Discussions

The compulsion to sustain and increase food grains production

The world human population according to the United Nations prediction is expected to reach 9.4 billion by 2050. The world must therefore develop the capacity to feed 10 billion within the next 40–50 years. Most of this capacity will need to result from greater yields on existing cropland. “The 9-billion People Question” (9BPQ) addressed a worldwide dilemma that is central to most if not all plant scientists – How can our society grow enough food to feed 2 billion additional human beings in less than 40 years (Parker 2011)? Rice (*Oryza sativa*) will play a key role in solving the 9BPQ as rice feeds half the world and it is that half that will double in size in the foreseeable future. If this can be achieved without proportionate increases in the use of water or fertilizer (sustainable intensification), and within the context of climate change (Hirel et al 2007; Cattivelli et al 2008; Foulkes et al 2009; Royal Society 2009), the damaging environmental effects of expanding the global cropped area will be minimized. Increased stability in yield and in crop stress resistance is therefore required, along with better use of water and fertilizer, to ensure food security and environmental protection in future decades.

Effects of climate change

Major changes to agricultural systems worldwide in the last five decades have contributed to, and interacted with, new food systems. Von Braun (2007) highlighted the transforming role of the interacting driving forces of population increase, income growth, urbanization, and globalization on food production, markets, and consumption. To these
forces can be added the twin elements of climate variability and climate change which have direct effects on both food production and food security (Parry et al 2004). It is well known that the sensitivity of agricultural systems to climate differs between systems depending on whether they are temperature- or water-limited, and whether they are operating near their optimum or not. Fuhrer (2006) concluded that there was ample evidence to demonstrate the sensitivity of agricultural systems to climate change, and that the range of effects on potential productivity was from extremely negative in areas that were already water-limited to positive in areas that were temperature-limited. Similarly, the effects of climate variability and change on food security are also location-specific and, more importantly, societally-specific with countries and groups with low income and limited adaptive capacity facing significant threats to food security (von Braun 2007). In particular, food insecurity is expected to be increased by climate change although the size of the effect is affected more by socio-economic factors than by climate change per se (Easterling et al 2007).

While many studies have demonstrated the sensitivities of plants and of crop yield to a changing climate, a major challenge for the agricultural research community is to relate these findings to the broader societal concern with food security. Globally atmospheric CO₂ has increased, with accompanying changes in pathogen and pest incidence and to farming practices. Many pests and pathogens exhibit considerable capacity for generating, recombining, and selecting fit combinations of variants in key pathogenicity, fitness, and aggressiveness traits that there is little doubt that any new opportunities resulting from climate change will be exploited by them. However, the
interactions between crops and pathogens and pests are complex and poorly understood in the context of climate change (Gregory et al 2009).

Climate change models predict a gradual increase in CO₂ concentration and temperature all over the world, but are not precise in predicting future changes in local weather that will directly affect crop productivity and outbreaks of epidemics. Extreme weather events that will occur with climate change will influence when and where diseases will occur and therefore many impose severe risks on crop failure (Gautam et al 2013). Rice plants are reported in greenhouse tests to be more susceptible to *Pyricularia oryzae* and *Rhizoctonia solani* (Kobayashi et al 2006) under elevated levels of CO₂. One hypothesis they proposed was that the higher number of tillers observed under elevated CO₂ concentrations may have increased the chance for fungal sclerotia to adhere to the leaf sheath at the water surface. Consequently, the potential risks for infection of leaf blast and epidemics of sheath blight would increase in rice grown under elevated CO₂ concentration (Kobayashi et al 2006). Therefore it is imperative to watch for the stability in reaction of rice varieties to pathogens and grain yield performance to prevent production losses.

**Supporting rice production with improved varieties**

Rice research network has made significant contributions to rice improvement in all the rice growing countries. The All-India Co-ordinated Rice Improvement Project (AICRIP) trials started in 1965 are primarily aimed at disseminating germplasm and elite breeding stock, for evaluation and direct use as commercial release, or indirect use as parents in
variety improvement program as the secondary aim. In AICRIP, there is a two-way flow of elite germplasm, breeding material and information among participating national agricultural research systems in all states. Ecosystem-oriented yield nurseries evaluated intensively in replicated trials are focused towards rainfed upland, rainfed lowland, semi-deep and deep water and irrigated rice areas. By the identification and introduction of $D_{GWG}$ gene into varieties, non-lodging dwarf stature was achieved with an improvement only in yields harvested. Compared to indica land races, the harvest index increased along with a reduction in plant height in the first “high-yielding” varieties TN1, IR8 and Jaya. Exploiting the advantage of METs of AICRIP, a number of varieties were released with similar yield potential but with varied maturity duration (early, medium, and late), grain size, appearance, scent and quality, and resistance to one or more pathogens and insect pests that cause damage (Muralidharan et al 1996).

