Vegetable Science (2023) Vol. 50 (Special Issue): 177-188

doi: 10.61180/vegsci.2023.v50.spl.05

ISSN- 0970-6585 (Print), ISSN- 2455-7552 (Online)

www.isvsvegsci.in

REVIEW ARTICLE

Chili: Breeding and Genomics

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Abstract

Chili or hot pepper is an important vegetable cum spice crop, which has huge commercial applications in food, nutrition, pharmaceutical and cosmetic industries. The *Capsicum* genus originated in Central America with about 35 species, of which five are domesticated for cultivation. Color and pungency-related components such as capsanthins, capsaicinoids and capsinoids are unique to *Capsicum* genus. There exists large variability in the genus and genetic resources have been explored for breeding varieties/ hybrids with resistance/ tolerance to biotic and abiotic stresses with enhanced fruit quality. In the present climate change scenario, there is an evolution of various pests and diseases, which requires continuous exploration of germplasm including related cultivated and wild species for novel genes/alleles. Conventional breeding has led to the development of improved lines/varieties/hybrids. Whole genome sequence information and the pan genome of chili are publicly available, which can help in the development of molecular markers associated with key traits of importance. Advancements in genomic resources and next-generation sequencing techniques can be employed to accelerate breeding programs.

Keywords: Breeding, Chili, Genomics, Markers, Resistance.

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Citation: Reddy, M.K., Kumar, R., Ponnam, N., Prasad, I., Barik, S.P., Pydi, R., Timmarao, S., Narigapalli, P., Shaik, M. and Pasupula, K. (2023). Chili: Breeding and Genomics. Vegetable Science 50(spl): 177-188.

Source of support: Nil

Conflict of interest: None.

Received: 06/08/2023 **Accepted:** 11/12/2023

Introduction

Chili belongs to the *Capsicum* genus which originated in Central and South America. *C. annuum* var. *glabriusculum* is wild progenitor of cultivated chili (Aguilar-Melendez *et al.*, 2009). *Capsicum* genus consist of thirty-five species (Carrizo García *et al.*, 2016) and among them five species (*C. annuum, C. chinense, C. frutescens (C.annuum var glabriusculum*; Taxonomic serial no. 30493 (ITIS, 2022), *C. pubescens and C. baccatum)* are domesticated species. Further, another distinctive domesticated species *C. assamicum* has been reported from the North-eastern part of India (Purkayastha *et al.*, 2012).

World's dry chili production increased significantly over the previous 20 years (2000 to 2020) (www.fao.org/faostat), from 2.46 to roughly 4.15 million tonnes. Dry chili area has decreased by 5.49% over the last 20 years, and today is 1.61 million hectares. India is the largest producer of dry chili in world with an area of 7.02 lakh hectares and an annual production of 20.49 lakh tonnes (Spice Board, 2020-21). Dry chili contributes the highest among total spice exports from India with 5.57 lakh tonnes with Rs. 8429.92 crores of economic value (Spice Board, 2020-2021). Indian dry chili is majorly exported to China (Value of Rs. 3144.53 crores), followed by Thailand, Bangladesh, USA, Sri Lanka, Indonesia, UAE, Malaysia, UK and Vietnam. The major dry chili cultivated states in India are Andhra Pradesh (25.27%),

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Madhya Pradesh (17.40%), Telangana (12.69%) and Karnataka (12.19%), accounting for 67.55% of total cultivated area and 87.62% of total dry chili production. The largest chili markets in the Asian continent are in Guntur (Andhra Pradesh) and Haveri (Karnataka) of India. The total area under green chili cultivation is 3.08 lakh ha with an annual production of 35.92 lakh MT with an average productivity of 11.64 MT/ha (Horticulture Statistics Division, 2017-18). India has exported 52,370 MT of green chilies, worth 310.44 crores rupees during 2021-22 (APEDA).

