Review Article

Breeding Oats for Biotic and Abiotic Stresses

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A B S T R A C T

Oats rank around sixth in world cereal production statistics, following wheat, maize, rice, barley and sorghum. In many parts of the world, oats are grown for use as grain as well as for forage and fodder, straw for bedding, hay, haylage, silage and chaff. Livestock grain feed is still the primary use of oat crops, accounting for an average of around 74 percent of the world's total usage.In India, breeding of oats begun in nineteen-eighties and is grown as the most important cereal fodder crop in North Western, Central India, extending to the eastern regions.As a fodder crop, it has excellent protein quality, fat and mineral content. It is a palatable, succulent and nutritious crop.Many diseases cause serious direct damage, mainly by reduction of the fodder yield. Among them diseases such as crown rust, stem rusts and leaf blotch. Several resistance genes against the major diseases, i.e. crown rust, stem rust, powdery mildew, BYDY, etc., from oat gene pool have been discoveredin over 31 wild oat species. Several breeding strategies such as marker-assisted selection (MAS), marker-assisted back-crossing (MABC), marker-assisted gene pyramiding and marker-assisted recurrent selection (MARS) are extensively being exploited for incorporating resistance gene introgression into elite cultivars. With the advancement of new sequencing technologies and a rapid development in bioinformatics, complete oat genome sequencing is no longer out of reach. Oat genome sequencing would pave new pathways for breeders to develop a large number of sequence-based markers such as SNPs which will help in identifying the disease resistance genes through exploiting linkage disequilibrium mapping and genomic selection.

Introduction

Oats rank around sixth in world cereal production statistics, following wheat, maize, rice, barley and sorghum (FAO 2015). Currently, oat remains an important grain and forage crop in many parts of the world grown on 13.2 million hectares with a grain production of 26.2 million metric tons in 2003 (USDA, Foreign Agricultural Service. Commodity production, supply, and disposition database http://fas.usda.gov/psd). The Russian Federation is the largest producer followed by Canada and the USA. Land area devoted to oat has fallen substantially the past several decades with oat being displaced by

higher value crops, such as soybean in the USA. Oat grain has always been an important form of livestock feed, and provides a good source of protein, fibre and minerals, but world oat grain production declined as farm mechanization increased between 1930 and 1950. In many parts of the world, oats are grown for use as grain as well as for forage and fodder, straw for bedding, hay, haylage, silage and chaff. Livestock grain feed is still the primary use of oat crops, accounting for an average of around 74 per cent of the world's total usage.

In India, breeding of oats begun in nineteen-eighties and is grown as the most important cereal fodder crop in North Western, Central India, extending to the eastern regions. India has a wide range of research centres and agro-ecological zones to develop suitable varieties for different zones as well as different systems of fodder production. India has a well-managed system for evaluation of breeding lines for release and notification for cultivation by farmers.

It has excellent growth habit, good quality herbage and recovers quickly after cutting. Oat requires a long and cool season for its growth; therefore, it is successfully grown in the plains and hilly areas of the country. In India it is grown in Punjab, Haryana, Jammu & Kashmir, Himachal Pradesh, Uttar Pradesh, Madhya Pradesh, Rajasthan, Maharashtra and Bengal. Variety of soils is suitable for oats cultivation. Reasonably fertile and well-drained soil is suited if temperature and moisture conditions are favourable; although maximum oat yields are usually not achieved until sufficient lime is added to bring the soil pH up to range of 5.3-5.7. Oat has been shown to tolerate acid soils with a pH of 4.5. The total area covered under oat cultivation in the country is about 5,00,000 ha. Oats have assumed considerable importance in India as fodder as well as grain for animal feed

particularly calves and young stock, horses, poultry and sheep.

