



REVIEW ARTICLE

Cabbage: Breeding and Genomics

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Abstract

Plant breeding has had a tremendous influence on crop improvement. However, due to dwindling germplasm resources, identification of variability for incorporation into new cultivars is becoming more difficult. Therefore, there has been recourse to alternative approaches including mutagenesis, tissue culture and genetic transformation to aid breeding programs. Development and application of molecular markers derived from genes, commonly called genic markers or sometimes functional markers, is gaining momentum in plant genetics and breeding. Presently, marker discovery, genotyping and molecular breeding practices would be routine in crop improvement in many crop species including Brassica. Molecular markers are known as particularly effective and reliable tools for the characterization of genome architectures and the investigation of gene polymorphisms in cabbage also. Cabbage breeding, genomics and their applications have been discussed in detailed in this review article.

Keywords: Cabbage, Breeding, Biotic stress, Abiotic stress, Quality.

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Introduction

The family *Brassicaceae*, also called the “mustard family” contains the most important model species *A thaliana* and also many important agricultural species including three diploids (*B. rapa*, *B. nigra*, and *B. oleracea*) and three tetraploids (*B. juncea*, *B. napus* and *B. carinata*) (Schranz *et al.*, 2006). The *Brassicaceae* family comprises more than 372 genera and about 4060 species, many of which are economically important species (Bayer *et al.*, 2019). The *Brassica* genus is also the economically most important genus within the tribe Brassicaceae, consisting of 37 different species. *Brassica oleracea* L. comprises many major vegetable crops such as cabbage, cauliflower, broccoli, kale and collards, Brussels sprouts and kohlrabi. Vegetable *Brassicaceae* are of great valuable crops throughout the world. Among them, cabbage is one of the most important vegetable crops grown in many countries of the world. White cabbage belongs to the variety of *capitata*, whose name comes from the Latin word ‘capita’ which means ‘head’. Leaves are shaped, as the word means, into distinctive cabbage heads that can vary in shape, color and texture of the leaves, resulting in a wide number of cabbage cultivars with cultivation potential under different climatic conditions (Björkman *et al.*, 2011). Cabbage is botanically known as *Brassica oleracea* var. *capitata* L. The *capitata* variety presents 4 forms: alba (white cabbage), rubra (red cabbage), sabauda

(savoy cabbage) and *acuta* (cone cabbage). Historical evidence indicates that modern hard-head cabbage cultivars are descended from wild non-heading *Brassicas*, Cole wart' (*Brassica oleracea* var. *sylvestris*) originating in the eastern Mediterranean. It is commonly accepted that the origin of cabbage is in North European Countries, the Baltic Sea coast (Baldwin, 1995) and the Mediterranean region and believed to have been first domesticated in Western Europe. It is also considered that modern-day white and red-headed cabbage was evolved in Germany by 1150 AD (Helm, 1963), while savoy had probably originated in Italy. The exact date of the introduction of cabbage in India is not known, but it was introduced to India by the Portuguese and cultivated during the Mughal period (1542>) as mentioned in Ain-i-Akbari (Thamburaj and Singh, 2013). From ancient times, it has been known that it has many medicinal properties like its juice reduces constipation, an antidote to mushroom poisoning, treatment for hangovers and headaches and is used as a laxative, an antidote to drunkenness, stop sunstroke, or to relieve fevers, soothe swollen feet and to treat childhood croup, anti-inflammatory activity like treatment of swelling, protection of breast inflammation mostly used by breastfeeding woman (Alexandra and Andreea-Daniela, 2020). Cabbage has a richness of phytochemicals such as polyphenolics, glucosinolates, enzyme myrosinase carotenoids and vitamins that have shown antioxidant, anticancer, and anti-obesity properties (Oloyede *et al.*, 2021).

Globally, Cole crops are being grown on an area 3.77 million ha with an annual production of 96.39 million tonnes. Among them, cabbage and other *Brassicas* contribute 2.53 million ha and 70.86 million tones of production. Cabbage is being grown in 141 countries as depicted in global distribution maps. However, the area and production scenario of cabbage is skewed towards two countries, i.e., China and India. Both these countries have a share of almost 48.3% in the global area of cabbage. The accumulative share of these crops holds 13th and 4th rank in global area and production under vegetable crops, respectively. The Cabbage and other *Brassicas* have higher average productivity (29.35 MT/ha) than the global average of overall vegetable crops (19.69 MT/ha). However, in India, the average yield of cabbage (23.2 t/ha) is higher than the overall national vegetable productivity of India (15.5 t/ha) (Figure 1). Asia-Pacific has witnessed the highest production of cabbages and other brassicas, with China being the leading country, in terms of production and export. China is the largest exporter of cabbages and other brassicas in the world and has accounted for 34% of global exports in 2019.

The classical breeding techniques are insufficient and time-consuming for genetic improvement. Biotechnological approaches have opened new dimensions over the last few decades and provide sets of tools to complement breeding

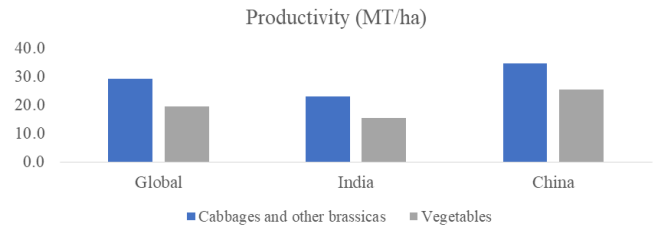


Figure 1: Productivity of cabbage and other *Brassicas*

efforts aimed at crop improvement in various ways. These sets of tools encompass such areas as *in vitro* culture techniques, transgene technology, DNA-based mapping, DNA-based marker-assisted selection, gene cloning and sequencing technologies. Furthermore, tools for analysis of the transcriptome, proteome and metabolome have also attained an unprecedented level of sophistication. These tools have been referred to as being part of the functional genomics toolbox (Colebatch *et al.*, 2002). Generally, Gene transformation using *Agrobacterium* bacteria is one of the most popular methods and by using genetic engineering, plays a significant role in adding specific characteristics to existing cultivars. However, a prerequisite for transferring genes into plants is the availability of efficient regeneration and transformation methods. An efficient *in vitro* regeneration system to allow the genetic transformation of *Brassica* is a crucial tool for improving its economic value.

