tester H 77/833-2 exhibited positive DRI values in this relatively severe terminal drought stress environment, indicating their superior ability to maintain grain number per plot under these conditions.

4.3.5.2.3. Combining ability for DRI

4.3.5.2.3.1. General Combining Ability (gca)

The results of combining ability analyses for the early-onset terminal drought stress treatment, using DRI values of individual replications, are presented in the form of tabulated *gca* effects of the lines and testers in Table 43.

Introgression line 197-10-11 exhibited significant positive *gca* effects, whereas the tester PPMI 301, donor parent 863B, and introgression line 197-12-2 showed significant negative *gca* effects for DRI of panicle number per plot and DRI of effective tiller numbers per plant. Among the testers, introgression lines and their parents, donor parent 863B was the only highly significantly positive combiner for DRI of panicle yield per plot, grain yield per plot, panicle harvest index, harvest index and grain number per panicle.

Introgression lines 197-12-2 and 197-10-11, respectively exhibited significantly positive and negative *gca* effects for DRI of grain number per panicle. For DRI of stover yield per plot, the testers H 77/833-2 and PPMI 301 showed significantly positive and negative *gca* effects, respectively. Hence tester H 77/833-2 can be recommended for use as a male parent to develop hybrids for early-onset terminal drought stress situations. Among the introgression lines, 197-10-18, and 197-10-11, and among testers H 77/833-2 exhibited significantly positive *gca* for DRI of biomass yield per plot.

For DRI of harvest index, the tester PPMI 301 and drought tolerance donor parent 863B were the only significantly positive combiners among testcross hybrid parental lines and testers. In comparison with the late-onset stress treatment, in the early-onset stress treatment donor parent 863B, showed relatively better *gca* for DRI values of harvest index. Among introgression lines, 197-10-18 exhibited negative *gca* effects and 202-7-12 showed positive *gca* effects for DRI of both plant height and panicle diameter.

For DRI of 100-grain mass, drought tolerance donor parent 863B was the only testcross hybrid parent to exhibit significantly positive DRI in the early-onset stress environment. For DRI of grain number per panicle the tester H 77/833-2 and

Table 43. Estimates of gca effects of DRI values under relatively severe early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Lines & Testers	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B	-0.34	-1.44**	-1.36**	1.23**	2.03**	2.57**	1.47**	0.45	0.51	1.12**	0.20	-0.42	0.50	2.54**	1.28**	0.19
ICMB 841	0.45	-0.85	-0.77	-0.33	-0.70	-0.09	-0.13	-0.27	-0.35	-0.30	0.37	0.09	-0.47	-0.35	0.13	-0.32
197-10-18	0.11	0.08	0.23	-0.16	-0.63	-0.10	-0.73	0.83	0.70*	-0.86*	-1.10*	-0.30	-1.09*	-0.61	0.31	0.23
202-8-11	0.36	-0.11	-0.06	-0.16	-0.51	-0.44	0.00	0.04	-0.02	-0.06	-1.01	0.14	-0.07	0.09	-0.28	-0.22
197-12-2	0.65	-0.97*	-1.39**	-0.18	0.29	1.26*	0.76	-0.41	0.37	0.50	0.69	-0.25	0.53	0.42	1.13**	-0.30
202-8-9	0.46	0.36	0.16	-0.03	-0.52	-0.37	-0.48	0.67	0.52	-0.85*	-0.77	-0.13	-0.70	-0.78	-0.14	0.26
202-7-12	0.15	0.58	0.62	0.02	-0.31	-0.90	-0.05	-0.56	-1.16*	0.37	1.55**	0.49	1.29*	-0.83	-0.07	0.89*
202-8-27	0.01	0.65	0.61	-0.22	-0.47	-0.39	-0.40	0.35	0.25	-0.55	0.98	0.76	0.54	-0.63	-0.33	-0.39
197-10-11	0.11	1.20**	1.03*	0.46	0.37	-1.12*	-0.40	0.91	0.70*	-0.28	-0.04	0.37	0.00	0.18	-0.97*	-0.35
202-7-4	-0.63	0.15	0.21	-0.52	-0.35	-0.28	-0.02	-0.42	-1.07**	0.15	-1.04*	-0.44	-0.90	-0.72	-0.11	-0.29
202-7-10	-0.17	0.68	0.38	-0.06	0.23	0.11	-0.15	-0.26	0.15	0.11	0.85	-0.32	0.27	0.41	-0.24	-0.17
202-8-8	0.16	-0.34	-0.27	-0.46	0.11	0.01	0.08	-0.57	-0.06	0.37	-0.49	0.79	-0.22	0.18	-0.12	-0.04
197-1-12	0.44	0.05	-0.01	0.50	0.52	0.06	0.21	0.17	0.57	0.05	-0.04	-0.10	-0.18	0.31	-0.32	0.12
202-6-26	-0.78	0.00	0.26	-0.47	-0.50	-0.29	-0.55	-0.72	-0.68*	-0.31	-0.21	-0.28	0.51	-0.49	-0.16	-0.14
197-18-1	-0.98*	-0.03	0.36	0.38	0.46	-0.05	0.38	-0.21	-0.42	0.53	0.06	-0.41	-0.02	0.30	-0.13	0.53
PPMI 301	-0.21	-0.48*	-0.48**	0.14	0.19	0.13	0.28	-0.61**	-0.428**	0.59**	0.29	-0.21	-0.11	-0.30	0.62**	0.32
RIB 335/74	0.10	0.13	0.14	-0.37	-0.30	-0.27	-0.22	-0.01	0.02	-0.28	0.02	0.18	0.26	0.00	-0.28	-0.36
H 77/833-2	0.11	0.36	0.35	0.23	0.12	0.14	-0.06	0.62**	0.40**	-0.31	-0.31	0.03	-0.16	0.30	-0.34*	0.04

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

introgression line 197-10-11 exhibited significantly negative *gca* and tester PPMI 301, donor parent 863B, and introgression line 197-12-2 were the significantly positive combiners, as in late-onset stress treatment. For DRI of grain number per plot the only line 202-7-12 showed positive *gca* effects in this severe stress environment.

4.3.5.2.3.2. Specific Combining Ability for DRI

The *sca* effects of testcross hybrids for DRI of observed agronomic traits in this ealy-onset terminal drought stress environment are presented in Table 44. Among testcross hybrids, 202-7-4 × PPMI 301 and 863B × RIB 335/74 showed negative *sca* effects for DRI of plant number per plot. For DRI of panicle yield per plot, hybrid ICMB 841 × RIB 335/74 showed negative *sca* effects. Among testcross hybrids, negative *sca* effects for DRI of grain yield per panicle were exhibited by 863B × PPMI 301; for DRI of panicle harvest index were exhibited by 202-7-12 × RIB 335/74 and for DRI of biomass yield per plot were exhibited by 202-8-9 × PPMI 301, and 197-10-18 × RIB 335/74. For DRI of biomass yield per plot, significantly positive *sca* effects were showed by testcross hybrids 197-10-18 × PPMI 301, 197-10-11 × RIB 335/74 and 202-8-9 × H 77/833-2.

For DRI of panicle length, only testcross hybrid 202-6-26 × PPMI 301 exhibited significant positive *sca* effects. Among testcross hybrids, 197-10-18 × PPMI 301 and 197-10-11 × H 77/833-2 exhibited significant positive *sca* effects for DRI of grain number per panicle and grain number per plot. Similarly for DRI of grain number per plot the best testcross hybrids with positive *sca* effects were 202-8-11 × RIB 335/74, and 202-7-10 × RIB 335/74 exhibited significantly positive *sca* effects.

Table 44. Estimates of sca effects of testcross hybrids with DRI values under relatively severe early-onset terminal drought stress conditions, ICRISAT-Patancheru, drought nursery, summer-2004.

Hybrids	Plant No./plot	Panicle No./plot	ET	Panicle yield (g/plot)	Grain yield (g/plot)	Grain yield (g/panicle)	Panicle H.I. (%)	Stover yield (g/plot)	Biomass yield (g/plot)	H.I. (%)	Plant height (cm)	Panicle length (cm)	Panicle diameter (mm)	100-grain mass (g)	Grain No./panicle	Grain No./plot
863B × PPMI 301	0.58	0.54	0.28	-0.96	-1.39	-1.78*	-1.12	-0.55	0.24	-0.72	-0.97	-0.03	0.96	-0.69	-1.11	-0.95
ICMB 841 × PPMI 301	-0.21	0.54	0.43	0.57	0.11	-0.27	0.26	-0.03	0.41	0.29	-0.67	0.13	-0.41	0.22	-0.44	0.58
197-10-18 × PPMI 301	-0.07	-0.35	-0.33	1.35	0.92	0.57	0.09	1.10	1.81**	-0.27	0.40	0.52	1.15	-1.23	1.48*	1.56*
202-8-11 × PPMI 301	-0.40	-0.07	0.37	0.69	-0.17	-0.29	-0.63	0.57	0.82	-0.99	0.71	0.14	-0.22	-0.01	-0.38	-0.17
197-12-2 × PPMI 301	0.25	-1.20	-0.92	-0.65	-0.52	1.48	-0.61	-1.09	-1.09	0.46	-0.99	0.10	-0.85	-0.92	1.60*	-0.07
202-8-9 × PPMI 301	1.22	0.10	-0.20	-0.67	-0.51	-0.43	0.19	-1.26	-1.71**	0.24	-0.10	-1.03	-0.49	-0.27	0.03	-0.05
202-7-12 × PPMI 301	1.42	0.70	0.00	-0.40	0.13	-0.68	0.13	-0.13	-0.42	0.09	0.48	-0.52	-0.44	-0.30	-0.11	0.16
202-8-27 × PPMI 301	0.23	-0.75	-0.80	-0.17	0.09	0.82	0.70	1.21	0.17	-0.79	-0.22	-0.12	0.99	0.00	0.63	0.02
197-10-11 × PPMI 301	-0.33	1.36	1.24	0.52	1.23	-0.67	0.59	0.30	-0.29	0.77	0.38	-0.15	0.06	0.11	-0.72	-0.11
202-7-4 × PPMI 301	-1.90**	0.51	1.44*	0.34	0.63	0.10	0.52	-0.16	0.38	0.13	0.73	-0.31	-0.35	0.30	-0.04	0.27
202-7-10 × PPMI 301	-0.55	-0.50	0.07	-0.14	-0.30	0.35	-0.12	0.58	0.69	-0.29	-0.08	0.54	-0.28	1.08	-0.90	-0.63
202-8-8 × PPMI 301	-0.40	-0.62	-0.52	0.65	0.17	0.55	-0.36	-0.62	0.02	0.72	-0.24	-0.06	0.17	1.60	-0.15	-0.33
197-1-12 × PPMI 301	0.54	0.05	-0.37	0.11	0.00	0.49	0.12	0.08	-0.15	0.41	-0.92	-0.93	-1.11	0.42	0.25	-0.09
202-6-26 × PPMI 301	0.27	-0.05	-0.21	-1.07	-0.70	-0.63	-0.21	0.06	-0.55	-0.29	0.72	1.64*	0.87	-0.44	-0.49	-0.24
197-18-1 × PPMI 301	-0.64	-0.26	-0.49	-0.16	0.31	0.39	0.46	-0.06	-0.35	0.23	0.78	0.06	-0.05	0.16	0.36	0.06
863B × RIB 335/74	-1.58*	-0.79	-0.28	0.35	0.09	1.09	0.05	-0.06	0.01	0.31	0.55	-0.49	0.12	0.97	0.44	-0.40
ICMB 841 × RIB 335/74	-0.34	-0.94	-0.38	-1.66*	-1.10	-0.39	-0.46	-0.18	-1.00	-0.47	-0.01	-0.71	-0.57	-0.61	-0.42	-1.28
197-10-18 × RIB 335/74	0.18	-0.61	-0.37	-0.53	-0.66	-0.48	-0.89	-1.33	-1.19*	0.17	-0.61	-0.39	-0.98	0.45	-0.75	-1.24
202-8-11 × RIB 335/74	0.83	0.34	-0.08	0.50	1.34	0.67	1.08	-0.49	-0.44	1.36	0.40	0.22	0.99	-0.48	1.05	1.54*
197-12-2 × RIB 335/74	-0.35	1.19	0.90	0.40	-0.35	-1.73	-0.16	0.23	0.13	-0.66	-0.18	-0.41	0.42	-0.08	-1.44*	0.15
202-8-9 × RIB 335/74	-0.92	-0.18	0.15	-0.14	0.10	0.24	0.70	-0.07	-0.02	0.44	1.14	0.44	0.40	0.19	0.39	-0.46
202-7-12 × RIB 335/74	-0.22	-0.15	-0.07	0.69	-0.31	-0.03	-1.49*	0.56	0.73	-1.07	0.32	-0.15	0.91	0.24	-0.28	-0.57
202-8-27 × RIB 335/74	0.46	0.56	0.29	0.56	0.36	0.22	-0.13	0.24	0.91	-0.05	-0.61	0.45	-1.20	0.97	-0.22	0.23
197-10-11 × RIB 335/74	0.31	-1.37	-1.17	-0.88	-1.09	0.06	-0.47	0.84	1.40*	-1.38	0.01	0.69	0.04	1.32	-0.55	-1.57*
202-7-4 × RIB 335/74	0.96	-0.38	-0.69	-0.58	0.02	0.51	0.47	-0.40	0.18	0.49	0.39	0.26	0.59	-1.46	0.86	0.62
202-7-10 × RIB 335/74	0.91	1.13	0.65	0.39	0.06	0.12	0.38	-0.19	-0.17	0.73	-0.45	0.66	-1.34	-1.32	0.96	1.56*
202-8-8 × RIB 335/74	0.23	1.37	1.30	-0.59	0.68	-0.35	1.49*	0.22	-0.61	0.31	0.46	0.04	-0.09	-0.71	0.29	1.37
197-1-12 × RIB 335/74	0.19	-0.25	-0.30	0.18	-0.20	-0.22	0.02	0.27	-0.04	-0.25	0.00	-0.07	0.72	-0.32	-0.37	-0.17
202-6-26 × RIB 335/74	-0.97	-0.16	0.22	1.27	0.79	0.52	-0.44	-0.14	0.26	0.15	0.17	-0.66	0.79	0.48	0.41	0.44
197-18-1 × RIB 335/74	0.32	0.23	-0.15	0.06	0.28	-0.25	-0.15	0.50	-0.15	-0.07	-1.58	0.09	-0.80	0.37	-0.36	-0.23
863B × H 77/833-2	1.00	0.25	0.00	0.61	1.31	0.69	1.07	0.61	-0.26	0.41	0.42	0.51	-1.09	-0.28	0.67	1.35
ICMB 841 × H 77/833-2	0.55	0.41	-0.05	1.09	0.98	0.66	0.20	0.21	0.59	0.18	0.69	0.58	0.98	0.40	0.86	0.70
197-10-18 × H 77/833-2	-0.11	0.95	0.71	-0.82	-0.26	-0.09	0.80	0.23	-0.62	0.10	0.21	-0.13	-0.17	0.78	-0.73	-0.32
202-8-11 × H 77/833-2	-0.43	-0.28	-0.29	-1.19	-1.16	-0.38	-0.45	-0.08	-0.38	-0.37	-1.11	-0.37	-0.76	0.49	-0.67	-1.37
197-12-2 × H 77/833-2	0.10	0.01	0.02	0.26	0.87	0.25	0.77	0.86	0.96	0.19	1.18	0.31	0.43	1.00	-0.16	-0.08
202-8-9 × H 77/833-2	-0.30	0.08	0.05	0.81	0.42	0.19	-0.89	1.33	1.73**	-0.68	-1.04	0.59	0.09	0.09	-0.42	0.51
202-7-12 × H 77/833-2	-1.20	-0.56	0.07	-0.29	0.18	0.71	1.37	-0.43	-0.31	0.97	-0.81	0.66	-0.47	0.06	0.39	0.42
202-8-27 × H 77/833-2	-0.68	0.19	0.51	-0.38	-0.45	-1.04	-0.57	-1.46	-1.07	0.84	0.83	-0.34	0.21	-0.96	-0.41	-0.25
197-10-11 × H 77/833-2	0.02	0.01	-0.06	0.36	-0.14	0.61	-0.11	-1.14	-1.12	0.60	-0.38	-0.54	-0.10	-1.43	1.26*	1.68*
202-7-4 × H 77/833-2	0.94	-0.12	-0.75	0.24	-0.65	-0.61	-0.99	0.56	-0.56	-0.62	-1.12	0.05	-0.24	1.16	-0.82	-0.89
202-7-10 × H 77/833-2	-0.36	-0.63	-0.72	-0.25	0.24	-0.47	-0.26	-0.38	-0.52	-0.44	0.53	-1.20	1.62	0.24	-0.06	-0.94
202-8-8 × H 77/833-2	0.17	-0.76	-0.77	-0.05	-0.85	-0.21	-1.13	0.40	0.59	-1.03	-0.22	0.01	-0.08	-0.89	-0.14	-1.04
197-1-12 × H 77/833-2	-0.73	0.21	0.67	-0.30	0.20	-0.27	-0.14	-0.35	0.19	-0.16	0.92	1.00	0.39	-0.10	0.12	0.26
202-6-26 × H 77/833-2	0.71	0.21	-0.02	-0.19	-0.09	0.10	0.64	0.08	0.28	0.15	-0.90	-0.99	-1.65	-0.03	0.08	-0.20
197-18-1 × H 77/833-2	0.32	0.03	0.64	0.10	-0.59	-0.14	-0.31	-0.44	0.50	-0.16	0.80	-0.14	0.85	-0.53	0.01	0.16

** Significant at 0.01 level of probability; * Significant at 0.05 level of probability

DISCUSSION

CHAPTER V

DISCUSSION

In a modern sense, plant breeding may be defined as systematic crop improvement by genetic change. Although plant-breeding efforts have been continuous since the beginnings of agriculture, the breeding process retained its primarily empirical character during the discovery of many of the foundation concepts of biology (Sturtevant, 1965). Thus the first plant breeding activities involved unconscious selection for agricultural suitability. In the millennia that followed, plant breeding developed into an empirical art and ultimately into a modern scientific enterprise characterized by predictive methods. The most successful application of predictive methods to plant breeding has arrived as molecular markers technology has begun to be applied to crop improvement (Goldman, 2000).

Genetic markers offer the possibility of achieving breeding goals more precisely than through direct phenotypic selection. The fundamental attraction of DNA-based assays [homology to primer sequence (i.e., SSR) or recognition site (i.e., RFLP)] is the immense number of 'characters' they reveal for investigating the organization of genomes and for the construction of dense genetic maps. Improving drought tolerance has been considered as a valid plant-breeding target to minimize yield losses resulting from drought stress. Phenotypic traits associated directly with drought tolerance are limited; however, several investigations noted that effective tillering ability (van Oosterom *et al.*, 2001), developmental asynchrony and plasticity (Ramond, 1968; Ong, 1984; Lambert, 1983; Craufurd and Bidinger, 1988b; Mahalakhsmi *et al.*, 1987; Mahalakhsmi and Bidinger, 1985b), biomass partitioning (Carberry and Campbell, 1985;

Craufurd and Bidinger, 1988b), flowering time and grain yield potential (Bidinger *et al.*, 2001); and terminal drought tolerance (Mahalakhsmi *et al.*, 1987) are associated with agronomic performance under conditions of drought stress.

The advent of saturated molecular marker-based genetic maps in pearl millet (Liu *et al.*, 1994) promised rapid progress towards the improvement of pearl millet for genetically complex traits like drought tolerance. In pearl millet, using a mapping population based on the cross of parents ICMB 841 and 863B a number of genomic regions for grain yield *per se* and for drought tolerance of grain yield were mapped on linkage group (LG) 2 and explained up to 23% of the phenotypic variation, some of these QTLs were common across stress environments (Yadav *et al.*, 2004). Hence in the present study an attempt was made to transfer the entire LG2 from drought tolerance donor parent 863B to drought sensitive recurrent parent ICMB 841 via backcrossing with molecular-marker-assisted selection (MMAS). The objectives of the study were: to complete transfer of one of three major drought tolerance QTLs from donor parent 863B to recurrent parent ICMB 841 and to evaluate the hybrid performance of the potentially improved version(s) of ICMB 841, relative to the original recurrent parent, under fully-irrigated and managed terminal drought stress conditions.

Marker-Assisted Selection:

Two agronomically elite seed parents, ICMB 841 and 863B, were previously crossed to develop a segregating population for genetic linkage map construction and trait analysis. Parent 863B was bred at ICRISAT-Patancheru by direct selfing and selection within *Iniadi* landrace material from Togo and was chosen as a parent for its superior combining ability for grain filling under terminal drought stress conditions (F.R.

Bidinger, unpublished). The other parent, ICMB 841 (Singh *et al.*, 1990), lacks tolerance to terminal drought stress (F.R. Bidinger, unpublished) and is the maintainer of the female parent of several high yielding hybrids of commercial importance in India. The $F_{2:3}$ segregating population from the parents was developed at ICRISAT-Patancheru, in India, and the UK's Institute for Grassland and Environmental Research (IGER) contributed to RFLP and SSR genotyping of the F_2 population, phenotyping its testcross hybrids and QTL mapping with the combined data set to tag genomic regions that control terminal drought tolerance (Yadav *et al.*, 2004).

From the QTL mapping analysis, it was inferred that a number of genomic regions contributing to the control of grain yield *per se* and to drought tolerance of grain yield mapped on LG2 and explained up to 23% of the phenotypic variation in grain yield among mapping population testcrosses grown under terminal drought stress conditions (Yadav *et al.*, 2004). Some of these QTLs were common across stress environments. Identification of these consistent putative QTLs for terminal drought tolerance on LG2 paved way for the present study.

A survey of parental polymorphism using a total of 78 SSR primer pairs was initially conducted for linkage map construction. Out of 78 SSR primer pairs tested, 28 detect polymorphism (35.9%) between the mapping population and backcross progeny parents (863B and ICMB 841) that can be scored on silver-stained polyacrylamide gels. In the present study, RFLP probes were also utilized for tracking segregation in genomic regions wherever the SSR markers were found to be less in number (especially on LG1, LG4, LG6 and LG7).

Among these two-marker systems, SSR markers are profoundly simpler and quicker to use because of their technical simplicity, stable inheritance, and high level of polymorphism (Chen *et al.* 1997). SSR primer pairs usually produce single marker locus markers; the other marker systems, RFLP probe-enzyme combinations, often identify several loci. RFLP markers were used successfully in pearl millet for marker-assisted selection of downy mildew resistance using donor parent ICMP 451 and recurrent parent H 77/833-2 (Sharma, 2001). Similar markers were used in QTL mapping of downy mildew resistance with PT 732B and P 1449-2 (Nepolean, 2002), W 504-1-1 and P 310-17 (Kolesnikova, 2001), and Tift 238D1 and IP 18293 (Azhaguvel, 2001). The other aspect of RFLP analysis is that it involves radioactive labeling, and is very laborious and time consuming. In this study, 23 polymorphic RFLP probe-enzyme combinations were used primarily for screening the progenies for background selection in pearl millet genomic regions lacking previously mapped SSR markers that were polymorphic for the parental combination of 863B and ICMB 841. The goal of background selection is to speed recovery of the recurrent parent genome across the whole genome outside of regions explicitly targeted for donor genome introgression (Tanksley *et al.*, 1989; Frisch *et al.*, 1999).

In the BC_3F_1 generation of this study, 38 backcross families were genotyped. In this generation both foreground selection (heterozygotes for LG2 alleles of both parents) and background selection (homozygous for alleles of recurrent parent ICMB 841) were applied to select among the backcross progenies for individuals heterozygous on LG2 and homozygous elsewhere for ICMB 841 alleles. Based on genotypic data from 51 markers, one backcross family was selected for further backcrossing and genotyping. Using

genotypic data from these 38 backcross families, a linkage map was constructed using MAPMAKER/EXP to better know the relative positions of individual markers and to compare their order with the standard genetic linkage map of pearl millet. All of the 51 polymorphic markers aligned to the expected positions on the seven linkage groups without any distortions–may be due to the small number of individuals that were taken for this study.