As a fodder crop, it has excellent protein quality, fat and mineral content. It is a palatable, succulent and nutritious crop. The average yield varies from 45 to 55 tons of green fodder per hectare. It forms an excellent combination when fed along with other winter legumes like berseem, lucerne, senji, shaftal and wild pea or vetch. When mixed with berseem, oat provides balanced feed to milch animals. Its straw is soft and superior to wheat and barley.

Oat diseases: An overview

Losses due to oat diseases

Oatgrain has always been an important form of livestock feed and serves as a good source of excellent protein, fibre and minerals. However, the world oat production has declined from 26.30 million metric tonnes in 2003 to projected production of 23.16 metric tonnes in 2018/2019 (USDA, Foreign Agricultural Service, Commodity production, supply, and disposition database, owing to several factors including various biotic and abiotic stresses.

Roughly, direct yield losses caused by pathogens, animals and weeds are altogether responsible for losses ranging between 20 and 40 per cent of global agricultural productivity (Teng and Krupa 1980; Teng 1987; Oerke *et al.,* 1994; Oerke 2006). The phrase 'losses between 20 and 40 per cent' therefore inadequately reflects the true costs of crop losses to consumers, public health, societies, environments, economic fabrics and farmers. On an average it is estimated that 20–30 per cent losses occur due to diseases, while yield loss will be complete incase of severe disease epidemics. Plant protection in general and the protection of crops against plant diseases in

particular have an obvious role to play in meeting the growing demand for food quality and quantity (Strange and Scott 2005).

In 350B.C. Theophrastus, the father of botany, first recorded occurrence of plant diseases and differences among oat plants with respect to the disease reactions. Among the diseases in oats that significantly reduce production the world over, the most important ones are crownrust, stemrust, powdery mildew, *Fusarium* headblight, leaf blotch, smut and barley yellow dwarf virus (BYDV). Diseases reduce total biomass production by either causing death of plants, killing of branches, general stunting, damage to leaf tissues or damage to reproductive organs including fruits and seeds.

The crown rust disease is considered the most serious and destructive disease. The annual yield losses averaged 5.1 per cent on account of this disease during the period 2001–2005 in Canada (Chong *et al.,* 2011), with highest losses of 11.2 per cent and 8.8 percent in 2001 and 2005, respectively (McCallum et al., 2007). The *Fusarium* headblight (scab) is yet another destructive disease of oat. There are several examples of major famines or food losses of crop plants associated with pest and disease epidemics in the past. The prevention of epidemics and ultimately the reduction of losses in yield have been of great concern.

Disease susceptibility in oats and severity

The optimum conditions for a disease to occur and develop are a combination of three factors – susceptible host, virulent pathogen and favorable environmental conditions. In traditional agriculture owing to the presence of genetic heterogeneity and natural biological control, the natural population and wild species of crop plants rarely shows epidemics. On the contrary, modern agriculture technology has introduced important changes:

(1) it has narrowed down the genetic base of cultivars, which alters the dynamic imbalance between host and parasites, which in turn results in epidemics; (2) it has generated more or less continuously distributed populations and has changed the whole ecosystem, creating habitats profoundly altered for host and parasites.

Many diseases cause serious direct damage, mainly by reduction of the fodder yield. Among them diseases such as crown rust, stem rusts and leaf blotch caused by *Pyrenophora* spp., *Septoria* spp. and BYDV, respectively, cause severe direct damage through reduction of the fodder yield, while other diseases like scab and ergot cause indirect damage by compromising the quality of the product. Based on the causal organism, the diseases occurring in oats can be categorized into three classes based on the type of pathogen (Table 1).