Genetic Resources and Diversity

The genus *Brassica* is the most economically important genus within the *Brassicaceae* family. Since the last century, several cytogenetic investigations were carried out to determine chromosome numbers and chromosome pairing in interspecific *Brassica* hybrids. The cytogenetic relationship of the main species of the *Brassica* genus was depicted in the U triangle (U 1935) in which *Brassica nigra* (L.) Koch (n = 8), *Brassica oleracea* L. (n = 9), and *Brassica rapa* L. (n = 10) represent the three diploid species in the vertices, and they developed by intercrossing to the three amphidiploid species, *Brassica carinata* A. Braun (n = 17), *Brassica juncea* (L.) Czern. (n = 18), and *Brassica napus* L. (n = 19). Genome A was attributed to *B. rapa* L. (*B. campestris* in the past), the genome B to *B. nigra*, and genome C to *B. oleracea*. The genome-C is represented by *B. oleracea*, which diversified itself into several botanical varieties and related crops by domestication processes, such as var. *acephala*, var. *botrytis*, var. *capitata*, var. *gemmifera*, var. *gongylodes*, var. *italica*, and var. *sabauda*, which are represented, respectively, by kale, cauliflower, cabbage, Brussels sprout, kohlrabi, broccoli and Savoy cabbage crops. The somatic hybrids are expected to be used as bridging plant material to introduce the C3–C4 intermediate trait into *Brassica* crop species. Somatic hybrids were also generated between *Arabidopsis*

thaliana and cabbage (Yamagishi *et al.*, 2008). Liu *et al.* (2014) published whole genome sequences of cabbage (line O2–12) and revealed a multilayered asymmetrical evolution of the *Brassica* genomes and mechanisms of polyploid genome evolution underlying speciation.

Genetic diversity involves classification of individuals on the basis of their relationship with each other. Before crossing two cultivars, the plant breeder should first try to find out how diverse the two cultivars are from each other. Genetic diversity can be studied by using morphological traits and biochemical markers, however molecular markers are preferred as they are based on the genotype of an individual and are free from the confounding effects of the environment. Genetic diversity involves classification of individuals on the basis of their relationship with each other. Before crossing two cultivars, the plant breeder should first try to find out how diverse the two cultivars are from each other. Genetic diversity can be studied by using morphological traits and biochemical markers, however molecular markers are preferred as they are based on the genotype of an individual and are free from the confounding effects of the environment. Genetic diversity is pre-requisite and important factor for hybrid development. Hybrids between genetically-diverse parents manifest greater heterosis than those of closely-related parents. Researchers have employed different molecular markers to quantify the genetic diversity level in cabbage. Kibar *et al.* (2016) studied 22 cabbage inbred lines, 28 experimental cabbage hybrids using 34 quantitative characters using Principal Component Analysis (PCA) and reported that the first three principal components accounted for 39.76% of the total variability among the 28 cabbage hybrids and 45.34% of the total variability among 22 cabbage parents for all the traits investigated. El-Esawi *et al.* (2016) reported 24.3% genetic variation among accessions while 75.7% within the accessions in cabbage using SSR markers from Ireland. Saxena *et al.*, 2011 studied the genetic relationship and diversity among seven cabbage cultivars using RAPD and SSR markers and found that cultivars January King Sel. Improved and Golden Acre are highly divergent cultivars as demonstrated by both the marker systems and found 84.44% and 87.6% polymorphism using these two marker systems, respectively.

Genetic resources encompass all the various forms of germplasm that are available for collection, storage and use. The genetic diversity of crops, represented by traditional local cultivars and wild relatives has been disappearing rapidly during recent decades. Local landraces are being replaced rapidly by improved cultivars and hybrids due to yield advantages. Hence, *in situ* conservation of cabbage genetic resources is currently difficult for cabbage. However, *ex-situ* conservation is a common approach. The Horticultural Research International, Wellesbourne, Warwick,

UK; Instituut voor de Veredeling van Tuinbouwgewassen, Wageningen, Netherlands; Instituto del Germoplasm, Bari, Italy; Indian Agricultural Research Institute, New Delhi; Indian Agricultural Research Institute Regional Station, Katrain, Himachal Pradesh and the National Bureau of Plant Genetic Resources, New Delhi are managing significant collections of cabbage germplasm. Germplasm conservation through *in vitro* propagation of cabbage is feasible using hypocotyle and cotyledon culture (Gambhir *et al.*, 2017), protoplast culture (Yang *et al.*, 1994) and anther culture (Sretenovic-Rajicic *et al.*, 2002).

Breeding Objectives

In cabbage, the main objectives of breeding are crop uniformity, high yield, field appearance and adequate size and shape of economic parts, and good color. It is difficult to achieve a high level of uniformity in case of open-pollinated varieties and in F_1 hybrids using conventionally developed inbred lines due to the cross-pollination nature of cabbage. Production of F_1 hybrids with a great extent of uniformity and in a reduced time span could be possible by use of doubled haploid (DH) lines. At present, most of the cabbage varieties grown in the world are F_1 hybrids (Tanaka and Niikura, 2006) that realize high yields and early maturity through heterosis. Heterosis breeding is only possible if there is an efficient method of producing F_1 seed on a large scale which requires some control of reproduction or pollination mechanism. Two pollination control mechanisms viz., self-incompatibility (SI) and male sterility (particularly CMS) are used for commercial hybrid seed production of cabbage. However, CMS system will help to overcome the problems of instability of SI level and complexities in the maintenance of SI lines. Thakur and Vidyasagar (2016) compared the SI and CMS systems for the performance of hybrids in cabbage and reported that the CMS-based hybrids excelled in their performance for the majority of the characters whereas for few characters, SI system-based hybrids were better. Development of diseases and insect-pests resistant varieties/hybrids is an important objective to reduce pesticide residue effect from food and environment. Qualitative traits have relatively high importance in vegetable breeding. Red-colored cabbage is gaining attraction due to its high anthocyanin content. A selective approach for glucosinolates is mainly required because some have harmful health effects. The development of climate-resilient varieties/hybrids is desirable in changing climatic scenarios like the development of tropical lines in cabbage.