The one selected backcross family (BC_4F_1) was transplanted to the field for backcrossing. In the initial stages of seedling growth, leaf samples were taken for DNA extraction and marker genotyping. Simultaneously useful morphological characters like presence of hairiness on the nodal ring (*Hn/hn*), leaf sheath (*Hsh/hsh*), and leaf blade (*Hl/hl*), green node color (*Rn/gn*) and yellow anther color typical of recurrent parent ICMB 841 were used as additional criteria to select among the progenies. With these available morphological markers facilitating recovery of background genotype of ICMB 841, it was possible to reduce the amount of lab consumables costs involved in the marker-assisted selection process. In this generation similar selection to that conducted in the BC_3F_1 was carried out, but with smaller numbers of markers for background selection and the full set of markers for LG2 (foreground selection). Two backcross families (BC_5F_1) were selected for generation advance (by selfing and backcrossing) based upon the occurrence of the heterozygous condition on LG2 and homozygosity for recurrent parent alleles on the remaining linkage groups.

Each of 18 progenies across the two selected BC_5F_1 families was taken up for genotyping. With morphological markers as well as both foreground and background (full MAS) markers, twelve lines were selected for further selfing and backcrossing with

ICMB 841. Formula by Sedcole (1977) helped to calculate the number of plants needed to have a 95% chance of getting at least one plant of the desired genotype based on expected Mendelian ratios. In these selected progenies, only partial MAS was carried out using eight polymorphic SSR marker loci distributed across LG2. To reduce population size for genotyping, initial screening was done with two markers–one each on "above" and "below" the target region on LG2.The experimental results of Stam and Zeven (1981), Young and Tanksley (1989a), and Frisch and Melchinger (2000) indicated that without background selection, this introgressed segment could remain fairly long over a large number of backcross generations, hence contributing a major part of the donor genome still present on the final breeding product. With this foreground marker data, 13 individuals (all selfed BC_5F_2 plants) were selected based on their homozygosity for various portions of the donor genome across LG2.

Testcross hybrid development:

The 13 selected segmental introgression homozygotes varied in the length of the homozygous region that they carried from the donor genome. These introgression homozygote progenies along with their two parents (863B and ICMB 841) were crossed with three different testers, namely PPMI 301, RIB 335/74 and H 77/833-2, to produce 45 testcross hybrids. All three testers were considered to be relatively sensitive to terminal drought stress, and are male parents of released pearl millet hybrid cultivars in India, namely Pusa 322, RHB 30 and HHB 67 respectively.

The selected progenies were phenotyped as testcross hybrids rather than using the derived inbred lines for several reasons: i) to restore heterotic vigor to backcross-derived inbreds that might otherwise be too weak for effective screening under stress conditions;

ii) to use the dominantly inherited early flowering of the testers to reduce variation in flowering time among the test units in order to focus the product assessment on specific drought tolerance traits rather than traits or responses associated with drought escape; and iii) to have test units that approximate the genetic structure of the F_1 hybrids grown by farmers rather than inbreds from many backcross-derived progenies.

Downy mildew screening:

Simultaneously, 45 testcross hybrids along with their 15 inbred line parents, three testers and two controls were screened against three different pearl millet downy mildew isolates of Indian origin [Patancheru (Sg153), Durgapura (Sg151) and Jamnagar (Sg140)] in three replicates. Since most of the seed of testcross hybrids were taken for field trials, only a small number of remnant seeds were available for screening against these pathogen isolates in a single replication each.

Downy mildew incidence (DMI%) was found to be high for screens involving both the Patancheru and Durgapura isolates. For the Jamnagar isolate, the mean value of downy mildew incidence was low but differences between the 15 inbreds were significant none-the-less. The operational heritabilities of screens against all the three isolates were high when calculated on an entry-mean basis. Among the three testers, H 77/833-2 was found to be highly susceptible to all three pathogen isolates, while PPMI 301 exhibited variable levels of resistance to the three pathogen isolates, and RIB 335/74 was consistently resistant to all three pathogen isolates. Among introgression line parents, 863B was highly resistant to two of the three pathogen isolates.

Among experimental inbreds, introgression lines 202-8-9 and 202-8-27 were found to resistant to all three pathogen isolates. For introgression line testcross hybrids,

due to paucity of seeds, only one replication could be evaluated to crudely estimate the *gca* and *sca* effects for disease reaction, so statistical analysis of variance of this data set was not possible. Hence, this data gives an extremely preliminary overall idea on the performance of individual testcross hybrids for downy mildew incidence. The mean performance of the testcross hybrids of introgression lines 197-1-12, 197-10-11, 202-8-27 and testers PPMI 301 and RIB 335/74 showed very low values for downy mildew incidence suggesting that these lines and testers may have negative general combining ability for downy mildew incidence incited by the three pathogen isolates used in this study.

Similarly, the estimates of *gca* effects of the lines 197-10-11 and 197-1-12 showed the most of negative *gca* effects and the testers PPMI 301 and RIB 335/74 also exhibited negative *gca* effects for downy mildew incidence across screens against the three pathogen isolates. Similarly, negative *sca* effects were recorded for the experimental DM resistant hybrids produced with inbred lines 197-10-11 and 197-1-12 and resistant testers PPMI 301 and RIB 335/74. However, these results must be considered preliminary since the results were from a single replication only. Further screening to confirm these results will be necessary once seed is available for this.

Fully irrigated non-stress conditions

Under fully irrigated conditions, hybrids of tester RIB 335/74 exhibited early flowering followed by those of PPMI 301 and H 77/833-2. Almost all the testcross hybrids of tester RIB 335/74 exhibited early flowering (42 days) equal to the donor parent testcross, 863B × RIB 335/74. Hybrids of introgression line 202-7-12 flowered very late with all three testers. In contrast, the hybrids of terminal drought tolerance donor parent 863B and

introgression lines 197-18-1 and 202-6-26 flowered very early (ca. 2-3 days earlier than other entries) with all three testers. Selection for early flowering helps the plant in escaping from terminal drought tolerance by reducing growth duration (Rattunde *et al.*, 1989).

Usually effective tiller number per plant was low for hybrids of donor parent 863B with all three testers. Most of the introgression line testcross hybrids exhibited effective tiller numbers per plant equal to or greater than testcrosses of the recurrent parent ICMB 841. Among introgression line testcrosses, those of 197-10-18 produced low numbers effective tillers with all three testers. Among testers, hybrids of H 77/833-2 produced the largest number of effective tillers per plant. Production of large numbers of tillers provides potential compensation for damage to the main shoot or primary tillers during midseason drought stress, but can increase vulnerability to terminal drought stress (Mahalakhsmi and Bidinger, 1985a, 1986; Mahalakshmi *et al.*, 1987; Bidinger *et al.*, 1987a).

Under fully irrigated non-stress conditions, introgression line testcross hybrids of testers PPMI 301 and H 77/833-2 yielded *ca.* 300-500 g more than the testcross hybrids of tester RIB 335/74 for both panicle yield and grain yield per plot. Among introgression line testcrosses, those of 202-6-26, 197-18-1 and 197-10-18 produced larger panicle yield and grain yield per panicle. Grain yield per panicle was highly influenced by effective tiller number, panicle length, panicle diameter, and hundred grain mass. Selection for limited tillering and large panicles can be achieved by selecting for higher grain yield per panicle (Bidinger *et al.*, 1987b; Yadav, 1994). Among testers, hybrids of PPMI 301 showed the largest grain yield per panicle followed by hybrids of H 77/833-2 and RIB

335/74. The difference in grain yield per panicle the between hybrids of introgression line parents 863B and ICMB 841 were very high (40-50%) with all three testers. Among introgression lines, hybrids of 197-18-1, 197-12-2 and 202-6-26 had higher grain yield per panicle with all three testers.

Panicle harvest index for introgression line testcross hybrids was high for the tester PPMI 301 and transgressive segregants were identified for this character among the introgression lines with testcrosses of 197-12-2 having higher panicle harvest index values than those of the better parent, 863B. This trait indicates the plant's ability to set and fill grains. It integrates the effects of all the physiological traits bearing on the effectiveness of assimilate production and translocation under stress (Bidinger and Mahalakhsmi, 1993). As expected, hybrids of introgression lines 197-12-2, 197-18-1 and 202-6-26 showed higher panicle harvest index values than those of recurrent parent ICMB 841, across all three testers.

For stover yield per plot, hybrids of tester H 77/833-2 exhibited higher yield than did those of PPMI 301 and RIB 335/74. As tester H 77/833-2 was having the greatest tillering ability, the recurrent parent ICMB 841 produced more stover with tester H 77/833-2 than with other two testers. In contrast, hybrids of introgression lines 197-10-11 and 197-18-1 produced large stover yield per plot across three testers. Similarly, total shoot biomass yield per plot was the highest for the hybrids of tester H 77/833-2 followed by those of PPMI 301 and RIB 335/74. Among introgression line testcrosses, those of 197-18-1, 197-10-7, 202-7-12, 202-8-9 and 197-10-18 showed higher biomass yields per plot with all three testers. The lowest yielders for biomass yield per plot among introgression line testcrosses were those of 202-8-27, 202-7-4 and 202-7-10.

Due to higher grain yields per plot produced by hybrids of tester PPMI 301, the overall harvest index values was large for hybrids of this tester when compared to those of RIB 335/74 and H 77/833-2. Among introgression line testcrosses, hybrids of 197-12-2, 202-6-26 and 197-18-1 showed higher harvest index values with testers PPMI 301 and RIB 335/74. Usually hybrids of tester H 77/833-2 exhibit higher tiller numbers and hence higher biomass yields, that tend to result in reduced harvest index values. However, hybrids of introgression lines, 202-7-10 and 197-1-12 with tester H 77/833-2 exhibited high harvest index values. Hybrids of these introgression lines had lower biomass yields, suggesting the efficient transfer of assimilates from leaves and stems to the panicles for grain yield production (Winkel and Do, 1992).

Between two drought tolerance mapping population parents used in developing the introgression lines in this study, the drought tolerance donor parent 863B produced taller hybrids than the recurrent parent ICMB 841, when crossed with all three testers. Among the three testers, RIB 335/74 contributed more height in its hybrids with both of these parents followed equally by PPMI 301 and H 77/833-2. Among introgression line testcrosses, hybrids of 202-7-12 and 202-8-27 were taller and shorter respectively, than those of the other introgression lines across all three testers. For panicle length, only a marginal difference was observed between hybrids of the donor and recurrent parents. Among testers, hybrids of H 77/833-2 produced shorter panicles (by 3-5 cm) when compared to hybrids of the other two testers.

Testcrosses of the donor parent 863B showed substantial differences for panicle diameter with their counterparts involving the recurrent parent ICMB 841. Among testers, hybrids of PPMI 301 exhibited the largest panicle diameters followed by hybrids

of RIB 335/74 and H 77/833-2. Almost all the introgression line testcross hybrids exhibited panicle diameters similar to those of the recurrent parent ICMB 841 when crosses involved the same tester. Similarly, hybrids of the donor parent had higher hundred grain mass with all three testers than their counterparts involving the recurrent parent. Almost all the testcross hybrids of introgression lines had hundred-grain mass values either to equal or less than those of their counterparts involving the recurrent parent. None of these testcross hybrids surpassed the hundred-grain mass of testcrosses of donor parent 863B. Among testers, hybrids of PPMI 301 produced heavier grains than those of the other two testers.

Grain number per panicle is an important trait to study the genetic potential of a genotype under stress and non-stress conditions (Bidinger *et al.*, 1987a). Among testers, hybrids of PPMI 301 had the highest numbers of grains per panicle under non-stress conditions followed by hybrids of H 77/833-2. Although the panicle diameter and panicle length of H 77/833-2 testcross hybrids were smaller than those of RIB 335/74 testcross hybrids, H 77/833-2 produced larger numbers of grains per panicle. Among introgression line testcrosses, hybrids of 197-18-1 and 197-1-12 had large numbers of grains per panicle with all three testers. For grain number per plot, hybrids of tester H 77/833-2 produced larger numbers of panicles and hence surpassed the plot grain numbers of hybrids of testers PPMI 301 and RIB 335/74. Due to the low number of panicles per plot exhibited by testcrosses of the donor parent 863B, hybrids of the recurrent parent ICMB 841 produced more grains per plot with all three testers under these fully irrigated non-stress conditions.

The dominance genetic variance component was significant for flowering time, stover yield per plot, plant height, panicle length, and 100-grain mass and can be exploited in hybrid cultivar breeding programmes. In assessing the relative contributions of lines and testers, it was observed that lines contributed more than testers to testcross hybrid variation for plant height and grain number per panicle under these fully irrigated non-stress conditions. Based on the general combining ability analysis, the introgressions line 202-8-27 and tester RIB 335/74 were the best combiners for early flowering but showed negative combining ability for both grain and stover yield-related characters. This relationship between flowering time and grain and stover yield performance was as expected under fully irrigated non-stress conditions where delay in flowering is expected to allow time for greater accumulation of biomass prior to crop maturity. The donor parent 863B conferred early flowering on its testcrosses and exhibited positive combining ability for grain-related characters but not for stover-related characters. Among testers, PPMI 301 had positive combining ability for grain yield related characters including panicle harvest index, harvest index, panicle length, panicle diameter, 100-grain mass and grain number per panicle. As expected, combining abilities of tester H 77/833-2 were often significantly different from those of PPMI 301 (Yadav *et al.*, 2004).

Under fully irrigated conditions, MAS-improved introgression lines showed very good variability for a range of agronomic characters. Among introgression lines and their parents, ICMB 841, 202-8-11, 202-8-9 and 202-8-27 were the best combiners for panicle numbers per plot and effective tiller number per plant. Since all the introgression lines were the backcross-derived progenies of recurrent parent ICMB 841, many of them exhibited general combining ability values similar to those of ICMB 841 for most of the

observed characters. Exceptions included introgression lines were 197-18-1, 202-8-11, 197-12-2, 202-8-9, 202-8-27 and 202-7-12. These lines with better general combining ability values under non-stress conditions than their recurrent parent, for several observed traits, can be exploited for the production of hybrids, synthetics and OPVs. Introgression line 197-12-2 showed positive combining ability for panicle harvest index and grain number per panicle.

The specific combining ability effects observed for introgression line testcross hybrids under these fully irrigated non-stress conditions indicated that 202-7-10 × RIB 335/74 exhibited better than expected (based on the trial mean and general combining abilities of its parents) performance for early flowering and number of grains per panicle. Similarly, 863B × PPMI 301 showed positive *sca* effects for stover yield and grain number per plot. These testcross hybrids with good *sca* effects can be considered for exploitation in hybrid breeding programmes.

Late-onset terminal drought stress conditions:

In the early-onset terminal drought stress treatment, irrigation was terminated so that drought stress commenced from the mid-flowering stage. In the late-onset terminal drought stress treatment, irrigation was terminated so that drought stress commenced about 1 week after the mid-flowering stage. In both the early and late-onset terminal drought stress treatments, symptoms of drought stress started to appear approximately 10 days after the last irrigation. Hence there was no variation observed in the flowering time of introgression line testcross hybrids in these stress treatments in comparison with the fully irrigated non-stress treatment.

Testcross hybrids of the donor parent 863B, introgression line 202-8-27 and tester RIB 335/74 maintained their earliness in flowering across moisture regimes. Similarly, testcrosses of introgression lines 197-12-2, 197-10-11, 197-18-1 and testers PPMI 301 and H 77/833-2 exhibited late flowering across all three moisture regimes. Interestingly, testcrosses of several late-flowering introgression lines like 197-12-2 and 197-18-1 maintained their superior grain and stover yield characters, respectively, under late-onset terminal drought stress conditions. Among testers, hybrids of PPMI 301 and H 77/833-2 showed the same behavior as the above two introgression lines. These results were found to be perfectly matching with earlier reports (Yadav *et al.*, 2004) involving drought tolerance screening of testers PPMI 301 and H 77/833-2 in hybrid combinations with mapping population progenies derived from the drought tolerance donor and recurrent parents (863B and ICMB 841, respectively) used to generate the introgression lines used in the present study.

Yield reduction under conditions of terminal drought stress can occur both due to a decrease in number of panicles per plant and a decrease in grain mass per panicle (Bidinger *et al.*, 1987a; Mahalakshmi *et al.*, 1987). By comparing the panicle numbers per plot in the late-onset and early-onset terminal drought stress moisture regimes with those in fully irrigated non-stress conditions (Tables 45 and 46), it was observed that some hybrids of introgression lines 197-12-2 and 202-7-10 (with tester PPMI 301 in both the early-onset and late-onset stress environments); introgression lines 202-6-26, 202-8-8, 202-8-9, as well as recurrent parent ICMB 841 (with tester PPMI 301 in the more severe early-onset stress environment); donor parent 863B, recurrent parent ICMB 841, and introgression lines 197-10-18, 202-7-4, and 202-8-9 (with tester RIB 335/74 in the more

severe early-onset stress environment), and recurrent parent ICMB 841 as well as introgression lines 197-12-2, 202-7-4, 202-7-12, 202-8-8, 202-8-9 and 202-8-11, (with tester H 77/833-2 in the more severe early-onset stress environment), exhibited up to 19 to 53 panicles more per plot in the control moisture regime despite having essentially equal numbers of plants per plot in the terminal drought stress and fully irrigated control treatments. This suggests that in terms of panicle number maintenance, tester PPMI 301 produced hybrids that were relatively more vulnerable to the milder late-onset terminal drought stress and tester H 77/833-2 produced hybrids that were relatively more vulnerable to the more severe early-onset terminal drought stress. However, even hybrids of the drought tolerance donor parent 863B produced lower numbers of panicles, with all three testers, in the drought stress treatments than in the fully irrigated non-stress control moisture regime. Testcross hybrids of the donor parent 863B and tester PPMI 301 exhibited more panicle yield per plot under late-onset terminal drought stress when compared to other introgression lines and testers (Table 45). The reduction in panicle yield per plot when compared with fully irrigated non-stress conditions was in the range of 200-700 g for the late-onset terminal drought stress regime. In comparisons among the testers, these panicle yield losses were observed to be greatest in hybrids of H 77/833-2 followed by those of PPMI 301 and RIB 335/74. Panicle yield losses were also observed to be greater with hybrids of introgression lines 202-6-26, 202-7-10 and 202-8-9 with tester PPMI 301; recurrent parent ICMB 841 and introgression lines 202-7-12 and 197-18-1 with tester RIB 335/74; and recurrent parent ICMB 841 and introgression lines 197-10-11, 197-10-18, 197-12-2, 197-18-1, 202-7-4, 202-7-12, 202-8-8, 202-8-9, 202-8-11 and 202-8-27 with tester H 77/833-2.

Table 45. Difference between control and late-onset terminal drought stress and its percentage (%) difference

Hybrids	FT	FT %	Plnopt	Plnopt %	Pnnopt	Pnnopt %	ET	ET %	Pnypt	Pnypt %	Grydpt	Grydpt %	Grydpn	Grydpn%	PnHI	PNHI %
863B × PPMI 301	0	0 0	-3	-4 5	4	3 6	0 13	7 7	441 1	16 4	432 2	21 1	2 86	15 2	3 8	5 0
ICMB 841 × PPMI 301	0	0 0	2	2 8	11	6 7	0 09	4 1	461 0	16 8	443 8	23.5	1 86	16 0	5 4	7 8
197-10-18 × PPMI 301	1	2 2	6	8 3	-21	-15 0	-0 49	-22 8	296 9	11 0	336 1	17 6	3 92	28 6	5 3	7 5
202-8-11 × PPMI 301	1	2 3	-2	-2 8	-21	-13 3	-0 20	-10 6	391 6	14 5	396 0	21 4	3 55	30 0	5 6	8 2
197-12-2 × PPMI 301	0	0 0	-8	-11 9	30	19 4	0 65	33 6	373 9	14 3	442 0	22 2	0 69	5 2	7 4	9 7
202-8-9 × PPMI 301	0	0 0	0	0 0	7	3 9	0 22	9 4	604 9	21 7	516 0	27 5	2 40	23 1	4 5	6 7
202-8-27 × PPMI 301	0	0 0	0	0 0	2	1 2	0 03	1 1	298 1	11 0	270 8	15 1	1 62	15 5	3 8	5 7
202-7-12 × PPMI 301	1	2 2	-6	-9 0	-24	-16 7	-0 13	-5 8	550 3	20 4	664 0	33 9	5 92	43 6	13 0	18 0
197-10-11 × PPMI 301	-1	-2 2	5	6 7	-40	-28 6	-0 70	-26 3	260 6	10 4	318 2	18 5	5 55	42 1	6 1	9 0
202-7-4 × PPMI 301	0	0 0	0	0 0	-12	-7 6	-0 17	-7 0	289 2	11 4	358 3	20 2	2 97	26 2	6 8	9 7
202-7-10 × PPMI 301	1	2 2	1	1 5	32	18 0	0 48	20 4	631 7	23 4	708 1	35 4	2 33	20 5	12 1	16 3
202-8-8 × PPMI 301	-1	-2 3	0	0 0	6	3 9	0 08	2 8	203 4	8 2	254 9	14 4	1 68	14 0	5 5	7 7
197-1-12 × PPMI 301	0	0 0	-4	-5 9	0	0 0	0 09	4 7	367 8	13 8	380 2	20 1	2 81	21 9	5 9	8 2
202-6-26 × PPMI 301	0	0 0	2	2 9	12	7 7	0 12	5 3	708 4	25 1	676 1	32 3	3 41	25 4	7 4	10 0
197-18-1 × PPMI 301	1	2 2	-1	-1 4	-32	-23 4	-0 49	-22 8	447 6	16 7	466 1	23 3	5 90	38 7	6 3	8 5
Average		**0.4**		**-0.9**		**-2.7**		**-0.4**		**15.7**		**23.1**		**24.4**		**9.2**
863B × RIB 335/74	1	2 4	-3	-4 6	23	17 3	0 43	20 7	374 8	15 1	318 2	17 1	0 18	1 3	1 8	2 4
ICMB 841 × RIB 335/74	1	2 3	-3	-4 4	18	8 7	0 43	14 0	438 8	18 9	432 3	29 4	1 72	23 6	8 1	12 8
197-10-18 × RIB 335/74	1	2 3	0	0 0	13	6 3	0 21	8 9	326 3	14 1	381 6	25 0	1 22	16 8	7 4	11 3
202-8-11 × RIB 335/74	0	0 0	-4	-6 0	1	0 5	0 22	9 0	182 3	8 6	282 6	21 7	1 72	25 6	6 8	11 5
197-12-2 × RIB 335/74	1	2 3	-2	-2 9	-5	-3 2	-0 01	-0 4	232 0	10 7	245 5	16 5	1 79	19 1	4 1	6 0
202-8-9 × RIB 335/74	1	2 3	-3	-4 3	-6	-2 9	0 02	0 9	384 7	16 3	366 4	24 8	1 85	25 6	6 2	9 9
202-8-27 × RIB 335/74	0	0 0	0	0 0	-7	-3 5	-0 12	-5 3	356 6	16 4	257 6	20 4	1 62	25 6	4 1	7 0
202-7-12 × RIB 335/74	0	0 0	-3	-4 3	-2	-1 1	0 11	4 9	473 8	20 2	553 2	35 8	2 97	36 1	13 2	20 1
197-10-11 × RIB 335/74	1	2 3	9	11 8	-17	-9 3	-0 59	-20 3	385 5	15 8	365 0	23 8	2 52	29 9	6 3	10 0
202-7-4 × RIB 335/74	1	2 4	0	0 0	-1	-0 5	0 01	0 3	289 5	13 0	280 5	19 9	1 58	21 3	4 9	7 8
202-7-10 × RIB 335/74	0	0 0	-5	-7 7	-28	-18 3	-0 22	-8 0	269 2	12 4	305 7	22 3	4 28	41 8	7 4	11 7
202-8-8 × RIB 335/74	0	0 0	1	1 4	-10	-6 1	-0 20	-8 5	261 4	11 3	295 0	19 6	2 25	24 3	5 8	8 9
197-1-12 × RIB 335/74	0	0 0	4	5 3	-23	-13 1	-0 49	-20 7	310 5	14 1	384 6	27 5	3 03	37 2	10 3	16 2
202-6-26 × RIB 335/74	0	0 0	0	0 0	-15	-8 9	-0 19	-6 3	347 2	14 8	382 8	25 4	2 67	30 2	8 1	12 6
197-18-1 × RIB 335/74	-1	-2 4	1	1 5	-27	-16 6	-0 46	-16 4	435 6	17 3	455 9	26 9	4 07	38 2	8 0	11 9
Average		**0.9**		**-0.9**		**-3.4**		**-1.8**		**14.6**		**23.7**		**26.4**		**10.7**

Table 45. Difference between control and late-onset terminal drought stress and its percentage (%) difference (Cont...)