The annual production oriented surveys have shown a wide prevalence of diseases on at least some varieties under cultivation in different districts and states of India (DRR 1975-2014). Although in none of the years epidemics of devastating proportion like that of Irish potato ((Large 1940; Strange 2003) or the Great Bengal Famine (Padmanabhan 1973) was encountered in the Indian rice production scene, several accurate estimates have been made on the loss of yields due to epidemic outbreaks of rice diseases. In epidemics, the most conservative estimates for the production yield losses in actual districts affected were 8 to 13% from blast (Rajarajeswari and Muralidharan 2006a), and 3 to 16% from bacterial leaf blight epidemics (Rajarajeswari and Muralidharan 2006b). Further, a single tungro epidemic that may occur sporadically can inflict yield loss of
53% in a district, 23% in any one state and 2% in all-India rice production (Muralidharan et al 2003a). Over 500,000 tonnes of rice valued at Rs 2911 millions (at 2003 prices) was lost in an epidemic of tungro in one district. Therefore, it is clear that epidemics can cause considerable, if not devastating, production and economic losses limited to some farm fields. Rice varieties released for commercial cultivation in India with some level of resistance to pathogens have definitely prevented the threat of a national calamity from these epidemics although they still continue to occur at a few places and at varying intensities in India (DRR 1975-2014).

**Re-evaluation of old released varieties**

The importance of re-evaluation of varieties under commercial cultivation was realized in all crops, more importantly in food grain crops as reports are continuously made on the level of yield losses from different cropped fields, districts, states or countries. Genetic uniformity invites disaster because it makes a crop vulnerable to attack from a pest or disease that strikes one plant and quickly spreads throughout the crop. Fortunately epidemics on the scale of southern corn leaf blight epidemic of 1970–1971 in the USA (Ullstrup 1972) was not witnessed again as numerous varieties were released and in any one rice growing area, normally more than 20 rice varieties are encountered in contiguous fields in India (DRR 1975-2014).

Epidemic outbreaks focus on the importance of continued vigil on pathogen and crop varieties. The epidemic of cotton leaf curl disease (CLCuD) in Pakistan and north-eastern India during the 1990s involved multiple multipartite begomoviruses, with many
plants containing more than one species, a single species of betasatellite and various alphasatellites. All previously resistant cotton varieties started showing symptoms of CLCuD from 2001 onwards. The begomovirus associated with resistance break down was also found to be a recombinant (Sattar et al 2013).

Seldom shift from a minor to a major status of a pathogen may occur. A major success in plant breeding for disease resistance is the broad-spectrum, durable control of powdery mildew (*Blumeria graminis* f. sp. *hordei*) of barley conferred by recessive alleles of *Mlo*. The widespread use of *mlo* resistance to control mildew may have inadvertently stimulated the emergence of *Ramularia* leaf spot as a major disease of barley (McGrann et al 2014). Plant pathogens are continually evolving to survive. Plants have developed a set of mechanisms to face the challenge of foreign pathogens through a long history of co-evolution (Muralidharan 2005). The continuous changes in host plants, pathogens, production technology and environment are reasons for periodical re-evaluation of variety performances and adaptation.

Analyses of old varieties help understand the yield potential and stability of varieties. Nsarellah et al (2011) re-assessed the adaptation of the main registered durum wheat (*Triticum turgidum* var. *L. durum*) varieties in Morocco. The varieties from the medium breeding era were widely adapted and possessed the ability to exploit favorable environments. The oldest varieties were widely adapted but were devoid of high yield potential in the more favorable environments. Internationally coordinated public wheat breeding efforts have focused in recent decades on increasing resistance to disease and
abiotic stress (Reynolds and Borlaug 2006; Braun et al 2010). Increasingly it is felt important to rigorously re-test all the old varieties to assess their stability in the level of resistance and in grain production capacity. For the first time, in the present investigations over one-hundred commercially released rice varieties in India have been re-tested during three kharif and two rabi seasons for stability of yield and resistance to four major pathogens viz., *Pyricularia oryzae*, *Rhizoctonia solani*, *Xanthomonas oryzae* pv. *oryzae* and rice tungro virus.