Genetic improvement through conventional breeding

Traditional/Conventional plant breeding has significantly improved crop yield by genetically manipulating agronomical as well as economically important traits. It includes the identification of variability in locally available germplasm or from introductions such as landraces or

other breeding programs, wild species, or genera. To compensate for lack of genetic variability, plant breeders resorted to the identification of spontaneous mutants or even mutations induced by physical or chemical means. The identified variants from all these sources served as the basis for establishing parental lines for eventual hybridization and selection for desired qualitative or quantitative traits. Depending on the traits to be selected for and whether the plants are self-pollinating or cross-pollinating, the breeder sets realistic objectives to maximize the identification of desired traits in the progeny of the crosses. In summary, the objectives of a breeding program determine the choice of parents, choice of breeding method, selection criteria and selection timing. The main conventional methods of breeding commonly utilized in cabbage include introduction, mass selection, pedigree method, backcross, recurrent selection, hybridization, heterosis, synthetics and composites. The choice of the best method or combination of them depends mainly on the type of inheritance (monogenic, oligogenic or polygenic) of the traits to be improved.

Varietal Development

Many varieties like Golden Acre, Pride of India, Copenhagen Market, September, Pusa Drum Head, Late Large Drum Head etc. are either introductions or selections. Pusa Mukta (EC 24855 × EC 10109) was developed by hybridization and notified by CVRC in 1989. Among red cabbage Kinner Red, a selection from exotic material has been recommended by Dr. YS Parmar UHF, Nauni, Solan, H.P. At present, more than 80 germplasm lines of cabbage have been developed and maintained at IARI Regional Station, Katrain, Kullu, H.P. (Singh *et al.*, 2022). Another significant achievement in cabbage breeding is the development of tropical lines e.g. DTC-507-4, 513, 528 (released as Pusa Ageti) etc. at the ICAR-IARI, New Delhi. One genotype of tropical cabbage (VRCAB-101) having a slightly flattish and compact head that induces robust bolting and flowering at 10.1-22.4 °C temperature (average of two seasons i.e. December 2014 to January 2015 and December 2015 to January 2016) has been observed at ICAR-IIVR, Varanasi and the population has been advanced to next generation for further evaluation. Many open-pollinated varieties of cabbage differing in maturity, head shape and size, color and shape of leaves are available. The popular varieties grown are listed below:

Golden Acre: This is an introduction, which was recommended for commercial cultivation by IARI RS, Katrain. The plants have shorter frames, few outer leaves, short stems and small cup-shaped leaves. Heads is round and compact with interior white of excellent quality. It is an early variety and yields 25 t/ha.

Pusa Drum Head: This variety was developed by IARI RS, Katrain and it was released and notified in 1968. It is a late maturing variety taking 80-90 days for head formation.

Plants have wider frame, light green leaves, few outer leaves and short stem. The head is partially covered, less compact and flat weighing 3-4 kg. It possesses field resistance to a black leg (*Phoma lingam*).

Pusa Mukta: This variety was developed at ICAR-IARI, RS, Katrain by hybridization of EC-24855 × EC-10109 and it was released and notified during 1989. Plants have a short stalk, medium plant spread, few outer leaves having wavy margin and puckered leaf blades. Heads are not perfectly round but slightly flat, moderately resistant to black rot. The variety gives a higher yield than Golden Acre but bursts early in the field.

September: An introduction from Germany and recommended by the Tamil Nadu State Department of Agriculture, is popular in the Nilgiri hills. It has solid, round to slightly oblong heads weighing 3-5 kg. Leaves are dark green with wavy margin. The stalk is long and heads usually tilt on one side. It has a very good staying capacity in the field. It takes around 100 days to maturity.

Pusa Ageti: This is a tropical variety developed at ICAR-IARI, New Delhi. It produces seeds under sub-tropical conditions and forms marketable heads at a temperature range of 15 to 30°C but day temperature should not be above 35°C. Heads weigh 600 to 1200 g, gets ready for harvest in 75 to 90 days and yields 11 to 33 t/ha depending upon the time of planting.

Pride of India: The plant type of this variety is similar to Golden Acre but it is about a week later in maturity. Head weighs between 1.0 to 1.5 kg. This is an introduction recommended by Dr.Y.S. Parmar UHF, Nauni, Solan, H.P.

Kinner Red: This is a red cabbage variety recommended by Dr. Y.S. Parmar UHF, Nauni, Solan, H.P. The Head is oval shaped and weighs 500-600 g and takes 70-80 days for head formation.

Hybrid Breeding

Cabbage is one of the cole crops where F₁ hybrids have become very popular. The public sector has also come forward and the first indigenous hybrid 'Pusa Cabbage-1' (KGMR-1) was developed by utilizing SI line, was released and notified during 2012 from the ICAR-IARI RS, Katrain. First CMS system-based F₁ hybrid 'Pusa Hybrid-81' of cabbage was released and notified in 2019. Recently, two CMS-based hybrids Pusa Hybrid-82 (KTCBH-822) and Pusa Red Cabbage hybrid-1 were released and notified during 2022. Cytoplasmic male sterility (CMS) system was transferred successfully from an exotic line (EC 173419) to cabbage at ICAR-IARI, RS, Katrain (Parkash, 2008). Presently 15 Ogura-based CMS lines along with their respective maintainers and eight stable self-incompatible lines of cabbage are available and being utilized for the development of F₁ hybrids at the ICAR-IARI, RS, Katrain (Parkash *et al.*, 2015). Two CMS lines of 'no-chill' cabbage were maintained and the conversion process of four lines of tropical 'no-chill' cabbage into CMS

lines was continued by backcross at ICAR-IARI, New Delhi. The CMS lines were characterized using 13 morphological characters. Few low-chill CMS and SI lines of cabbage have been developed at CSK HPKV, Palampur and are in the process of utilization.