Color and pungency extracts are used in both the food, feed, pharmaceutical and cosmeceutical industries. Biochemical composition of fruit color and pungency are carotenoids and capsaicinoids, respectively. Capsaicin, dihydrocapsaicin and nor-dihydrocapsaicin are major alkaloids among capsaicinoids having wide applications in the food, medicine and pharmaceutical and other industries (Baenas *et al*., 2019). Capsinoids (capsiate and dihydrocapsiate) are low/non-pungent analogs of capsaicinoids that have similar pharmacological applications (Lang *et al*., 2009). Capsaicin is being used as an effective agent to cure neuropathic pain as Qutenza® (Aitken *et al*., 2017).

There are various cases of paprika oleoresin being used as cosmetic colorants in bath oils, shampoo, shower gels, and beauty products such as eye makeup and lipsticks (Baenas *et al*., 2019). Chili fruit extracts rich in lutein and zeaxanthin compounds are used in skin and facial care serums or nutritional supplements (https://zss-skincare.com). By-products of chili fruits, rich in bioactive compounds are successfully used in cosmeceutical industries for various beauty and healthcare products with no side effects (Barik *et al*., 2022).

Among the different chili-based industries one of the most important is paprika, 70% of which is used as spice in soups, sauces and meat products. Mild and non-pungent types of chili in ground form, or oleoresin extracts is internationally referred to as paprika. Besides having a special place in the global diet as ripe dried spice and green fruit (vegetable), chili is broadly utilized as a vital condiment in recipes to impart a natural red color. The main specialty of this additive is the magnitude of its red color, which positively impacts consumer acceptance as well as commercial value. It was categorized as a natural food additive (EFSA, 2015). According to Grand View Research, the global market for oleoresins was valued at US$1.44 billion in 2018, and it is forecasted that the market will grow at a compound annual growth rate of 4.7% to 2025.

Hybridization and Crossability

Various intraspecific and interspecific hybridizations have been conducted so far (Sunil *et al*., 1998, Naresh *et al*., 2016). It was reported that fertile hybrids can be obtained by interspecific crosses within *Capsicum annuum* complex at varying degrees (Baral and Bosland, 2004; Panda *et al*., 2004; Jarret and Dang, 2004). On the other hand, no fertile hybrids were produced in cross between *Capsicum annuum* and *Capsicum pubescens*. Varying rate of successful fertile hybrid were obtained by crossing between wild and semi-domesticated *C. annuum* var. *glabriusculum*, and *C. annuum* var. *annuum* (Hernández-Verdugo *et al*., 2001; Guzmán *et al*., 2005).

Genetic Resources

World Vegetable Center, Taiwan holds large germplasm of chili along with other international organizations such as the United States Department of Agriculture and New Mexico State University (NMSU). National Bureau of Plant Genetic Resources (NBPGR), New Delhi acts as an essential nodal center for germplasm exploration, collection and conservation. AICRP (Vegetable Crops), National Institutes like ICAR-IARI, ICAR-IIVR, ICAR-IIHR and Horticultural Research Station like Lam farm, Devihossur along with state agricultural university's viz., Dr. YSR Horticultural University, Punjab Agricultural University are active centres for chili germplasm collection, conservation and maintenance.

India is considered as the secondary center of origin for *Capsicum* sp. owing to its wide range of diversity with respect to fruit color and pungency. Few land races have been recognized with GI tag including Byadagi Dabbi (Karnataka), Naga mirchi (Kohima, Nagaland), Guntur Sannam (Guntur, Andhra Pradesh), Mizo chili (Mizoram), Bhiwapur Chili (Nagpur, Maharashtra), Hathei chili (Manipur), Edayur chili (Malappuram, Kerala), Khola chili (Goa), Dalle Khursani (Sikkim) and Harmal chili (Goa). In India, especially the North Eastern regions have been recognized as the home for highly pungent hot pepper genotypes (Sarwa *et al*., 2013; Gaur *et al*., 2016). The very popular natural hybrid 'Bhoot Jolokia' (*C. chinense* X *C. frutescens*) (Mathur *et al*., 2000 and Bosland and Baral, 2007) was recorded on the official list of Guinness World Records, 2007 for its high Scoville Heat Unit (SHU). Genetic resources have been screened against various biotic and abiotic stresses globally, various sources of resistance have been reported (Table 1) and genetics of various traits have been studied (Table 2).