Hybrids	FT	FT %	Plnopt	Plnopt %	Pnnopt	Pnnopt %	ET	ET %	Pnypt	Pnypt%	Grydpt	Grydpt %	Grydpn	Grydpn%	PnHI	PNHI %
863B × H 77/833-2	1	2.3	-3	-4.3	5	3.3	0.14	6.2	380.8	13.8	346.2	16.6	1.93	14.0	2.7	3.6
ICMB 841 × H 77/833-2	0	0.0	-3	-4.2	-2	-0.9	0.10	3.4	591.3	22.4	700.1	39.5	3.44	42.0	16.0	23.8
197-10-18 × H 77/833-2	0	0.0	-3	-4.6	-14	-7.2	-0.04	-1.4	693.2	25.5	785.3	42.0	4.43	45.8	15.3	22.3
202-8-11 × H 77/833-2	-1	-2.2	-2	-2.9	11	4.6	0.25	7.6	683.4	24.4	743.8	39.7	2.85	36.0	13.4	20.1
197-12-2 × H 77/833-2	-1	-2.2	1	1.4	-18	-10.3	-0.27	-8.8	384.1	15.0	411.0	23.8	3.09	30.6	6.7	9.9
202-8-9 × H 77/833-2	-1	-2.2	-2	-2.7	-10	-4.5	-0.06	-1.8	415.8	15.6	519.9	29.1	2.34	29.1	10.9	16.2
202-8-27 × H 77/833-2	1	2.2	4	5.3	-7	-3.3	-0.25	-10.3	543.2	20.6	548.8	32.6	2.79	34.5	9.2	14.4
202-7-12 × H 77/833-2	1	2.2	5	6.9	6	2.8	-0.12	-3.8	640.3	24.5	626.2	37.3	2.84	35.6	11.1	17.2
197-10-11 × H 77/833-2	0	0.0	-4	-5.7	16	7.0	0.40	13.2	699.6	26.2	754.7	41.3	2.89	36.0	13.9	20.4
202-7-4 × H 77/833-2	0	0.0	-3	-4.5	-1	-0.4	0.15	5.3	612.1	23.4	614.7	35.4	2.95	37.8	12.5	18.9
202-7-10 × H 77/833-2	1	2.1	-8	-12.9	-15	-8.0	0.13	3.8	451.7	19.5	558.9	34.2	3.72	41.8	13.8	19.5
202-8-8 × H 77/833-2	0	0.0	-6	-8.8	7	3.3	0.32	10.6	526.3	20.5	497.3	29.1	2.15	26.3	7.2	10.8
197-1-12 × H 77/833-2	0	0.0	-7	-10.4	-32	-17.3	-0.16	-5.6	380.9	15.1	482.0	27.9	3.77	39.6	10.3	15.1
202-6-26 × H 77/833-2	0	0.0	-6	-9.7	9	4.2	0.43	12.8	476.8	19.4	543.8	32.6	2.39	30.4	11.1	16.3
197-18-1 × H 77/833-2	-1	-2.2	1	1.4	-3	-1.4	-0.09	-3.1	427.6	16.3	543.0	29.6	2.58	29.6	11.4	16.3
Average		**0.0**		**-3.7**		**-1.9**		**1.9**		**20.2**		**32.7**		**34.0**		**16.3**
ICMB 93333 × PPMI 301	0	0.0	1	1.4	20	15.9	0.21	10.3	614.2	21.7	565.4	25.3	2.64	14.6	4.0	5.1
ICMB 94111 × PPMI 301	-1	-2.3	-4	-5.9	3	2.2	0.17	8.6	519.6	18.7	499.8	23.6	3.50	21.7	4.6	6.0
ICMB 97111 × PPMI 301	0	0.0	-2	-2.9	-24	-17.6	-0.27	-13.8	490.9	18.4	417.7	20.7	4.41	29.6	2.1	2.8
ICMB 98222 × PPMI 301	-1	-2.2	3	4.3	2	1.7	-0.09	-5.4	690.5	23.9	561.4	25.7	5.29	27.0	1.5	2.0
ICMB 99111 × PPMI 301	1	2.2	-5	-7.5	1	0.7	0.16	7.2	691.5	25.7	607.2	29.8	4.14	30.7	4.8	6.4
ICMB 99222 × PPMI 301	0	0.0	3	4.3	-39	-34.2	-0.63	-38.6	478.3	16.3	439.3	18.9	7.77	37.9	2.5	3.2
ICMB 841 × PPMI 301	-1	-2.4	-1	-1.4	9	5.8	0.22	9.6	360.0	13.6	305.1	15.5	1.20	9.3	1.6	2.2
863B × PPMI 301	1	2.3	1	1.4	-1	-1.0	0.03	2.0	279.5	10.7	372.9	18.2	3.56	18.1	6.5	8.3
ICMH 451	0	0.0	2	2.7	20	14.7	0.24	13.0	539.8	22.8	531.5	29.5	2.80	20.5	6.8	8.9
Average		**-0.3**		**-0.4**		**-1.3**		**-0.8**		**19.1**		**23.0**		**23.3**		**5.0**

First column of a trait = difference between control and late stress treatment value
Second column of a trait = percentage of this difference

Table. 45 Difference between control and late-onset terminal drought stress and its percentage (%) difference (Cont...)

Hybrids	Stydpt	Stydpt %	Bidypt	Bidypt %	HI	HI %	Plht	Plht %	Pnln	Pnln %	Pndi	Pndi %	HGM	HGM %	Grnopn	Grnopn %	Grnopt	Grnopt %
863B × PPMI 301	511.2	23.1	651.3	13.3	3.4	25.6	7	4.2	1.3	5.5	1.6	4.9	-0.007	-0.8	318	14.8	45200	19.2
ICMB 841 × PPMI 301	532.4	24.7	987.2	20.2	1.0	4.9	-6	-4.1	1.3	5.3	0.8	3.3	0.153	20.2	-88	-5.7	5800	2.3
197-10-18 × PPMI 301	577.8	26.7	857.7	17.7	0.3	1.7	-10	-6.8	0.6	2.5	0.5	2.1	0.175	21.9	114	6.7	-16500	-6.9
202-8-11 × PPMI 301	400.1	19.4	800.1	16.8	1.9	11.3	-2	-1.4	2.3	9.2	0.0	0.0	0.167	21.7	173	11.2	-4700	-2.0
197-12-2 × PPMI 301	559.4	26.3	937.1	19.8	1.2	6.1	-4	-2.6	1.2	4.8	0.4	1.6	0.162	19.8	-268	-16.5	7500	3.1
202-8-9 × PPMI 301	160.6	7.6	802.7	16.2	4.1	25.4	-7	-4.6	0.4	1.7	0.9	3.9	0.143	20.1	38	2.7	21000	8.0
202-8-27 × PPMI 301	439.3	22.9	732.4	15.8	0.1	0.6	-20	-14.9	0.8	3.3	1.8	7.7	0.125	16.8	-17	-1.2	-5000	-2.1
202-7-12 × PPMI 301	390.9	17.5	948.5	19.2	7.5	39.0	12	7.0	0.1	0.4	0.5	2.1	0.181	23.5	474	26.9	41400	16.2
197-10-11 × PPMI 301	731.0	30.3	1009.6	20.6	0.5	2.4	-6	-3.9	0.8	3.3	1.6	6.6	0.163	22.5	434	24.2	-17100	-7.3
202-7-4 × PPMI 301	114.1	6.3	403.5	9.3	5.1	54.7	1	0.7	1.0	4.2	1.3	5.3	0.176	24.3	23	1.5	-15900	-6.5
202-7-10 × PPMI 301	670.9	30.8	1336.1	27.4	5.2	19.0	13	8.2	1.6	6.7	0.7	2.8	0.157	21.0	-17	-1.1	48300	17.9
202-8-8 × PPMI 301	408.4	19.1	611.0	13.3	1.3	9.8	0	0.0	3.1	11.8	2.9	11.6	0.067	9.3	125	7.3	19500	7.9
197-1-12 × PPMI 301	576.8	24.7	972.0	19.4	0.9	4.6	-13	-8.9	0.4	1.6	0.5	2.1	0.115	15.1	155	9.1	14900	6.1
202-6-26 × PPMI 301	840.6	37.8	1593.4	31.5	0.3	1.0	5	3.3	1.1	4.5	1.1	4.6	0.133	18.2	123	6.7	42000	14.9
197-18-1 × PPMI 301	285.6	12.4	739.1	14.8	4.2	28.4	-7	-4.7	0.2	0.8	-1.6	-6.6	0.191	24.7	289	14.7	-7300	-2.8
Average		**22.0**		**18.3**		**15.6**		**-1.9**		**4.4**		**3.5**		**18.6**		**6.7**		**4.5**
863B × RIB 335/74	794.1	35.6	1162.1	24.7	-3.7	-20.2	-2	-1.1	0.6	2.3	0.6	2.0	0.049	5.4	-74	-4.7	26000	12.5
ICMB 841 × RIB 335/74	640.2	34.8	1064.3	25.6	0.5	2.0	5	3.2	1.0	4.3	0.6	3.0	0.128	21.6	8	0.7	24800	10.0
197-10-18 × RIB 335/74	391.0	21.3	718.8	17.2	2.8	11.0	-3	-2.0	-0.9	-3.8	3.1	14.0	0.082	13.3	7	0.6	17300	7.1
202-8-11 × RIB 335/74	206.4	13.5	364.7	10.0	1.9	11.0	-13	-8.9	-1.4	-6.0	0.6	3.0	0.087	15.7	68	5.8	15100	6.5
197-12-2 × RIB 335/74	145.6	8.3	351.2	9.0	2.6	26.1	-3	-1.9	-0.3	-1.2	0.5	2.3	0.083	13.2	80	5.5	10500	4.5
202-8-9 × RIB 335/74	199.8	10.9	585.8	14.0	4.2	46.9	-1	-0.7	1.3	5.4	1.2	5.6	0.118	19.3	78	6.6	13000	5.4
202-8-27 × RIB 335/74	287.7	16.8	648.8	16.8	1.9	13.6	-6	-4.2	1.9	7.6	2.5	11.6	0.14	23.7	99	8.9	9800	4.5
202-7-12 × RIB 335/74	269.0	14.9	734.6	17.7	8.8	52.5	-6	-4.0	0.5	2.1	2.7	12.5	0.164	27.0	182	13.6	33000	12.9
197-10-11 × RIB 335/74	337.2	17.9	727.1	16.8	3.4	19.2	0	0.0	0.5	2.2	2.1	9.9	0.165	26.6	101	7.3	-9600	-3.9
202-7-4 × RIB 335/74	409.1	23.5	719.6	18.1	0.2	1.2	-1	-0.7	1.0	4.1	1.6	7.5	0.153	22.0	-3	-0.3	400	0.2
202-7-10 × RIB 335/74	739.4	40.9	1007.8	25.3	-1.6	-8.8	-10	-6.9	0.7	2.9	1.3	6.1	0.099	17.1	553	31.2	17500	7.3
202-8-8 × RIB 335/74	232.7	13.2	485.6	11.9	3.3	13.0	-5	-3.4	1.4	5.8	1.3	6.0	0.101	16.4	147	9.7	7400	3.0
197-1-12 × RIB 335/74	179.1	11.3	494.0	13.0	6.8	57.1	-6	-4.3	1.0	4.3	1.2	5.8	0.072	13.5	461	29.4	42300	16.1
202-6-26 × RIB 335/74	280.7	17.4	628.9	15.9	4.5	34.6	12	7.8	1.6	6.9	1.2	5.5	0.101	16.4	261	18.2	27300	11.3
197-18-1 × RIB 335/74	390.0	19.6	826.7	18.2	4.2	26.5	-5	-3.3	0.2	0.8	-0.2	-0.9	0.119	19.8	425	24.2	24100	8.7
Average		**20.0**		**16.9**		**19.0**		**-2.0**		**2.5**		**6.3**		**18.1**		**10.4**		**7.1**

Table. 45 Difference between control and late-onset terminal drought stress and its percentage (%) difference (Cont...)

Hybrids	Stydpt	Stydpt %	Bidypt	Bidypt %	HI	HI (%)	Plht	Plht (%)	Pnln	Pnln %	Pndi	Pndi %	HGM	HGM %	Grnopn	Grnopn %	Grnopt	Grnopt %
863B × H 77/833-2	220.6	9.6	589.3	11.7	2.3	12.6	3	1.8	0.6	3.0	0.0	0.0	0.098	12.9	-22	-1.2	5900	2.1
ICMB 841 × H 77/833-2	405.2	15.8	1023.2	19.6	9.3	54.9	2	1.3	0.0	0.0	1.3	6.7	0.145	24.2	209	15.8	47200	16.2
197-10-18 × H 77/833-2	374.8	15.0	1068.8	20.4	9.2	78.8	5	3.2	0.0	0.0	2.0	10.1	0.084	14.5	606	36.6	102800	32.0
202-8-11 × H 77/833-2	759.6	27.5	1440.1	25.9	6.0	30.7	7	4.5	0.9	4.3	1.9	9.6	0.133	21.8	241	18.8	71600	23.2
197-12-2 × H 77/833-2	313.1	13.3	698.4	14.2	3.4	16.6	-2	-1.4	-0.3	-1.5	-0.6	-3.2	0.124	20.3	211	12.8	9500	3.3
202-8-9 × H 77/833-2	194.0	8.3	641.8	12.8	6.6	25.5	2	1.4	0.3	1.5	0.6	3.2	0.099	16.5	190	14.1	34300	11.7
202-8-27 × H 77/833-2	168.6	7.9	696.7	14.6	7.6	53.4	2	1.4	-0.8	-4.3	-0.2	-1.1	0.136	22.0	197	15.1	30400	11.2
202-7-12 × H 77/833-2	616.7	24.5	1232.7	24.1	5.5	42.9	7	4.5	-0.1	-0.5	0.6	3.2	0.108	18.2	267	20.1	64700	22.8
197-10-11 × H 77/833-2	621.7	24.5	1331.5	25.6	7.5	51.3	1	0.7	1.8	8.4	2.2	10.8	0.096	16.4	321	23.7	92500	29.8
202-7-4 × H 77/833-2	497.4	21.4	1103.2	22.4	8.3	34.5	-4	-2.7	0.8	4.0	0.6	3.2	0.124	21.0	307	23.4	59900	20.3
202-7-10 × H 77/833-2	259.2	12.7	721.4	16.5	7.6	29.7	-1	-0.7	0.7	3.5	1.1	5.8	0.127	21.1	370	25.4	48200	17.8
202-8-8 × H 77/833-2	253.5	11.2	774.2	16.0	5.2	23.3	-3	-2.0	0.8	3.8	0.5	2.6	0.105	17.2	151	11.2	38100	13.5
197-1-12 × H 77/833-2	196.2	8.8	554.8	11.8	6.6	39.9	-2	-1.3	0.2	1.0	0.8	4.1	0.100	16.6	460	28.6	43000	14.8
202-6-26 × H 77/833-2	395.3	17.0	869.5	18.2	5.9	36.8	9	5.8	0.7	3.3	0.8	4.0	0.108	17.7	167	12.9	49400	18.0
197-18-1 × H 77/833-2	365.1	14.3	803.2	15.5	6.3	53.6	4	2.6	0.1	0.5	0.8	4.1	0.140	22.2	147	10.6	25000	8.6
Average		**15.5**		**18.0**		**39.0**		**1.3**		**1.8**		**4.2**		**18.8**		**17.8**		**16.4**
ICMB 93333 × PPMI 301	91.2	3.7	548.6	10.4	5.1	28.0	-10	-5.6	0.0	0.0	1.6	5.5	0.133	17.2	-95	-4.0	32900	11.3
ICMB 94111 × PPMI 301	485.9	19.7	998.9	19.1	2.1	13.5	7	4.2	2.6	9.7	4.9	14.7	0.161	17.9	116	6.4	22500	9.6
ICMB 97111 × PPMI 301	455.7	23.4	944.2	20.5	-0.6	-3.3	-1	-0.6	1.9	8.5	1.9	6.6	0.058	7.1	460	24.9	44100	17.6
ICMB 98222 × PPMI 301	564.1	23.2	1242.7	23.4	1.1	10.6	-9	-5.6	0.0	0.0	1.0	3.1	0.156	17.8	301	13.3	25400	10.2
ICMB 99111 × PPMI 301	613.6	26.5	1300.7	26.0	2.1	11.0	-11	-7.3	2.2	9.7	-0.6	-2.2	0.178	23.1	194	11.0	31700	11.9
ICMB 99222 × PPMI 301	719.6	29.0	1200.9	22.2	-1.8	-8.8	9	5.1	-0.9	-3.9	0.1	0.3	0.199	22.4	447	19.5	-7900	-3.0
ICMB 841 × PPMI 301	381.3	18.1	738.7	15.6	-0.9	-3.9	5	3.2	0.8	3.9	0.6	2.0	0.164	22.1	-286	-16.3	-20600	-7.7
863B × PPMI 301	539.2	25.7	956.1	20.2	-1.6	-6.1	-2	-1.2	1.1	4.7	0.1	0.3	0.110	12.1	118	5.5	14000	6.2
ICMH 451	-11.5	-0.5	540.7	11.3	7.8	35.1	-8	-4.3	-0.8	-3.2	1.6	6.4	0.177	19.6	2	0.1	28000	13.8
Average		**18.8**		**18.7**		**8.5**		**-1.3**		**3.3**		**4.1**		**17.7**		**6.7**		**7.8**

First column of a trait = difference between control and late stress treatment value
Second column of a trait = percentage of this difference

For grain yield-related characters like grain yield per plot and grain yield per panicle under late-onset terminal drought stress conditions, hybrids of tester H 77/833-2 (32.7%) showed subsequently higher grain losses followed by RIB 335/74 (23.7%) on comparison with fully irrigated non-stress conditions. These results were found to agree well with expectations based upon the earlier report of Yadav *et al.* (2004), who associated differences in the grain yield under conditions of terminal drought stress loss among (ICMB 841 × 863B)-derived mapping population progeny testcrosses to testers PPMI 301 and H 77/833-2 to the presence of QTLs on LG2 and LG7. Among introgression line testcrosses, hybrids of 202-8-8, 197-12-2 and 197-18-1 showed relatively small grain yield loss per plot across all three testers in this relatively mild late-onset terminal drought stress regime. Testcrosses of the donor parent 863B and tester PPMI 301 showed high mean values, with higher grain yield per plot in this moisture regime than hybrids of other parental lines used in this experiment.

By comparing the grain yield per panicle in this late-onset stress regime with that in the fully irrigated non-stress treatment, it was observed that among testers hybrids of PPMI 301 showed great absolute differences than hybrids of the other two testers—perhaps because hybrids of PPMI 301 had the heaviest panicles and therefore greater potential for loss. Among introgression line testcrosses, hybrids of 197-12-2 and 202-8-8 showed reduced levels of grain yield loss per panicle in response to this late-onset terminal drought stress treatment. For panicle harvest index, among testcross hybrids of both PPMI 301 and RIB 335/74 exhibited better maintenance than those of tester H 77/833-2. The overall *per se* reduction in panicle harvest index with introgression line testcross hybrids was high (16%) with H 77/833-2 in this late-onset terminal drought

stress regime. But these results contradict the earlier findings of Yadav *et al.* (2004), which highlighted the presence of putative drought tolerance QTLs on LG2 that could be detected with high-tillering tester H 77/833-2 and relatively mild late-onset terminal drought stress treatments. These putative QTLs may be false positives since they were detected only under less severe late-onset terminal drought stress conditions. This observation also indicates the importance of the year and season for drought tolerance screening experiments. Clearly it will be necessary to repeat the drought tolerance assessment of the introgression lines generated in the current study before any firm conclusions can be drawn. Among introgression lines, testcrosses of 197-12-2, 202-8-8, 202-8-27, 197-18-1 and the donor parent 863B showed panicle high harvest index values in the late-onset terminal drought stress regime. Among introgression line testcross hybrids of 197-12-2 and 202-8-27, the reduction in panicle harvest index values under late-onset stress conditions were relatively smaller, but hybrids of the latter had larger numbers of panicles per plot.

For developing testcross hybrids for stover yield maintenance under late-onset terminal drought stress conditions, tester H 77/833-2 was the best followed by RIB 335/74. Tester PPMI 301 was the worst for this trait, exhibiting a greater reduction of stover yield per plot among its testcross hybrids in response to the late-onset terminal drought stress moisture regime. Testcross hybrids of introgression lines 202-8-9, 197-12-2 and 197-1-12 consistently maintained their stover yield per plot with both of the better-performing testers, namely H 77/833-2 and RIB 335/74. With tester PPMI 301, hybrids of introgression lines 202-8-9, 202-7-4 and 197-18-1 were the best at maintaining their stover yields per plot. Interestingly, hybrids of both donor parent 863B and introgression

line 202-8-27 with tester H 77/833-2 were also relatively good at maintaining their stover yields in this late-onset terminal drought stress environment. Among introgression lines 202-8-9 was the best at conferring its hybrids with the ability to maintain stover yield per plot in this stress regime. For this introgression line, the behavior of the introgressed genomic region was found to match well with the expectations for this trait and stress regime based upon earlier results of Yadav *et al.* (2004).

Among testcross hybrids, only those of tester PPMI 301 exhibited limited influence of the late-onset terminal drought stress conditions by maintaining their harvest index values at levels similar to those under fully irrigated non-stress conditions. Introgression line testcross hybrids of tester H 77/833-2 showed much variation in harvest index values under late-onset terminal drought stress conditions. However, testcrosses of donor parent 863B and introgression line 197-12-2 with H 77/833-2 showed less influence of late-onset terminal drought stress conditions on their harvest index values. With PPMI 301 and RIB 335/74, introgression lines 197-10-18, 202-7-10, 202-8-8, 202-8-9, 202-8-11 and 202-8-27 consistently exhibited better maintenance of harvest index values. The observed effects of tester H 77/833-2 on harvest index maintenance was contradictory with earlier reports of Yadav *et al.* (2004) They reported detection of QTLs for harvest index maintenance on LG2 with tester H 77/833-2 under late-onset terminal drought stress conditions. This contradiction may be due to a false positive QTL due the small size of the mapping population used, or due to the milder late-onset terminal drought stress conditions observed in the ICRISAT-Patancheru drought nursery during 1999 when this putative QTL was detected.

By comparing the results of the fully irrigated control and late-onset terminal drought stress conditions for grain and stover related characters, the allelic composition of the introgression lines in genomic regions between SSR markers *Xpsmp*2066 and *Xpsmp*2255 were found to be in good agreement with observed drought tolerance differences. Similarly, these results showed that simultaneous improvement of grain yield and stover yield could be possible (Yadav *et al.*, 2004). For biomass yield per plot under late-onset terminal drought stress conditions, H 77/833-2 was the best pollinator followed by RIB 335/74. Due to the larger number of tillers produced by hybrids of H 77/833-2, the biomass yield loss due to the late-onset terminal drought stress treatment was compensated for. Among introgression lines, testcrosses of 197-10-18, 202-8-9, 202-7-10 and 197-18-1 produced higher biomass yields in these moderately severe late-onset terminal drought stress conditions. However, these introgression lines showed less/poor in grain yield production in this environment due to biomass partitioning (Bidinger *et al.*, 1977; Passioura, 1977; Slafer and Araus, 1998).