The requirement of F_1 hybrid seed is very high (> 150 q) and is being taken care of through private seed merchants and National and State Seed Corporations. Some of the hybrids have been identified through AICRP i.e. Sri Ganesh Gol (from MAHYCO in 1992), Nath-401 (from Nath Seeds in 1993), BSS-32 in the name of Swarna (from Bejo Sheetal in 1995), Nath 501 (from Nath Seeds in 1997), and Quisto (from Syngenta in 1998). The other hybrids (Bahar, Pragati and Unnati from Pro Agro; Kalyani, Kranti and Hari Rani Gol from Mahyco; Hero, Mitra and Aditya from Sungrow; Yamuma, Ganga and Kaveri from IAHS; Masrgan, Meenaxi and Kuwaxi from Century; Vishesh and Uttam from Hindustan Lever; H-30, 50, 10 and 20 from NSC; Gloria, Runa and Ratan from Dechan-Feldt; Rare Ball from Kaneko; Green Challenger from Hungnong are brought under cultivation without testing under AICRP. Similarly, many heat-tolerant cabbage hybrids were introduced e.g. Golden Cross, KK Cross, OS Cross, Resistlaka, Green Cornet, Autumn Queen, Green Ball (Takii); Green Boy, Green Express, Herculis, Stone Head, Regalia (Sakata). Japanese seed companies have also undertaken seed multiplication of their self-incompatible lines in South Asian Countries. A brief description of cabbage hybrids developed/released by public sector in India is given as below:

Pusa Cabbage-1 (KGMR-1): This is the first public sector cabbage hybrid developed at IARI RS, Katrain and it was released and notified in, 2012. Its leaves are slightly serrated at the margin, round, medium waxy and green. The head is very compact, attractive, fully covered with good staying capacity in the field and takes 60 days after transplanting to first harvest. It carries field resistance to black rot disease with a yield range of 35 to 40 t/ha.

Pusa Hybrid-81: This is the first CMS-based hybrid developed by the IARI Regional Station, Katrain, which was released and notified in 2019. The hybrid has dark green, 12 to 14 non-wrapping waxy leaves, plant height is 22 to 25 cm, round and very compact head covered with outer leaf. It matures in 60 to 65 days after transplanting. It has very good field staying capacity (20–25 days) after head formation. It has given an average yield of 43.5 t/ha in multi-location trials.

Pusa Hybrid-82 (KTCBH-822): This is a CMS system-based hybrid developed by the IARI Regional Station, Katrain. It has been released and notified by the CVRC in 2022. The hybrid has dark green, 11 to 14 non-wrapping waxy leaves, plant height is 19 to 22 cm. Head is flat in shape, very compact and covered with outer leaf. It matures in 65 to 75 days after transplanting. It has a very good field staying capacity (25–30 days) after head formation. The average yield of 40.3

t/ha in multi-location trials which is 19% higher than the commercial check.

Pusa Red Cabbage Hybrid-1: This is the first hybrid of red cabbage from the public sector (IARI Regional Station, Katrain) in India, developed by using a cytoplasmic male sterility (CMS) system. It was released by the Delhi State Seed Sub Committee in 2021 and notified by the CVRC in 2022. The average head weight and yield under multi-location evaluation trials is 1.10 kg and 43.63 t/ha, respectively, which is 10.50 and 21.40% higher in yield over the commercial hybrids, Pusa Cabbage-1 and Primero, respectively. It matures in 70-75 days after transplanting and has an excellent field staying capacity (25–30 days). The anthocyanin concentration in the edible portion is 7.94 mg/100 g (7.5 times higher than that in white cabbage, 1.05 mg).

Quality Traits

Genotypes viz., Red Cabbage, KIRC 1-1, KIRC 2, C 6, KIRC 1A, EC 490162 and MR 1 were found with high carotenoids (>900 $\mu\text{g}/100$ g fresh head weight) and C 3, C 2, C 4, Pusa Mukta, C 8, C 6 (all savoy types), CMS 3 and EC 490162 were most promising genotypes for high ascorbic acid content (>45 mg/100 g fresh head weight). It is also indicated that the inclusion of savoy-type genotypes in the breeding programs would be beneficial to improve the ascorbic acid content of cabbage heads. In the past decade, much interest has been devoted to the positive effects of glucosinolates, a class of phytochemicals whose breakdown products are reported to possess cancer-preventive activity (Kamal *et al.*, 2022). Although the primary function of glucosinolates in plants is presently unknown, several studies have suggested that they play an allelopathic role in plant resistance against fungi, nematodes, herbivores, and weeds (Sotelo *et al.*, 2015). In the past decades, the importance of these plant secondary metabolites has increased after the discovery of their potential in cancer prevention, as biofumigants in agriculture, and in crop protection. Moreover, the presence of glucosinolates in Arabidopsis has promoted a great research effort into the study of these metabolites (Halkier and Gershenzon, 2006). In a field trial, a total of 146 cabbage (*B. oleracea* var. *capitata*) genotypes were analyzed and accessions identified with increased concentrations of glucosinolates (Bhandari *et al.*, 2020). Hanschen and Schreiner (2017) reported that broccoli and red cabbage were mainly rich in 4- methylsulfonyl butyl glucosinolate (glucoraphanin), whereas cauliflower, savoy cabbage and white cabbage contained mainly 2-propenyl (sinigrin) and 3-(methylsulfinyl) propyl glucosinolate (glucoiberin). A set of 70 white cabbage accessions were characterized for the variability of biochemical compounds at Vavilov Institute of Plant Genetic Resources (VIR); the accumulation by different genotypes of protein, sugars, ascorbic acid, carotenoids, chlorophylls, amino acids, organic acids, fatty acids, and

phenolic compounds was determined. The sources of high levels of nutritive and biologically active substances were found, mostly within central Russian and Dutch white cabbage accessions (Solovyova *et al.*, 2014). Parkash *et al.* (2019) studied the effect of 'Ogura' cytoplasm introgression on different quality traits in 17 lines of cabbage. In general, the concentration of different nutritional compounds increased 3–5 times in some lines, while a 4–5-fold reduction was noticed in others. However, a drastic elevation in the concentration of cupric ion-reducing antioxidant capacity (CUPRAC) and ferric-reducing ability of plasma (FRAP) was observed in the CMS lines RRMA (29 times) and 5A (78 times), respectively. The best performing cytoplasmic male sterile (CMS) lines, viz. RRMA, RJA, PMA, RCA, 208A and 5A with higher concentrations of different nutritional compounds can be utilized in future breeding programs for quality F₁ hybrid development in cabbage.