**Development and release of high-yielding varieties with resistance to diseases**

The aim of AICRIP program is to improve yielding ability, increase efficiency in the use of external inputs and incorporate resistance to biotic and abiotic stresses (Muralidharan and Siddiq 1997). The multi-locational or multi- environmental (METs) testing of breeding stock developed at different research centres is organized by AICRIP. The evaluation of genotype x environment interactions in different ecosystems has been the rationale for the multidisciplinary approach to rice improvement research. Depending on genotype sensitivity to photoperiod, a promising superior genotype is identified based on three to four years data from the METs. Each year, genotypes are tested in METs at a minimum of 5 to a maximum of 53 locations in 16 states of India. In the first year, the newly evolved genotypes are tested in replicated local yield trials. The selected breeding lines from these experiments are included in the zonal coordinated trials called initial variety trial (or initial evaluation trial - IET). Simultaneously, these breeding lines are also put to screening nursery tests for identifying their reaction to diseases and pests. The breeding lines that yield consistently well for two years are grouped to form advanced
variety trials (or uniform variety trials) and tested for two more seasons. Agronomic data on these elite breeding lines are also generated during this period. After a careful scrutiny by different research centres, selected breeding lines are evaluated in on-farm trials for obtaining reaction of farmers and extension workers on the yield performance and acceptability. Considering yield records, agronomic data and the reaction to diseases and pests, candidate breeding lines are identified for release as varieties at the annual workshop by the coordinating unit. These are then named and released as new high yielding varieties to cultivators by the state or central variety release committee (Prasad et al 2001). Yet, these released commercial varieties were not systematically studied for stability or change in reactions to pathogens or in grain yields capacity. Therefore, the present study assumes greater importance.

**Futility of detached leaf assay for identifying resistance to *Pyricularia oryzae***

Typical techniques of screening for resistance in germplasm of most crop plants involve field ratings for the presence of lesions and other damage caused by pathogen. A disadvantage of this method is dependence on favourable environmental conditions or controlled facilities in a greenhouse for the pathogen development before rating can be taken. Variation in virulence of pathogen populations also will likely influence these tests, producing differences in observed cultivar susceptibility between locations. To bypass these inherent difficulties in conducting field tests, a detached leaf method is used for assessing variety resistance in several plant species. This makes it potentially better method of screening for disease resistance, as it is cost effective, space saving and a faster method of conducting screening tests on large sample size (Jackson et al 2008).
This method has the advantage of having control over the environmental conditions which have been a common source of errors in past analyses (Purdy et al 1983).

Several techniques using detached leaves have been developed to study host–pathogen interactions, including maize rust (Kushalappa and Hegde 1971), *Fusarium* head blight of wheat (Browne and Cooke 2004), *Septoria tritici* blotch (Arraiano et al 2001), yellow rust of barley (Osman-ghani 1982), and powdery mildew of barley (Brown and Wolfe 1990). These methods were successfully focused on host resistance. Most detached-leaf studies have utilized the cytokinin kinetin and benzimidazole to maintain green tissues healthy and delay senescence. Dolar (1997) tested resistance of detached chickpea leaflets to two different races of *Ascochyta rabiei* (Pass.) Labr. and found it to be successful. For several legume crops, detached leaf screening for response to pathogen have been reported (Balducchi and McGee 1987; Onfroy et al 2007).

A detached pod or leaf assay conducted in vitro is only of benefit to the plant breeder if it correlates well to field responses (Irwin et al 2003). Detached plant-part screening assays are useful because they enable assessments to be made under highly-controlled conditions, serve as rapid screening techniques that can be adopted by breeding programs and can assist our understanding of host-pathogen interactions (Huang et al 2005; Bradley et al 2006; Ergon and Tronsmo 2006). Detached leaves of differential oat cultivars produced the same reactions to *Puccinia coronata* as whole plants screened under standard conditions in a growth chamber using benzimidazole and kinetin (100
mg/l). Jackson et al (2008) had proposed detached leaf system as useful for the evaluation of host resistance under highly controlled conditions.