For panicle length, marginal variation was observed in responsive to this late-onset stress, with increasing sensitivity among testers from H 77/833-2 and RIB 335/74 to PPMI 301. Hence, long-panicled hybrids of tester PPMI 301 were the most subject to reduction in panicle length by the late-onset terminal drought stress moisture regime. Testcrosses of most of the introgression lines exhibited less panicle length in response to this mild moisture stress regime, as did those of the testcrosses of recurrent parent ICMB 841; however, hybrids of 197-12-2 showed marginal increases in panicle length across testers RIB 335/74 and H 77/833-2 under these late-onset terminal drought stress conditions.

The testcrosses of recurrent parent ICMB 841 exhibited only very small decreases, or even increases, in panicle diameter and grain number per panicle in response to this stress regime, comparable to those of the larger-panicled donor parent 863B. Thus it was not surprising that among the introgression line testcrosses, only the hybrids of 197-12-2 and 197-18-1 showed even marginal improvement in these traits relative to the recurrent parent under late-onset terminal drought stress conditions were. For panicle diameter maintenance, increased variation among testcross hybrids was exhibited by tester RIB 335/74. For 100-grain mass, all testcrosses had smaller grains under late-onset terminal drought stress conditions than in the fully irrigated control, except the combination of donor parent 863B × PPMI 301. Among introgression lines, testcrosses of 197-1-12, 197-10-18, 197-12-2, 202-8-8 and 202-8-27 showed the smallest decreases in grain size in response to this mild stress. Among testers, increased responsiveness to drought stress for grain number per panicle and grain number per plot was exhibited from hybrids of PPMI 301 (least responsive), RIB 335/74 and H 77/833-2 (most responsive). Hybrids of tester H 77/833-2 showed the greatest percentage of reduction in grain number per panicle as well as per plot. Among introgression line testcrosses, hybrids of 197-12-2, 202-8-9, 197-10-11 and 197-18-1 maintained their grain numbers relatively well under these relatively mild late-onset terminal drought stress conditions.

Based on combining ability analysis, it was easy to classify the introgression lines into two categories: First group produced hybrids with increased number of panicles per plot, less of grain yield per panicle, higher stover yield, lower harvest index values, smaller panicle diameter and hence poor grain numbers per plot and per panicle. The

members of this first group were introgression lines 202-8-11, 202-8-9, 202-8-27, 197-10-11 and 202-7-4. The second group, which produced hybrids with the opposite complex of characters, consisted of introgression lines 197-12-2, 202-7-10 and the donor parent 863B. This classification is based on the concept of differences in biomass partitioning (Bidinger *et al.*, 1987a). Under late-onset terminal drought stress conditions, the *sca* effects of testcross hybrids indicated that recurrent parent hybrid ICMB 841 gave higher than expected grain yield with tester PPMI 301. Similarly, with testers RIB 335/74 and H 77/833-2 the donor parent 863B exhibited significant *sca* effects for higher grain yield per panicle, stover yield and grain number per plot under these conditions, indicated better than expected hybrid performance.

Early-onset terminal drought stress conditions:

In the early-onset terminal drought stress environment, drought stress commenced at the mid-flowering stage and symptoms of drought stress started to appear approximately 10 days after the last irrigation, which occurred at the time the trial was in the boot leaf growth stage. Among testcross hybrids, those of late-flowering high tillering tester H 77/833-2 flowered 1-2 days (197-12-2) later in this environment when compared with fully irrigated non-stress conditions. This delayed-flowering response of the H 77/833-2 testcrosses is probably beneficial under a non-terminal mid-season drought stress moisture regime, but was not beneficial in this experiment. Under these more severe drought stress conditions, the plant numbers per plot may be reduced due to death or lodging of plants. For plant numbers per plot, testcrosses of introgression lines 202-6-26 and 197-18-1 showed poor plant stands in this moisture regime, so the observations on their relative performance in these moisture regimes were confounded with these

difference in plant stand and this experiment should be repeated to permit fair comparisons with the other testcrosses.

As in the control treatment, hybrids of tester H 77/833-2 had highest number of panicles per plot followed by those of RIB 335/74. Similarly, hybrids of introgression lines 202-8-11, 202-8-9, 202-8-27, 202-7-12 and 197-10-11 had large number of panicles per plot (Table 46). Among testers, hybrids of RIB 335/74 (36.2%) showed less reduction in panicle yield per plot than those of H 77/833-2 (40.7%) and PPMI 301 (41.0%). The panicle yield loss percentages of introgression line hybrids with testers PPMI 301 and RIB 335/74 were never more than that of the counterpart recurrent parent testcrosses. However, several of the introgression line testcrosses with H 77/833-2 suffered greater percentages of reduction in panicle yield than did ICMB 841 × H 77/833-2. Across testers PPMI 301 and RIB 335/74, hybrids of introgression lines 197-1-12, 197-10-11, 197-10-18, 197-18-1, 202-7-10, 202-8-11 and 202-8-27 maintained their panicle yields per plot better than did ICMB 841 in these severe drought stress conditions.

For grain yield per plot, highest yield reduction observed in this early-onset terminal drought stress environment among hybrids of tester H 77/833-2 (53.4%) followed by those of PPMI 301 (53.0%) and RIB 335/74 (50.7%). These results were found to be slightly contradictory with those of Yadav *et al.* (2004), who observed greater yield reductions among hybrids based on tester PPMI 301 than for those of tester H 77/833-2 under such relatively severe terminal drought stress conditions; however, as expected across testers the hybrids of drought tolerance donor parent 863B suffered less grain yield losses in this moisture regime than did those of recurrent parent ICMB 841. Among introgression line testcrosses, among introgression line hybrids with tester PPMI

Table. 46. Difference between control and early-onset terminal drought stress and its percentage (%) difference

Hybrids	FT	FT %	Plnopt	Plnopt %	Pnnopt	Pnnopt %	ET	ET %	Pnydpt	Pnydpt %	Grydpt	Grydpt %	Gypn	Gypn %	Pnhi	Pnhi %
863B × PPMI 301	0.0	0.0	-3.0	-4.5	3.0	2.7	0.1	8.6	1036.1	38.6	978.2	47.7	8.9	47.4	11.2	14.7
ICMB 841 × PPMI 301	-1.0	-2.2	0.0	0.0	23.0	14.0	0.3	13.5	1299.8	47.4	1133.3	59.9	6.3	53.8	17.0	24.7
197-10-18 × PPMI 301	0.0	0.0	1.0	1.4	15.0	10.7	0.2	8.5	1046.0	38.7	995.5	52.2	6.2	45.0	14.8	21.0
202-8-11 × PPMI 301	0.0	0.0	0.0	0.0	2.0	1.3	0.0	0.6	1067.9	39.5	1008.1	54.5	6.4	53.9	17.0	24.8
197-12-2 × PPMI 301	-1.0	-2.2	-5.0	-7.5	53.0	34.2	0.9	45.5	1099.7	42.0	1061.3	53.2	4.1	31.0	14.4	18.8
202-8-9 × PPMI 301	0.0	0.0	-6.0	-8.6	25.0	13.8	0.6	25.4	1289.1	46.2	1133.3	60.3	5.8	55.5	17.5	26.1
202-8-27 × PPMI 301	0.0	0.0	-1.0	-1.4	17.0	9.8	0.3	11.0	1109.5	41.1	918.6	51.2	4.7	45.2	12.6	19.0
202-7-12 × PPMI 301	0.0	0.0	-7.0	-10.4	-10.0	-6.9	0.1	4.4	1162.8	43.1	1074.8	54.9	7.9	57.8	14.8	20.4
197-10-11 × PPMI 301	-1.0	-2.2	5.0	6.7	-29.0	-20.7	-0.6	-21.4	831.6	33.3	818.9	47.6	8.0	60.8	14.9	21.9
202-7-4 × PPMI 301	-1.0	-2.3	6.0	8.8	2.0	1.3	-0.2	-7.2	991.2	39.2	886.0	50.0	5.7	50.1	12.1	17.3
202-7-10 × PPMI 301	0.0	0.0	-1.0	-1.5	19.0	10.7	0.3	14.0	1126.6	41.7	1090.2	54.4	5.1	45.3	15.8	21.3
202-8-8 × PPMI 301	0.0	0.0	0.0	0.0	25.0	16.4	0.3	11.9	957.4	38.6	879.7	49.7	5.0	41.8	13.5	18.9
197-1-12 × PPMI 301	0.0	0.0	-6.0	-8.8	16.0	10.7	0.4	19.6	1041.4	39.2	952.4	50.2	5.9	45.6	14.3	20.0
202-6-26 × PPMI 301	0.0	0.0	2.0	2.9	22.0	14.1	0.3	12.0	1272.3	45.1	1222.8	58.4	7.2	53.5	18.3	24.6
197-18-1 × PPMI 301	0.0	0.0	5.0	7.1	16.0	11.7	0.1	5.5	1110.3	41.3	1005.3	50.3	7.1	46.6	11.8	15.8
Average		**-0.6**		**-1.0**		**8.2**		**10.1**		**41.0**		**53.0**		**48.9**		**20.6**
863B × RIB 335/74	0.0	0.0	0.0	0.0	21.0	15.8	0.3	16.4	725.8	29.2	721.4	38.7	4.4	30.6	10.7	14.3
ICMB 841 × RIB 335/74	1.0	2.3	-2.0	-2.9	47.0	22.6	0.8	26.3	1061.3	45.6	886.6	60.2	3.9	53.2	18.7	29.5
197-10-18 × RIB 335/74	1.0	2.3	-3.0	-4.3	25.0	12.1	0.5	19.4	864.0	37.3	873.6	57.1	3.8	52.1	21.3	32.4
202-8-11 × RIB 335/74	-1.0	-2.4	-8.0	-11.9	13.0	6.4	0.5	22.3	702.4	33.0	641.4	49.2	3.1	45.8	13.2	22.3
197-12-2 × RIB 335/74	1.0	2.3	-4.0	-5.7	-1.0	-0.6	0.1	4.3	786.3	36.3	769.0	51.8	4.6	49.6	15.7	23.0
202-8-9 × RIB 335/74	0.0	0.0	-1.0	-1.4	19.0	9.3	0.3	11.7	937.5	39.6	799.5	54.0	3.5	48.8	14.5	23.2
202-8-27 × RIB 335/74	0.0	0.0	-2.0	-2.9	0.0	0.0	0.1	4.3	653.1	30.1	582.8	46.1	2.9	46.2	13.7	23.5
202-7-12 × RIB 335/74	1.0	2.3	-3.0	-4.3	5.0	2.6	0.2	10.0	835.1	35.5	851.2	55.0	4.5	54.6	20.0	30.4
197-10-11 × RIB 335/74	1.0	2.3	1.0	1.3	4.0	2.2	0.0	0.6	1009.0	41.4	878.6	57.3	4.8	57.1	17.5	27.8
202-7-4 × RIB 335/74	0.0	0.0	-2.0	-2.9	20.0	10.4	0.4	13.4	883.4	39.6	709.5	50.4	3.1	41.0	14.4	22.9
202-7-10 × RIB 335/74	0.0	0.0	-7.0	-10.8	-41.0	-26.8	-0.3	-12.6	678.0	31.3	614.0	44.8	6.2	60.8	13.7	21.6
202-8-8 × RIB 335/74	0.0	0.0	-1.0	-1.4	-19.0	-11.6	-0.2	-9.4	917.3	39.6	656.1	43.5	4.7	50.9	8.7	13.4
197-1-12 × RIB 335/74	0.0	0.0	0.0	0.0	8.0	4.6	0.1	3.8	750.8	34.0	694.5	49.6	3.9	47.7	15.1	23.8
202-6-26 × RIB 335/74	0.0	0.0	5.0	7.1	7.0	4.1	-0.1	-4.0	775.1	33.1	781.3	51.8	4.2	47.9	17.6	27.4
197-18-1 × RIB 335/74	-1.0	-2.4	-1.0	-1.5	2.0	1.2	0.0	1.3	960.0	38.0	857.8	50.6	5.3	49.6	13.4	19.9
Average		**0.4**		**-2.8**		**3.5**		**7.2**		**36.2**		**50.7**		**49.1**		**23.7**

Table. 46. Difference between control and early-onset terminal drought stress and its percentage (%) difference (Cont...)

Hybrids	FT	FT %	Plnopt	Plnopt %	Pnnopt	Pnnopt %	ET	ET %	Pnydpt	Pnydpt %	Grydpt	Grydpt %	Gypn	Gypn %	Pnhi	Pnhi %
863B × H 77/833-2	1.0	2.3	-3.0	-4.3	17.0	11.1	0.3	14.7	847.3	30.8	799.2	38.3	4.2	30.5	8.0	10.5
ICMB 841 × H 77/833-2	-1.0	-2.2	-3.0	-4.2	32.0	14.7	0.5	17.0	1037.4	39.2	931.4	52.5	3.6	44.1	15.7	23.4
197-10-18 × H 77/833-2	1.0	2.2	-6.0	-9.2	0.0	0.0	0.3	9.4	1336.8	49.1	1111.0	59.4	5.5	56.8	15.1	22.0
202-8-11 × H 77/833-2	-1.0	-2.2	-3.0	-4.3	39.0	16.3	0.6	19.4	1364.1	48.6	1136.1	60.6	4.2	52.8	15.0	22.5
197-12-2 × H 77/833-2	-2.0	-4.4	0.0	0.0	34.0	19.5	0.5	15.3	1035.2	40.6	836.0	48.3	3.7	36.5	8.0	11.8
202-8-9 × H 77/833-2	0.0	0.0	0.0	0.0	23.0	10.4	0.3	9.7	1067.6	40.2	1020.1	57.1	4.0	50.2	18.8	27.9
202-8-27 × H 77/833-2	1.0	2.2	6.0	7.9	10.0	4.7	-0.1	-2.9	1103.8	42.0	981.5	58.2	4.7	57.9	18.0	28.1
202-7-12 × H 77/833-2	0.0	0.0	4.0	5.6	21.0	9.9	0.1	4.4	1112.1	42.6	827.0	49.2	3.5	44.4	8.0	12.4
197-10-11 × H 77/833-2	0.0	0.0	-1.0	-1.4	14.0	6.1	0.2	7.8	1018.2	38.2	973.2	53.2	4.0	49.3	17.1	25.0
202-7-4 × H 77/833-2	0.0	0.0	-5.0	-7.5	35.0	15.6	0.8	26.6	1091.8	41.8	1013.8	58.4	3.9	49.9	19.0	28.7
202-7-10 × H 77/833-2	0.0	0.0	-5.0	-8.1	17.0	9.1	0.4	13.3	904.5	39.0	865.1	52.9	4.3	48.4	15.4	21.8
202-8-8 × H 77/833-2	-1.0	-2.2	-3.0	-4.4	46.0	22.0	0.8	25.3	1052.1	41.0	962.5	56.2	3.7	44.7	17.4	26.1
197-1-12 × H 77/833-2	-1.0	-2.2	-2.0	-3.0	13.0	7.0	0.3	9.5	966.6	38.2	864.4	50.1	4.5	47.0	12.4	18.2
202-6-26 × H 77/833-2	0.0	0.0	-6.0	-9.7	20.0	9.4	0.6	18.0	983.3	39.9	903.7	54.1	4.0	50.7	16.3	24.0
197-18-1 × H 77/833-2	0.0	0.0	4.0	5.5	21.0	9.9	0.1	4.6	1043.6	39.8	960.7	52.4	4.3	48.9	15.1	21.6
Average		**-0.4**		**-2.5**		**11.1**		**12.8**		**40.7**		**53.4**		**47.5**		**21.6**
ICMB 93333 x PPMI 301	0.0	0.0	3.0	4.1	34.0	27.0	0.4	17.6	1484.1	52.4	1342.4	60.1	8.3	46.1	14.1	17.9
ICMB 94111 x PPMI 301	0.0	0.0	-3.0	-4.4	19.0	14.2	0.4	20.3	1050.8	37.9	992.8	46.9	6.1	37.6	11.2	14.7
ICMB 97111 x PPMI 301	0.0	0.0	-4.0	-5.7	14.0	10.3	0.3	13.3	1216.2	45.6	1087.2	53.7	7.5	50.1	11.3	14.9
ICMB 98222 x PPMI 301	-1.0	-2.2	-3.0	-4.3	17.0	14.8	0.2	15.2	1293.4	44.8	1106.7	50.7	8.3	42.5	8.3	11.0
ICMB 99111 x PPMI 301	1.0	2.2	-8.0	-11.9	11.0	7.2	0.4	18.2	1299.7	48.3	1223.3	60.0	7.8	57.5	16.7	22.1
ICMB 99222 x PPMI 301	1.0	2.3	1.0	1.4	18.0	15.8	0.2	13.5	1240.3	42.3	1171.8	50.4	8.5	41.3	12.1	15.3
ICMB 841 x PPMI 301	0.0	0.0	-1.0	-1.4	29.0	18.8	0.5	22.2	998.9	37.8	892.0	45.3	3.7	28.8	9.1	12.2
863B x PPMI 301	0.0	0.0	-4.0	-5.8	-29.0	-28.2	-0.3	-20.1	977.9	37.3	1035.0	50.6	11.2	57.0	16.1	20.6
ICMH 451	0.0	0.0	1.0	1.4	11.0	8.1	0.2	10.8	1261.7	53.4	1063.4	58.93	6.8	49.5	8.8	11.5
Average		**0.3**		**-3.0**		**9.8**		**12.3**		**44.4**		**53.0**		**45.6**		**15.6**

First column of a trait = difference between control and early stress treatment value
Second column of a trait = percentage of this difference

Table 46. Difference between control and early-onset terminal drought stress and it's percentage (%) difference (cont...).

Hybrids	Stydpt	Stydpt %	Biydpt	Bidypt %	HI	HI (%)	Plht	Plht %	Pnln	Pnln %	Pndi	Pndi %	HGM	HGM %	Grnopn	Grnopn %	Grnopt	Grnopt %
363B × PPMI 301	934.3	42.2	1953.6	39.9	5.8	13.9	4	2.4	0.3	1.2	2.0	6.1	0.247	28.3	571	26.6	66000	28.0
CMB 841 × PPMI 301	660.0	30.6	1925.1	39.4	13.1	34.0	-16	-10.8	0.2	0.8	-0.7	-2.9	0.306	40.4	348	22.7	83300	33.0
197-10-18 × PPMI 301	317.1	14.6	1360.0	28.0	12.6	31.9	-8	-5.5	1.0	4.1	1.8	7.5	0.383	47.9	-121	-7.1	11600	4.9
202-8-11 × PPMI 301	463.4	22.5	1561.4	32.7	12.7	32.8	-11	-7.7	1.5	6.0	1.6	6.9	0.307	39.9	328	21.3	55600	23.3
197-12-2 × PPMI 301	1009.4	47.5	2107.1	44.4	6.6	15.6	0	0.0	3.1	12.3	1.7	6.9	0.349	42.6	-306	-18.8	49900	20.5
202-8-9 × PPMI 301	741.3	35.0	2087.2	42.0	11.9	32.1	2	1.3	3.3	13.9	3.8	16.3	0.321	45.1	251	17.5	75400	28.7
202-8-27 × PPMI 301	207.6	10.8	1303.1	28.2	13.0	33.5	-26	-19.4	-0.3	-1.2	-3.3	-14.1	0.293	39.5	102	7.3	42600	17.7
202-7-12 × PPMI 301	887.9	39.7	2035.1	41.3	8.0	20.2	9	5.3	2.0	8.0	-0.3	-1.2	0.347	45.1	386	21.9	45000	17.6
197-10-11 × PPMI 301	711.3	29.5	1550.2	31.6	8.1	23.5	-2	-1.3	1.9	7.8	2.2	9.0	0.245	33.9	723	40.2	50800	21.8
202-7-4 × PPMI 301	558.0	31.0	1497.7	34.6	9.6	23.3	-6	-4.1	2.6	10.8	4.4	18.1	0.285	39.4	260	16.6	49400	20.2
202-7-10 × PPMI 301	732.9	33.6	1911.7	39.2	10.2	24.7	-6	-3.8	1.7	7.0	2.4	9.7	0.222	29.7	360	23.9	91100	33.8
202-8-8 × PPMI 301	932.8	43.7	1879.7	40.8	6.4	16.6	0	0.0	1.9	7.2	2.1	8.4	0.23	31.9	277	16.3	71600	28.9
197-1-12 × PPMI 301	807.0	34.5	1856.7	37.0	8.3	21.7	-6	-4.1	2.6	10.6	4.2	17.2	0.271	35.7	250	14.7	47700	19.4
202-6-26 × PPMI 301	866.7	38.9	2149.0	42.4	12.4	30.0	-7	-4.6	0.0	0.0	-2.7	-11.3	0.304	41.5	364	19.8	80400	28.5
197-18-1 × PPMI 301	805.4	34.9	1932.6	38.6	7.8	19.5	-12	-8.1	3.3	12.9	1.8	7.3	0.276	35.7	297	15.1	50700	19.8
Average		**32.6**		**37.3**		**24.9**		**-4.0**		**6.8**		**5.6**		**38.4**		**15.9**		**23.1**
863B × RIB 335/74	517.3	23.2	1252.0	26.6	7.5	18.8	18	10.2	2.2	8.5	5.6	18.3	0.238	26.4	78	4.9	36300	17.5
ICMB 841 × RIB 335/74	515.0	28.0	1572.2	37.8	14.0	39.3	0	0.0	1.1	4.6	0.0	0.0	0.222	37.5	253	21.2	93800	37.7
197-10-18 × RIB 335/74	568.0	30.9	1458.5	35.0	13.2	36.1	1	0.7	0.7	2.9	3.4	15.3	0.231	37.4	283	23.9	79700	32.5
202-8-11 × RIB 335/74	275.8	18.0	1004.2	27.4	7.1	21.5	-10	-6.8	-1.0	-4.2	-3.8	-19.1	0.193	34.8	164	14.0	46200	19.7
197-12-2 × RIB 335/74	280.8	16.0	1045.9	26.7	12.2	32.2	-3	-1.9	1.5	6.1	-2.4	-11.0	0.200	31.7	353	24.2	71500	30.3
202-8-9 × RIB 335/74	57.4	3.1	925.8	22.1	13.5	38.2	-11	-7.4	0.0	0.0	-1.2	-5.6	0.222	36.4	237	20.1	71800	29.7
202-8-27 × RIB 335/74	51.7	3.0	675.8	17.5	10.8	33.3	-17	-11.9	-0.6	-2.4	0.9	4.1	0.171	29.0	274	24.8	50600	23.0
202-7-12 × RIB 335/74	419.4	23.3	1194.4	28.8	13.6	36.3	-13	-8.6	-0.5	-2.1	-6.9	-31.9	0.234	38.6	318	23.7	70400	27.4
197-10-11 × RIB 335/74	119.4	6.3	1123.6	26.0	15.5	43.3	1	0.6	-2.0	-8.6	-2.5	-11.7	0.172	27.7	573	41.2	97100	39.3
202-7-4 × RIB 335/74	526.7	30.2	1400.0	35.3	7.5	21.7	-2	-1.3	1.5	6.2	0.0	0.0	0.336	48.4	-91	-8.3	25600	12.1
202-7-10 × RIB 335/74	453.0	25.1	1129.7	28.4	8.2	23.6	-9	-6.2	0.2	0.8	0.9	4.2	0.220	38.1	623	35.1	17000	7.1
202-8-8 × RIB 335/74	415.3	23.6	1329.0	32.6	8.8	23.6	-8	-5.4	-0.7	-2.8	-0.5	-2.3	0.237	38.6	374	24.6	26900	10.9
197-1-12 × RIB 335/74	62.1	3.9	843.1	22.2	13.7	36.7	-13	-9.3	-0.1	-0.4	-4.0	-19.4	0.150	28.1	450	28.7	73300	28.0
202-6-26 × RIB 335/74	405.7	25.1	1177.0	29.7	11.4	29.9	-5	-3.3	1.9	4.2	-3.1	-14.1	0.199	32.3	333	23.3	65900	27.3
197-18-1 × RIB 335/74	405.8	20.4	1407.6	31.1	10.0	26.7	1	0.7	1.2	5.0	0.2	0.9	0.181	30.2	476	27.1	76700	27.5
Average		**18.7**		**28.5**		**30.7**		**-3.3**		**1.2**		**-4.8**		**34.3**		**21.9**		**24.7**