Chili Genome and its Characters

The chili genome is one of the most complex with a size of ~3Gb. The complete genome of pepper is distributed in 12 chromosomes. There are 2,139 distinct gene families found only in members of the Solanaceae plant family, and 756 distinct gene families found only in hot peppers. The family size have been found to be varied among the hot pepper gene families. (Kim *et al.* 2014). Whole genome sequencing has been carried out in some accessions of *C. annuum, C. chinense and C. baccatum* and publicly available as reference genomes (Table 3). Recently 383 cultivars (335 *C. annuum*, 11 *C.chinense*, 13 *C. frutescens* and 4 *C.baccatum*) were

Table 1: Resistance sources of pepper against various biotic stresses (Diseases and insect pests)

Disease/Pest	*Resistant sources*
Viral Diseases	
Begomoviruses	
Pepper golden mosaic virus (PepGMV) and Pepper huasteco yellow vein virus (PHYVV)	BG-3821 (*C. chinense*) (Anaya-Lopez *et al*., 2005)
ChiLCV	Bhut Jolokia 001 (Adluri *et al*., 2017).
PepLCV	GKC-29, EC-497636, BS-35 (Kumar *et al*., 2006)
	VI012005, PBC495, PBC144, PBC143, PBC149 (Kenyon *et al*., 2014) Kalyanpur Chanchal (Singh *et al*., 2016)
Pepper yellow leaf curl Thailand virus	9852-123 (Barchenger *et al*., 2019)
Tomato leaf curl New Delhi virus & ChiLCV	DLS-Sel-10, PBC142, PBC145, WBC-Sel-5, PBC345 (Srivastava *et al*., 2015; 2017)
Chili leaf curl virus	IHR4615, IHR4630, and IHR4517 (Yadav *et al*., 2022)
Cucumber mosaic virus (CMV)	Sapporo-oonaga, Nanbu-onaga (Suzuki *et al*., 2003) Bukang (Kang *et al*., 2010) LS1839-2-4 (Suzuki *et al*., 2003) IHR2451, IHR4503 (Naresh *et al*., 2016) PI439381-1-3 (*C. baccatum*) (Suzuki *et al*., 2003) PBC688 (*C. frutescens*) (Guo *et al*., 2017)
Poty viruses	
TEV, PVY (0), PepMoV	PI 159236, PI 152225 (*C. chinense*) (Murphy *et al*., 1998)
PVY (0)	Yolo Y (Kang et. al., 2005)
TEVT, PVY (0, 1)	*C. annuum* Florida VR2 (Kang et. al., 2005)
PepMoV	Avelar (Guerini and Murphy, 1999)
	CM334 (Caranta et. al., 1999)
PVMV	Perennial (Caranta et. al., 1996)
ChiVMV	NW4 (Lee et. al., 2013) IHR2451and IHR4503 (Naresh *et al*., 2016) CV3, CV4, CV8, and CV9 (Lee *et al*., 2017)
Tospoviruses (TSWV)	PI152225, PI159234 (*C. chinense*) (Jahn *et al*., 2000) CNPH 275, PI-15, ECU-973, C00943 (Cebolla-Cornejo *et al*., 2003) AC09-207 (*C. chinense*)
GBNV	EC631810, IIHR4360, IIHR4577, IIHR4578, IIHR4582, IIHR4585, IIHR4587, IIHR4588 (Pavithra *et al*., 2019)
Fungal diseases	
Phytophthora root rot	CM334 (Kim *et al*., 2008) PI201232 and PI201234 (Silvar *et al*., 2006)
Anthracnose fruit rot	PBC80, PBC81, PI594137 (*C. baccatum*) and PBC932 (*C. chinense*) (Gniffke et. al., 2013)
Powdery Mildew	H3 ((Daubeze *et al*., 1995; Lefebvre *et al*., 2003) Pimenta Cheiro and PI 152225 (Blat *et al*., 2005) VK515R (Jo *et al*., 2017)
Bacterial diseases	
Bacterial wilt	IIHR-B-HP-130 (Naveena *et al*., 2020) Perennial, Narval, PI 322719, LS2341, YCM334 (*C. annuum*), Heiser 6240, LS 2390 (*C. frutescens*), LS1716, PBC385, PBC066, CNPH145 (HC10) (*C. baccatum*) (Parisi *et al*., 2020) CNPH 3800, Dedo-de-moca 1, 2, 3 (*Capsicum baccatum*), Pimento-de-Bode red 2, Pimento-de-Bode red 4, Pimento-de-Bode yellow 1, (*Capsicum chinense*), Malagueta 4, Malagueta 5 (*Capsicum frutescens*) (Rossato *et al*., 2018) PCWR-1-3-08, PCWR-Cap-4-08, PCWR-33-1-3-08 and PCWR-33-3-1-08 (Singh *et al*., 2018)

