SCIENCE ET CHANGEMENTS PLANÉTAIRES

SECHERESSE

VOLUME 24
NUMÉRO 4
OCT.-NOV.-DÉCEMBRE 2013

Addressing farming challenges in semi-arid zones

Surmonter les défis de l'agriculture en zones sèches

Numéro coordonné
par Jérôme Bossuet et Vincent Vadez

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DE LA FRANCOPHONIE

ISSN 1147-7806

Cahiers d'études et de recherches francophones

SECHERESSE

Research Article

Sécheresse 2013 ; 24 : 261–73

Pest and diseases: Old and new threats – Modern breeding tools to tailor new crop cultivars

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Abstract

Full yield potential of any crop cannot be harnessed completely due to several challenges such as biotic and abiotic, faced by the crops at various growth stages. Biotic stresses caused by viruses, bacteria, fungi, pathogen, parasites, pests and weeds pose major threat to sustainable productivity by reducing yield from 30% in general to complete yield loss in some severe epidemic cases. Crop protection measures for safe-guarding crops such as use of synthetic pesticides, weedicides, etc. have largely been helpful in curtailing the losses, however, their haphazard use have caused adverse environmental and health hazards. Genetic alternatives such as introgression/pyramiding of genes/quantitative trait loci associated with resistance to target pest and diseases, on the other hand, is much ecological and eco-friendly approach. Although, there are several biotic stress agents for any crop, however, only a few pests or diseases cause major yield loss. It is beyond the scope of this review to cover all the pests and diseases affecting all the crops, thereby, focus has been given on major pests and diseases of representative crops such as rice (cereal), chickpea (legume) and tomato (vegetable). Special emphasis has been given on the current status and future prospects of deploying modern breeding approaches for developing improved cultivars with high resilience to major biotic stresses in order to achieve maximum genetic yield potential in all the crops.

Key words : biotic stress, disease resistance, genomics-assisted breeding.

Résumé

Ravageurs et maladies : anciennes et nouvelles menaces – Les outils modernes de sélection pour confectionner de nouvelles variétés de plantes adaptées

Le plein potentiel de rendement d'une culture ne peut jamais être totalement atteint du fait de plusieurs obstacles tels que les contraintes biotiques et abiotiques que rencontrent ces cultures aux différents stades de croissance. Les stress biotiques causés par les virus, bactéries, champignons, pathogènes, parasites, ravageurs et adventices représentent un problème majeur dans la recherche d'une productivité agricole durable, en réduisant les rendements de 30 % en général jusqu'à la perte totale de la récolte dans certains cas d'attaques extrêmes. Les mesures de protection des plantes telles que l'usage de pesticides et herbicides synthétiques ont permis de réduire les pertes mais leur utilisation hasardeuse a causé des dommages sur l'environnement et pour la santé. Des approches alternatives basées sur la génétique des plantes comme l'introgression, le pyramidage de gènes et la sélection par QTL (*quantitative trait loci*) de variétés résistantes aux maladies et ravageurs sont plus

To cite this article: Khera P, Pandey MK, Varshney RK, 2013. Pest and diseases: Old and new threats – Modern breeding tools to tailor new crop cultivars. *Sécheresse* 24: 261-73. doi: 10.1684/sec.2014.0410

doi: 10.1684/sec.2014.0410

Reprints : R.K. Varshney

écologiques. Même si chaque plante est confrontée à plusieurs types de stress biotiques, seuls quelques ravageurs ou maladies causent des pertes importantes de rendement. Cet article ne se veut pas exhaustif mais se focalise sur les principaux ravageurs et maladies de cultures représentatives comme le riz (céréale), le pois chiche (légumineuse) et la tomate (légume). Une attention particulière a été portée sur la situation actuelle et les évolutions futures du déploiement des outils modernes de sélection des plantes pour créer des cultivars améliorés très résistants aux principaux stress biotiques, comme réponse pour atteindre le potentiel maximum de rendement pour toutes les plantes cultivées

Mots clés : résistance aux maladies, sélection génomique assistée des plantes, stress biotique.

At the turn of the mid-century, world population is expected to reach nine billion (UNDP, 2006) thereby, pressing the demand for more food and fodder (Lutz and Samir, 2010). Since, the majority of our calorie intake is obtained from cereals followed by legumes and vegetables, major contribution towards world food security is expected from these crops (Bruinsma, 2009). An obvious solution to attain this higher demand is through either expansion of the cropped area or increased productivity. However, due to continuous constraints on natural resources because of population pressure and varying climate change scenario, increasing crop area is not a realistic alternative in near future (Wall and Smit, 2005). Hence, the only feasible alternative left for sustainable agriculture is to increase the overall crop yield per unit area on the available agricultural land. Crop specialists all over the world are putting great effort in increasing the yield barrier. However, during the last decade there has been stagnation in yield increase in several important crops such as rice, wheat and maize. Legumes on the other hand not participated much in the yield increase per unit area. Apart for the struggle towards breaching the yield barrier, another way to increase yield is to put much greater effort towards protecting the yield loss through making crop plants more resilient to different stress factors.

Nowadays, crops face countless challenges in the form of insects attack, pathogen infection, drought, and temperature fluctuations due to climate change. If pest related losses are taken into consideration, it contributes to 14 to 25% on average of the total global agricultural production (see DeVilliers and Hoisington, 2011). Estimated losses due to pests among some major crops were estimated to be 26% for soybean, 28% for wheat, 31% for maize, 37% for rice and 40% for potatoes (Oerke, 2006; Oerke and Dehne, 2004). However, crop losses in the range of 15-30% against pests are known in cotton, chickpea, pigeon pea, tomato and sunflower (see Dhaliwal *et al.*, 2010). Furthermore, losses due to pathogens, animal pests and weeds were estimated to be 16, 18, and 34%, respectively. While synthetic pesticides have provided effective control over many pests, their continuous and indiscriminate use causes various adverse and harmful effects on environment along with development of pesticide resistance in pests and pest resurgence (Sharma *et al.*, 2008). Since pesticides are not specific to a particular type of organism, many non-target organisms are also killed during crop protection exercises. In addition, pesticide residue in food causes health hazards in humans. It is estimated that around US$10 billion of pesticide is annually used for crop protection (Oerke, 2006).