Table 46. **Difference between control and early-onset terminal drought stress and it's percentage (%) difference (cont...).**

Hybrids	Stydpt	Stydpt %	Biydpt	Bidypt %	HI	HI (%)	Plht	Plht (%)	Pnln	Pnln %	Pndi	Pndi %	HGM	HGM %	Grnopn	Grnop %	Grnopt	Grnopt %
863B x H 77/833-2	225.2	9.8	1039.6	20.6	8.6	20.8	11	6.6	-2.7	-13.5	5.5	20.6	0.191	25.2	135	7.4	48300	17.6
ICMB 841 x H 77/833-2	655.7	25.6	1718.5	32.9	10.8	31.5	-4	-2.6	-3.0	-15.6	-4.1	-21.2	0.192	32.1	191	14.4	85200	29.3
197-10-18 x H 77/833-2	359.7	14.3	1658.6	31.7	14.1	39.6	4	2.6	-1.9	-9.5	0.9	4.5	0.182	31.4	676	40.8	145600	45.4
202-8-11 x H 77/833-2	955.5	34.6	2379.1	42.7	10.2	30.4	12	7.8	-1.8	-8.7	-0.4	-2.0	0.166	27.2	461	35.9	145300	47.1
197-12-2 x H 77/833-2	544.9	23.1	1583.0	32.2	7.5	21.5	-15	-10.2	-1.4	-6.9	-4.0	-21.0	0.138	22.5	310	18.8	98900	34.7
202-8-9 x H 77/833-2	136.3	5.9	1178.9	23.6	14.8	41.6	-2	-1.4	-1.9	-9.4	-1.4	-7.4	0.203	33.9	318	23.6	97100	33.2
202-8-27 x H 77/833-2	750.2	35.2	1858.6	39.0	11.6	32.5	-20	-14.2	-4.0	-21.2	-5.3	-29.2	0.24	38.9	377	28.9	82700	30.4
202-7-12 x H 77/833-2	837.3	33.3	1989.6	38.8	6.3	19.1	2	1.3	-3.7	-18.5	-4.5	-23.6	0.214	36.1	149	11.2	54800	19.3
197-10-11 x H 77/833-2	698.6	27.5	1708.0	32.8	10.6	29.9	1	0.7	-1.0	-4.6	-2.0	-9.8	0.207	35.3	287	21.1	79900	25.8
202-7-4 x H 77/833-2	656.1	28.2	1731.4	35.1	11.3	32.0	5	3.4	-1.0	-4.9	-0.4	-2.1	0.159	26.9	396	30.2	125300	42.5
202-7-10 x H 77/833-2	533.1	26.2	1448.1	33.2	10.4	27.4	-11	-7.4	0.4	2.0	-6.8	-35.6	0.166	27.5	426	29.2	99900	36.9
202-8-8 x H 77/833-2	577.5	25.5	1639.4	34.0	12.4	35.2	-6	-4.1	-2.6	-12.5	-2.1	-10.9	0.202	33.1	249	18.4	101100	35.9
197-1-12 x H 77/833-2	446.8	20.2	1424.2	30.2	10.6	28.9	2	1.3	-2.7	-13.3	-3.4	-17.6	0.176	29.1	431	26.8	90300	31.0
202-6-26 x H 77/833-2	572.1	24.6	1547.8	32.4	11.7	33.5	10	6.4	0.8	3.7	1.4	7.0	0.208	34.0	308	23.8	81900	29.8
197-18-1 x H 77/833-2	796.3	31.2	1838.2	35.5	9.8	27.5	-6	-3.9	-0.7	-3.4	-4.2	-21.6	0.211	33.4	315	22.6	82000	28.3
Average		**24.3**		**33.0**		**30.1**		**-0.9**		**-9.1**		**-11.4**		**31.1**		**23.6**		**32.5**
ICMB 93333 x PPMI 301	827.1	33.7	2326.3	44.0	12.9	30.3	20	11.2	1.1	4.7	4.0	13.8	0.311	40.3	228	9.7	97000	33.4
ICMB 94111 x PPMI 301	742.4	30.1	1807.4	34.5	7.6	18.8	3	1.8	3.4	12.6	6.3	18.8	0.268	29.8	210	11.6	56500	24.0
ICMB 97111 x PPMI 301	180.2	9.3	1419.0	30.8	15.1	34.7	0	0.0	0.0	0.0	4.5	15.6	0.252	30.8	527	28.5	85300	34.1
ICMB 98222 x PPMI 301	661.4	27.3	2003.0	37.7	9.6	23.1	21	13.0	-2.2	-10.0	11.2	34.3	0.298	34.1	328	14.4	65000	26.0
ICMB 99111 x PPMI 301	668.5	28.9	1941.1	38.8	13.5	33.3	-13	-8.6	-0.1	-0.4	2.4	8.7	0.315	41.0	490	27.8	88500	33.1
ICMB 99222 x PPMI 301	1216.8	49.1	2444.5	45.2	3.3	7.6	29	16.3	1.1	4.7	7.0	22.4	0.329	37.0	167	7.3	56000	21.4
ICMB 841 x PPMI 301	940.6	44.6	1902.6	40.1	1.9	4.6	8	5.2	0.1	0.4	11.9	38.8	0.234	31.6	-52	-3.0	52000	19.4
863B x PPMI 301	308.3	14.7	1332.2	28.2	13.5	31.2	13	7.9	0.3	1.2	7.8	25.4	0.393	43.4	554	25.6	30500	13.5
ICMH 451	793.4	32.9	2076.6	43.5	9.7	25.8	30	16.0	-1.2	-4.8	2.9	11.5	0.318	35.3	334	22.1	72400	35.8
Average		**30.1**		**38.1**		**23.3**		**7.0**		**1.0**		**21.1**		**35.9**		**16.0**		**26.7**

First column of a trait = difference between control and early stress treatment value
Second column of a trait = percentage of this difference

301 those of 197-10-11, 202-7-4 and 202-8-8 best maintained their grain yield per plot; similarly, hybrids of RIB 335/74 with 197-1-12, 202-7-10, 202-8-8, 202-8-11 and 202-8-27 best maintained their grain yields per plot; and hybrids of H 77/833-2 with 197-12-2, 202-7-10 and 202-7-12 were the best at maintaining their grain yield. Based on these results, it was inferred that the genomic regions in between SSR markers *Xpsmp*2066 and *Xpsmp*2059 (lower arm of LG2) are playing a major role in maintaining grain yield per plot under these relatively severe drought stress conditions.

Among testers, hybrids of RIB 335/74 (49.1%) exhibited more grain loss per panicle under early-onset terminal drought stress conditions, followed by those of PPMI 301 (48.9%) and H 77/833-2 (47.5%), when compared with grain yield per panicle under fully irrigated non-stress conditions. The comparatively high yield losses with tester RIB 335/74 may be due to larger panicle length and panicle diameter, and the tendency of these hybrids to lodge following relatively early collapse of their stems under these drought stress conditions. Among introgression line testcrosses, hybrids of 197-12-2, 197-1-12 and 197-18-1 maintained their grain yields per panicle relatively well across all three testers, but hybrids of drought tolerance donor parent 863B were clearly superior for this, especially those with testers RIB 335/74 and H 77/833-2.

For panicle harvest index under these early-onset terminal drought stress conditions, tester H 77/833-2 maintained higher harvest index values followed by PPMI 301 and RIB 335/74, but the reductions in panicle harvest index relative to the fully irrigated control were greatest (23.7%) for hybrids of tester RIB 335/74 and least (20.6%) for those of tester PPMI 301. These results were found to be similar to those in earlier reports of Yadav *et al.* (2004). In comparison with the fully irrigated non-stressed

conditions, among introgression lines testcrosses of PPMI 301, those with 197-1-12, 197-12-2, 202-7-4, 202-8-8, 202-8-27 and 197-18-1 best maintained panicle harvest index values; similarly, among introgression line testcrosses of RIB 335/74 those with 197-18-1, 202-7-4, 202-7-10, 202-8-11, and 202-8-8 best maintained panicle harvest index values; and among introgression line testcrosses of H 77/833-2, those with 197-1-12, 197-12-2, and 202-7-12 best maintained panicle harvest index values. These results helped to confirm that the genomic regions between *Xpsmp*2066 and *Xpsmp*2059 (lower arm of LG2) were associated with maintenance of panicle harvest index under these terminal drought stress conditions. These genomic regions were also highly associated with grain yield per plot and its maintenance under these conditions. This finding strongly supports earlier reports of (Yadav *et al.*, 2004; Yadav *et al.*, 2002; Bidinger *et al.*, 1987) in pearl millet, in essence confirming the presence of a major drought tolerance QTL in this genomic region with donor parent 863B providing a more favorable allele than recurrent parent ICMB 841. Further, it lends support to similar reports from maize (Ribaut *et al.*, 1997a), barley (Teulat *et al.*, 2001) and wheat (Blum, 1988a).

Under early-onset terminal drought stress conditions, RIB 335/74 was the best pollinator in terms of giving hybrids with consistent lower stover yield reductions (18.7%) than over those of the other two testers. Between other two testers, H 77/833-2 maintained smaller (24.3%) losses in stover yield per plot followed by PPMI 301 (32.6%). Among introgression line testcrosses, hybrids of PPMI 301 with 197-10-18, 202-8-11 and 202-8-27 gave relatively small stover yield reductions under these severe early-onset terminal drought stress conditions; similarly hybrids of RIB 335/74 with 197-1-12, 197-10-11, 202-8-9 and 202-8-27 maintained their stover yields relatively well; and

those of H 77/833-2 with 197-1-12, 197-10-18 and 202-8-9 also maintained their stover yields relatively well. The genomic region associated with superior performance of introgression line hybrids with testers PPMI 301 and H 77/833-2 was uniform, covering SSR marker loci between *Xpsmp*2072 to *Xpsmp*2231; whereas for RIB 335/74, the drought tolerant genotypes in terms of stover yield maintenance fall in the genomic regions exactly similar to those for grain yield and panicle harvest index values (lower arm of LG2). However, the earlier studies (Yadav *et al.*, 2004) have not indicated any QTL region of interest for stover yield drought tolerance in pearl millet for these tester backgrounds. For maintenance of biomass yield per plot, RIB 335/74 (28.5%) was the best tester as its hybrids exhibited relatively low biomass yield reductions followed by those of H 77/833-2 (33.0%) and PPMI 301 (37.3%). The same genomic regions associated with stover yield maintenance under these conditions were observed also for biomass yield maintenance across all three testers.

Among introgression line testcross hybrids, those of tester RIB 335/74 showed higher rates of reduction in harvest index values (30.7%) in response to this severe early-onset terminal drought stress moisture regime, followed by those of H 77/833-2 (30.1%) and PPMI 301 (24.9%). Under these early-onset terminal drought stress conditions, PPMI 301 was the best tester for hybrid development aimed at maintenance of harvest index. These results were in agreement with report of Yadav *et al.*, (2004). Testcross hybrids of PPMI 301 with introgression lines 197-12-2, 202-8-8 and 197-18-1 maintained their harvest index values relatively testcrosses of 197-18-1, 202-6-26, 202-7-4, 202-7-10, 202-8-8 and 202-8-11 with RIB 335/74 also maintained their harvest index values relatively well; as did those of H 77/833-2 with 197-12-2, 197-18-1, 202-7-10 and 202-7-

12. The genomic regions (lower arm of LG2) associated with maintenance of harvest index values under severe early-onset stress highly correlated well with the genomic regions for drought tolerance of panicle harvest index, grain yield per plot and stover yield per plot.

Hybrids of tester H 77/833-2 showed lower rates of increase in plant height under early-onset terminal drought stress conditions (0.9%) than did those of RIB 335/74 (3.3%) and PPMI 301 (4.0%). The hybrid of tester PPMI 301 with introgression line 202-8-27 showed much improvement (26 cm; corresponding to 19.4%) in height of its plants in this treatment relative to the fully irrigated control. Improvements in panicle length and panicle diameter were also observed among hybrids of tester H 77/833-2. In contrast, testcrosses of RIB 335/74 exhibited marginally shorter and thicker panicles in this moisture regime compared to the fully irrigated control, and those of PPMI 301 exhibited reduction in both panicle length and panicle diameter.

Much less variation for 100-grain mass was observed among the hybrids of tester H 77/833-2 than among those of testers RIB 335/74 and PPMI 301. Hybrids of tester PPMI 301 demonstrated substantial reductions in 100-grain mass (38.4%) in this relatively severe early-onset terminal drought stress regime compared with the fully irrigated non-stress conditions. For grain number per panicle and grain number per plot, reductions among testcross hybrids in this stress environment relative to the fully irrigated control were least for PPMI 301 (15.9% and 23.1%, respectively), followed by RIB 335/74 (21.9% and 24.7%), and H 77/833-2 (23.6% and 32.5%). Hence, tester PPMI 301 was the best for development of testcross hybrids suited for maintenance of grain

number per panicle and grain number per plot under early-onset drought stress conditions.

Combining ability analysis indicated that the best combiner for both grain- and stover-related characters in this relatively severe early-onset terminal drought stress environment was donor parent 863B. This parent confers early flowering, which facilitate escape from terminal drought stress situations. The most widely used sources of earliness, low tillering, combined with a large main panicle and large grain size are the *Iniadi* type landraces from Western Africa (Andrews and Bramel-cox, 1993; Andrews and Anand Kumar, 1996), and 863B was bred by direct selfing and selection within a sample of this germplasm. For panicle number per plot, introgression lines 202-8-11, 202-8-9, 202-8-27, 202-7-12 and 197-10-11 showed the best *gca* effects in this environment. H 77/833-2 showed positive *gca* effects for all stover-yield related characters. These results were concordance with the report of Yadav *et al.* (2004). Among introgression lines, 197-12-2 and 197-18-1 were selected as the best combiners for grain-yield related characters; 202-8-9 and 197-10-11 were selected as best combiners for stover yield-related characters in this early-onset terminal drought stress environment.

Under these relatively severe early-onset terminal drought stress conditions, the testcross hybrids with the best *sca* effects for grain yield-related characters were 197-10-18 × PPMI 301, 202-8-8 × RIB 335/74, 202-8-11 × RIB 335/74, 202-7-10 × RIB 335/74, and 197-10-11 × H 77/833-2. Similarly, testcross hybrids with best positive significant *sca* effects for biomass yield per plot were 197-10-18 × PPMI 301, 197-10-11 × RIB 335/74, and 202-8-9 × H 77/833-2.

Pooled analysis across three moisture regimes:

Genotype × environment interactions (GEI) are ubiquitous for quantitative traits like drought tolerance—in fact, drought tolerance is an expression of GEI!. Significant GEI tends to hinder genetic progress in a breeding program, as it requires that the breeding program focus upon performance in specific environments rather than simply seeking entries that perform well across all environments. Pooled analysis over three moisture regimes was performed for the stover and grain yield-related characters to assess the importance of GEI for the agronomic traits observed in this three moisture regime experiment.

Across the three moisture regimes (fully irrigated control, late-onset terminal drought stress and early-onset terminal drought stress), the line × tester effects were significant for grain and stover yield-related characters, indicating that the parents in this trial could best be exploited in hybrid breeding programmes. Across environments, lines were significant sources of variation for grain yield per panicle, harvest index, plant height and panicle diameter, indicating that the poor heritability of the remaining observed traits and their significant influence by environmental variation. Similarly, environment × testers were significantly different for all the characters except for flowering time, plant number per plot, panicle number per plot, effective tiller number per plant, plant height, and grain number per panicle. Non-significant environment × line × testers effects indicated that the line × testers interaction effects were nil for all the observed characters across three moisture regimes.

Among testers, PPMI 301 was the best combiner for developing hybrids for grain yield-related characters. Similarly, for stover yield H 77/833-2 was the best combiner.

Introgression line 197-18-1 exhibited positive *gca* effects both for stover yield per plot and grain yield per panicle, panicle harvest index, harvest index, 100-grain mass and grain number per panicle. For stover yield introgression lines 202-8-9, 197-10-18 and 197-10-11 showed significant *gca* effects. Since *gca* of a genotype is due to additive and additive × additive interaction effects, these best general combiners can be utilized in both hybrid and synthetic development programmes.

Pooled analysis of introgression line testcross hybrids over three moisture regimes indicated that the testcross hybrids ICMB 841 × PPMI 301 and 202-7-10 × RIB 335/74 exhibited significant *sca* effects for early flowering and large grain numbers per panicle. Similarly significant *sca* effects were observed across environments for testcross hybrids 202-8-8 × RIB 335/74 and 863B × H 77/833-2 for grain number per plot.

DRI values for late-onset terminal drought stress conditions:

Drought response indices (DRI) were calculated for the terminal stress treatments using linear terms for both yield potential and time to flowering (Bidinger *et al.*, 1987b). Results of Yadav and Bhatnagar, (2001) indicated that DRI might be useful for identifying cultivars with high performance under stress particularly when days to flower differ considerably among test entries.

The recurrent parent hybrid ICMB 841 with tester PPMI 301 (a hybrid combination approximating commercially released cultivar Pusa 322 = ICMA 841 × PPMI 301), indicated positive DRI for grain yield per plot and grain yield per panicle, harvest index, panicle diameter, grain number per panicle and grain yield per plot. Similarly, testcross hybrids with positive DRI values for grain yield-related characters like grain yield per plot, panicle harvest index, and harvest index included 197-12-2 ×

PPMI 301, 202-8-9 × PPMI 301, 202-7-10 × PPMI 301, 202-6-26 × PPMI 301, 197-12-2 × RIB 335/74, 202-8-9 × RIB 335/74 and 197-10-18 × H 77/833-2. These observations indicate there is a positive association between DRI of grain yield and stover yield related characters, which is confined to the genomic regions between SSR markers *Xpsmp*2066 and *Xpsmp*2059 (lower arm of LG2).

Among testcross hybrids that showed positive DRI values for stover yield were 202-8-27 × PPMI 301, 202-7-12 × PPMI 301, 202-6-26 × PPMI 301, 197-10-18 × PPMI 301, 202-6-26 × RIB 335/74, 197-10-18 × H 77/833-2, 197-12-2 × H 77/833-2, 202-7-12 × H 77/833-2, 202-6-26 × H 77/833-2 and 197-18-1 × H 77/833-2 suggesting the genomic regions between the SSR markers *Xpsmp*2066 and *Xpsmp*2255 play a major role in determining both stover and grain yield-related characters under late-onset terminal drought stress conditions.

Combining ability analysis using DRI values indicated that tester PPMI 301 was the best combiner for DRI of grain yield-related characters and H 77/833-2 was the best tester for DRI of stover yield under late-onset terminal drought stress conditions. Similarly, the best combiners under late-onset terminal drought stress conditions among introgression lines were 197-12-2 and the donor parent 863B for DRI of grain yield; introgression line 202-8-9 for DRI of stover yield.

Combining ability analysis demonstrated that the best combiners among testers were PPMI 301 for grain yield-related characters under late-onset terminal drought stress conditions, and H 77/833-2 and RIB 335/74 for stover yield-related characters. As expected the donor parent 863B exhibited positive *gca* effects for grain yield-related characters followed by introgression line 197-12-2, which also exhibited positive *gca*

effects. Similarly, among introgression lines positive *gca* effects were observed for 197-10-18, 202-8-9, 202-8-27, 197-10-11 and 197-1-12 stover yield-related characters.

Significant *sca* effects were observed under late-onset terminal drought stress conditions for testcross hybrids 202-7-12 × H 77/833-2 and 863B × H 77/833-2 respectively observed for harvest index and grain number per plot.

DRI values for early-onset terminal drought stress conditions:

For grain yield-related characters recurrent parent ICMB 841 and introgression line 197-1-12 exhibited positive DRI values with PPMI 301 and RIB 335/74. Similarly, for harvest index, ICMB 841, 197-12-2, 202-7-10, 197-1-12, 197-18-1 with PPMI 301 and RIB 335/74; 197-10-18 and 197-1-12 with H 77/833-2 showed positive DRI values.

Best combiners for the grain yield-related characters with DRI values under early-onset drought stress conditions were donor parent 863B, 197-12-2, and 197-18-1 and similarly among testers was PPMI 301. Best combiners with positive *gca* for biomass yield per plot with DRI values under early-onset drought stress conditions were 197-10-18, 197-10-11, and tester H 77/833-2.

A peculiarity of biomass partitioning was observed involving the donor parent 863B and introgression line 197-18-1. Under relatively severe early-onset terminal drought stress conditions both of them appear to divert assimilates from stems and leaves to grain yield. Hence their significant *gca* moved from stover yield to grain yield under this more severe stress.

Significant *sca* with DRI values under severe early-onset terminal drought conditions both for yield- and biomass-related characters among testcross hybrids were

197-10-18 x PPMI 301, 197-10-11 x RIB 335/74, 202-7-10 x RIB 335/74, 202-8-9 x H 77/833-2 and 197-10-11 x H 77/833-2.

Conclusions:

QTL analysis enables the identification of genes contributing substantially to responses responsible for superior performance across a wide range of environments. The strong associations of allelic composition in genomic regions between *Xpsmp*2066 and *Xpsmp*2255 on LG2 that were observed in this study for both downy mildew and the different grain and stover yield-related characters, and observation of expression of these genomes across environments (whether these be moisture regimes in case of the yield-related traits or pathogen isolates differing in virulence in case of the greenhouse downy mildew screens) increases confidence about the real value of marker-assisted selection as a tool to facilitate pearl millet hybrid improvement. This genomic region has consistently shown involvement in the genetic control for these different traits over multiple genetic backgrounds, locations and years (Azhaguvel, 2000; Sharma, 2001; Yadav *et al.*, 2002, 2003, 2004; Nepolean, 2002) which makes this region a good candidate for further study.

The future priorities of the present study should be first to repeat the field drought tolerance screens and greenhouse downy mildew screens, and then to fine map the QTLs for different agronomic characters that are associated with the genomic regions for terminal drought tolerance on LG2 in pearl millet. Development of NILs for this particular region, including a set of recombinant lines (Sub NILs) derived from introgression lines 197-12-2 and 202-7-12, should be undertaken in order to fine map this region either by substitution mapping (Alpert and Tanksley, 1996; Han *et al.*, 1997;

Monforte and Tanksley, 2000; Saito *et al.*, 2003) or by the deficiency mapping technique of Pasyukova *et al.* (2000).

The other prospects of MAS can be used to pyramid several disease resistance genes and drought tolerance genes into a single economically important inbred genotype such as ICMB 841. A modified three-way hybrid seed production method explained by Witcombe and Hash (2000) can be exploited to generate hybrids segregating for pyramids of different disease resistance and drought tolerance gene complements using A-, B-, and R-lines that have been bred by marker-assisted selection.

The genomic similarities now being discovered among all the cereal crops imply that the entire family can be viewed as a single genetic system (Kellogg, 1998). Candidate genes identified by mutant phenotypes in one species can also be examined for effects on related traits on other species (Gale and Devos, 1998). The results of the present study on the terminal drought stress tolerance QTL on pearl millet LG2 suggest that it should be compared with QTLs for drought tolerance located on syntenic genomic regions on chromosome 2 in rice (Zhang, 2001), on chromosome 1 in maize (Tuberosa *et al.*, 2002a,b, 2003), and linkage group A in sorghum (Haussmann *et al.*, 2002).