In the present investigations, detached leaves inoculated with *P. oryza* spore drops produced very clear lesions. Irrespective of the ecosystem for which a variety was released for commercial cultivation, overall means showed production of 17 to 30 lesions/54 spore drops placed on detached leaves (Table 3). All these leaf lesions were fully developed that later coalesced in detached leaves of all the varieties tested (Plate 1). Lesions developed in all detached leaves tested irrespective of whether a variety was known as resistant, moderately resistant or susceptible as evident from 30 to 37% lesions development in detached leaves of Rasi, IR64 or IR 72 (resistant), and 65% lesions in detached leaves of Mahsuri (susceptible) (Table 2). Kar and Mishra (1975) found benzimidazole, kinetic, etc to increase the activities of peroxidase and polyphenol oxidase enzymes in detached floated leaves. As a result of increased levels of oxidative enzymes, the total phenolics accumulated in detached and darkened rice detached leaves; but in attached leaf senescence in light, no such accumulation of phenolics occurred. This elevated enzyme activities may be the critical factor in making detached leaf susceptible to the *P. oryza*.

Detached leaf method for the fungal inoculation and disease evaluation has recently been suggested as one of the methods for a better measurement of host resistance by minimizing confounding factors from plant architectures and environmental conditions. The results from the detached leaf assays in the present
investigation clearly demonstrated that irrespective of the source of resistance either known or un-known in varieties, all the 80 varieties tested showed typical blast lesion development in detached leaves (Table 2). Therefore, detached leaf test to evaluate disease reactions of rice germplasm and to map of blast resistance genes as advocated by Jia et al (2013) has no practical value as this test shows only one reaction of susceptibility to \textit{P. oryzae} that will lead to erroneous conclusions.

**Stability in the reaction of released rice varieties to four major pathogens**

Severity or incidence is a quantitative measurement of the intensity of certain damage caused by pathogens. Severity is the area or volume of plant tissue that is damaged, usually relative to the total area or volume. With sheath blight and tungro virus, severity is also measured with an arbitrary scale indicating the degree of whole plant symptom development. Always a comparative reaction of test varieties is taken in relations to that of susceptible check in making final judgement on a varietal reaction to the pathogen. In the present study, the susceptible checks \textit{viz., HR12} for \textit{P. oryza}, and \textit{TN1} for \textit{R. solani, X. oryzae pv. oryzae} and tungro virus, were killed by the respective pathogens (score = 9) in all the repeat tests, and in all the replicatios. This indicated that disease pressure on varieties was high in these tests and the reactions scored are valid and useful for analysis.

The reaction of 118 varieties \textit{P. oryzae} was categorized in AICRIP’s METs and declared as 47 resistant (scores <5), 32 moderately resistant (scores \leq 5 to<7) and 39 susceptible (scores \geq 7) (Fig. 3). The present tests revealed (Table 4) that only 34 were resistant, 60 were moderately resistant and 24 were susceptible to blast infection in these
repeat tests. Only five varieties *viz.*. ASD18, Dhanrasi, DRRH2, Gurjari and Sabita had changed reaction to blast from resistance to susceptibility (Table 4, 15; Fig. 4). This change was due to the altered disease scores from 3.0 to 6.5 in three varieties, and to 7 in two others (Table 16). From moderate resistance to susceptibility, seven varieties had changed reactions to blast disease. While six varieties had shown a changed reaction score from 6 to 7, only one *viz.* Ratna changed from score 6 to 8 (Table 16). Ratna has already been de-notified to stop commercial cultivation (Rani et al 2011).

The reaction of 118 varieties *R. solani* was categorized in METs and declared as none resistant (scores <5), 22 moderately resistant (scores \( \leq 5 \) to<7) and 96 susceptible (scores \( \geq 7 \)) (Fig. 5). Similar to the original disease scores claimed at release of varieties, no variety was resistance to sheath blight disease (Fig. 6, Table 15). The present tests revealed (Table 6) that 19 were moderately resistant and 99 were susceptible to sheath blight infection (Fig. 6). From moderate resistance to susceptibility, 14 varieties had changed reactions to sheath blight. Nine varieties had shown a change from disease scores 6 to 7, while five others were with scores <7.8 (Table 16).