Bacterial spot	Globál (Cherry type) (Palotás, 2016) UENF 1381 (Moreira *et al*., 2012) KC01617, KC01760, KC01779, KC01137, KC01777, KC00939 (Byeon *et al*., 2016)
Root knot Nematodes	
Root-knot nematodes	UFGFR 05 (*C. frutescens*) (Marques *et al*., 2019) UFGCCH 24 – 'Bode Roxa' (*Capsicum chinense*) (Marques *et al*., 2020)
Insect pests	
Thrips	X-1068, X-743, X-1047, NP-46A, Caleapin Red, Chamatkar, BG-4 (Dhall, 2015) RU27, RU32 and RU28 (Capsicum chinense (Visschers, 2020) AC 1979, Bisbas, Keystone Resistant Giant CM 331(*C. annuum*), No. 1553, Aji Blanco Christal (*C. baccatum*) (Maharijaya *et al*., 2011; 2015) EC378630, EC391082, EC378633, IC214991 (Sarath Babu *et al*., 2002) IC572492, IC342390, IC337281 (Rameash *et al*., 2015).\ CGN16795 (Pauline van Haperen et. al., 2021)
Mites	Navsari Jwala, RHRC Erect and ACG-77 (Desai *et al*., 2006) IC572481, EC596952 (Rameash *et al*., 2017) Kalyanpur red, Punjab lal, LEC 1, GoliKalyanpur (Dhall, 2015)

Table 2: Genetics of resistance to biotic stresses in pepper (Diseases and insect pests)

Disease/Pest	*Genetics*
Viral diseases	
Begomo viruses	Digenic with duplicate recessive epistasis (Garcia-Neria and Rivera Bustamante, 2011). Single recessive gene (Rai *et al*., 2014) Monogenic dominant (Yadav *et al*., 2022)
Cucumber mosaic virus (CMV)	Partially dominant (Pochard and Daubeze, 1989) Single dominant (Kang *et al*., 2010) Polygenic recessive (Naresh *et al*., 2016)
Poty viruses	
TEV, PVY (0), PepMoV	*pvr1*, Recessive (Yeam et. al., 2005)
PVY (0)	*pvr2* ($pvr2^1 = pvr1^1$)Recessive (Ruffel *et al*., 2002)
TEVT, PVY (0, 1)	*pvr2* ($pvr2^1 = pvr1^1$)Recessive (Ruffel *et al*. 2002)
PepMoV	*pvr3* Recessive (Parrella *et al*., 2002)
	Pvr4, Dominant (Grube et .al., 2000)
	Pvr7, Dominant (Grube *et al*., 2000)
PVMV	*pvr6 -* $pvr1^1$or $pvr1^{2,}$ Recessive (Ruffel *et al*., 2006)
ChiVMV	Monogenic dominant (Lee et. al., 2013 and Lee *et al*., 2017) Monogenic recessive (Naresh *et al*., 2016)
Tospoviruses (TSWV)	Single dominant gene (Boiteux *et al*., 1993). Monogenic dominant gene and non-allelic gene action in PI159236 and PI152225 (Hoang *et al*., 2013)
Fungal diseases	
Phytophthora root rot	Recessive to dominant nature (Reifschneider *et al*., 1992) Polygenic (Thabuis *et al*., 2003) Polygenic in nature with additive and epistatic effects (Lefbrve *et al*., 1996) Monogenic dominant (Manish *et al*., 2022)
Anthracnose fruit rot	Monogenic recessive (Mahasuk *et al*., 2009) Duplicate gene action (Lin *et al*., 2007) Polygenic (Lee *et al*., 2010)