SUMMARY

CHAPTER VI

SUMMARY

The findings from this study taken up to attempt marker-assisted selection backcross (MABC) transfer of one to three drought tolerance QTLs from donor parent 863B to recurrent parent ICMB 841 and to evaluate and compare the hybrid performance of the MAS-derived introgressed version(s) of ICMB 841, under two terminal drought stress moisture regimes and a control non-stress moisture regime are summarized below:

- Out of 78 pearl millet SSR primer pairs tested, 28 detected polymorphism (35.9%) between the mapping parents, namely donor parent 863B and recurrent parent ICMB 841.
- A total of 23 polymorphic RFLP probe-enzyme combinations were used primarily for screening the progenies for background selection and to track segregation in genomic regions whenever the polymorphic SSR markers were found to be less in numbers (especially on LG1, LG4, LG6, LG7).
- Analysis of segregation of 28 SSR marker and 23 RFLP probes in the backcross generations with MAPMAKER resulted in construction of a linkage map providing reasonably with full coverage of all seven linkage groups of pearl millet. Marker order in this map was as expected based on previously published results.
- Using several selection strategies (morphological and molecular marker-assisted selection), 13 segmental introgression homozygotes for the donor genome in LG2 were identified and crossed with three different testers that are relatively sensitive to drought.

- Greenhouse screening for downy mildew incidence of both introgression lines and testcross hybrids against three Indian pathogen isolates revealed that at least one genomic region from 863B that is probably not associated with LG2 plays a vital role in the variation level of resistance expressed in seedling screens.
- Field evaluation post rainy season under designated drought nursery conditions helped to assess testcross hybrids for drought response using three moisture regimes (Non-stress fully irrigated; late-onset terminal drought stress; and early-onset terminal drought stress). For late-onset terminal drought stress conditions H 77/833-2 and PPMI 301 were the best testers that could be used to develop hybrids for drought tolerance of stover yield and grain yield related characters, respectively.
- Similarly, the best performing introgression lines for late-onset terminal drought stress conditions were 197-10-18, 202-7-10, and 197-12-2. These results indicated that genomic regions on LG2 between SSR markers *Xpsmp*2066 and *Xpsmp*2255 played a major vital role in maintaining both grain and stover yield-related characters under these relatively mild stress.
- For more severe early-onset terminal drought stress conditions, the genomic regions between SSR markers *Xpsmp*2066 to *Xpsmp*2059 (lower arm of LG2) appear to be playing a major role in drought response of grain and stover yield-related characters.
- Results in total confirmed the presence of a major drought tolerant QTL in this genomic region with donor parent 863B providing a more favourable allele.

REFERENCES

REFERENCES

Akaji, H., Yokozeki, Y., Inagaki, A. and Fujimura, T. 1996. Microsatellite DNA markers for rice chromosomes. *Theor. Appl. Genet.*, **93**: 1071-1077.

Alagarswamy, G. and Bidinger, F.R. 1985. The influence of extended vegetative period and d_2 dwarfing gene in increasing grain number per panicle and grain yield in pearl millet. *Field Crops Res.*, **11**: 265-279.

Ali, M.L., Pathan, M.S., Zhang, J., Bai, G., Sarkarung, S. and Nguyen, H.T. 2000. Mapping QTL for root traits in recombinant inbred population from two *indica* ecotypes in rice. *Theor. Appl. Genet.*, **101**: 756-766.

Allard, R.W. 1960. **In**: Principles of Plant Breeding. John Wiley and Sons Inc., New York.

Alpert, K.B. and S.D. Tanksley, 1996. High-resolution mapping and isolation of a yeast artificial chromosome containing fw2.2: a major fruit weight quantitative trait locus in tomato. *Proc. Natl.Acad. Sci.*, **93**: 15503-15507.

Amoukou, A.I. 1993. Incompatibilite post-zygoytique chez le mil *Pennisetum glaucum*. **In**: Le Mil en Afrique, Diversity Genetique et Agro-physiologique: Potentialites et Contraintes pour l'Amelioriation et la Culture, Hamon S, (ed.). Paris: ORSTOM. pp. 107-117.

Anand kumar, K. 1989. Pearl millet: Current status and future potential. *Outlook on Agric.*, **18**: 46-53.

Andrews, D.J. and Anand Kumar, K. 1996. Use of West African pearl millet landrace *Iniadi* in cultivar development. *Pl. Genet. Res. Newsletter* **105**: 15-22.

Andrews, D.J. and Bramel-Cox, P.J. 1993. Breeding cultivars for sustainable crop production in low-input dry land agriculture in the tropics. **In**: Proceedings of International Crop Science I. Buxton D.A. (ed.). Crop Science Society of America Inc. Madison, USA. pp. 211-233.

Apuya, N.R., Frazier, B.L., Keim, P., Roth, E.J. and Lark, K.G. 1988. Restriction fragment length polymorphisms as genetic markers in soybean, *Glycine max* (L.) Merrill. *Theor. Appl. Genet.*, **75**: 889-901.

Arunachalam, V. and Chandrashekaran, S. 1993. RFLP approach to breeding for quantitative traits in plants – a critique. *J. Genet.*, **72 (2&3)**: 73-83.

Azam Ali, S.N. 1983. Season estimates of transpiration from a millet crop using a porometer. *Agric. Meteor.*, **30**: 13-24.

Azam Ali, S.N., Gegory, P.J. and Monteith, J.L. 1984. Effect of planting density on water use and productivity of pearl millet (*Pennisetum typhoides*) growing on stored water. *Expl. Agric.*, **20**: 203-214.

Azhaguvel, P. 2001. Linkage map construction and identification of QTLs for downy mildew (*Sclerospora graminicola*) resistance in pearl millet (*Pennisetum glaucum* (L.) R. Br.). Ph.D. thesis, Tamil Nadu Agricultural University, Coimbatore, India.

Basten, C.J., Zeng, S.B. and Weir, B.S. 1994. ZMAP-A QTL cartographer. **In**: Proceedings of the 5th World Congress on Genetics Applied to Livestock Production: Computing strategies and Software. Smith, C., Gavora, J.S., Benket, B., Chesnais, J., Fairfull, W., Gibson, J.P., Kennedy B.W. and Burnside, E. B. (eds.). Guelph, Ontario, Canada, pp. 65-66.

Basten, C.J., Zeng, S.B. and Weir, B.S. 1997. QTL Cartographer: A reference manual and tutorial for QTL mapping. Department of Statistics, North Carolina State University, Raleigh, North Carolina: USA.

Beckmann, J. and Soller, M. 1983. Restriction fragment length polymorphisms in genetic improvement: methodologies, mapping & costs. *Theor. Appl. Genet.*, **67**: 35-43.

Beckmann, J. and Soller, M. 1986. Restriction fragment length polymorphisms and genetic improvement of agricultural species. *Euphytica* **35**: 111-124.

Beckmann, J.S. and Weber, J.L. 1992. Survey of human and rat microsatellites. *Genomics* **12**: 627-631.

Begg, J.E. 1965. The growth and development of a crop of bulrush millet (*Pennisetum typhoides* S. & H.). *J. Agric. Sci. Camb.*, **65**: 341-349.

Belliard, J. and Pernes, J. 1984. *Pennisetum typhoides* (B) S & H. **In**: Halevy, A.H., (ed.). Handbook of Flowering, Vol. IV. Boca Raton, FL. pp. 23-37.

Bernatzky, R. and Tanksley, S.D. 1986. Towards a saturated linkage map in tomato based on isozymes and random cDNA sequences. *Genetics* **112**: 887-898.

Bernacchi, D., Beck-Bunn, T., Emmatty, D., Eshed, Y., Inani, S., Lopez, J., Petiard, V., Sayama, H., Uhlig, J., Zamir, D. and Tanksley, S. 1998. Advanced backcross QTL analysis of tomato. II. Review of near-isogenic lines carrying single-donor introgressions for desirable wild QTL-alleles derived from *Lycopersicon hirsutum* and *L. pimpinellifolium*. *Theor. Appl. Genet.*, **97**: 170-180.

Bhattacharjee, R., Bramel, P.J., Hash, C.T., Kolesnikova-Allen, M.A. and Khairwal, I.S. 2002. Assessment of genetic diversity within and between pearl millet landraces. *Theor. Appl. Genet.*, **105**: 666-673.

Bidinger, F.R. 2002. Field screening for Drought Tolerance-Principles and illustrations. **In**: Field screening for Drought Tolerance in crop plants with emphasis on rice. Saxena, N.P. and John C O'Toole, (eds.). 11-14 Dec. 2000, ICRISAT, Patancheru, India. pp. 109-124.

Bidinger, F.R. and Hash, C.T. 2003. Pearl millet. Chapter 5 **In**: Physiology and biotechnology integration for plant breeding. Nguyen, H.T. and Blum, A. (eds.). Marcel Dekker, New York (in press). pp. 225-270.

Bidinger, F.R. and Mahalakhsmi, V. 1993. Selection for drought tolerance. **In**: Cereals program, ICRISAT 1993. Annual Report, 1992. ICRISAT, Patancheru, India. pp. 57-59.

Bidinger, F.R., Chandra, S. and Raju, D.S. 2001. Genetic variation in grain-filling ability in dwarf pearl millet [*Pennisetum glaucum* (L.) R. Br.] restorer lines. *Theor. Appl. Genet.*, **102**: 387-391.

Bidinger, F R., Mahalakshmi, V. and Rao, G.D.P. 1987a. Assessment of drought resistance in pearl millet (*Pennisetum americanum* (L.) Leeke). I Factors affecting yields under stress. *Aust. J. Agric. Res.*, **38**: 37-48.

Bidinger, F.R., Mahalakshmi, V. and Rao, G.D.P. 1987b. Assessment of drought resistance in pearl millet (*Pennisetum ameicanum* (L.) Leeke). II Estimation of genotype response to stress. *Aust. J. Agric. Res.*, **38**: 49-59.

Bidinger, F.R., Musgrave, R.B. and Fischer, R.A. 1977. Contribution of stored pre-anthesis assimilates to grain yield in wheat and barley. *Nature* **270**: 431-433.

Blum, 1988a. Improving wheat grain filling under stress by stem reserve mobilization. *Euphytica*, **100**: 77-83.

Blum, A. 1988b. Plant breeding for stress environments. CRC Press, Florida, USA.

Bonierbale, M.B., Plaisted, R.L. and Tanksley, S.D. 1988. RFLP maps based on common set of clones reveal modes of chromosomal evolution in potato and tomato. *Genetics* **120**: 1095-1103.

Botstein, D., White, R.L., Skolnick, M. and Davis, R.W. 1980. Construction of a genetic map in man using restriction fragment length polymorphisms. *Am. J. Hum. Genet.*, **32**: 314-331.

Bramel-Cox, P.J., Andrews, D.J. and Frey, K.J. 1986. Exotic germplasm for improving growth rate and grain yield in pearl millet. *Crop Sci.*, **26**: 687-690.

Brunken, J.N., de Wet, J.M.J. and Harlan, J.R. 1977. The morphology and domestication of pearl millet. *Econ. Bot.*, **31**: 163-174.

Burr, D., Burr, F.A., Thompson, K.H., Albertson, M.C. and Stuber, C.W. 1988. Gene mapping with recombinant inbreds in maize. *Genetics* **118**: 519-526.

Carberry, P. and Campbell, L.C. 1985. The growth and development of pearl millet as affected by photoperiod. *Field Crops Res.*, **11**: 207-217.

Carberry, P., Campbell, L.C. and Bidinger, F.R. 1985. The growth and development of pearl millet as affected by plant population. *Field Crops Res.*, **11**: 193-205.

Cavalli, L.L. 1952. An analysis of linkage in quantitative inheritance. **In**: Quantitative inheritance. Reeve, E.C.R. and Waddington, C.H. (eds.). His Majesty's Stationary Office, London, pp. 135-144.

Ceccarelli, S. and Grando, S. 1996. Drought as a challenge for the plant breeder. *Pl. Growth Reg.*, **20**: 149-155.

Cha, K.W., Lee, Y. J., Koh, H. J., Lee, B.M., Nam, Y.W. and Paek, N.C. 2002. Isolation, characterization, and mapping of the stay-green mutant in rice. *Theor. Appl. Genet.*, **104**: 526-532.

Champoux, M.C., Wang, G.L., Sarkarung, S., Mackill, D.J., O'Toole, J.C., Huang, N. and McCouch, S.R. 1995. Locating genes associated with root morphology and drought in rice *via* linkage to molecular markers. *Theor. Appl. Genet.*, **90**: 969-981.

Charmet, G., Robert, N., Perretant, M.R., Gay, G., Sourdilla, P., Groos, C., Bernard, S. and Bernard, M. 1999. Marker-assisted recurrent selection for cumulating additive and interactive QTLs in recombinant inbred lines. *Theor. Appl. Genet.*, **99**: 1143-1148.

Charreau, C. 1972. Problemes pose par l'utulisation agricole des sols tropicaux par des cultures annuelles. . *L'Agronomie Tropicale* **20**: 905-929.

Chase, R.G., Wendt, J.W. and Hossner, L.R. 1989. A study of crop growth variability on sandy Sahelian soils. **In**: Soil, Crop and Water Management Systems Rainfed Agriculture in the Sudano-Sahelian Zone, ICRISAT, Patancheru, India: pp. 229-240.

Chen, X., Temnykh, S., Xu, Y., Cho, Y.G. and McCouch, S.R. 1997. Development of a microsatellite framework map providing genome-wide coverage in rice (*Oryza sativa* L.). *Theor. Appl. Genet.*, **95**: 553-567.

Chopart, J.L. 1983. Etude du systeme racinaire du mil (*Pennisetum typhoides*) dans un sol sableux du Senegal. . *L'Agronomie Tropicale* **38**: 37-51.

Churchill, G.A. and Doerge, R.W. 1994. Empirical threshold values for quantitative trait mapping. *Genetics* **138**: 963-971.

Crasta, O.R., Xu, W.W., Rosenow, D.T., Mullet, J. and Nguyen, H.T. 1999. Mapping of post-flowering drought resistance traits in grain sorghum: Association between QTLs influencing premature senescence and maturity. *Mol. Gen. Genet.*, **262**: 579-588.

Craufurd, P.Q. and Bidinger, F.R. 1988a. Effect of the duration of the vegetative phase on crop growth, development and yield in two contrasting pearl millet hybrids. *J. Agric. Sci. Camb.*, **110**: 71-79.

Craufurd, P.Q. and Bidinger, F.R. 1988b. Effect of the duration of the vegetative phase on shoot growth, development and yield in pearl millet (*Pennisetum americanum* (L.) Leeke). *J. Exp. Bot.*, **39**: 124-139.

Craufurd, P.Q. and Bidinger, F.R. 1989. Potential and realized yield in pearl millet (*Pennisetum americanum)* as influenced by plant population density and life-cycle duration. *Field Crops Res.*, **22**: 211-225.

Cregan, P.B., Jarvik, T., Bush, A.L., Shoemaker, R.C., Lark, K.G., Kaya, N., Van Toai, T.T., Lohnes, D.G., Chung, J. and Mc Couch, S.R. 1999. An integrated genetic linkage map of the soyabean genome. *Crop Sci.*, **39**: 1464-1490.

Dancette, C. 1983. Besoins en eau du mil au Senegal, adaptation en zone semi-aride tropicale. . *L'Agronomie Tropicale* **38**: 267-280.

Darvasi, A., Weinreb, A., Minke, V., Weller, J.I. and Soller, M. 1993. Detecting marker-QTL linkage and estimating QTL gene effect and map location using a saturated genetic map. *Genetics* **134**: 943-951.

Dave, H.R. 1987. Pearl millet hybrids. **In**: Proceedings International Pearl millet Workshop. (Witcombe, J.R. and Beckerman, S.R. (eds.). ICRISAT, Patancheru, India. pp. 121-126.

de Wet, J.M.J. 1987. Pearl millet (*Pennisetum glaucum*) in Africa and India. **In**: Proceedings of the pearl millet workshop, 7-11, April, ICRISAT-Patancheru, India, pp. 259-267.

de Wet, J.M.J., Bidinger, F.R. and Peacock, J.M. 1992. Pearl millet (*Pennisetum glaucum*) - a cereal of the Sahel. **In**: Desertified Grasslands, their Biology and Management. Chapman, G.P. (ed.). London: Academic Press, Inc. pp. 259-267.

Devos, K.M., Pittaway, T.S., Busso, C.S. and Gale, M.D. 1995. Molecular tools for the pearl millet nuclear genome. *Int. Sorghum and Millets Newsletter* **36**: 64-66.

Diers, B.W., Keim, P., Fehr, W.R. and Shoemaker, R.C. 1992. RFLP analysis of soybean seed protein and oil content. *Theor. Appl. Genet.*, **83**: 608-612.

Do, F., Winkel, T., Cournoc, L. and Louguet, D. 1996. Impact of late season drought on water relations in a sparse crop of millet (*Pennisetum glaucum* (L.) R. Br.). *Field Crops Res.*, **48**: 103-113.

Dolstra, O., Denneboom, C., de Vos, A.L.F. and van Loo, E.N. 2003. Marker-assisted selection in improvement of quantitative traits of forage crops. Marker Assisted Selection: Session I: MAS in plants: www:http://fao.org.

Dreher, K., Khairallah, M., Ribaut, J.M. and Morris, M. 2003. Money matters (I): Costs of field and laboratory procedures associated with conventional and marker-associated maize breeding at CIMMYT. *Mol. Breed.*, **11**: 221-234.

Dudley, J.W. 1993. Molecular markers in plant improvement: Manipulation of genes affecting quantitative traits. *Crop Sci.*, **33**: 660-668

Eathington, S.R., Dudley, J.W. and Rufener, II G.K. 1997. Usefulness of marker-QTL associations in early generation selection. *Crop Sci.*, **37**: 1686-1693.

Edwards, M.D., Stuber, C.W. and Wendel, J.F. 1987. Molecular markers facilitated investigation of quantitative trait loci in maize. 1. Numbers, genomic distribution and types of gene action. *Genetics* **115**: 113-125.

Edwards, M.D. and Page, N.J. 1994. Evaluation of marker-assisted selection through computer simulation. *Theor. Appl. Genet.*, **88**: 376-382.

Eglinton, J.K., Baum, M., Grando, S., Ceccarelli, S. and Barr, A.R. 2001. Towards understanding the genetic basis of adaptation to low rainfall environments. **In**: Proceedings of the 10th Australian Barley technical symposium. www.regional.org.au/

Eldin, M. 1983. Analyse de l'effect des deficits hydriques sur la recolte du mil au Niger, consequences agronomiques. **In**: Hamon S, ed. Le Mil en Afrique, Diversity Genetique et Agro-physiologique: Potentialites et Contraintes pour l'Amelioriation et la Culture, Paris: ORSTOM. pp. 149-160.

Elston, R.D. and Stewart, J. 1971. A general method for the genetic analysis of pedigree data. *Hum. Hered.*, **21**: 523-542.

Everson, E.H. and Schaller, C.W. 1955. The genetics of yield difference associated with awn barbing in barley hybrid (Lion × Altas^{10}) × Altas. *Agron. J.*, **47**: 276-280.

FAO and ICRISAT, 1996. The world sorghum and millet economies: facts, trends and outlook. Food and Agricultural Organization of the united nations (FAO), Rome, Italy, and International Crops Research Institute for The Semi Arid Tropics (ICRISAT), Patancheru, AP, India.

FAO, 2000. Crop production yearbook 2000. Food and Agricultural Organization of the united nations, Rome, Italy.

Fatokun, C.A., Menancio-Hautea, D.I., Danesh, D. and Young, N.D. 1992. Evidence for orthologous seed weight genes in cowpea and mung bean based on RFLP mapping. *Genetics* **132**: 841-846.

Feinberg, A.P. and Vogelstein, B. 1983. A technique for radiolabelling DNA restriction endonuclease fragments to high specific activity. *Anal. Biochem.*, **132**: 6-13.

Figdore, S.S., Kennard, W.C., Song, K.M., Slocum, M.K. and Osborn, T.C. 1988. Assessment of degree of restriction polymorphisms in *Brassica*. *Theor. Appl. Genet.*, **75**: 833-840.

Foolad, M.R. 1999. Genetics of salt and cold tolerance in tomato: Quantitative analysis and QTL mapping. *Pl. Biotech.*, **16**: 55-64.

Frisch, M., Bohn, M. and Melchinger, A.E. 1999. Comparison of selection strategies for marker-assisted backcrossing of a gene. *Crop Sci.*, **39**: 1295-1301.

Frisch, M. and Melchinger, A.E. 2000. The length of the intact donor chromosome segment around a target gene in marker-assisted backcrossing. *Genetics* **151**: 1343-1356.

Fussell, L.K., Bidinger, F.R. and Bieler, P. 1991. Crop physiology and breeding for drought tolerance: research and development. *Field Crops Res.*, **27**: 183-199.

Fussell, L.K., Serafini, P.G., Bationo, A. and Klaij, M.C. 1987. Management practices to increase yield and yield stability of pearl millet in Africa. **In**: Proceedings of the pearl millet workshop, 7-11 April, ICRISAT Center, Patancheru, India. pp. 255-268.

Gale, M.D. and Devos, K.M. 1998. Comparative genetics in the grasses. *Proc. Natl. Acad. Sci.*, **95**: 1971-1974.

Gale, M.D. and Witcombe, J.R. 1992. DNA markers and marker-mediated applications in pearl millet breeding. **In**: Biotechnology and crop improvement in Asia. Moss, J.P. (ed.). ICRISAT, Patancheru, India. pp. 323-332.

Garcia-Huidobro, J., Monteith, J.L. and Squire, G.R. 1982. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.) I. Constant temperature. *J. Exp. Bot.*, **33**: 288-296.

Geldermann, H. 1975. Investigation on inheritance of quantitative characters in animals by gene markers. I. Methods. *Theor. Appl. Genet.*, **46**: 300-319.

GENSTAT 6th Edition, 2002. The guide to Genstat ® release 6.1. Payne, R.W. 2002. Part 2: Statistics, VSN International Limited, Oxford, UK.

Gibson, T.B. and Thoday, J.M. 1962. Effect of disruptive selection VI. A second chromosome polymorphism. *Heredity*, **17**: 1-26.

Gimelfarb, A. and Lande, R. 1995. Marker-assisted selection and marker-QTL associations in hybrid populations. *Theor. Appl. Genet.*, **91**: 522-528.

Goldman, I.L. 2000. Prediction in plant breeding. *Pl. Breed. Rev.*, **19**: 15-39.

Graham, G.I., Wolff, D.W. and Stuber, C.W. 1997. Characterization of a yield quantitative trait locus on chromosome 5 of maize by fine mapping. *Crop Sci.*, **37**:1601-1610.

Gregory, P.J. 1986. Responses to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). VIII. Root development. *J. Exp. Bot.*, **34**: 744-756.

Gregory, P.J. and Squire, G.R. 1979. Irrigation effect on roots and shoots of pearl millet (*Pennisetum typhoides*). *Expl. Agric.*, **15**: 241-252.

Hackett, C.A. 1997. Model diagnostics for fitting QTL models to trait and marker data by interval mapping. *Heredity*, **79**: 319-328.

Haley, C.S. and Knott, S.A. 1992. A simple regression method for mapping quantitative trait loci in line crosses using flanking markers. *Heredity* **69**: 315-324.

Han, A., Ullrich, S.E. Kleinbofs, A. Jones, B.L. Hayes, P.M and Wesenberg, D.M. 1997a. Fine structure mapping of the barley chromosome 1 centromere containing malting quality QTLs. *Theor. Appl. Genet.*, **95**: 903-910.

Han, F., Romagosa, I., Ullrich, S.E., Jones, B.L., Hayes, P.M. and Wesenberg, D.M. 1997b. Molecular marker assisted selection for malt quality traits in barley. *Mol. Breed.*, **3**: 427-437.

Hanna, W.W., Wells, H.D. and Burton, G.W. 1985. Dominant gene for rust resistance in pearl millet. *J. Hered.*, **76**: 134.