Status of oat genetic resources to combat disease

Crop genetic resource refers to the biological diversity existed among the crop plants found in a distinct ecosystem of habitats. Genetic resources are the rich source of genetic diversity and serve as an essential raw material for improving crops and developing new value-added products. A wide spectrum of genetic diversity exists in oats with respect to morphological differentiation at both genus and species level. Based upon agro-morphological parameters, several researchers have described oats' genetic resources for the benefit of human kind. The collection of genotypes as well as the conservation of gene pools of cultivated and wild species is essential for genetics and plant the world's oat collections have been estimated to be about 131,000 accessions stored by 125 institutions in 63 countries which are considered as eighth most numerous germplasm collections after

wheat, rice, barley, maize, bean, sorghum and soybean. The largest world collection of cultivated oats is maintained by Canada (~40,000), followed by the USA (~22,000) and Vavilov Institute of Plant Industry (VIR, Russia) (~12,000) which has a collection of about 10,000 accessions of 4 cultivated and 2000 accessions of 21 wild species. About 2 per cent of total oat accessions (2110) of world's collection (WC) are held in India. In India, National Bureau of Plant Genetic Resources (NBPGR), New Delhi, and Indian Grassland and Fodder Research Institute (IGFRI), Jhansi, are maintaining 940 (13 species) and 450 oat accessions, respectively.

Conservation of wild gene pool of any crop plant is of utmost importance as they carry valuable genes for desirable traits such as yield, quality and biotic and abiotic stresses for crop improvement programmes. Wild species are helpful in providing basic information on species relationship and evolution pattern of crop plants. More than 24 per cent of accessions in world's oat collections are classified as wild species. Mostly the wild species of oats comprised of numerous hexaploid species which are included in to primary genepool. Nearly 31,000 accessions of oat wild species are maintained in 29 oat collections, of which 13 hold more than 20 accessions (Brazil, Canada, China, Germany, Israel, Morocco, Norway, Poland, Russia, Spain, Sweden, UK and USA) (FAO/WIEWS).

The cultivated species of oats are *A. sativa*, *A. byzantina*, *A. strigosa* and *A. abyssinica*. Around 75,000 accessions of cultivated species are conserved in the world collections (Boczkowska *et al.,* 2016).

Harnessing genetic variation for disease resistance

Genetic variation is the prerequisite in any breeding programme. The breeding of disease-resistant varieties of crop has perhaps received more attention than any other phase of plant breeding. Use of fungicide and other methods of disease control has given effective control of diseases. However, host plant resistance is the most preferable means of crop protection of all kinds as it combines the advantages of cost-effectiveness and ecological soundness. In case of breeding resistant varieties to diseases and pests, it is imperative to search for source of resistance, i.e. the donors from which the resistant gene(s) may be transferred. The supply of genes for resistance, for disease(s), insect pest(s) and nematode(s), is the first concern in an ongoing resistance breeding programme. The primary and secondary centre of origin (gene centres) of cultivated plants is the best places to find genuine resistance to common diseases and pests. Resistance to diseases may be obtained from germplasm collection, wild/weedy relative species, mutations, somaclonal variations and unrelated organisms. Often the genes from wild species have resistance against a wide range of races. Such genes have been called 'super genes'. Therefore, resistance available from wild relative is attractive even when other sources of resistance are available. I. A. Watson (1970) noted that the new races/biotypes of parasites overcome the resistant gene(s) being used in the cultivars. Thus, it is emphasized that the wild relative or species become increasingly important sources of germplasm in the breeding of manycrops.

Several resistance genes against the major diseases, i.e. crown rust, stem rust, powdery mildew, BYDY, etc., from oat gene pool (Table 2) have been discovered in over 31 wild oat species. *A. sterilis* exhibits multiple resistance to several oat diseases, i.e. crown rust, stem rust, powdery mildew and cereal cyst nematode. Powdery mildew resistance has been transferred into variety HiFi through synthetic amagalon of *A. magna* × *A. longiglumis* cross. During 1925–1946, several

disease- resistant cultivars were developed utilizing the Victoria and Bond which are derived from wild red oat and cultivated hexaploid species *A.sativa*. This served as a source for development of many disease-resistant oat varieties for different regions.