The reaction of 118 varieties to *Xanthomonas oryzae* pv. *oryzae* was categorized in METs and declared as 9 resistant (scores <5), 26 moderately resistant (scores \( \leq 5 \) to<7) and 83 susceptible (scores \( \geq 7 \)) (Fig. 7). The present tests revealed (Table 8) that none was resistant, 21 were moderately resistant and 97 were susceptible to bacterial leaf blight infection (Fig 8). Only six varieties *viz.*. ADT36, GR101, IR36, PR111, PR116 and Sabita had changed reaction to bacterial leaf blight from resistance to susceptible. This
change was due to the altered disease scores from 3.0 to 6.7 in three varieties, to 7.0 in two varieties, and to 7.8 in one other variety (Table 15). From moderate resistance to susceptibility, 17 varieties had changed reactions to bacterial leaf blight disease. Six varieties had shown a changed reaction from scores 6 to 7, nine varieties from scores 6 to 8, Narendra118 from score 6 to 8.3 and ASD20 from 6 to 8.7.

The reaction of 118 varieties tungro virus disease was categorized in METs and declared as 5 resistant (scores <5), 17 moderately resistant (scores ≤ 5 to <7) and 96 susceptible (scores ≥ 7) (Fig. 9). The present tests revealed (Table 10) that 7 were resistant, 61 were moderately resistant and 50 varieties were susceptible to rice tungro virus infection (Fig 10). Only two varieties viz., Dinesh and DRRH2 had changed reaction to rice tungro virus from resistance to susceptibility (Table 15) while three others had changed from moderate resistance to susceptibility (Table 16).

**Durability of resistance in varieties released for commercial cultivation**

To all the four pathogens tested in the present study, a few changes in reactions of varieties earlier known to be resistant or moderately resistant were also recorded: 13 changed from resistance to susceptible (5 to *P. oryzae*, 6 to *X. oryzae pv oryzae*, and 2 to rice tungro virus); and 45 from moderate resistant to susceptible (11 to *P. oryzae*, 14 to *R. solani*, 17 to *X. oryzae pv oryzae*, and 3 to rice tungro virus) (Figs. 4, 6, 8, 10; Table 15). However, 24 of these varieties recorded a marginal increase in scores bordering moderate resistance and susceptibility (6 to *P. oryzae*, 9 to *R. solani*, 8 to *X. oryzae pv oryzae*, and 1 to rice tungro virus) (Table 16).
Thus evidence from the present repeat tests on the reactions of varieties to pathogens (*P. oryzae, R. solani, X. oryzae pv oryzae* and rice tungro virus) leads to a conclusion that the reactions of most varieties categorized in METs and declared as resistant, moderately resistant or susceptible have more or less remained very stable despite passage of several years and decades after their release. With the exception of a few varieties, most of them showed a borderline reaction change from moderate resistance to susceptibility (Table 16). It was of interest to note that a few varieties have actually improved on their performance to display resistance in the present tests in comparison with that claimed at their release. This is illustrated by the changed reaction of varieties recorded in the present tests (Fig. 4, 6, 8 and 10; Tables 4, 6, 8, and 10) from susceptibility to resistance (8 to *P. oryzae* and 4 to rice tungro virus), or from susceptibility to moderate resistance (19 to *P. oryzae*, 11 to *R. solani*, 9 to *X. oryzae pv oryzae*, and 42 varieties to rice tungro virus). The reason for such changes could be due to elimination of susceptible plants in apparently mixed population of breeding lines released as varieties.

Generally for such changes in resistance or moderate resistance to susceptible reaction of varieties, or susceptible to resistance or moderate resistance, the most common explanations given are the changed virulence of pathogens, environmental conditions or the disease escape in the tests. In a few instances, admixtures or impurity of seeds may also lead to changed reactions. The minor changes recorded may also be due to the minor deficiencies in the scoring system using the decimal scale which is
apparently in a pronounced quantitative scale when classifying varieties as moderate resistance or susceptible.

Observations on the severity leaf blast reaction are recorded as: 0-3 scores represent no lesions to small roundish to slightly elongated necrotic grey spots; and 4 to 9 scores quantitatively assess disease proportion as per cent leaf area affected by leaf blast lesions. All most always some test genotypes score moderately higher ratings (>5 but >7 scores). Accumulated data (DRR 1965-2014) indicate that it is always these moderately resistant genotypes that remain stable in their reactions to leaf blast in tests over years and therefore, get selected. Using such a classification of disease rating in METs, numerous high-yielding cultivars with blast resistance have been released for commercial cultivation in India. Dinaker and Muralidhran (2007) investigated on several components of resistance in 22 varieties and confirmed the appropriateness of using 0-9 decimal scoring of disease proportion to select cultivars with durable resistance to blast. Cultivars tested in their experiments have been released for commercial cultivation in farmers’ fields 15-27 years ago, after selection through METs for 5-7 years across 30-50 locations in the country. They concluded on the stable and durable resistance to leaf blast disease in these varieties.