Harinarayana, G., Anand Kumar, A. and Andrews, D.J. 1999. Pearl millet in global agriculture. **In**: Pearl Millet Breeding. Khairwal, I.S., Rai, K.N., Andrews, D.J. and Harinarayana, G. (eds.). Oxford and IBH, New Delhi. pp. 479-506.

Harrison, B.J. and Mather, K. 1950. Polygenic variability in chromosomes of *Drosophilla melanogaster* obtained from the wild. *Heredity* **4**: 295-312.

Hash, C.T. 1991. ICRISAT pearl millet breeding and the potential use of RFLPs. in report meeting, Rockefeller Foundation Conference: The establishment of sorghum and millet RFLP network to support breeding in developing countries (USA), 6-10 May, pp. 28-29.

Hash, C.T. 1997. Research on downy mildew of pearl millet. **In**: Integrating research evaluation efforts: Proceedings of an International Workshop, 14-16, Dec 1994, Bantilan, M.C.S. and Joshi, P.K. (eds.). ICRISAT, Patancheru, India. pp. 121-128.

Hash, C.T., Singh, S.D. Thakur, R.P. and Talukdar, B.S. 1999. Breeding for disease resistance. **In**: Pearl Millet Breeding. Khairwal, I.S., Rai, K.N. Andrews, D.J. and Harinarayana, G. (eds.). Oxford & IBH: New Delhi, India. pp. 337-379.

Hash, C.T. 2000. Concepts for application of marker techniques in Africa. **In**: Application of molecular markers in plant breeding: Training manual for a seminar held at IITA, Ibadan, Nigeria, 16-17 Aug 1999. Haussmann, B.I.G., Geiger, H.H., Hess, D.E., Hash, C.T. and Bramel-Cox, P. (eds.). International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, A.P. India. pp. 155-169.

Hash, C.T. and Bramel-Cox, P.J. 2000. Marker applications in pearl millet. **In**: Application of molecular markers in plant breeding: Training manual for a seminar held at IITA, Ibadan, Nigeria, 16-17 Aug. 1999. Haussmann, B.I.G., Geiger, H.H., Hess, D.E., Hash, C.T. and Bramel-Cox. P. (eds.). International Crops Research Institute for the Semi-Arid Tropics (ICRISAT): Patancheru, A.P. India. pp. 112-127.

Hash, C.T. and Witcombe, J.R. 1994. Pearl millet mapping populations at ICRISAT. **In**: Use of molecular markers in sorghum and pearl millet breeding for developing countries. Witcombe, J.R. and Duncan, R.R. (eds.). ODA: London, UK. pp. 69-75.

Hash, C.T. and Witcombe, J.R. 2002. Gene management and breeding for downy mildew resistance. **In**: John F. Leslie (ed.). Sorghum and millet diseases. pp. 27-36.

Hash, C.T., Singh, S.D., Thakur, R.P. and Talukdar, B.S. 1999. Breeding for disease resistance. **In**: Pearl Millet Breeding. Khairwal, I.S., Rai, K.N., Andrews, D.J. and Harinarayana, G. (eds.). Oxford & IBH Publishing Co. Pvt. Ltd.: New Delhi, India. pp. 337-379.

Hash, C.T., Witcombe, J.R., Thakur, R.P., Bhatnagar, S.K., Singh, S.D. and Wilson, J.P. 1997. Breeding for pearl millet disease resistance. **In**: Proceedings of the International conference on genetic improvement of sorghum and pearl millet, September 22-27, 1996. INTSORMIL, Publication No. 97-5. INTSORMIL and ICRISAT. pp. 337-372.

Hash, C.T., Yadav, R.S., Cavan, G.P., Howarth, C.J., Liu, H., Qi, X., Sharma, A., Kolesnikova-Allen, M.A., Bidinger, F.R. and Witcombe, J.R. 2000. Marker-assisted backcrossing to improve terminal drought tolerance in pearl millet. **In**: Proceedings of a Strategic Planning Workshop on "Molecular Approaches for the Genetic Improvement of Cereals for Stable Production in Water-limited environments", June 21-25, 1999, CIMMYT, El Batan, Mexico Ribaut, J-M and Poland, D. (eds.). CIMMYT, Mexico. pp. 114-119.

Haussman, B.I.G., Mahalakhsmi, V., Reddy, B.V.S., Seetharama, N., Hash, C.T. and Geiger, H.H. 2003. QTL mapping of stay-green in two sorghum recombinant inbred populations. *Theor. Appl. Genet.*, **106**: 133-142.

Helentjaris, T., Slocum, M., Wright, S., Schaefer, A. and Nienhuis, J. 1986. Construction of genetic linkage maps in maize and tomato using restriction fragment length polymorphisms. *Theor. Appl. Genet.*, **72**: 761-769.

Hensen, I.E. 1982. Osmotic adjustment to water stress in pearl millet in a controlled environment. *J. Exp. Bot.*, **33**: 78-87.

Henson, I.E. and Mahaklakshmi, V. 1985. Evidence for panicle control of stomatal behaviour in water-stressed plants of pearl millet. *Field Crops Res.*, **11**: 281-290.

Henson, I.E., Alagarswamy, G., Bidinger, F.R. and Mahalakshmi, V. 1982a. Stomatal responses of pearl millet (*Pennisetum americanum* (L.) Leeke) to leaf water status and environmental factors in the field. *Pl.Cell Environ.*, **5**: 65-74.

Henson, I.E., Mahalakshmi, V., Bidinger, F.R. and Alagarswamy, G. 1982b. Osmotic adjustment to water stress in pearl millet (*Pennisetum americanum* (L.) Leeke) under field conditions. *Pl. Cell Environ.*, **5**: 147-154.

Henson, I.E., Alagarswamy, G., Mahalakshmi, V. and Bidinger, F.R. 1983. Stomatal response to water stress and its relationship to bulk leaf water status and osmotic adjustment in pearl millet (*Pennisetum americanum* (L.) Leeke). *J. Exp. Bot.*, **34**: 442-450.

Hill, A.P. 1975. Quantitative linkage: A statistical procedure for its detection and estimation. *Ann. Hum. Genet.*, **38**: 439-449.

Hittalmani, S., Parco, A., Mew, T.. Zeigler, R.S. and Huang, N. 2000. Fine mapping and marker-assisted pyramiding of major genes for blast resistance in rice. *Theor. Appl. Genet.*, **100**· 1025-1042.

Holloway, J.L. and Knapp, S.J. 1994. Gmendel 3.0 User Guide. Department of Crop and Soil Science, Oregon State University: Corvallis, OR 97331, USA.

Hospital, F. and Charcosset, A. 1997. Marker-assisted introgression of quantitative trait loci. *Genetics* **147**: 1469-1485.

Hospital, F., Chevalet, C. and Mulsant, P. 1992. Using markers in gene introgression breeding programs. *Genetics* **132**: 1199-1210.

Hospital, F., Moreau, L., Lacoudre, A., Charcosset, A. and Gallais, A. 1997. More on the efficiency of marker-assisted selection. *Theor. Appl. Genet.*, **95**: 1181-1189.

Huang, N., Angeles, E.R., Domingo, J., Magapantay, G., Singh, S., Zhang, G., Kumaravadivel, N., Bennet, J. and Khush, G.S. 1997. Pyramiding of bacterial blight resistance genes in rice: Marker-assisted selection using RFLP and PCR. *Theor. Appl. Genet.*, **95**: 313-320.

Huda, A.K.S. 1987. Simulating the growth of sorghum and pearl millet in the semi-arid tropics. *Field Crops Res.*, **15**: 309-325.

Inukai, T., Zeigler, R.S., Sarkarung, S., Bronson, M., Dung, L.V., Kinoshita, T. and Nelson, R.J. 1996. Development of pre-isogenic lines for rice blast resistance by marker-aided selection from a recombinant inbred population. *Theor. Appl. Genet.*, **93**: 560-567.

Jayakar, S.D. 1970. On the detection and estimation of linkage between a locus influencing a quantitative character and a marker locus. *Biometrics* **26**: 441-464.

Jensen, J. 1989. Estimation of recombination parameters between a quantitative trait loci (QTL) and two marker gene loci. *Theor. Appl. Genet.*, **78**: 613-618.

Jones, E.S. 1994. Mapping quantitative trait loci for resistance to downy mildew in pearl millet. Ph.D. thesis, University of Wales, Bangor, UK.

Jones, E.S., Breese, W.A. and Shaw, D.S. 2001. Inoculation of pearl millet with the downy mildew pathogen, *Sclerospora graminicola*: Chilling inoculum to delay zoospores release and avoid spray damage to zoospores. *Pl. Pathol.*, **50**: 310-316.

Jones, E.S., Breese, W.A., Liu, C.J., Singh, S.D., Shaw, D.S. and Witcombe, J.R. 2002. Mapping quantitative trait loci for resistance to downy mildew in pearl millet: Field and glass house screens detect the same QTL. *Crop Sci.*, **42**: 1316-1323.

Jones, E.S., Liu, C.J., Gale, M.D., Hash, C.T. and Witcombe, J.R. 1995. Mapping quantitative trait loci for downy mildew resistance in pearl millet. *Theor. Appl. Genet.*, **91**: 448-456.

Jones, N., Ougham, H. and Thomas, H. 1997. Markers and mapping-we are all geneticists now. *New Phytol.*, **137**: 165-177.

Kapoor, R.L., Kakkar, P.S. Khairwal, I.S., Beniwal, C.R., Nijhawan, D.C. and yadav, H.P. 1989. Bajra hybrid HHB 67–A Major break through. *Haryana Farming* **18**: 17.

Kearsey, M.J. and Farquhar, A.G.L. 1998. QTL analysis in plants: where are we now? *Heredity* **80**: 137-142.

Kebede, H., Subudhi, P.K. and Rosenow, D.T. 2001. Quantitative trait loci influencing drought tolerance in grain sorghum (*Sorghum bicolor* L. Moench). *Theor. Appl. Genet.*, **103**: 266-276.

Keim, P., Diers, B.W., Olson, T.C. and Shoemaker, R.C. 1990. RFLP mapping in soyabean: association between marker loci and variation in quantitative traits. *Genetics* **126**: 735-742.

Kellogg, E.A. 1998. Relationships of cereal crops and other grasses. *Proc. Natl. Acad. Sci.*, **95**: 2005-2010.

Kerns, M.R., Dudley, J.W. and Rufener, II G.K. 1999. Tester and type of progeny affect QTL detection in maize. *Maydica* **44**: 69-83.

Knapp, S.J. 1994. Mapping quantitative trait loci. **In**: DNA-Based Markers in Plants. Phillips, R.L. and Vasil, I.K. (eds.). Kluwer Academic: Dordrecht, The Netherlands. pp. 58-96.

Knapp, S.J. 1998. Marker-assisted selection as a strategy for increasing the probability of selecting superior genotypes. *Crop Sci.*, **38**: 1164-1174.

Knapp, S.J., Bridges Jr., W.C. and Birkes, D. 1990. Mapping quantitative trait loci using molecular marker linkage maps. *Theor. Appl. Genet.*, **79**: 583-592.

Kolesnikova M. A., 2000. Mapping new quantitative trait loci (QTL) for downy mildew resistance in pearl millet. Ph.D. thesis, Russian National Academy of Sciences, Moscow.

Kouressy, M., Niangado, O., Vaksmann, M. and Reyniers, F.N. 1998. **In**: Le Futur des Céréales Photopériodique pour une Production Durable en Afrique Tropicale Semi-Aride, Bacci, L., Reyniers F.N. (eds.). Florence, Italie: Ce.S.I.A. - Accademia dei Georgofili, 1998. pp 59-75.

Kowal, J.M. and Kassam, A.H. 1978. Agricultural Ecology of Savanna - a Study of West Africa. Oxford; Clarendon Press, pp.403.

Lacape, J-M., Nguyen, T.B., Hau, B. and Giband, M. 2003. Targeted introgression of cotton fiber quality QTLs using molecular markers. Markers Assisted Selection: Session I: MAS in plants: www:http://fao.org

Lahiri, A.N. and Kharabanda, B.C. 1965. Studies of plant-water relationships: effects of moisture deficit at various developmental stages of bulrush millet. *Proc. Natl. Inst. Sci.*, **31**: 14-24.

Lambert, C. 1983. Influence de la precocite sur le devellopement du mil *(Pennisetum typhoides* Stapf et Hubbard) en conditions naturelles. I Elaboration de la touffe. *L'Agron. Trop.*, **38**: 7-15.

Lande, R. and Thompson, R. 1990. Efficiency of marker-assisted selection in the improvement of quantitative traits. *Genetics* **124**: 743-756.

Lander, E.S. and Botstein, D. 1989. Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. *Genetics* **121**: 185-199.

Lander, E.S., Green, P., Abrahamson, J., Barlow, A., Daly, M.J., Lincoln, S.E. and Newburg, L. 1987. MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. *Genomics* **1**: 174-181.

Landry, B.S., Kesseli, R.V., Barry Farrara and Michelmore, R.W. 1987. A genetic map of lettuce (*Lactuca sativa* L.) with restriction fragment length polymorphism, isozyme, disease resistance and morphological markers. *Genetics* **116**: 331-337.

Law, C.N. 1967. The location of factors controlling a number of quantitative characters in wheat. *Genetics* **56**: 445-461.

Lawson, D.M., Lunde, C.F. and Mutschler, M.A. 1997. Marker-assisted transfer of acylsugar-mediated pest resistance from the wild tomato, *Lycopersicon pennellii*, to the cultivated tomato, *Lycopersicon esculentum*. *Mol. Breed.*, **3**: 307-317.

Lawson, W., Goulter, K., Henry, R., Kong, G. and Kochman, K. 1998. Marker-assisted selection for sunflower rust resistance loci. **In**: Plant and Animal Genome VI conference, CA.

Lee, M. 1995. DNA markers and plant breeding programs. *Adv. Agron.*, **55**: 265-344.

Lilley, J.M., Ludlow, M.M., McCouch, S.R. and O'Toole, J.C. 1996. Locating QTL for osmotic adjustment and dehydration tolerance in rice. *J. Exp. Bot.*, **47**: 1427-1436.

Lin, Y.R., Schertz, K.F. and Paterson, A.H. 1995. Comparative analysis of QTLs affecting plant height and maturity across the *Poaceae*, in reference to an intra-specific sorghum population. *Genetics* **140**: 391-411.

Lincoln, S., Daly, M. and Lander, E. 1992a. Mapping genes controlling quantitative traits with MAPMAKER/QTL 1.1. Whitehead Institute Technical Report. 2nd edition.

Lincoln, S., Daly, M. and Lander, E. 1992b. Constructing genetic maps with MAPMAKER/EXP 3.0. Whitehead Institute Technical Report. 3rd edition.

Lindhout, P., Van Heusden, S., Pet, G., Van Ooijen, J.W., Sandbrink, H., Verkerk, R., Vrielink, R. and Zabel, P. 1994. Perspective of molecular marker-assisted eding for earliness in tomato. *Euphytica* **79**: 279-286.

Liu, C.J., Witcombe, J.R., Pittaway, T.S., Nash, M., Hash, C.T., Burro, C.S. and Gale, M.D. 1994. An RFLP-based genetic linkage map of pearl millet (*Pennisetum glaucum*). *Theor. Appl. Genet.*, **89**: 481-487.

Lynch, M. and Walsh, B. 1998. Genetics and Analysis of Quantitative Traits. Sinauer Associates Inc: Sunderland, MA, USA.

Mace, E.S., Buhariwalla, H.K. and Crouch, J.H. 2004. A High Throughput DNA extraction protocol for tropical molecular breeding programs. *Pl. Mol. Biol. Reporter* (in press).

Mahalakshmi, V. and Bidinger, F.R. 1985a. Flowering response of pearl millet to water stress during panicle development. *Ann. Appl. Biol.*, **106**: 571-578.

Mahalakshmi, V. and Bidinger, F.R. 1985b. Water stress and time of floral initiation in pearl millet. *J. Agric. Sci. Camb.*, **105**: 437-445.

Mahalakshmi, V., and Bidinger, F.R. 1986. Water deficit during panicle development in pearl millet: yield compensation by tillers. *J. Agric. Sci. Camb.*, **106**: 113-119.

Mahalakshmi, V., Bidinger, F.R. and Raju, D.S. 1987. Effect of timing of water stress on pearl millet (*Pennisetum americanum*). *Field Crops Res.*, **15**: 327-339.

Mahalakshmi, V., Monyo, E.S., Payne, W., Quattara, S. and Bidinger, F.R. 1997. Breeding pearl millet for drought tolerance. **In**: The International conference on genetic improvement of Sorghum and Pearl millet. INTSORMIL and ICRISAT, September 22-27, 1996. Lubbock, Texas. pp. 443-457.

Maiti, R.K. and Bidinger, F.R. 1981. Growth and Development of the Pearl Millet *Pl. Res. Bulletin*, No. 6. Patancheru, ICRISAT, India, pp. 14.

Malyshev, S.V. and Kartel, N.A. 1997. Molecular markers in mapping of plant genomes. *Mol. Biol.*, **31**: 163-171.

Manly, K.F. 1993. A Macintosh program for storage and analysis of experimental genetic mapping data. *Mamm. Genome* **1**: 123-126.

Manly, K.F. and Olsen, J.M. 1999. Overview of QTL mapping software and introduction to Mapmanager QTL. *Mamm. Genome* **10**: 327-334.

Martin, B., Nienhuis, J., King, G. and Schaefer, A. 1989. Restriction fragment length polymorphisms associated with water use efficiency in tomato. *Science* **243**: 1725-1728.

Martinez, O. and Curnow, R.N. 1992. Estimation of the locations and sizes of the effects of quantitative trait loci using flanking markers. *Theor. Appl. Genet.*, **85**: 480-488.

Mather, K. 1949. Biometrical genetics, Ist edn. Methuen: London.

Mather, K. and Harrison, R.J. 1949. The manifold effect of selection. *Heredity* **3**: 1-52.

McCouch, S.R., Chen, X., Panaud, O., Temnykh, S., Xu, Y., Cho, Y.G., Huang, N., Ishii, T. and Blair, M. 1997. Microsatellite marker development, mapping and applications in rice genetics and breeding. *Pl. Mol. Biol.*, **35**: 89-99.

McCouch, S.R., Kochert, G., Yu, Z.H., Wang, Z.Y., Khush, G.S., Coffman, W.R. and Tanksley, S.D. 1988. Molecular mapping of rice chromosomes. *Theor. Appl. Genet.*, **76**: 815-824.

McIntire, J. and Fussell, L.K. 1989. On-farm experiments with millet in Niger: Crop establishment, yield loss factors and economic analysis. *Expl. Agric.*, **25**: 217-233.

McPherson, H.G. and Slatyer, R.O. 1979. Mechanisms regulating photosynthesis in *Pennisetum typhoides*. *Aust. J. Biol. Sci.*, **26**: 329-339.

Melchinger, A.E. 1990. Use of molecular markers in breeding for oligogenic disease resistance. *Pl. Breed.*, **104**: 1-19.

Michelmore, R.W. 1995. Molecular approaches to manipulation of disease resistance genes. *Annu. Rev. Phytopathol.*, **33**: 393-427.

Minocha, J.L. and Sidhu, J.S. 1981. Establishment of trisomic stocks and linkage groups in *Pennisetum typhoides*. Final research report of PL-480 project, submitted to Punjab Agricultural University, Ludhiana.

Mohammed, H.A., Clark, J.A. and Ong, C.K. 1988a. Genotypic differences in temperature response of tropical crops. I. Germination characteristics of groundnut (*Arachis hypogea* L.) and pearl millet (*Pennisetum typhoides* S. & H.). *J. Exp. Bot.*, **39**: 1121-1128.

Mohammed, H.A, Clark, J.A. and Ong C.K. 1988b. Genotypic differences in temperature response of tropical crops. II. Light interception and dry matter production of pearl millet. *J. Exp. Bot.*, **39**: 1137-1143.

Mohan, M., Nair, S., Bhagwat, A., Krishna, T.G., Yano, M., Bhatia, C.R. and Sasaki, T. 1997. Genome mapping, molecular markers and marker-assisted selection in the improvement of quantitative traits. *Mol. Breed.*, **3**: 87-103.

Monforte, A.J. and Tanksley, S.D. 2000. Fine mapping of a quantitative trait loci (QTLs) from *Lycopersicon hirsutum* chromosome 1 affecting fruit characteristics and agronomic traits: breaking linkage among QTLs affecting different traits and dissection of heterosis for yield. *Theor. Appl. Genet.*, **100**: 471-479.

Monforte, A.J., Asins, M.J. and Carbonell, E.A. 1996. Salt tolerance in *Lycopersicon* species. IV. Efficiency of marker-assisted selection for tolerance improvement. *Theor. Appl. Genet.*, **93**: 765-772.

Moreau, L., Charcosset, A., Hospital, F. and Gallais, A. 1998. Marker-assisted selection efficiency of fruit size. *Genetics* **148**: 1353-1365.

Moreau, L., Lamarie′, S., Charcosset, A. and Gallais, A. 2000. Economic efficiency of one cycle of marker-assisted selection. *Crop Sci.*, **40**: 329-337.

Morris, M., Dreher, K., Ribaut, J.M. and Khairallah, M. 2003. Money matters (II). Costs of maize inbred line conversion schemes at CIMMYT using conventional and marker-assisted selection. *Mol Breed.*, **11**: 235-247.

Nene, Y.L. and Singh, S.D. 1976. Downy mildew and ergot of pearl millet. *PANS*, **22**: 366-385.

Nepolean, T. 2002. Identification of QTLs for yield and its component traits and downy mildew [*Sclerospora graminicola* (Sacc.) J. Schrot.] resistance in pearl millet [*Pennisetum glaucum* (L.) R. Br.] Ph.D. thesis, Tamil Nadu Agricultural University, Coimbatore, India.

Nguyen, 2001. http://www.plantstress.com/admin/Files/QTLs_for_resistance.html

Niemann-Sorenson, A. and Robertson, A. 1961. The association between blood groups and several production characters in three Danish cattle breeds. *Acta Agric. Scand.*, **11**: 163-196.

Ong, C.K. 1983a. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.) I. Vegetative development. *J. Exp. Bot.*, **34**: 322-336.

Ong, C.K. 1983b. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.) II. Reproductive development. *J. Exp. Bot.*, **34**: 337-348.

Ong, C.K. 1983c. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.) IV. Extension of individual leaves. *J. Exp. Bot.*, **34**: 1731-1739.

Ong, C.K. 1984. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.) V. Development and fate of tillers. *J. Exp. Bot.*, **35**: 83-90.

Ong, C.K. and Monteith J.L. 1985. Response of pearl millet to light and temperature. *Field Crops Res.*, **11**: 141-160.

Ong, C.K. and Squire, G.R. 1984. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.) VII. Final number of spikelets and grains. *J. Exp. Bot.*, **35**: 1233-1240.

Panaud, O., Chen, X.L. and McCouch, S.R. 1996. Development of microsatellite markers and characterization of simple sequence length polymorphism (SSLP) in rice (*Oryza sativa* L.). *Mol. Gen. Genet.*, **252**: 597-607.

Passioura, J.B., 1977. Grain yield, harvest index and water use of wheat. *J. Aust. Inst. Agri. Sci.*, **43**: 117-120.

Pasyukova, E.G., Vieira, C. and Mackay, T.F.C. 2000. Deficiency mapping of quantitative trait loci affecting longevity in *Drosophila melanogaster*. *Genetics* **156**: 1129-1146.

Paterson, A.H., Lander, S.E., Hewit, J.D., Peterson, S., Lincoln, S.E. and Tanksley, S.D. 1988. Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. *Nature* **335**: 721-726.

Paterson, A.H., Tanksley, S.D. and Sorrells, M.E. 1991. DNA markers in plant improvement. *Adv. Aagron.*, **46**: 39-90.

Payne, W.A. 1997. Managing yield and soil water use of pearl millet in the Sahel. *Agron. J.*, **89**: 481-890.

Payne, W.A. 2000. Optimizing water use in sparse stands of pearl millet. *Agron. J.*, **92**: 808-814.