A much ecological and environmental friendly technology towards crop protection is to make cultivars resistant to various pests and diseases through introgression/pyramiding of genes and quantitative trait loci (QTL) controlling these biotic stresses. The genetic alternative has a significant role towards integrated crop management (ICM). Advances towards plant genomics approaches in this direction, including modern genomics and genetic engineering technologies have opened up new avenues for plant breeding. In this context, genomics-assisted breeding (GAB) has emerged as a powerful tool for breeders for enhancing genetic gain in crop breeding in less time and more accuracy. However, there is an urgent need to reduce the obstacles that bounds the routine implementation of complex genomic datasets by breeders. Part of the solution lies in the capacity building for next generation breeders in utilization of modern breeding approaches in order to integrate basic and applied genomics for developing improved cultivars. This chapter discusses some modern breeding approaches and successful examples wherein these modern tools have been used to develop improved varieties with special reference to pest and diseases.

Challenges in crop production: pest and disease resistance

Plant pests/diseases have been continuously posing serious damage to crop plants with their dynamic evolutionary nature. Although disease control measures were partly successful for some crops for few diseases but plant host-pathogen based resistance emerged as the best available sustainable option which avoid use of hazardous chemicals and hence are eco-friendly. It is estimated that diseases typically reduce plant yields by 10-20% each year. A plant shows resistance from preformed defences and infection-induced responses and the disease outcome is determined by the three-way interaction, *i.e.* pathogen, plant, and environment. Large variation for resistance has been observed among the crop specific-gene pool and resistance is usually pathogen species-specific or pathogen strain-specific. The other is a parasite gene called the avirulence (*Avr*) gene. Plants producing a specific resistance (*R*) gene product will show resistance against a pathogen that produces the corresponding avirulence (*Avr*) gene product. The two major classes of resistance gene namely NBS-LRR *R*-genes with a nucleotide binding site (NBS) and the cell surface pattern recognition receptors (PRR) *R*-genes with a leucine rich repeat (LRR) play important role in host-plant defence mechanism (Song *et al.*, 1995; McHale *et al.*, 2006). Some of the major challenges for crop production have been discussed in three crops namely rice, chickpea and tomato representing cereals, legumes and vegetables in this section.

Rice

Rice is a staple food crop for more than half of the world's population. Due to its wide cultivation across several ecosystem and geography, it invites numerous biotic stresses in the form of viruses, bacteria, fungi, parasites, pests, pathogen and weeds. Insect pests cause more than 25% yield loss (Dhaliwal *et al.*, 2010). Among diseases, the three most devastating diseases of rice are bacterial blight, blast and sheath blight. Bacterial blight caused by *Xanthomonas oryzae* pv. *oryzae* (Xoo) is one of the oldest known diseases of rice. When plants are infested by Xoo, it can cause yield losses in the range of 20-30%, which may sometimes go up to 50% (Mew, 1987; Ou, 1985). In young plants, the leaves show peculiar symptoms called as '*kresek*', wherein water-soaked pale-green streak are formed near the margins and tip. These streaks later coalesce and develop into yellowish-white and wavy edges. The whole leaf of the susceptible cultivar may wilt, leading to drying up and death of plants. In older plants, leaves become yellowish, wilt and dry (Swings *et al.*, 1990). Another important disease of rice is blast caused by *Magnaporthe oryzae*, a plant-pathogenic ascomycete fungus, which can cause yield loss of up to 50% annually (Scardaci *et al.*, 1997). Early symptoms of rice blast are greyish spots with dark borders on all parts of shoot and leaves, which grow into whitish-grey spindle-shaped lesions with necrotic borders. If not controlled, the lesions may expand, coalesce and kill the leaves (Jia *et al.*, 2000). Sheath blight, caused by the soil borne fungus *Rhizoctonia solani* (Kühn.), is one of the major diseases of rice. Yield losses of more than 50% have been reported (Chahal *et al.*, 2003) in high-inputs rice production areas. The symptoms of sheath blight appear as a greyish-water soaked lesion on the sheaths of leaf. These lesions enlarge quickly having uneven dark brown margins with whitish centre, giving it a snake skin look. At advanced stages of infestation, the lesions coalesce and girdle entire culm, leaf sheath, flag and boot leaf, encircling tiller to death.

Major pests of rice are planthoppers, gall midge, stem borers and leaffolders. Among planthoppers, brown planthopper (BPH) *Nilaparvata lugens* (Stal.) and while backed planthopper (WBPH) *Sogatella furcifera* (Horvath.) are of importance. Plant hoppers suck sap from the phloem vessels through their sucking mouth parts, thereby making plants devoid of food which results in wilting and drying of the entire plant (Bentur *et al.*, 2011). Furthermore, BPH being a vector of rice ragged stunt virus and rice grassy stunt virus, the damage increases when insect and virus attack combines. It is noteworthy here that another important pest of rice, green leafhoppers *Nephotettix* spp is a vector of rice tungro virus. Rice gall midge, *Orseolia oryzae* (Wood-Mason) is emerging as a major pest and causes silver shoot of paddy. Another important pest of rice is yellow stem borer (YSB), *Scirpophaga incertulas* (Walker.). YSB infests at all the stages of plant development, however maximum damage is observed at panicle exertion stage when the larva bores into the plant feeding on the growing tip. Among rice leaffolders, *Cnaphalocrocis medinalis* (Guenee.) is the most dominant and well-known species in Asia, other species which are less predominant are *Marasmia exigua* (Butler.), *M. exigua* and *B. arotraea* (Bentur *et al.*, 2011). The leaffolder larva causes damage through a peculiar mechanism. Firstly it folds the rice leaf, and stitching both the leaf blades together, secondly it feeds the green mesophyll tissue by scraping with the fold (Bentur *et al.*, 2011).