Marker-assisted breeding

With the discovery of DNA markers, plant breeding has experienced a new technological revolution by the development of a large array of DNA markers which makes breeders task easy for the selection of complex traits especially those which are difficult to assess phenotypically. Marker-assisted breeding (MAB) serves as boon to breeders to carry out effective and speedy selection based upon the DNA markers. With the development of a wide variety of DNA markers and genetic maps, MAB can be used for traits conditioned by qualitative as well as quantitative genes.

By practicing MAB in breeding programmes, the rate of genetic gain is twice the genetic gain obtained from traditional phenotypic selection. It includes several breeding strategies such as marker-assisted selection (MAS), marker-assistedback- crossing (MABC), marker-assisted gene pyramiding and marker-assisted recurrent selection (MARS). The success of marker-assisted breeding depends on the avail- ability of a tightly linked trait-molecular marker (disease resistance gene).

Since oat genomic resources are not as developed as in other cereal crops (rice, wheat, maize, etc.), the DNA marker system is less developed too. The first molecular marker RFLP developed by Botstein *et al.,* (1980) has been utilized by many oat researchers and strengthens the linkage and comparative mapping for the discovery of crown rust and stem rust resistance genes. Marker-assisted breeding for disease resistance and other

agronomic traits has been well discussed by Rines *et al.,* (2006) and Kapoor and Batra (2016).

Genomics perspectives and future scope for disease resistance breeding

Staple crops such as wheat, rice, barley, maize, pearl millet and sorghum are enriched with a large number of genomic resources in comparison to oats. The progress made in molecular genetic research in oats in comparison to other staples is less owing to the genomic complexity and non-availability of complete genome sequence. DNA marker-based genetic linkage maps developed in various oat genetic populations reveal marker-trait association useful for the identification of genes/ QTLs for their further utilization in marker-assisted breeding. But most of the identified genes/QTLs/markers in oats are linked to agronomic and nutritional value traits as the crop is considered as an important food grain crop owing to its high protein content.

Although several linkage maps have been developed in oats by many scientists using numerous mapping populations till date, only one consensus map (Chaffin *et al.,* 2016) is available in oats which depicts the genetic locations of several resistance genes. A major reason for this lacuna may be the lack of oat genome sequence which could provide insights into the plant architecture and genomic relationship between different oat genomes. Deducing the complete oat sequence is a challenge for scientists mainly because of polyploidy nature of oats. Highly precise and reliable next-generation sequencing DNA markers like SNP (single nucleotide polymorphism) which are widely used in the present era of genomics can however prove useful in delineating the genome sequence of oats. With the advancement of new sequencing technologies and a rapid

development in bioinformatics, complete oat genome sequencing is no longer out of reach. High-throughput genotyping is a pre- requisite for marker-assisted breeding (MAB), genomic selection (GS), genome- wide association studies (GWAS), TILLING which is the next-generation mutagenesis technique and the CRISPR/Cas9, most recently developed genome editing platform. In this regard sequencing of oat genome would be highly beneficial. It will enable fine mapping and cloning the disease resistance genes which is a challenge to DNA marker technology aimed for disease resistance.

Marker-assisted breeding (MAB) is the most suitable methodology in plant breeding for disease resistance breeding. It is highly useful in the selection of desirable individuals with major disease resistance genes/QTLs. However, minor genes/ QTLs also played a major role in disease resistance and tend to produce more durable varieties. As the genetic architecture of resistance shifts from single major R genes to a diffused architecture of many minor genes, the best approach for molecular breeding will shift from marker-assisted selection to genomic selection.