The low levels of changes in the reaction of 120 varieties to four major pathogens recorded in the present investigations, however, lead to conclude on the very stable resistance imparted and claimed in these varieties at the time of release. The METs performed at 5 to 53 locations in 16 states of India for a minimum period of three years in
screening nurseries ensure that the genotypes are many times exposed to various virulence populations and environmental conditions that are present at different locations in different years before they are selected on consistent performance and qualified for release as commercial varieties. The durability identified in the present tests further proves the strength of METs of AICRIP as earlier emphasized in other studies (Muralidharan et al 1996; Muralidharan et al 2003a, b, 2004b; Dinaker and Muralidharan 2007).

**Comparison of yields harvested in field tests with predicted yields using models**

The mean grain yields actually observed and recorded in the three kharif (first set) and rabi (second set) seasons data on the 100 varieties were also derived for each ecosystem (first and second sets, Table 17). Using the yield models developed by Muralidharan et al (1996, 2002), the mean grain yields were predicted (Table 17 third set) as the expected grain yields for each ecosystem (see page 60, Materials and Methods). As these models predicted yields only for the kharif season yields, the differences between the kharif and rabi seasons on estimated mean yields (first and second sets) in the present investigations, were used to adjust model by adding the differences to the derived yields (fourth set, Table 17) to rabi seasons data (second set) for a comparison.

While the overall model derived mean yield was 3.24 t/ha, the mean grain yields obtained seasons from varieties released was 3.50 t/ha in kharif, and 4.0 t/ha in rabi seasons. In general tillers and tillers with panicles were higher in kharif crop than that of rabi crop of all the varieties studied. Grain weight was more in rabi (94 to 124 g/10 hills)
except deep water rice (83 g/10 hills), compared to kharif (89 to 108 g/10 hill). In rabi seasons, panicle weight was slightly higher in the varieties, but the straw weight was lower. Such differences apparently contributed to higher grain yields in rabi.

Positive Pearson correlation coefficients (Table 17) were estimated for mean grain yields of 100 varieties released for different ecosystems in kharif ($r = 0.578$ non-significant) and rabi ($r = 0.779$ highly significant at $P= 0.01$) seasons with those of model derived mean yields for kharif and the adjusted model derived mean yields for rabi, respectively. Comparison of paired means $t$-test showed significant differences in the mean yields. The apparent cause was that the mean grain yields of 100 varieties were estimated only under irrigated conditions in the present investigations in all seasons tested. It also proved that rice varieties released for rainfed uplands, semideep and deep water ecosystems possessed the potential to produce higher yields in favorable (irrigated) ecosystem. This is an excellent achievement of breeders as the ecosystems depend largely on the vagaries of the weather. These varieties can contribute to higher production under favorable conditions of weather for crop growth like that of irrigated ecosystem.

A comparison of mean grain yields in field estimation of 100 varieties in kharif seasons was made with model derived yields for different rice ecosystems (Fig. 11). The difference between the mean grain yields actually harvested in kharif seasons and Muralidharan et al (1996) models derived yield showed minor decreases in yields in varieties released for hills (HRIR), irrigated (IRE, IRM, IRME), rainfed lowland (RSL) and scented rice (SCR) ecosystems. Altogether the total number of varieties tested in
these six ecosystems was 87. However, there were increases (0.58, 0.93 and 1.9 t/ha) in a total of only 13 of the released varieties tested (9 for rainfed upland (RUP), and 2 each for semideep water (SDW) and deep water (DW) ecosystems). It is again pertinent to point out that the yield tests in the present studies were made only in irrigated ecosystem at DRR Rajendranagar farm which apparently provided more favourable conditions for crop growth and productivity. Even granting for the deviation to high yields in 13 commercially released varieties than what was predicted with models, 87% of varieties tested produced grain yield that were near or negligibly different from the model predicted yields of the varieties (Fig. 11). Therefore, it is very much evident that 87 of the 100 released varieties tested demonstrated a very stable yield performance as shown earlier in a few released varieties through AICRIP (Prasad et al 2001).