Chickpea

The important biotic stresses affecting chickpea are ascochyta blight (AB), fusarium wilt (FW), botrytis grey mold (BGM) and pod borer (PB). AB caused by the fungus *Ascochyta rabiei* (Pass.) Labrousse, is one of the most devastating disease and can even cause complete yield loss (Singh and Reddy, 1996). Early symptoms are wilting of individual plants or group of seedlings, leading to drying and death of plant. On leaves, pods and stems, circular patches having greyish centre with brownish margins can be seen (Pande *et al.*, 2005). *Fusarium oxysporum* f.sp. *cicero* a soil-borne fungus causes a devastating disease, FW in chickpea with a yield loss of up to 90% (Singh and Reddy, 1991). It is vascular disease which causes blackening or browning of xylem, leading to wilting and death of the entire plant. BGM caused by *Botrytis cinerea* Pers. ex. Fr., is one of the main foliar disease (Pande *et al.*, 2006). Drooping and breakage of the infested terminal branches is a common symptom of BGM (Grewal *et al.*, 1992). *Helicoverpa armigera* or PB larva causes major yield loss; it initially feeds on young leaves, killing them completely. When the plant grows, the larva feeds on the developing seeds and leaves (Sharma *et al.*, 2008). Breeding for resistance to PB is a huge challenge in chickpea.

Tomato

Tomato (*Solanum lycopersicum* L.) is a major vegetable crop, grown in almost all parts of the world[1]. Apart from its various uses, it is a good source of antioxidant such as tocopherol, chlorogenic acid, rutin, xanthophylls and plastoquinones (Leonardi *et al.*, 2000). Diseases cause most of the economic losses in the fresh market segment as well as in tomato processing industries[2]. Fungi, bacteria, viruses, nematodes together cause over 200 diseases in tomato (Lukyanenko, 1991). Among this plethora of diseases, fungi cause major economic losses and hence, few major fungal diseases are discussed here. Fusarium wilt caused by *Fusarium oxysporum* f.sp. *Lycopersici*, and verticillium wilt caused by *Verticillium dahliae* and *V. albo-atrum*, are common and devastating soil borne fungal diseases of tomato. The early signs for both the diseases in small plants show yellowing, drooping and wilting of lower leaves. However in case of fusarium wilt, the symptoms shows on one side of the plant while the whole plant is affected uniformly in case of verticillium wilt[3]. Another serious soil borne fungal disease of tomato is fusarium crown and root rot, caused by *Fusarium oxysporum* f.sp. *radicis-lycopersici*. Symptoms show swelling of crown with orange and brown lesions, root-rot and decay of lower stem. As the disease progresses, the stem whither, leading to wilting of the plant within 2-3 weeks (Can *et al.*, 2004). Early blight, caused by *Alternaria solani* and *A. tomatophila*, is another common and destructive disease. It occurs mainly in the area where there is high relative humidity, frequent rainfall and heavy dew. The symptoms include dark brown lesions with concentric rings on older leaves, and as the lesion expand the leaves eventually defoliate (Barksdale and Stoner, 1977). Another major fungal disease which causes annually major economic loss is late blight, caused by the oomycete *Phytophthora infestans* (Mont.) de Bary. Its symptoms include dark brown lesions appearing first at the top of node or stem, progressing down the stem.

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[1] http://faostat.fao.org/site/567/DesktopDefault.aspx?PageID=567#ancor

[2] http://faostat.fao.org/

[3] http://ccesuffolk.org/assets/Horticulture-Leaflets/Fusarium-and-Verticillium-Wilts-of-Tomato.pdf

The disease begins when the sporangia start germinating on the host tissue through extension of germ tubes or through zoosporogenesis (Hardham and Blackman, 2010). As disease progress further, leaflets dry up, die, thereby spreading to rest of the leaves, leading to defoliation. Powdery mildew caused by *Oidium lycopersici*, *O. neolycopersici* sp. *nov.* and *Leveillula taurina* (Chunwongse *et al.*, 1994; Kissa *et al.*, 2001) occurs mainly where tomatoes are grown in green houses, however its occurrence in commercial field is also observed. The symptoms show powdery white lesions on leaf surface and stems. As the disease furthers, the lesions merge and devastates the plant. The diseased plant produce less and small unmarketable tomatoes (Jones *et al.*, 2001).

Among the bacterial diseases, bacterial canker caused by *Clavibacter michiganensis* sp. *michiganensis* and bacterial wilt caused by *Ralstonia solanacearum* are considered most serious and widespread. These diseases are difficult to control due to high genetic variation in pathogen, complexity of resistance traits and wide distribution of pathogen (Hayward, 1991; Yang and Francis, 2007). Bacterial canker causes variety of symptoms on plants depends on its age, mode of infection and environmental factors. However, most common symptom observed in young plants are dark brown lesions on leaf margins, wilting, stunting, vascular discoloration leading to the death of plant (Ftayeh *et al.*, 2010). In case of bacterial wilt, the pathogen disrupts the water transport system of the plant by affecting its vascular system, leading to wilting and death (Hayward, 1991). Among the major viral diseases, tomato mosaic virus (ToMV) and tomato yellow leaf curl virus (TYLCV) cause considerable yield loss. ToMV, transmitted mechanically, is considered as a highly stable virus. The early disease symptoms include yellow mottling of leaves and blister like lesions, which may appear fern-like at later stages. Fruit production will be stunted, and even if few tomatoes are produced, it would be of low quality (Scott, 2007). TYLCV, a whitefly transmitted geminivirus, is a devastating disease in the tropical and sub-tropical areas of the world (Navot *et al.*, 1991). The disease symptoms consist of upward curling of margins of leaflet, young leaves turns yellow, reduction in leaf area, flower abortion and stunting, thereby resulting in severe yield loss (Moriones and Navas-Castillo, 2000).

From germination to harvesting stage, a large number of insects attack tomatoes, causing considerable crop loss. Among the insects that feed on leaves, show discoloured blotches, cause plant injury by boring buds, stem end and fruits, includes tomato fruitworm, tobacco budworm, tomato pinworm and vegetable leafminer. Another class of chewing insects which makes holes in seedling leaves, tender leaf tissue includes blister beetles, cabbage looper, colorado potato beetle, flea beetles and hornworms. Plant injury from sap-sucking insects such as tomato aphids, green peach aphid, greenhouse whitefly, silverleaf whitefly, stink bug and western flower thrips causes discoloration of leaf, deformation of leaf or fruit and defoliation. Cutworm and southern potato wireworm on the other hand feeds on lower stems and roots causing irregular holes (Foolad, 2007; Foolad and Panthee, 2012).