Table.1 Diseases of common occurrence in oats

Type of disease	Diseases	Causal organism
Fungal	Crown rust	*Puccinia coronata* **f. sp.** *avenae*
	Stem rust	*Puccinia graminis* **f. sp.** *avenae*
	Helminthosporium leaf blotch	*Drechslera avenae*
	Septoria leaf blotch	*Septoria avenae*
	Powdery mildew	*Erysiphe graminis avenae*
	Loose smut	*Ustilago avenae*
	Fusarium head blight (Scab)	*Fusarium graminearum*
	Anthracnose	*Colletotrichum graminicola*
Bacterial	Halo blight	*Pseudomonas coronafaciens*
	Seed and seedling diseases	*Bipolaris sorokiniana, Fusarium* **and** *Pythium* **spp.**
	Bacterial stripe blight	*Pseudomonas syringae* **pv.** *striajaciens*
Viral	Soil-borne oat mosaic	*Oat mosaic virus*
	Barley yellow dwarf	*Barley yellow dwarf virus*

Table.2 Source of disease resistance among wild oat species

Species	Genome	Sources of resistance to					
		Powdery mildew	Crown Rust	Stemrust	BYDV	Smut	Septoria leaf blight
A. bruhnsiana	Cv	+	+				
A. ventricosa	Cv	+	+	+			
A. clauda	Cp	+	+	+	+		
A. pilosa	Cp	+	+	+			
A. prostrata	Ap	+	+				
A. damascena	Ad	+	+	+	+		+
A. longiglumis	Al	+	+	+	+		+
A. canariensis	Ac		+	+	+		+
A. wiestii	As	+	+			+	+
A. hirtula	As	+	+	+	+		+
A. atlantica	As	+					+
A. strigosa	As	+	+	+	+	+	+
A. barbata	AB	+	+	+	+	+	+
A. vaviloviana	AB	+	+		+	+	+
A. abyssinica	AB	+	+	+		+	
A. agadiriana	AB?	+					
A. magna	AC		+	+	+		
A. murphyi	AC	+	+		+		+
A. insularis	AC?		+	+			
A. macrostachya	CC?	+	+	+	+		+
A. fatua	ACD	+	+	+	+	+	+
A. occidentalis	ACD	+	+	+	+		
A. ludoviciana	ACD	+	+	+	+		+
A. sterilis	**ACD**	+	+	+	+	+	+

Source: Loskutov and Rines (2011)

Table.3 Molecular markers linked with crown rust and stem rust resistance

Gene	Marker	Linked marker/QTL
Crown rust		
Pc38	RFLP	**Cdo673, wg420**
Pc39	RFLP	**Cdo666**
Pc48	RFLP	**cdo337**
Pc54	RFLP	**cdo1435B**
Pc58a,b,c	RFLP	**PSR637, RZ516D**
Pc59	RFLP	**Cdo549B**

Pc68	RAPD	**ubc269**
	SNP	**Pc68-SNP1, PC68-SNP2**
	AFLP	**U8PM22, U8PM25**
	SDS-PAGE	**AveX, AveY, AveZ**
	RGA/RFLP	**Orga1**
	SCAR	**ubc269a SCAR**
Pc71	RFLP	**cdo783, cdo1502**
Pc81,82	AFLP	**isu2192, OP C18**
Pc83,84,85	STS	**Agx4, Agx9, Agx7**
Pc91	RFLP	**UMN145**
	DArT	**oPT-0350**
	SCAR	**oPT-0350-cdc**
	KASP	**oPT-0350-KOM4c2**
Pc92	RFLP	**OG176**
Pc94	AFLP	**AF94a**
	SCAR	**SCAR94-1, SCAR94-2**
	SNP	**Pc94-SNP1a**
Pca	RGA/RFLP	**Isu2192**
		L7M2.2
		B9-1
Pcx	RFLP, RAPD	**Xcdo1385F, XpOP6(A), Xacor458A**
Stem rust		
Pg3	RAPD	**ACOpR-1, ACOpR-2**
	SCAR/CAPS	**Pg3 SCAR/CAPS**
Pg4	SCAR/CAPS	**Ubc254s SCAR**
Pg9	Acid-PAGE	**avenin band**
	RFLP, RAPD	**Xcdo1385F, Xacor458A**
	SCAR/CAPS	**Pg9 SCAR/CAPS**
Pg13	SDS-PAGE	**56.6-kDa polypeptide locus**
	RFLP, RAPD	**Xmog12B, Xacor254C**
	SCAR	**Pg13SCAR**