**Diversity in varieties for stable yields**

Grasses have coevolved with humans since the dawn of agriculture; 10000 years ago. They represent the most productive and widely grown crop family and provide a foundation for human life across the globe. Grain producing grasses such as rice (*Oryza* spp.), maize (*Zea mays*), sorghum (*Sorghum bicolor*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and oats (*Avena sativa*) provide the majority of calories consumed by people worldwide (FAO 2009). Sugarcane (*Saccharum officinarum*) and sweet sorghum produce the bulk of water soluble carbohydrates, mainly sucrose, for use in human and animal foods, along with directly fermentable substrate for ethanol production (Waclawovsky et al 2010). Forage grasses and crop residues provide much of the biomass consumed by ruminant agricultural and wild pastoral animals as well as lignocellulosic feed stocks for second-generation biofuel production (Mitchell et al 2008;
Yields from primary crops such as maize, rice, and wheat are predicted to decline over the next two decades especially in semi-arid regions of the world due to climate change (Lobell et al 2008).

Empirical studies have shown that higher levels of plant species diversity can result in greater above-ground productivity (Hector et al 2002; van Ruijven and Berendse 2005; Roscher et al 2011) and ecosystem stability (Tilman et al 2006). Previous studies on the relationships between plant diversity, stability and productivity of ecosystems have focused on diversity at the species level (Tilman 2001), yet these relationships are also observed at the functional group and genotype level (Hector et al 2002; Hughes and Stachowicz 2011). The potential of plant diversity to increase or stabilize productivity is of great interest in crop systems (Zhu et al 2000). It is evident that stability in varieties for resistance to pathogens and grain yields must also be diverse in their genetic make-up.

In the present study, DNA fingerprinting of 100 released rice varieties with five ISSR primers produced interpretable and variable banding patterns. The total number of bands produced in 90 varieties varied: 466 in ISSR 876 (the least), 625 in both ISSR 811 and ISSR 812, 766 in ISSR842 and 885 in ISSR 884 (the highest). The ability of ISSR primers to discriminate between varieties also varied: failed to discriminate between 22 varieties with ISSR 811, 11 varieties with ISSR 812, 51 varieties with ISSR842, 13 varieties with ISSR 876 and 17 varieties with ISSR 884. The resolving power was high in a di-nucleotide 5’ anchored ISSR primer 884 (Rp = 19.67) and a di-nucleotide 3’ anchored ISSR primer 842 (Rp = 17.02). Yet, none of the primers was able to uniquely discriminate between the 90 varieties studied. Dendrograms generated with the five
primers showed more or less similar placement of varieties into respective clusters and subdivisions with some exceptions. There was no exclusive ecosystem grouping of varieties although they were released as suitable for nine specific rice ecosystems. Similarly there was no exclusive grouping based on maturity duration of varieties. These results confirmed the diversity in released rice varieties.

**Released rice varieties are diverse and stable for reaction to pathogens and yields**

Rice ecosystems are characterized by elevation, rainfall pattern, depth of flooding and drainage, and by the adaptation of rice to these agroecological factors. Genotypes are evaluated every year in METs. AICRIPs aim was to study the performance of breeding lines developed for various ecosystems and to identify stable genotypes with wide adaptability. They differ in the genetic expression of maturity period and photosensitivity (Muralidharan et al 1996). The periodic release of cultivars after 1980 resulted in yield stability, at the cost of a marginal reduction in yields. The remarkable diversity attained in rice varieties can be illustrated with the quick success in releasing a resistant variety to a newly discovered gall midge biotypes (Muralidharan et al 1996). A test of breeding lines developed before knowledge on this new biotype in the area where the ruling Phalguna rice variety became very susceptible, enabled identification of resistance in more than 30 lines (Muralidharan et al 1987). This demonstrated that breeding lines are rigorously and repeatedly exposed to known and unknown virulent pathogen populations and variable environmental stresses in METs to facilitate selection of stably resistant or moderately resistant lines. Therefore, maintenance breeding aimed at retaining the levels of resistance considered critical to yield stability (Hargrove et al 1980; Khush 1990) was
proved to be no longer needed in rice improvement programs as suggested by Prasad et al (2001).