Modern breeding approaches

Although methods in classical plant breeding have contributed immensely towards genetically insulating crops from various biotic stress during the last century, however, in the current scenario of crop production wherein multiple and new threats have arisen, conventional breeding alone does not seem to be an effective approach. Modern breeding approaches have emerged as a saviour towards developing improved cultivars in a fast and effective manner. With the advent of next generation sequencing (NGS) and high-throughput genotyping technologies in the area of genomics, last decade has witnessed numerous advances in the area of molecular biology and bioinformatics. Now genomic tools for breeding applications are available in almost all important crops. Once the marker-trait or genotype to phenotype associations is established, this knowledge can be used in product development.

The benefits of modern breeding approaches include not only developing improving cultivars but also shielding the leading cultivars from pests and diseases by introgressing various genes and QTL through gene pyramiding. Large number of breeding populations can be screened at the early seedling stage in addition to drastically reducing the time period for developing a variety. This approach is called as marker-assisted selection (MAS). There are, however, several instances where pest and disease resistance genes were found in wild crop relatives (WCR). Through utilization of molecular breeding approaches like advanced-backcross QTL (AB-QTL) these genes have been introgressed in the elite cultivars. Recently, novel breeding approaches such as marker-assisted recurrent selection (MARS) and genomic selection (GS) have been developed by coupling genomics tools with conventional breeding schemes along with precise multi-season phenotyping and dense genotyping (Varshney and Dubey, 2009; Phillips, 2010). Hence an all-inclusive approach, where all genomic technologies are used in plant breeding is now termed as 'genomics-assisted breeding' (GAB) (Varshney *et al.*, 2005) (*figure 1*). Through utilization of these modern breeding approaches, plant

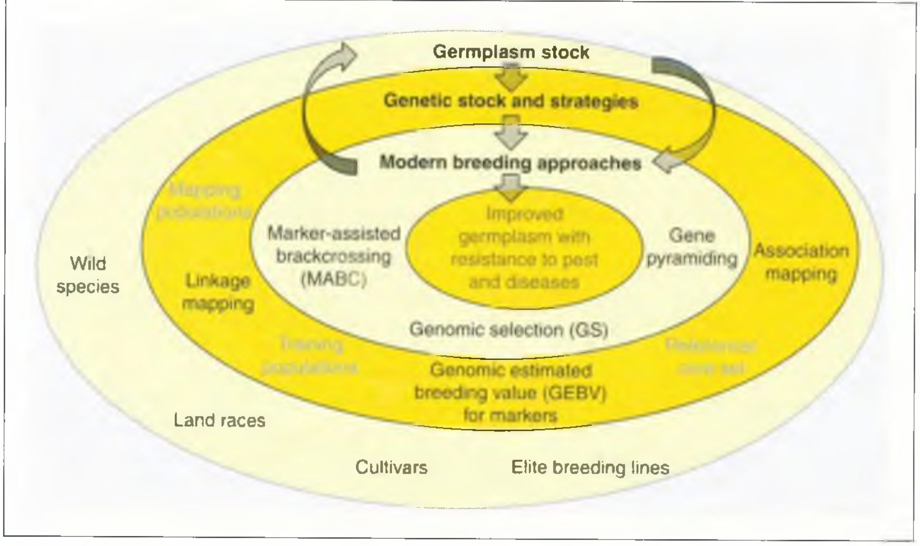

Figure 1. Integrated genomics and breeding approaches for developing improved germplasm with resistance to pest and diseases.

breeding has reached to such levels wherein genomics tools are being efficiently integrated in regular crop improvement programs in a cost-effective way for speedy development of improved cultivars.

Trait mapping and validation of markers

In order to successfully reap the benefits of modern breeding approaches, the first step is to have tight linkage between molecular marker and trait of interest. Linkage and association mapping are the two main approaches used for trait mapping (Varshney *et al.*, 2009a). Once the marker-trait linkage is established, confirmed and validated, it can then be routinely used aptly in crop improvement program. The prerequisite to achieve this is to have in place, appropriate genomic tools and precise phenotyping techniques. Researchers in the past have put lot of efforts in this direction. As a result, there are numerous types of molecular markers, genetic maps, transcriptome resource and genome sequence available in a range of crops. But, among molecular markers, simple sequence repeat (SSR) and single nucleotide polymorphism (SNP) markers have undoubtedly arisen as a preferred choice (Gupta *et al.*, 1999; Gupta and Varshney, 2000; Varshney and Dubey, 2009). However, with the introduction of next generation sequencing (NGS) technologies and high-throughput genotyping platforms, SNP marker is gaining popularity (Varshney *et al.*, 2009b; Varshney *et al.*, 2009c). It is evident that last decade has witnessed immense growth towards development of genomic tools however, effort towards establishing high-throughput precision phenotyping platform have not been satisfactory (Mir *et al.*, 2012; Cobb *et al.*, 2013). Accurate phenotyping is still a major challenge for several complex traits towards efficient utilization of molecular tools and forming strong marker-trait association. Nevertheless, sophisticated robotics based digital image analysis platform, which includes, chlorophyll fluorescence analysis, imaging of pathogen affected leaf area, fluorescence-based conidial quantification, video tracking system, data management and statistical analysis are now fast gaining importance (Lucas, 2010; Walter *et al.*, 2012). The Australian Plant Phenomics Facility established at Adelaide and Canberra, Australia is one such initiative towards alleviating the phenotyping bottleneck[4].

Once, the genomic tools and precise phenotyping methods are available, trait mapping can be initiated either through linkage or association mapping approaches. In case of linkage mapping, a suitable mapping population is developed by crossing contrasting parental genotypes for the target trait. During the past few decades various linkage mapping populations have been developed for marker discovery work, which includes, F_2, three-way, back cross, recombinant inbred lines, immortal F_2s and chromosome substitution segment lines in a number of crops. Subsequently, segregating (mapping) populations are genotyped with the markers polymorphic between the parental lines and based on these genotyping data, genetic maps are developed. In parallel, the populations are phenotyped for traits of interest. Analysis of genotyping and phenotyping data together by using QTL mapping programmes provides QTL(s) and markers associated with traits (Collard *et al.*, 2005; Varshney *et al.*, 2009a). By using linkage mapping based approach, a number of QTLs conferring resistance to biotic stress have been identified in several crops (see Varshney *et al.*, 2013).