Source: Gnanesh *et al.,* (2014)

Genomic selection (GS) or genome-wide selection (GWS) is also a form of marker-assisted selection which is based on the statistical prediction models and selection methodology. These statistical models will be able to predict accurately for disease resistance and will outperform the multiple linear regressions applied in marker-assistedbreeding.GShasbecomefeasibleinplant sduetothediscoveryand development of a large number of SNP markers by genome sequencing (Dhillon and Chhuneja, 2014). Thus, use of GS in oats for disease resistance becomes a powerful approach in oat breeding programmes. Many QTLs have been identified using the bi-parental population utilizing DNA markers in crop plants, but such QTLs have limited application in MAS as parental genotypes because these genotypes are often not representatives of

germplasm pool which is actively used in breeding programmes, and markers linked to QTL are not always transferable to other genetic backgrounds (Snowdon and Friedt, 2004). Genome-wide association studies (GWAS) emerged as an alternative approach which has over come the limitations of bi-parental linkage mapping. GWAS is most commonly used for detecting the variants for complex human diseases. Recently, it has been utilized in maize, rice, wheat and sorghum for the identification of marker-trait association for agronomic traits (Huang *et al.,* 2010; Jia *et al.,* 2013; Li *et al.,* 2013; Morris *et al.,* 2013), but there are some reports available where GWAS have been utilized for identifying disease resistance genes in maize, rice and wheat. Inoats, few GWAS are available where marker-trait associations have been determined for grain quality traits (Newell *et al.,* 2012; Asoro *et al.,* 2013). But the rear some studies where GWAS have been utilized for the identification of QTLs/loci linked with disease resistance. Klos *et al.,* (2017) identified 29 SNPs on 12 linkage groups related to crown rust reaction and *Pc48*, *Pc58a*, *Pc68*, *Pc71*, *Pc91* and *PcKM*QTLs shown to be linked with seedling resistance genes using genome-wide association mapping (GWAM). Presently, GWAS has become a potential approach which will open new frontiers in disease resistance research in oats.

TILLING (targeting induced local lesions in genomes) is a reverse genetic approach which utilizes traditional mutagenesis to discover spontaneous mutation. It is helpful in generating an allelic series of genes for a particular trait of interest. TILLING has been exploited for many agronomical traits in many crop plants. There is a plenty of scope of utilization of TILLING for the identification of genes involved in regulatory path- ways of defense related genes in oats. Till date, there are no reports available on

utilization of TILLING in oats for disease resistance. Recently, CRISPR/Cas9, a new genome editing technology, is used worldwide among the plants as well as animals for different traits for their improvisation. Once oat genomes become a reality, there would be ample opportunity for precise site-directed mutagenesis using CRISPR/Cas9. CRISPR/Cas9 system can also be utilized for defect elimination at specific position in oat genome which regulates pathogenesis genes and would be useful for correcting disease resistance in susceptible oat cultivars. Considering the above, delineating the complete genome sequence in oats would openupnewvistasindiseaseresistancebreedinga ndhelpaccelerate'precisionoat breeding'.

In conclusion, oat genome sequencing would pave new pathways for breeders to develop a large number of sequence-based markers such as SNPs which will help in identifying the disease resistance genes through exploiting linkage disequilibrium mapping and genomic selection. Exploring new genome editing techniques would not only allow precise breeding but also provide a remarkable new opportunity for oat breeders. Integrating traditional breeding methodologies with modern genomics-assisted breeding to develop consensus linkage maps would open new vistas for the identification and precise mapping of major as well as minor genes/QTLs governing resistance against the economically important diseases. Meticulous planning and effective utilization of oat genetic resources would therefore provide ample scope for breeders to develop disease resistance cultivars in oats.

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