As farmers adopt modern cultivars and improved cultural practices, they generally shift to monoculture and this has been assumed to lead to genetic simplification of rice cultivated in many farmlands. When a single cultivar is planted over large areas, vulnerability to pests and diseases has been speculated (NAS 1972). A large number of improved rice cultivars released since the early 1940s trace maternally to *Cina* (Hargrove et al 1980). Other popular land races used in crosses include Latisail and Peta. Chang and Vergara (1972) also expressed concern about the lack of diversity of cytoplasm. However, the genetic makeup of some varieties discussed in the present study includes female progenitors, with *Cina* (IR 36, IR 50, IR 8, Swarnadhan, and Savitri); and *Mayang Ebos* cytoplasm (Mahsuri) (Prasad et al 2001). Including Jaya, Rasi, IR 8, IR 36, IR 50 and Savitri, most semidwarf improved rice cultivars developed worldwide, derive their dwarfing gene from the Chinese dwarf *DGWG*. However, after 50 years of continued use, no weakness in *Cina* cytoplasm has been detected so far (Hargrove et al 1980; DRR 1975-2014). The genetic makeup of these stable varieties has been shown to possess considerable variation (Prasad et al 2001).

Recently, genetic diversity in representative sets of high yielding varieties of rice released in India between 1970 and 2010 was studied at molecular level employing hypervariable microsatellite markers (Choudhary et al 2013). Cluster analysis clearly grouped the 100 genotypes into their respective decadal periods i.e., 1970s, 1980s, 1990s
and 2000s. The trend of diversity over the decadal periods estimated revealed increase of diversity over the periods in year of release-wise classification of rice varieties.

**Durability due to quantitative resistance**

Quantitative resistance affects quantitative components of pathogenicity (e.g., rate of infection, latent period, rate of sporulation), which are dependent on the host, the pathogen and the interaction between host and pathogen (Lannou 2012). Quantitative resistance is frequently assumed to be more durable than qualitative resistance (Parlevliet 2002), which has been experimentally shown, for example, in the case of wheat leaf rust on the cultivar, Apache (Papaix et al 2011). Even if differential efficiencies of quantitative resistance have been shown among sites (Andrivon et al 2007) and among pathogen isolates (Talukder et al 2004; Le Guen et al 2007; Marcel et al 2008; Delmotte et al 2013), the erosion of quantitative resistance at one site over time has not been demonstrated (Mundt et al 2002). It is indeed difficult to detect gradual changes in efficiencies of quantitative resistance (McDonald and Linde 2002), since these efficiencies are influenced by environmental conditions (Young 1996; Pariaud et al 2009; Lannou 2012). Since diverse mechanisms have been proposed to explain quantitative resistance (Poland et al 2009: Kou and Wang 2010: Vergne et al 2010), different corresponding adaptation process becomes a necessity for the pathogen with only a few leading to the emergence of generalist pathogen populations. The results obtained by Caffier et al (2014) stress the need to look for diversified quantitative resistance factors that combine complementary modes of action on the pathogen, resulting in trade-offs between quantitative components of pathogenicity (Lannou 2012; Azzimonti et al 2013; Pariaud et
al 2013), and to optimize the management of cultivar distribution in space and time (Sapoukhina et al 2013) to limit the possibilities of step-by-step evolution in pathogen populations (Bourget et al 2013). Theoretical approaches predict that host quantitative resistance selects for pathogens with a high level of pathogenicity, leading to erosion of the resistance. However, this process of erosion has not been experimentally demonstrated (Caffier et al 2014). Genetic diversity as observed in landraces of rice and its wild relatives enables the plants to evolve and differentiate into various cultivars adapted to different environments (Morishima and Oka 1995).

The present study demonstrated for the first time beyond doubt that varieties released for commercial cultivation, barring a few exceptions, are stable or durable for the reaction to \textit{P. oryzae}, \textit{R. solani}, \textit{X. oryzae pv oryzae}, and rice tungro virus and produce stable grain yields. Li et al (1999) concluded that a high level of durable resistance to \textit{X. oryzae pv. oryzae} may be achieved by the cumulative effects of multiple QTLs, including the residual effects of "defeated" major resistance genes. It is therefore apparent that breeder across different centres in the country have pooled diverse resistance genes in the varieties nominated to AICRIP for an evaluation and METs successfully aided in the selection of those possessing quantitative resistance genes resulting in the stability or durability of reaction to pathogens even decades after their selection and release for commercial cultivation. The diversity in these durably resistant varieties has successfully prevented vulnerability and yield instability in rice production in India.