In recent years, association mapping approach which utilizes linkage disequilibrium in germplasm for establishing marker-trait association is gaining importance. Some of its benefits over linkage mapping are that it saves lot of precious resources in terms of time and labour, as there is no necessity for developing any mapping population, and germplasm collections can directly be employed for phenotyping and genotyping. The panel of genotypes used in association mapping can be phenotyped for several traits; therefore the same genotypic data can be used for identification of markers associated with different traits. It offers higher resolution as it utilizes the variations due to meiotic recombination accumulated in natural population during the course of evolution. Even though currently association mapping is at its nascent stage, it is rapidly becoming a preferred method to study complex traits (Varshney *et al.*, 2009a). Recently marker-trait association using this approach have been performed in several crop species such as maize (Kump *et al.*, 2011; Tian *et al.*, 2011; Hung *et al.*, 2012; Poland *et al.*, 2011; Riedelsheimer *et al.*, 2012; Wang *et al.*, 2012), rice (Huang *et al.*, 2010; Zhao *et al.*, 2011; Huang *et al.*, 2012), barley (Yu and Buckler, 2006; Cockram *et al.*, 2010; Pasam *et al.*, 2012), wheat (Neuman *et al.*, 2011), oilseed rape (Rezaeizad *et al.*, 2011), Ontorio bean (Shi *et al.*, 2011). Certainly this approach has potential to discover complex molecular mechanism underlying insect resistance as discussed recently by Kloth *et al.* (2012).

After establishing a tight marker-trait association, as mentioned above, for the resistance to a particular pest and disease, it is essential to validate these markers before utilizing them in breeding programmes. Depending upon the availability of germplasm source, there are several possibilities on validating the marker. In first case, if the recipient is same as contrasting parent used for identifying QTL/gene from the donor, then there is no need for validation. In second case, if the donor used for introgression of the desired trait is the same wherein QTL/gene was discovered, however, the recipient is different, then we simply need to see marker polymorphism between the genetic background of donor and target genotypes for validation. In the third case, when we don't have the same donor which was used for marker discovery, nevertheless, we have other donors for the same trait; then we should first screen the marker on the genotypes we have, considering that they are showing the same level of resistance as in the donor reported earlier. If the same marker allele is observed in the donor, then polymorphism can be tested with the recipient genotypes, for its subsequent use in breeding programmes. However, many times, a different allele is observed in other resistance sources, in such cases a more reliable validation can be done by developing a mapping population with the germplasm sources available with the breeder and establishing the reported marker-trait association in the same. We consider that validation process is extremely critical for the success of any molecular breeding program.

Marker-assisted selection (MAS)

MAS is an indirect selection process for trait of interest based on genotype in place of phenotype which can be practiced at any generation using trait linked markers. The major genes controlling economically important traits are very less in the plants such as disease resistance, male sterility, self-incompatibility, aroma, seed shape, color, and plant architecture. In order to check the efficiency of MAS, earlier MAS applications were demonstrated with the predegree breeding approach where selection is practiced during F_2 generation based on phenotype. For example, Abenes *et al.* (1993) used MAS for

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[4] http://www.plantphenomics.org.au/

selection of brown planthopper resistance (*Bph3*) and bacterial blight resistance (*Xa21*) using PCR-based markers in rice during F_2 generation. Similarly, PCR-based MAS for *Xa21* gene was employed by Reddy *et al.* (1997) in rice improvement program. However, it was later realized that since MAS can be used to handle few genes/loci at one time, this approach was then either used for adding one or two genes into the background of elite cultivar through marker-assisted backcrossing (MABC) or pyramiding of 3-5 genes/loci using linked markers.

Marker-assisted backcrossing (MABC): introgression of gene and gene pyramiding

In order to transfer genomic regions for single or multiple pests and disease resistance in elite cultivars, marker-assisted backcrossing (MABC) approach has been quite successful. In this approach the donor parent is backcrossed 2-3 times with recipient parent followed by 1-2 generation of selfing. When improved cultivar is developed for multiple traits through markers, it is termed as gene pyramiding. In this approach, multiple genes conferring resistance to pests and diseases for the target environment are staked in the niche variety. This leads to the simultaneous expression of the genes stacked, thereby conferring long-term broad-spectrum resistance in the improved variety. To achieve the desired results and success in any gene pyramiding project, there are several critical factors, such as, number of genes to pyramid, genetic distance between gene and flanking markers, type of germplasm, presence of linkage drag, etc. To address these issues, and for faster recovery of recipient parent genome (RPG), background selection can be utilized and if there is linkage drag from donor, recombination selection can be exploited. It is always recommended to utilize background and recombination selection in MABC program for quicker product delivery.