Biotic Stress Resistance

Screening for biotic stresses has been carried out primarily at ICAR-IARI, RS, Katrain. Resistance to cabbage yellows (*Fusarium oxysporum* f.sp. *conglutinans*) has been noticed in AC 238, Spitzkool and EC93559 whereas resistance to black rot (*Xanthomonas campestris*) has been reported in EC10109, Sel.8, Spitzkool, and Greenland Hammer. MR-1, an introduction from USA carries multiple disease resistance to Sclerotinia rot, *Rhizoctonia solani*, downy mildew, black rot and soft rot (*Erwinia carotovora*). As regards the genetics of resistance there are variable reports in literature. Type A resistance (stable at wider temperature range) to cabbage yellow disease is controlled by a single dominant gene whereas Type B (unstable at temperatures above 25°C) is polygenic. Resistance to Sclerotinia rot is under the control of a major recessive gene with modifiers. For downy mildew (*Peronospora parasitica*), the resistance is monogenic dominant against each race. Resistance to black rot is polygenic dominant. In cabbage, cultivars Large Blood Red and Red Pickling (all red types) were identified to possess preferential resistance against caterpillars (*Pieris Brassicae*) and susceptible to aphid (*Brevicoryne Brassicae*). The white cabbage varieties All Season and Round Sure Head showed resistance to these pests and vice versa. AC 208 of bluish green colour has resistance to black rot. Cabbage IRCH-4 to 6 and KK Cross have shown tolerance to aphids. Some of the genetic resources for biotic stress in cabbage is given in Table 1.

Under the National Agricultural Technology Project entitled "Development of insect pests and disease resistant superior varieties of cabbage and cauliflower" a total of 21 genotypes of cabbage have been deposited with the NBPGR, New Delhi. This included sources of resistance and lines having resistance/tolerance to diseases viz., black rot, sclerotinia rot, downy mildew and *Atlenaria* leaf spot and important pests like diamondback moth and cabbage

Table 1: Genetic resources for biotic stresses in cabbage

Biotic stress	Varieties and lines resistant
Black rot	Green Hammer, EC-10109, Spitzkool, Harirani Gol, Kranti, MR-1, AC-204, AC-208, Pusa Mukta (EC 24855 × EC 10109), Delicious, Irodori, EC497641, EC497642, EC497644, EC494005. Hybrid DARL 801 has field tolerant to black rot disease developed by DIBER, Pithoragarh.
Downy mildew	MR-1 and spitzkool
Sclerotinia Rot	MR-1
Yellows	Copenhagen, Wisconsin Copenhagen, Marion Market, Wisconsin Golden Acre, Badger Market, Globe, Resistant Glory, Green Back, All Head Early, All Seasons, AC 238, Spitzkool and EC 93559.
Bacterial spot	EC497641, EC497642, EC497644
Other diseases	MR-1, cabbage carries multiple resistance to soft rot, wire stem, black rot and sclerotinia rot. Pusa Drumhead having some tolerance to black leg disease.
Cabbage butterfly caterpillars (<i>Pieris Brassicae</i>)	Large Blood Red and Red Pickling (all red types)
Aphid (<i>Brevicoryne Brassicae</i>)	All Season and Round Sure Head IRCH-4 to 6 and KK tolerant to aphid

butterfly. A screen of 27 cabbage cultivars revealed a range of preferences of cabbage aphid toward the tested accessions (De Melo *et al.*, 2013). 'Chato de Quintal', 'Ryuhō', and 'Taishita' were the less preferred cultivars by the aphid. Plant Sources of resistance against cabbage moth were detected in a screen of 21 local and commercial cabbage varieties and interactive effects of leaf traits, head compactness, and leaf glucosinolate content were identified (Cartea *et al.*, 2010). Among them three local varieties (MBG-BRS0057, MBG-BRS0074, and MBG-BRS0452) were highly susceptible at both natural and artificial infestation conditions being MBG-BRS0074 the most damaged variety. Two local varieties (MBG-BRS0402 and MBG-BRS0535) and commercial hybrids were identified as resistant or moderately resistant to *M. Brassicae*. Among them, 'Corazón de Buey' and 'Cabeza negra' were the most resistant and produced compact heads. Resistance against cabbage whitefly (*Aleyrodes proletella*) was tested in a collection of 432 accessions of *B. oleracea* and its wild relatives. It was shown that the wild relatives exhibited an earlier resistance than the breeding cultivars, which is probably due to the earlier formation of trichomes (Pelgrom *et al.*, 2015). There are some of disease-resistant hybrids developed by pvt. Seed companies are given in Table 2.