Payne, W.A., Lascano, R.J., Hossner, L.R., Wendt, C.W. and Onken, A.B. 1991. Pearl millet growth as affected by phosphorus and water. *Agron. J.*, **83**: 942-948.

Payne, W.A., Wendt, C.W. and Lascano, R.J. 1990. Root zone water balance of three low input millet fields in Niger, West Africa. *Agron. J.*, **82**: 813-818.

Phillips, R.L. 1999. Unconventional sources of genetic diversity: *de novo* variation and elevated epistasis. **In**: Plant Breeding in the Turn of the Millennium. Borem, A., Giudice, M.P. and Sakiyama, N.S. (eds.). University of Vicosa, Brazil. pp. 103-131.

Poncet, V., Lamy, F., Devos, K.M., Gale, M.D., Sarr, A. and Robert, T. 2000. Genetic control of domestication traits in pearl millet (*Pennisetum glaucum* L., *Poaceae*). *Theor. Appl. Genet.*, **100**: 147-159.

Prioul, J.L., Quarrie, S., Causse, M. and Dominique de Vienne. 1997. Dissecting complex physiological functions through the use of molecular quantitative genetics. *J. Exp. Bot.*, **48**: 1151-1163.

Qi, X., Pittaway, T.S., Lindup, S., Liu, H., Waterman, E., Padi, F.K., Hash, C.T., Zhu, J., Gale, M.D. and Devos, K.M. (in press). An integrated genetic map of pearl millet (*Pennisetum glaucum*).

Ramond, C. 1968. Pour une meillure connaissance de la croissance et du développement des mils *Pennisetum*. *L'Agronomie Tropicale* **23**: 844-863.

Rasmusson, J.M. 1935. Studies on the inheritance of quantitative characters in *Pisum*: I. Preliminary note on the genetics of flowering. *Hereditas* **20**: 161-180.

Rattunde, H.F., Witcombe, J.R. and Frey, K.J. 1989. Structure of variation among morphological and physiological traits in three pearl millet composites. *Euphytica* **43**: 233-244.

Ray, J.D., Yu, I., McCouch, S.R., Champoux, M.C., Wang, G. and Nguyen, H.T. 1996. Mapping quantitative trait loci associated with root penetration ability in rice. (*Oryza sativa* L.) *Theor. Appl. Genet.*, **92**: 627-636.

Reed, K.C. and Mann, D.A. 1985. Rapid transfer of DNA from agarose gels to nylon membranes. *Nucleic Acid Res.*, **13**: 7207-7221

Ribaut, J-M. and Betran, J. 1999. Single large-scale marker-assisted selection (SLS-MAS). *Mol. Breed.*, **5**: 531-541.

Ribaut, J-M., Jiang, C. Gonzalez de Leon, D. Edmeades, G.O. and Hoisington, D. 1997a. Identification of quantitative trait loci under drought conditions in tropical maize. 2. Yield components and marker-assisted selection strategies. *Theor. Appl. Genet.*, **94**: 887-896.

Ribaut, J-M., Hu, X., Hoisington, D.A. and Gonzalez-de-Leon, D. 1997b. Use of SSTs and SSRs as rapid and reliable pre-selection tools in a marker-assisted selection backcross scheme. *Pl. Mol. Biol. Rep.*, **15**: 154-162.

Ribaut, J-M., Jiang, C. and Hoisington, D. 2002. Simulation experiments on efficiencies of gene introgression by backcrossing. *Crop Sci.*, **42**: 557-565.

Ribaut, J-M., Hoisington, D.A., Deutsch, J.A., Jiang, C. and Gonzalez-de-Leon, D. 1996. Identification of quantitative trait loci under drought conditions in tropical maize. 1. Flowering parameters and the anthesis-silking interval. *Theor. Appl. Genet.*, **92**: 905-914.

Rodney Mauricio, 2001. Mapping quantitative trait loci in plants: Uses and caveats for evolutionary biology. *Nat. Rev.*, **2**: 370-381.

Romagosa, I., Han, F., Ullrich, S.E., Hayes, P.M. and Wesenberg, D.M. 1999. Verification of yield QTL through realized molecular marker-assisted selection responses in a barley cross. *Mol. Breed.*, **5**: 143-152.

Saiki, R.K., Gelfand, D.H., Stoffel, S., Scharf, S.J., Higuchi, R., Horn, G.T., Mullis, K.B. and Erlich, H.A. 1988. Primer directed enzymatic amplification of DNA with a thermostable DNA polymerase. *Science* **239**: 487.

Saito, K., Miura, K. Nagano, K. Hayano-Saito, Y. Araki, H. and Kato, A. 2001. Identification of two closely linked quantitative trait loci for cold tolerance on chromosome 4 of rice and their association with anther length. *Theor. Appl. Genet.*, **103**: 862-868.

Sax, K. 1923. The association of size differences with seed coat pattern and pigmentation in *Phaseolus vulgaris*. *Genetics* **8**: 552-560.

Schneider, K.A., Brothers, M.E. and Kelly, J.D. 1997. Marker-assisted selection to improve drought resistance in common bean. *Crop Sci.*, **37**: 51-60.

Sedcole, J.R. 1977. Number of plants necessary to recover a trait. *Crop Sci.*, **17**: 667-668.

Sharma, A. 2001. Marker-assisted improvement of downy mildew resistance in elite pearl millet (*Pennisetum glaucum*) parental line H 77/833-2. Ph.D. thesis, Chaudhary Charan Singh Haryana Agricultural University, Hisar, India.

Sharp, P.J., Kries, M., Sherry, P.R. and Gale, M.D. 1988. Location of β-amylase sequences in wheat and its relatives. *Theor. Appl. Genet.*, **75**: 286-290.

Sharp, P.J., Chao, S., Desai, S. and Gale, M.D. 1989. The isolation, characterization and application in the *Triticeae* of a set of wheat RFLP probes identifying each homoeologous chromosome arm. *Theor. Appl. Genet.*, **78**: 342-348.

Shasidar, H.E. Hash, C.T., Seetharama, N., Shailaja, and Hittalmani, N. 2000. Target traits for QTL analysis and marker-assisted selection strategy for drought tolerance in rice. **In**: Field screening for drought tolerance in crop plants with emphasis on rice. Saxena, N.P. and John C o'Toole, (eds.). ICRISAT, Patancheru, India. pp. 92-103.

Shen, L., Courtois, B., McNally, K.L., Robin, S. and Li, Z. 2001. Evaluation of near-isogenic lines of rice introgressed with QTLs for root depth through marker-aided selection. *Theor. Appl. Genet.*, **103**: 75-83.

Shetty, H.S. 1987. Biology and epidemiology of downy mildew in pearl millet. **In**: Proceeding of the International Pearl Millet Workshop. Witcombe, J.R. and Beckerman, S.R. (eds.). ICRISAT, Patancheru, AP, India. pp. 147-160.

Singh, S.D. and Gopinath, R. 1985. A seedling inoculation procedure for detecting downy mildew resistance. *Pl. Dis.*, **69**: 582-584.

Singh, S.D., Ball, S.L. and Thakur, R.P. 1987. Problems and strategies in the control of downy mildew. **In**: Proceedings International Pearl Millet Workshop. Witcombe, J.R. and Beckerman, S.R. (eds.). ICRISAT: Patancheru, Andra Pradesh, India. pp. 161-172.

Singh, S.D., Singh, P., Rai, K.N. and Andrews, D.J. 1990. Registration of ICMA 841 and ICMB 841 pearl millet parental lines with A1 cytoplasmic-genic male sterility system. *Crop Sci.*, **30**: 1378.

Singh, S.D., King, S.B. and Werder, J. 1993. Downy mildew disease of pearl millet. Information Bulletin no.37. International Crops Research Institute for the Semi-Arid Tropics: Patancheru, Andhra Pradesh, 502 324. India. pp. 36.

Singh, S.D., Wilson, J.P. Navi, S.S. Talukdar, B.S. Hess, D.E. and Reddy, K.N. 1997. Screening techniques and sources of resistance to downy mildew and rust in pearl millet. Information Bulletin. No. 48. ICRISAT: Patancheru, Andra Pradesh. 502 324, India.

Slafer, G.A. and Araus, J.L. 1998. Improving wheat responses to abiotic stress. **In**: Proceedings 9th International Wheat Genetics Symposium, Saskatoon, Canada, Vol. 1. pp. 201-213.

Soller, M. and Beckmann, J.S. 1990. Marker-based mapping of quantitative trait loci using replicated progenies. *Theor. Appl. Genet.*, **80**: 205-208.

Soller, M. and Beckmann, J.S. 1983. Genetic polymorphism in varietal identification and genetic improvement. *Theor. Appl. Genet.*, **47**: 179-190.

Soller, M., Genizi, A. and Brody, T. 1976. On the power of experimental designs for the detection of linkage between marker loci and quantitative loci in crosses between inbred lines. *Theor. Appl. Genet.*, **47**: 35-39.

Squire, G.R. 1979. The response of the stomata of pearl millet (*Pennisetum typhoides* S. & H.) to atmospheric humidity. *J. Exp. Bot.*, **118**: 925-933.

Squire, G.R. 1989. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.) IX. Expansion processes. *J. Exp. Bot.*, **40**: 1389-1389.

Squire, G.R., Marshall, B. and Ong, C.K. 1986. Development and growth of pearl millet (*Pennisetum typhoides*) in response to water supply and demand. *Expl. Agric.*, **22**: 289-299.

Squire, G.R., Ong, C.K. and Monteith, J.L. 1987. Crop growth in semi-arid environments. **In**: Proceedings of the International Pearl millet workshop, ICRISAT-Patancheru, India, pp. 219-231.

Stam, P. 1993. Construction of integrated genetic linkage maps by means of computer package-Joinmap. *The Pl. J.*, **5**: 739-744.

Stam, P. and Van Ooijen, J.W. 1995. JoinMap ™ version 2.0: Software for the calculation of genetic linkage maps CPRO-DLO: Wageningen, The Netherlands.

Stam, P. and Zeven, A.C. 1981. The theoretical proportion of the donor genome in near-isogenic lines of self-fertilizers bred by backcrossing. *Euphytica* **30**: 227-238.

Stapf, O. and Hubbard, C.E. 1934. Pennisetum. **In**: Flora of Tropical Africa, Prain, D. (ed.). Vol. 9. London: Crown Agents, 1934, pp 954-1070.

Stuber, C.W. 1992. Biochemical and molecular markers in plant breeding. *Pl. Breed. Rev.*, **9**: 37-61.

Stuber, C.W. 1994. Breeding multigenic traits. **In**: DNA-Based Markers in Plants. Phillips, R.L.and Vasil, I.K. (eds.) Kluwer Academic Press: Dordrecht, The Netherlands. pp. 97-115.

Stuber, C.W. 1995. Mapping and manipulating quantitative traits in maize. *Trends Genet.*, **11**: 477-481.

Stuber, C.W., Edwards, M. and Wendel, J. 1987. Molecular marker-facilitated investigations of quantitative trait loci in maize. 2. Factors influencing yield and its component traits. *Crop Sci.*, **27**: 639-648.

Stuber, C.W., Goodman, M. and Moll, R. 1982. Improvement of yield and ear number resulting from selection at allozyme loci in a maize population. *Crop. Sci.*, **22**: 737-740.

Stuber, C.W., Lincoln, S.E. Wolff, D.W. Helenjaris, T. and E.S. Lander, 1992. Identification of genetic factors contributing to heterosis in a hybrid from elite maize inbred lines using molecular marker. *Genetics* **132**: 823-839.

Stuber, C.W., Moll, R., Goodman, M., Schaffer, H. and Weir, B. 1980. Allozyme frequency changes associated with selection for increased grain yield in maize (*Zea mays* L.). *Genetics* **95**: 225-236.

Sturtevant, A.E. 1965. A history of genetics. Haper and Row, New York.

Subudhi, P.K., Rosenow, D.T. and Nguyen, H.T. 2000. Quantitative trait loci for the stay-green trait in sorghum (*Sorghum bicolor* L. Moench). *Theor. Appl. Genet.*, **101**: 733-741.

Suiter, K.A., Wendel, J.F. and Case, J.S. 1983. Linkage-I: A PASCAL computer program for the detection and analysis of genetic linkage. *J. Hered.*, **74**: 203-204.

Tanksley. S.D. and Nelson, J.C. 1995. Advanced backcross QTL analysis: a method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. *Theor. Appl. Genet.*, **92**: 191-203.

Tanksley, S.D. and Rick, C.M. 1980. Isozymic gene linkage map of the tomato: applications in genetics and breeding. *Theor. Appl. Genet.*, **57**: 161-170.

Tanksley, S.D., Medina-Filho, H. and Rick, C.M. 1982. Use of naturally occurring enzyme variation to detect and map genes controlling quantitative traits in an inter-specific backcross of tomato. *Heredity* **49**: 11-25.

Tanksley, S.D., Young, N.D., Patterson, A.H. and Bonier-bale, M.W. 1989. RFLP mapping in plant breeding: new tool for an old science. *Biotech.*, **7**: 257-263.

Tao, Y.Z., Henzell, R.G., Jordan, D.R., Butler, D.G., Kelly, A.M. and McIntyre, C.L. 2000. Identification of genomic regions associated with stay-green in sorghum by testing RILs in multiple environments. *Theor. Appl. Genet.*, **100**: 1225-1232.

Teulat, B., Merah, O., Souyris, I. and This, D. 2001. QTLs for agronomic traits from a Mediterranean barley progeny grown in several environments. *Theor. Appl. Genet.*, **103**: 774-787.

Thoday, J.M. 1961. Location of polygenes. *Nature* **191**: 368-370.

Toojinda, T., Baird, E., Booth, A., Broers, L., Hayes, P., Powell, W., Thomas, W., Vivar, H. and Young, G. 1998. Introgression of quantitative trait loci (QTLs) determining stripe rust resistance in barley: an example of marker-assisted line development. *Theor. Appl. Genet.*, **96**: 123-131.

Tuberosa, R., Salvi, S. Sanguineti, M.C. Landi, P. Maccaferri, M. and Conti, S. 2002a. Mapping QTLs regulating morpho-physiological traits and yield in drought-stressed maize: case studies, shortcomings and perspectives. *Ann. Bot.*, **89**: 941-963.

Tuberosa, R., Sanguinet, M.C. Landi, P. Giuliani, M.M. Salvi, S. and Conti, S. 2002b. Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QTLs for grain yield in the field at two water regimes. *Pl. Mol. Biol.*, **48**: 697-712.

Tuberosa, R., Salvi, S. Sanguineti, M.C. Maccaferri, M. Giuliani, S. and Landi, P. 2003. Searching for QTLs controlling root traits in maize: a critical appraisal. *Plant Soil* **255**: 35-54.

Tuinstra, M.R., Grote, E.M., Goldbrough, P.B. and Ejeta, G. 1996. Identification of quantitative trait loci associated with pre-flowering drought tolerance in sorghum. *Crop Sci.*, **36**: 1337-1344.

Tuinstra, M.R., Ejeta, G. and Goldsbrough, P.B. 1997. Heterogeneous inbred family (HIF) analysis: A method for developing near isogenic lines that differ at quantitative trait loci. *Theor. Appl. Genet.*, **95**: 1005-1011.

Ullstrup, A.J. 1973. An overview of the downy mildew of corn and sorghum. Report of a workshop on the downy mildew of sorghum and corn, Technical Report, Texas Agricultural Experimental Station, Department of Plant Sciences, 74: 5-12.

Utz, H.F. and Melchinger, A.E. 1995. PLABQTL: A computer program to map QTL, Version 1.0, University of Hohenheim, Germany.

Utz, H.F., Melchinger, A.E. and Schön, C.C. 2000. Bias and sampling error of the estimated proportion of genotypic variance explained by QTL determined from experimental data in maize using cross validation and validation with independent samples. *Genetics* **154**: 839-849.

Van Berloo, R. and Stam, P. 1998. Marker-assisted selection in autogamous RIL populations: a simulation study. *Theor. Appl. Genet.*, **96**: 147-154.

Van Ooijen, J.W. 1999. LOD significance thresholds for QTL analysis in experimental populations of diploid species. *Heredity* **83**: 613-624.

Van Ooijen, J.W. and Maliepaard, C. 1996. MapQTL™ verson 3.0: Software for the calculation of QTL positions on genetic maps. CPRO-DLO, Wageningen, The Netherlands.

van Oosterom, E.J., Whitaker, M.L. and Weltzien, R. E. 1996a. Integrating genotype by environment interaction analysis, characterization of drought patterns, and farmer preferences to identify adaptive plant traits in pearl millet. **In**: Plant Adaptation and Crop Improvement. Cooper, M. Hammer, G.L. (eds.). Wallingford, UK: CAB International, pp. 383-402.

van Oosterom, E.J., Mahalakshmi, V., Bidinger, F.R. and Rao, K.P. 1996b. Effect of water availability and temperature on the genotype-by-environment interaction of pearl millet in semi-arid tropical environments. *Eupytica* **89**: 175-183.

van Oosterom, E.J., Carberry, P.S., Hargreaves, J.N.G. and O'Leary, G.J. 2001. Simulating growth, and yield of tillering pearl millet II. Simulation of canopy development. *Field Crops Res.*, **72**: 67-91.

van Oosterom, E.J., O'Leary, G.J., Carberry, P.S. and Craufurd, P.Q. 2002. Simulating growth, development and yield of tillering of pearl millet III. Biomass accumulation and partitioning. *Field Crops Res.*, **79**: 85-106.

Visscher, P.M., Haley, C.S. and Thompson, R. 1996. Marker-assisted introgression in backcross breeding program. *Genetics* **144**: 1923-1932.

Wallace, J.S., Lloyd, C.R. and Sivakumar, M.V.K. 1993. Measurements of soil, plant and total evaporation from millet in Niger. *Agric. Forest Meteor.*, **63**: 149-169.

Weber, J.K. and May, P.E. 1989. Abundant class of human DNA polymorphisms which can be typed using the polymerase chain reaction. *Am. J. Hum. Genet.*, **44**: 388-396.

Weller, J., Soller, M. and Brody, T. 1988. Linkage analysis of quantitative traits in an interspecific cross of tomato (*Lycopersicon esculentum* × *L. pimpinellifolium*) by means of genetic markers. *Genetics* **118**: 329-339.

Weller, J.I. 1987. Mapping and analysis of quantitative trait loci in *Lycopersicon* (tomato) with the aid of genetic markers using approximate maximum likelihood methods. *Heredity* **59**: 413-421.

Weltzien R.E. and King, S.B. 1995. Recurrent selection for downy mildew resistance in pearl millet. *Pl. Breed.*, **114**: 308-312.

Williams, R.J., Singh, S.D. and Pawar, M.N. 1981. An improved field screening technique for downy mildew resistance in pearl millet. *Pl. Dis.*, **65**: 239-241.

Wilson, J.P. 1999. Pearl millet diseases: A compilation of information on the known pathogens of pearl millet, *Pennisetum glaucum* (L.) R. Br. Agriculture Handbook No.716. U.S.

Winkel, T. and Do, F. 1992. Caracteres morphologiques et physiologiques dc resistnce du mil [*Pennisetum glaucum* (L.) R.Br.] a la secheresse. *L'Agronomie Tropicale* **46**: 339-350.

Witcombe, J.R. and Hash, C.T. 2000. Resistance gene deployment strategies in cereal hybrids using marker-assisted selection: Gene pyramiding, three-way hybrids and synthetic parent populations. *Euphytica* **112**: 175-186.

Xu, W., Subudhi, P. K., Crasta, O. R., Rosenow, D. T., Mullet, J. E. and Nguyen, H. T. 2000. Molecular mapping of QTLs conferring stay-green in sorghum (*Sorghum bicolor* L. Moench). *Genome* **43** : 461-469.

Yadav, O.P. 1994. Genetic divergence in pearl millet accessions of Indian and exotic origin. *Ind. J. Genet. & Pl. Breed.*, **54**: 89-93.

Yadav, O.P. and S.K. Bhatnagar, 2001. Evaluation of indices for identification of pearl millet cultivars adapted to stress and non-stress conditions. *Field Crops Res.*, **70**: 201-208.

Yadav, O.P. and weltzien, E.R. 1999. Breeding for adaptation to abiotic stresses. **In**: Pearl millet breeding. Khairwal, I.S., Rai, K.N., Andrews, D.J. and Harinarayana, G. (eds.). Oxford & IBH, New Delhi, India: pp. 317-336.

Yadav, R.S., Hash, C.T., Bidinger, F.R. and Howarth, C.J. 1999. QTL analysis and marker-assisted breeding of traits associated with drought tolerance in pearl millet. **In**: Proceedings of the workshop on Genetic Improvement of Rice for Water-Limited Environments, Ito, O., O'Toole, J. and Hardy, B. (eds.). 1-3 Dec 1998, Los Banos, Phillipines: The International Rice Research Institute. pp. 211-223.

Yadav, R.S., Hash, C.T., Bidinger, F.R., Cavan, G.P. and Howarth, C.J. 2002. Quantitative trait loci associated with traits determining grain and stover yield in pearl millet under terminal drought stress conditions. *Theor. Appl. Genet.*, **104**: 67-83.

Yadav, R.S., Bidinger, F.R., Hash, C.T., Yadav, Y.P., Yadav, O.P., Bhatnagar, S.K. and Howarth, C.J. 2003. Mapping and characterization of QTL × E interactions for traits determining grain and stover yield in pearl millet. *Theor. Appl. Genet.*, **106**: 512-520.

Yadav, R.S., Hash, C.T. Bidinger, F.R. Devos, K.M. and Howarth, C.J. 2004. Genomic regions associated with grain yield and aspects of post-flowering drought tolerance in pearl millet across stress environments and tester background. *Euphytica*, **136**: 265-277.

Young, N.D. 1996. QTL mapping and quantitative disease resistance in plants. *Annu. Rev. Phytopathol.*, **34**: 479-501.

Young, N.D. 1999. A cautiously optimistic vision for marker-assisted breeding. *Mol. Breed.*, **5**: 505-510.

Young, N.D. and Tanksley, S.D. 1989a. RFLP analysis of the size of chromosomal segments retained around the Tm-2 locus of tomato during backcross breeding. *Theor. Appl. Genet.*, **77**: 353-359.

Young, N.D. and Tanksley, S.D. 1989b. Graphics-based whole genome selection using RFLPs. **In**: Current communications in molecular biology: Development and application of molecular markers to problems in plant genetics, Helentjaris, T. and Burr, B. (eds.). Cold Spring Harbor Press: Cold Spring Harbor, NY. pp. 123-129.

Young, N.D. and Tanksley, S.D. 1989c. Restriction fragment length polymorphism maps and the concept of graphical genotypes. *Theor. Appl. Genet.*, **77**: 95-101.

Young, N.D., Miller J. and Tanksley, S.D. 1987. Rapid chromosomal assignment of multiple genomic clones in tomato using primary trisomics. *Nucl. Acids Res.*, **15**: 9339-9348.

Zeng, Z.B. 1993. Theoretical basis for separation of multiple linked gene effects in mapping quantitative trait loci. *Proc. Natl. Acad. Sci.*, **90**: 10972-10976.

Zeng, Z.B. 1994. Precision mapping of quantitative trait loci. *Genetics* **136**: 1475-1468.

Zhang, X.Q., Ross, K. and Gustafson, J.P. 2000. Physical location of homoeologous groups 5 and 6 molecular markers mapped in *Triticum aestivum* L. *Genetics* **91**: 441-445.

Zheng, Z-B. 1993. Theoretical basis of separation of multiple linked gene effects in a mapping quantitative trait loci. *Proc. Natl. Acad. Sci.*, **90**: 297-303.

Zheng, Z-B. 1994. Precision mapping of quantitative trait loci. *Genetics* **136**: 10972-10976.

Zhou, P.H., Tan, Y.F., He, Y.Q., Xu, C.G. and Zhang, Q. 2003. Simultaneous improvement for four quality traits of Zhenshan 97, an elite parent of hybrid rice by molecular marker-assisted selection. *Theor. Appl. Genet.*, **106**: 326-331.