During the recent past there have been various examples wherein MABC is successfully applied to develop improved varieties in number of crops (*table 1*). Among cereals, rice is one of the leading crop where MABC has been used extensively for improving leading cultivars for resistance to different diseases and pests. Molecular breeding for bacterial blight (*Xa4*, *xa5*, *Xa7*, *xa13*, *Xa21*, *Xa22* and *Xa23*), blast (*Pi1*, *Piz5*, *Pi55*, *Pita* and *Piz*), brown plant hopper (*Bph14*, *Bph15*, *Bph18*, *Bph1*, *Bph2*, *Bph25* and *Bph26*) and Asian rice gall midge (*Gm-2*, *Gm-6(t)* and *Gm8*) is now routinely being practised, leading to the value addition of several improved varieties for Asia (Singh *et al.*, 2001; Gopalakrishnan *et al.*, 2008; Sundaram *et al.*, 2008; Perumalsamy *et al.*, 2010; Suh *et al.*, 2011; Hu *et al.*, 2012; Huang *et al.*, 2012; Singh *et al.*, 2012; Myint *et al.*, 2012; Sama *et al.*, 2012, Pandey *et al.*, 2013). In wheat, MABC approach has been used for fusarium head blight (*Qfhs.ndsu-3AS*), stripe rust (*Yr15*, *Yr17* and *Yr36*), leaf rust (*Lr1*, *Lr9*, *Lr1*, *Lr24*, *Lr28* and *Lr47*), stem rust (*Sr25* and *Sr38*), septoria (*Stb4*), powdery mildew (*Pm2*, *Pm4a*, *Pm12* and *Pm21*), wheat streak mosaic virus (*Wsm-1*), yellow dwarf virus (*Bdv2*), orange blossom wheat midge (*Sm1*), wheat stem sawfly (*Qss.msub-3BL*), hessian fly (*H25*) and cyst nematode (*CreX* + *CreY*). These MABC efforts led to development of improved cultivars/varieties around the world (Elias *et al.*, 2005; Nocente *et al.*, 2007; Brevis *et al.*, 2008; Bainotti *et al.*, 2009; DePauw *et al.*, 2009; Graybosch *et al.*, 2009; Randhawa *et al.*, 2009; Yu *et al.*, 2009; Kumar *et al.*, 2010). Similar type of efforts have been undertaken in other cereal crops like maize (Abalo *et al.*, 2009; Gupta *et al.*, 2010; Prasanna *et al.*, 2010a; Prasanna *et al.*, 2010b; Asea *et al.*, 2012), barley (Friedt and Ordon, 2007; Ordon *et al.*, 2009; Palloix and Ordon, 2011). At ICRISAT also, MABC approach was used to improve hybrid of a parental line of pearl millet, by introgressing a genomic region conferring resistance to downy mildew and HHB 67-improved line was developed (Hash *et al.*, 2006). Similar efforts are also underway to introgress genes and QTLs for enhanced resistance towards shoot fly, grain mold, *striga* resistance and staygreen trait in parental lines of hybrids and cultivars in sorghum (Kassahun *et al.*, 2010; Kumar *et al.*, 2011; Muth *et al.*, 2011: Deshpande and Vadez[5]).

Among legumes, soybean is one of the most important crop, as it is a main source of vegetable oil and protein content. The most devastating pest of soybean are nematodes; several varieties have been released in USA such as 'JTN-5109' and 'DS-880', through pyramiding of three genes *rhg1*, *Rhg4* and *Rhg5* for resistance towards soybean cyst nematode (Arelli and Young, 2009; http://www.ars-grin.gov/cgi-bin/npgs/acc/display.pl?1836762). In addition, soybean cultivar 'JTN-5109' and 'JTN-5303' conferring disease resistance have also been released in USA (Arelli *et al.*, 2006; Arelli *et al.*, 2007; Arelli *et al.*, 2009). Also, a soybean variety, 'Essex' has been released in USA by pyramiding *Rsv1*, *Rsv3* and *Rsv4* genes for soybean mosaic virus (Maroof *et al.*, 2008). Among bean, varieties resistance towards anthracnose 'USPT-ANT-1' (*Co-4*^{2} gene, Miklas *et al.*, 2003) and common bacterial blight 'ABCP-8' (SAP6 and SU91 linked QTL, [Mutlu *et al.*, 2005]) have been released in the USA. In the case of groundnut, much progress has been made towards development of varieties conferring nematode resistance (*Rma* gene) such as 'NemaTAM' (Simpson *et al.*, 2003), and efforts are underway to combine it with high oleic trait (Chu *et al.*, 2011). In addition, ICRISAT has successfully improved elite groundnut cultivars for rust resistance (Pandey *et al.*, 2012; Varshney *et al.*, 2013) and chickpea elite lines are being improved for fusarium wilt and ascochyta blight at ICRISAT using MABC approach (Chamarthi *et al.*, 2011; Varshney *et al.*, 2013).

Among fruits and vegetables, efforts towards molecular breeding for disease resistance in tomato have been quite exciting. Several seed companies and public sectors are actively involved in pyramiding genes and QTLs for traits in tomato such as bacterial canker (*Rcm2.0*, *Rcm5.1*), bacterial speck (*Pto*), bacterial spot (*Rx-3* QTL), blackmold (few QTLs), corky root rot (*Py-1*), fusarium wilt (*I-2C* and *I-3*), late blight (*Ph-2*, *Ph-3* and few QTLs), powdery mildew (*Lv*, *Ol-1* and *Ol-2*), tomato spotted wilt virus (*Sw-5*), tomato yellow leaf curl virus (few QTLs), tobacco mosaic virus (*Tm-2a*) and verticillium wilt (*Ve*) (Robert *et al.*, 2001; Brouwer and Clair, 2004; Coaker and Francis, 2004; Yang and Francis, 2005; Foolad, 2007; Gardner and Panthee, 2010; Panthee and Gardner, 2010; Foolad and Panthee, 2012). Similar efforts are underway in many other vegetable crops.

Advanced-backcross (AB-QTL) analysis

The past experience of marker-trait association in many crops has provided significant proof that irrespective of poorer phenotype, wild relatives/landraces or exotic germplasm are expected to more likely have QTLs for yield, quality, disease resistance, pest resistance and tolerance to several abiotic stresses (Wang and Chee, 2010). In order to simultaneously identify and introgress

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[5] personal communication.

Table 1. Selected examples of improved lines/cultivars/varieties developed with resistance to pest and diseases through molecular breeding approaches in some crops.