Table 2: Disease resistant hybrids developed by private seed companies

Company	Hybrids	Disease
Mahyco, Jalna	Harirani Gol, Kranti	Resistant to yellows and black rot
	Sri Ganesh Gol	Resistant to yellows
Century Seeds, New Delhi	Geetanjali	Tolerant to black rot and fusarium wilt
Beejo-Sheetal Seeds, Jalna	Swati, Sarita, Bajrang, Shanti, BSS-44, Swarna and Sonali	Resistant to fusarium
Pro Agro Seeds, New Delhi	Bahar	Tolerant to black rot
Sandoz seeds, Pune	Quisto and Vishwas	Tolerant to fusarium yellows

Abiotic Stress Resistance

The abiotic stresses are becoming an alarming situation for *Brassica* crop production worldwide due to quick changes of the global environment. The *Brassica* vegetables are soft and succulent and generally consist of more than 85% water. Therefore, water scarcity as well as excessive water significantly influences the yield and quality of these crops; abiotic stress particularly cold, salinity and drought stresses dramatically reduce the productivity of these crops. Most of the vegetable crops especially *Brassica* crops are sensitive to salinity stress during seedling and early growing stages. Therefore, it is well characterized that the response of plants to abiotic stresses depends on the plant growing stage and the duration and severity of the stress (Bray, 2002). Alfine-like transcription factors in *B. oleracea* (BoAL1, 4, 5, 6, 7, 8, 9, 10, and 12) have been reported in response to abiotic stresses like cold, salinity, drought and ABA (Kayum *et al.*, 2016). The heat tolerance trait in the interspecific somatic and sexual hybrids between cabbage (*B. oleraceae* var. *capitata*) × Chinese cabbage (*B. campestris* var. *peknensis*), was

Table 3: Abiotic stress tolerant varieties in cabbage

Abiotic stress	Varieties
Tolerance to high temperature	Green express, Green boy, KK Cross, Pusa ageti
Tolerant to bolting when grown in spring	Qiangan 1

intermediate between of the parents (Huang *et al.*, 2000). Different varieties that showed abiotic stress resistance are presented in Table 3.

Molecular Breeding Approaches

Molecular markers are the differences in nucleotide DNA at the corresponding site on homologous chromosomes which follow the Mendelian pattern of inheritance (in case of nuclear DNA Marker) or follow maternal inheritance (in case of organellar DNA marker). Recent advances in molecular biology, particularly the development of molecular markers and transformation technology, have been very promising for easy identification and manipulation of qualitative and quantitative traits. Molecular markers and genetic maps have been widely used to assist breeders in marker-aided selection in *Brassica* species (Snowdon and Friedt, 2004). Markers may be either phenotypic or genotypic, and marker-assisted breeding developed in the 1980s with the evolution of DNA marker technologies. Today, the main DNA markers used in breeding programs are random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), Simple Sequence Repeats, Sequence characterized Amplified Region (SCAR), expressed sequence tags (ESTs), single nucleotide polymorphism (SNP) etc. Each of these markers has a different set of advantages and limits. Cost and possible automation of the techniques are of particular importance for their adoption.

In *B. oleracea* and *B. rapa*, linkage maps have been extensively used to identify economically important complex polygenic traits and efforts are being made to transfer these genes using the linked markers to desirable

Table 4: Linked molecular marker in cabbage

Trait	Gene	Marker	Reference source
Black rot	BRQTL-C3, BRQTL-C6	SNP	Lee <i>et al.</i> (2015)
Genic male sterility	CDMs399-3	EST-SSR	Chen <i>et al.</i> (2013)
Head shape	QTLs (Htd 3.1, Htd 8.1)	SSR, InDel	Pang <i>et al.</i> (2015a, b)
Head splitting	QTLs (SPL-2-1, SPL-4-1)	SSR	Pang <i>et al.</i> (2015a, b)
Yellow-green leaf	<i>Ygl-1</i>	InDel	Liu <i>et al.</i> (2016)
Plant height, leaf length, head transverse diameter	QTLs Ph 3.1, LI 3.2, Htd 3.2	InDel	Lv <i>et al.</i> (2016)
Sclerotinia rot resistance	QTLs (6 for stem and 12 for leaf resistance)	SSR	Mei <i>et al.</i> (2012)
Fusarium wilt resistance	<i>FOC1</i>	InDel	Lv <i>et al.</i> (2014)
Petal colour	<i>Cpc-1</i>	InDel	Han <i>et al.</i> (2015)

commercial backgrounds. Notable examples are the mapping of disease resistance and cytoplasm male sterility restorer genes (Snowdon and Friedt, 2004). Linked markers to these economically important traits could be used to transfer this trait into commercial cultivars through marker-assisted selection, molecular manipulation of QTL/gene(s), and cloning and characterization of important genes.

Molecular markers have been utilized extensively for the preparation of saturated molecular maps (genetic and physical) and their association with genes/QTLs controlling the traits of economic importance has been utilized in several cases for marker-assisted selection (MAS) (Varshney *et al.*, 2005 and 2006). As a result of extensive efforts undertaken at the international level to identify molecular markers tightly linked with a large number of agronomic traits as well as tolerance/ resistance to abiotic and biotic stresses in major crop species, it has been possible to realize the potential of molecular markers to track loci and genome regions in several crop-breeding programs (Gupta and Varshney, 2004; Varshney and Tuberosa, 2007). Other important uses of molecular markers include germplasm characterization, genetic diagnostics, genome organization studies and phylogenetic analysis (Varshney and Tuberosa, 2007; Jain *et al.*, 2010). A comprehensive study on characterization and genetic diversity analysis was carried out by Parkash *et al.* (2017) in exclusively eight self-incompatible (SI) lines of cabbage using 13 morphological traits and 49 SSR markers. Study revealed that 49 SSR loci recorded high polymorphism and were effective for differentiating different self-incompatible lines under study. The SI genotype, S-645 and S-681 were found most divergent based on morphological and molecular studies, respectively. Hence, these genotypes have greater potential in future breeding programs for the development of high-yielding quality hybrids. A comprehensive study on characterization and genetic diversity analysis was carried out in 16 'Ogura'-based 'CMS' lines of cabbage using 14 agro-morphological traits and 29 SSR markers. The 29 SSR loci recorded high polymorphism and were found effective for differentiating different CMS lines under study. Hence, SSR markers can be utilized for germplasm characterization and association mapping for future breeding programs in 'Ogura'-based CMS lines of cabbage. In overall, based on agro-morphological and molecular studies genotype RRMA, ZHA-2 and RCA were found most divergent. Hence, they have immense potential in future breeding programs for the high-yielding hybrid development in cabbage (Parkash *et al.*, 2018). Cole genome has been sequenced by Liu *et al.* (2014), and number of linked molecular markers for important traits have been identified in cabbage (Table 4). The genomic sequences are useful tools for the development of robust DNA markers. The genetic maps in *Brassica* also serve the purpose of (a) understanding the relationship among the

genomes of the *Brassica*- cultivated diploid species and (b) utilization in applied genetics and breeding of the numerous *Brassica* crops.