Crop	**Cultivar/ breeding line/ *parental line***	**Resistant to Trait**	**Gene(s)/QTL (Q)**	**Place**	**Reference**
Rice	PR106	Bacterial blight	*xa5* + *xa13* + *Xa21*	India	Singh *et al.* (2001)
	Pusa Basmati 1	Bacterial blight	*xa13* + *Xa21*	India	Gopalakrishnan *et al.* (2008)
	Samba Mahsuri	Bacterial blight	*xa5* + *xa13* + *Xa21*	India	Sundaram *et al.* (2008)
	ADT43	Bacterial blight	*xa5* + *xa13* + *Xa21*	India	Perumalsamy *et al.* (2010)
	Huahui 1035	Bacterial blight	*Xa7* + *Xa21* + *Xa22* + *Xa23*	China	Huang *et al.* (2012)
	PR36944-450, PR36944-700	Bacterial blight	*Xa4* + *Xa7* + *Xa21*	Philippines	Perez *et al.* (2008)
	XH2431, 9311(*Xa27*), WH421	Bacterial blight	*Xa4* + *Xa21* + *Xa27*	China	Luo *et al.* (2012)
	Taraori Basmati, Basmati 386, Vasumati	Bacterial blight	*Xa21* + *xa13*	India	Pandey *et al.*, 2013
	KMR3, PRR78, IR58025B, Pusa 6B, Mahsuri	Bacterial blight	*Xa4* + *xa5* + *xa13* + *Xa21*	India	Shanti *et al.* (2009)
	Lu-Yuon-Zhan	Bacterial blight, Bacterial leaf strike	*Xa23* + *Rxo1*	China	Zhou *et al.* (2009)
	Pusa Basmati 1	Bacterial blight, blast and sheath blight	*xa13* + *Xa21* + *Pi54* + *qSBR11-1*	India	Singh *et al.* (2012)
	CO39	Blast	*Pi1* + *Piz-5* + *Pita*	Philippines	Hittalmani *et al.* (2000)
	Pusa1602	Blast	*Piz-5*	India	Singh *et al.* (2012)
	Pusa1603	Blast	*Pi55*	India	Singh *et al.* (2012)
	IR50	Blast	*Piz*	India	Narayanan *et al.* (2002)
	Zhenshan 97A	Blast	*Pi1*	China	Liu *et al.* (2003)
	CO39	Bacterial blight, blast	*Pi1* + *Piz5* + *Xa21*	India	Narayanan *et al.* (2004)
	Rongfeng B	Bacterial blight, blast	*Xa23* + *Pi1* + *Pi2*	China	Fu *et al.* (2012)
	Junambyeo	Brown planthopper	*Bph18*	Taiwan	Suh *et al.* (2011)
	Minghui 63	Brown planthopper	*Bph14* + *Bph15*	China	Hu *et al.* (2012)
	Tsukushibare	Brown planthopper	*Bph1* + *Bph2*	Japan	Sharma *et al.* (2004)
	ADR52	Brown planthopper	*BPH25* + *BPH26*	Japan	Myint *et al.* (2012)
	Duokang #1, Phalguna	Asian rice gall midge	*Gm-2*, *Gm-6(t)*	India	Katiyar *et al.* (2001)
	Improved Samba-Mahsuri (ISM)	Asian rice gall midge	*Gm8*	India	Sama *et al.* (2012)
Wheat	Ben	Fusarium head blight	*Qfhs.ndsu-3AS*	USA	Elias *et al.* (2005)
	Zak	Stripe rust	*Yr15*	USA	Randhawa *et al.* (2009)
	Westmore	Stripe rust	*Yr36*	USA	Brevis and Dubcovsky (2008)
	BIOINTA 2004	Leaf rust	*Lr47*	Argentina	Bainotti *et al.* (2009)
	HD2329	Leaf rust	*Lr24* + *Lr28*	India	Kumar *et al.* (2010)
	UC1113 (PI638741)	Stem rust (Ug99)	*Lr19* + *Sr25*	USA	Yu *et al.* (2009)
	Bolero, CelWorito, Serio, Spada and Thatcher	Leaf rust	*Lr1*, *Lr9*, *Lr24* and *Lr47*	Italy	Nocente *et al.* (2007)

Table 1. (*Continued*)

Crop	Cultivar/ breeding line/ parental line	Resistant to Trait	Gene(s)/QTL (Q)	Place	Reference
	Mace	Wheat streak mosaic virus	*Wsm-1*	USA	Graybosch *et al.* (2009)
	Goodeve	Orange blossom wheat midge	*Sm1*	Canada	DePauw *et al.* (2009)
	McNeal, Reeder, Hank	Wheat stem sawfly	*Qss.msub-3BL*	USA	http://www.wheatworld.org/pdf/dubcovsky.pdf
	Cataldo	Hessian fly	*H25*	USA	http://www.ars-grin.gov/cgi-bin/npgs/acc/display.pl?1698787
	D3-8-3, D3-8-5	Cyst nematode	*CreX* + *CreY*	France	Barloy *et al.* (2007)
Maize	CM137, CM138, CM139, CM150 and CM151	Turcicum leaf blight and Polysora rust	*RppQ*	India	Prasanna *et al.* (2010a); Prasanna *et al.* (2010b)
	NA	Corn borer resistance	QTLs on chrom. 7, 9 and 10		Willcox *et al.* (2002)
Barley	Steptoe	Stripe rust	*Bmy1*	USA	Toojinda *et al.* (1998)
	NA	leaf rust	*Rphq6*		van Berloo *et al.* (2001)
	NA	Barley yellow dwarf virus	*Yd2*		Jefferies *et al.* (2003)
	DH-lines	Barley yellow dwarf virus	*Ryd2* + *Ryd3*	Germany	Riedel *et al.* (2011)
	NA	Yellow mosaic virus	*rym4* + *rym5* + *rym9* + *rym11*		Werner *et al.* (2005)
Pearl Millet	HHB 67-improved	Downy mildew		India	Hash *et al.* (2006)
Soybean	JTN-5503	Soybean cyst nematode	*rhg1* + *Rhg4* + *Rhg5*	USA	Arelli *et al.* (2006, 2007)
	JTN-5109	Soybean cyst nematode	*rhg1* + *Rhg4* + *Rhg5*	USA	Arelli and Young (2009)
	Essex	Soybean mosaic virus	*Rsv1* + *Rsv3* + *Rsv4*	USA	Maroof *et al.* (2008)
Bean	USPT-ANT-1	Anthracnose	*Co-4*^{2}	USA	Miklas *et al.* (2003)
	ABCP-8	Common bacterial blight	*SAP6 and SU91 linked Q*	USA	Mutlu *et al.* (2005)
	ABC -Weihing	Common bacterial blight	*SU91 linked Q*	USA	Mutlu *et al.* (2008)
Groundnut	NemaTAM	Nematode resistance	*Rma*	USA	Simpson *et al.* (2003)
Cassava	CR41-10	Cassava mosaic disease	*CMD2*	Nigeria	Okogbenin *et al.* (2007)

desirable QTL alleles from exotic in to cultivated lines, another molecular breeding method, mentioned as advanced backcross (AB) QTL strategy was developed. This strategy was first explained by Tanksley *et al.* (1996) in tomato. In this method, an elite cultivar is crossed with the exotic germplasm followed by 2-3 backcrosses, then marker trait association is established and the same associated markers are used to track the introgression of QTLs by MABC. During the recent years, there have been lot of interest in this approach and many genes and QTLs for resistance to pests and disease, abiotic stress and agronomic traits have been identified from land races or wild relatives in important crops such as rice (Cheema *et al.*, 2008; Lu *et al.*, 2011; Eizenga *et al.*, 2013; Zhang *et al.*, 2013), wheat (Naz *et al.*, 2008; Buerstmayr *et al.*, 2011; Naz *et al.*, 2012; Ogbonnaya *et al.*, 2013), maize (Li *et al.*, 2008; Welcker *et al.*, 2011) and barley (Schmalenbach *et al.*, 2008; Saal *et al.*, 2011; Sayed *et al.*, 2012).

Marker-assisted recurrent selection (MARS)

While conducting QTL analysis, in addition to major QTLs, a large number of minor effect QTLs are identified. Major and minor QTLs interactions can now be easily visualized for better understanding of the complex genetics behind any trait (Isobe *et al.*, 2007). However, in majority of cases minor effect QTLs are not utilised due to their inconsistency across different seasons and environments. Nevertheless, if some minor QTLs are showing consistency, their introgression through MABC in elite cultivars is a big challenge. For such cases, a modern molecular breeding approach, marker assisted recurrent selection (MARS) has been proposed.

In the case of MARS, superior alleles for different QTLs (10-40 loci) are pyramided into a single genotype, thereby increasing the frequency of beneficial alleles having both additive and small individual effects in recurrent crosses (Ribaut *et al.*, 2010; Varshney *et al.*, 2012). Through this approach, it is proposed that the overall phenotypic variance for a trait would be increased, thereby leading to development of more durable crops against disease and pests in much shorter time and effort when compared to conventional breeding approaches (Bernardo and Charcosset, 2006). Efforts are underway in many crops to combine superior alleles for traits of interest (Kulwal *et al.*, 2011). Due to its benefits, private sector has shown a lot of interest towards using this technique in their breeding program (Eathington *et al.*, 2007). In several crops such as maize, rice, sorghum, wheat, beans, cowpeas and cassava efforts are underway to develop improved cultivars using this method. MARS approach has not been exclusively used for disease and pest resistance, because of involvement of elite cultivars, MARS approach in general, combines resistance to diseases and pests with other traits. In case, resistance to different races for a given disease or different diseases and pests are combined, MARS seems to be an effective approach.

Genome-wide or genomic selection (GS)

Next-generation sequencing (NGS) technologies, wherein the entire genome can be sequenced in a much shorter time, has paved the way towards development of various advances towards crop genetics and breeding such as re-sequencing of well-characterized species, *de novo* sequencing of crop species, genome wide association studies (GWAS), population genetics and evolutionary biology (Varshney *et al.*, 2009b). In addition to these, a much recent application of NGS or high-throughput genotyping technologies is foreseen as genomic selection (GS) for rapid crop improvement (Varshney *et al.*, 2012). Unlike MABC and MARS, GS can be used for selecting superior lines with high GEBV that leads to develop superior lines with better agronomic performance overall (Bernardo and Yu, 2007; Heffner *et al.*, 2009).

In GS, genomic-estimated breeding values (GEBVs) are used as a criteria for selection of superior lines and making new crosses. In order to calculate GEBV, the two most important prerequisites are generation of highly dense genotypic data covering the entire genome and multi-season historical phenotypic data on a 'training population'. The 'training population' is usually constituted of advanced breeding lines and elite cultivars. The whole GS relies on effective calculation of GEBV; hence it is very critical to have an appropriate statistical model to derive these values. Once the selection is made based on GEBVs, genotypic data of progenies from these crosses are generated, and GEBVs for all the progenies are calculated based on the model developed in training population. Consequently, progeny lines with higher GEBVs are selected and used for further breeding process (Varshney *et al.*, 2012). The idea here is to select individuals entirely based on higher GEBVs unlike traditional phenotypic selection. So far this approach has been well embraced for improving complex traits (Asoro *et al.*, 2011; Zhao *et al.*, 2012; Rincent *et al.*, 2012) but few efforts also demonstrated its utility in improving disease resistance (Rutkoski *et al.*, 2011; Lorenz *et al.*, 2012; Rutkoski *et al.*, 2012). Thus, this strategy has the potential to revolutionize plant breeding in faster delivery of product lines.

Future directions

The current climate change scenario is becoming a key force towards changing the population dynamics of pests and diseases (Dhaliwal *et al.*, 2010). Hence, there is a need to adapt effective management strategies to handle the new status of pest and diseases. Genomics-assisted breeding plays a very important role to efficiently develop safe and healthy crop varieties for target biotic stress in less time and cost-effective manner as compared with conventional breeding (Varshney *et al.*, 2009a). However, it is observed that the huge genomic resources developed are not being regularly used by plant breeders, particularly in the public sector (Ribaut *et al.*, 2010). This could be due to several challenges such as, inapt phenotyping infrastructure, lack of bioinformatics systems and dearth of modern or next generation molecular breeders who have experience in integrating new technologies in crop improvement programs (Tester and Langridge, 2010). However, initiatives such as Integrated Breeding Platform[6] wherein plant breeders can access phenotyping, genotyping and information technologies which could help them integrate these in their breeding programs. Ultimately following an integrated breeding approach towards crop improvement for biotic stress will ensure sustainable agriculture and food security mainly in developing countries.

Acknowledgements

Thanks are due to CGIAR Generation Challenge Programme, Bill and Melinda Gates Foundation, US Agency for International Agricultural Development (USAID), and Department of Biotechnology and Ministry of Agriculture of Government of India for funding research projects in the area of molecular breeding underway at Center of Excellence in Genomics (CEG), ICRISAT.

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[6] https://www.integratedbreeding.net/

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