Transgenics in Cabbage

Genetic transformation used for improving the traits and induce resistance against biotic and abiotic stresses. The advancement of genetic engineering can overcome the barriers associated with the sexual incompatibility of *Brassica oleracea* cultivars, resulting in hybrids with new desirable agronomic traits (Gerszberg, 2018). A transgenic approach was used by Jin *et al.* (2000) to target resistance to diamondback moth larvae in cabbage through *Agrobacterium tumefaciens*- mediated transformation with *Bacillus thuringiensis* (Bt) cry genes. Cabbage plants transformed with a synthetic Bt gene, *cryIAb3*, were all resistant to larvae of the diamondback moth, whereas all plants transgenic for *cryIIa3*, a wild-type Bt gene, were susceptible. The transgenic cabbage plants containing the wild-type *cryIIa3* gene were susceptible to diamondback moth larvae and showed the presence of a truncated *cryIIa3* transcript by Northern analysis (Jin *et al.*, 2000).

Kalia *et al.* (2018) investigated the insecticidal efficacy of *Cry1B/Cry1C* genes in transformed lines of cauliflower, and cabbage was assessed by feeding neonates of DBM on detached leaves. From large number of transformed lines analyzed, it is obvious that the *Cry1B/Cry1C* genes potentially exhibited insecticidal activity. Paul *et al.* (2005) transformed a tropical cabbage breeding line 'DTC 507' by a synthetic fusion gene of *Bacillus thuringiensis* encoding a translational fusion product of *Cry1B* and *Cry1Ab* δ -endotoxins by *Agrobacterium*-mediated transformation. Russell *et al.* (2017) reviewed progress on the deployment of pyramided Bt genes *cry1B* and *cry1C* for the control of *Plutella xylostella*, *Crociodomia pavonana*, *Hellula undalis* and *Pieris* spp. in cabbage and cauliflower. Different examples of desirable gene transfer in cabbage are given in Table 5.

Genome and transcriptome sequencing

The NGS technologies have been changed with reduced cost and time for sequencing compared to Sanger technology and making possible to perform millions of sequencing reactions in parallel. Second-generation sequencing (massively paralleled sequencing) technologies such as Roche/454 pyrosequencing and Illumina/Solexa sequencing are already profusely used to sequence plant species, and third-generation sequencing (also known as long-read sequencing) are currently under active development and incorporated to sequencing projects PacBio RS (Pacific Biosciences), Helicos (Helicos) or Ion Torrent (Life Technologies). Nowadays, it is feasible to sequence most crop genomes with a relatively modest budget, by combining Sanger with NGS technologies. However, as compared to whole genome sequencing, transcriptome

Table 5: Desirable gene transfer studies in cabbage

<i>B. oleracea</i> var. <i>capitata</i> cultivar	Technique of gene transfer	Gene transfer	Improvement in traits	References
161	<i>A. rhizogenes</i> (A ₄ K, A ₄ H)	<i>nptII</i> , <i>hph</i>	Resistance to kanamycin, hygromycin	Berthomieu and Jouanin (1992)
King Cole	<i>A. tumefaciens</i> (AB1)	<i>cry1a (c)</i>	Resistance to diamond back moth (<i>P. xylostella</i>)	Metz <i>et al.</i> (1995)
Yingchun, Jingfeng	<i>A. tumefaciens</i> (LBA4404)	<i>CpTI</i>	Insect tolerance to <i>Pieris rapae</i> L.	Hong-jun <i>et al.</i> (1997)
Hercules, Brunswick, Cape spitz, Copenhagen	<i>A. tumefaciens</i> (LBA4404)	<i>nptII</i>	Resistance to kanamycin	Pius and Achar (2000)
Scorpio, Testie	<i>A. tumefaciens</i> (EHA105)	<i>cry1la3</i>	Resistance to diamond back moth (<i>P. xylostella</i>)	Jin <i>et al.</i> (2000)
Uji	<i>A. tumefaciens</i> (LBA4404)	<i>GO</i>	Enhanced tolerance to black rot disease by <i>Xanthomonas campestris</i> pv. <i>campestris</i>	Lee <i>et al.</i> (2002)
		<i>hpt</i> , <i>bar</i> , <i>BcA9</i>	Polen male sterility	Lee <i>et al.</i> (2003)
Golden Acre	<i>A. tumefaciens</i> (GV2260)	<i>betA</i>	Enhanced salt tolerance	Bhattacharya <i>et al.</i> (2004)
DTC 507	<i>A. tumefaciens</i>	<i>cry1 b</i>	Resistance to diamond back moth (<i>P. xylostella</i>)	Paul <i>et al.</i> (2005)
Xiaguang	<i>A. tumefaciens</i> (LBA4404)	<i>vhb</i>	Increases submergence tolerance	Li <i>et al.</i> (2005)
N/A	<i>A. tumefaciens</i> (LBA4404)	<i>OC-I</i>	Insect resistance	Lei <i>et al.</i> (2006)
Summer Summit, KY cross	Biolistic method	<i>cry1Ab</i>	Resistance to diamond back moth (<i>P. xylostella</i>)	Liu <i>et al.</i> (2008)
KY Cross	<i>A. tumefaciens</i> (GV2260)	<i>AtHSP101</i>	Increase the high temperature tolerance	Rafat <i>et al.</i> (2010)
A21-3'	<i>A. tumefaciens</i> (LBA4404)	<i>cry1la8</i> , <i>cry1Ba3</i>	Resistance to diamond back moth (<i>P. xylostella</i>)	Yi <i>et al.</i> (2013)
AD BENTAM	<i>A. tumefaciens</i> (LBA4404)	<i>PMI</i> , <i>JMT</i>	PMI/mannose selection system; resistance to stress	Hur and Min (2015)
		<i>Bt CryIAb3</i>	Resistance to diamondback moth	Ravanfar <i>et al.</i> (2017)

sequencing has been a cheaper alternative. The RNA-seq is independent of a priori knowledge on the sequence under investigation, thereby also allowing analysis of poorly characterized species. It helps to study gene expression and identify novel RNA species and directly reveals sequence identity, crucial for the analysis of unknown genes and novel transcript isoforms. Liu *et al.* (2014) generated draft genome sequence of cabbage covering 98% of 630 Mb genome and compared it with *B. rapa* which revealed numerous chromosome rearrangements and asymmetrical gene loss in duplicated genomic blocks, asymmetrical amplification of transposable elements, differential gene co-retention for specific pathways and variation in gene expression. Glucosinolate biosynthesis-related genes were illustrated due to the consequence of genome duplication and gene divergence. Yang *et al.* (2018) assembled the cabbage mtDNA by whole genome sequencing (WGS) and assembled sequence reads in a circular structure of 219,975 bp. They observed differences in the arrangement

of bases at different regions, genome realignment of the plastid genome and mtDNAs and associated presence of heteroplasmy and reverse arrangement of the heteroplasmic blocks within the other mtDNAs which might be one of the causal factors for its diversity. They confirmed the existence of different mtDNAs in diverse *B. oleracea* subspecies.

CRISPR/Cas9

A recent tool for genome editing is a CRISPR-associated protein (Clustered regularly interspaced short palindromic repeats) consisting of a nuclease (Cas9) and two short single-strand RNAs (crRNA and tracrRNA) which are fused to form single-guide RNA (sgRNA) for genome editing. Cas9 and a gRNA form a ribonucleoprotein complex and bind to genomic DNA (Cong *et al.*, 2013). In Cole vegetables, using cabbage as a model plant and *PsbS* as the target gene, Jansson (2018) was the first to describe the gene-edited using CRISPR-Cas9 (a *Brassica* deletion mutant). Murovec *et al.* (2018) introduced preassembled ribonucleoprotein

complexes (RNPs) into cabbage protoplasts with PEG 4000. Four sgRNAs targeting two endogenous genes (the *FRI* and *PDS* genes, two sgRNAs per gene) were introduced and detected 1.15–24.51% mutation. Ma *et al.* (2019) in cabbage targeted phytoene desaturase gene (*BoPDS*), S-receptor kinase gene (*BoSRK*) and male-sterility-associated gene *BoMS1* genes by CRISPR/Cas9 gene editing using a construct with tandemly arrayed tRNA-sgRNA architecture. They reported that *BoSRK3* gene mutation suppressed self-incompatibility completely, and *BoMS1* gene mutation produced a completely male-sterile mutant. They also revealed that CRISPR/Cas9 system, coupled with an endogenous tRNA-processing system, is an efficient tool to improve cabbage traits. Direct modification of the *SRK* gene in the male sterile parent, the maintainer line and the paternal line using the CRISPR/Cas9 system reduce the costs of cabbage hybrid seed production. Lawrenson *et al.* (2019) described an *Agrobacterium*-mediated delivery approach to deliver Cas9 and dual sgRNAs into 4-day-old cotyledonary petioles of *Brassica oleracea* and detected nearly 10% of primary transgenic plants. In subsequent T1 and T2 generations, it segregated away from the T-DNA and enabled the recovery of nontransgenic, genome-edited plants carrying a variety of mutations at the target locus.

Future Prospective

Different aspects like crop uniformity for maturity, yield and yield attributing traits, along with the development of resistant lines to biotic and abiotic stresses, climate-resilient varieties and hybrids and rich in nutraceutical properties are the priority objectives of crop improvement in cabbage. The new challenges of plant breeding urge us to integrate the latest innovations in biology and genetics to enhance crop improvement. While the development of markers and the genetic map was an expensive and time-consuming task till a few years ago, the availability of gene/genome sequence data together with high-throughput marker discovery and genotyping platforms have made the development of genic markers easier and faster. The availability of high-throughput genome-wide and low-cost genotyping platforms provides opportunities to accelerate breeding practices through the use of markers in background selection during marker-assisted breeding.

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सारांश

पादप प्रजनन का फसल सुधार में एक महत्वपूर्ण योगदान रहा है। हालाँकि, जर्मप्लाज़्म की विलुप्ति नई किस्मों में नई वांछित परिवर्तनशीलता को शामिल करना अत्यंत कठिन होता जा रहा है, अतः फसल सुधार में वैकल्पिक तकनीकों का सहारा लिया गया है। प्रजनन में सहायता के लिए उत्परिवर्तन, ऊतक संवर्धन और आनुवंशिक परिवर्तन शामिल हैं। जीन से प्राप्त आणविक मार्करों का विकास और अनुप्रयोग, जिन्हें आमतौर पर जेनिक कहा जाता है। आणविक मार्करों के अनुप्रयोग से पादप आनुवंशिकी और प्रजनन में गति मिल रही है। वर्तमान में, मार्कर खोज, जीनोटाइपिंग और आणविक प्रजनन प्रथाएं के अनुप्रयोग से विभिन्न फसलों जैसे सरसो कुल की फसलों आदि के फसल सुधार कि दिशा को काफी गति मिल रही है। आणविक मार्करों के उपयोग से जीनोम आर्किटेक्चर और कुछ विशेष फिनोटिपिक विशेषताओं को सुनिश्चित करने में महत्वपूर्ण पाया गया है जो कि गोभी वर्गीय फसलों में भी देखा गया है। गोभी प्रजनन, जीनोमिक्स और उनके इस समीक्षा लेख में अनुप्रयोगों पर विस्तार से चर्चा की गई है।