Powdery Mildew	Polygenic dominant trait (Murthy and Deshpande, 1997; Blat *et al.*, 2005). Incomplete dominance (3 genes) (Anand *et al.*, 1987) Monogenic dominant gene (Jo *et al.*, 2017)
Bacterial diseases	
Bacterial wilt	Digenic (Kwon *et al.*, 2021) Digenic and complementary gene action with other minor genes (Naveena *et al.*, 2020) Monogenic recessive (Thakur *et al.*, 2014) Polygenic (Mimura *et al.*, 2009)
Bacterial spot	Polygenic recessive gene action with additive effect (Silva *et al.*, 2017) Digenic recessive (Jones *et al.*, 2005)
Root-knot nematodes	
Root knot nematode	Single dominant gene (Djian-Caporalino *et al.*, 2007)

Table 3: Publicly available pepper genomes

Cultivar/Species	*Method of sequencing*	*Genome size*	*Database*	*Reference*
CM334 (*Capsicum annuum*)	Illumina sequencing	3.48	http://peppergenome.snu.ac.kr.	Kim *et al.*, 2014
PBC81 (*C. baccatum*)	Illumina Hiseq 2500 system	3.9	http://peppergenome.snu.ac.kr.	Kim *et al.*, 2017
PI159236 (*C. chinense*)	Illumina Hiseq 2500 system	3.2	http://peppergenome.snu.ac.kr.	Kim *et al.*, 2017
Zunla-1 (*C. annuum*)	Illumina sequencing	3.26	http://peppersequence.genomics.cn	Qin *et al.*, 2014
Chiltepin (*C. annuum var. glabriusculum*)	Illumina sequencing	3.07	http://peppersequence.genomics.cn	Qin *et al.*, 2014
UCD-10X-F1 (CM334 x blocky pepper-breeding line)	Illumina HiSeq X Ten	3.5	https://solgenomics.net	Amanda M Hulse-Kemp *et al.*, 2018
Takanotsume (*Capsicum annuum*)	HiFi long-read sequencing technology.	3.058	https://plantgarden.jp	Kenta Shirasawa *et al.*, 2023

sequenced and pangenome was studied, which is available at PepperPan (Ou *et al.*, 2018).

Discovery of Molecular Markers in Chili

Most of the Molecular markers like simple sequence repeats (SSR) in pepper are developed either from genomic (Sanwen *et al.*, 2001; Lee *et al.*, 2004) or transcriptome sequencing projects. Nearly 11,500 SSRs were discovered or mined through *in-silico*-based methods. Information on publicly available molecular markers is presented in Table 4.

Breeding for Virus Resistance

In India, several viruses such as Chili leaf curl virus (ChiLCV), Tomato leaf curl Joydebpur virus (ToLCJoV), Tomato leaf curl New Delhi virus (ToLCNDV) and Chili leaf curl Vellanad virus (ChiLCVV) have been reported to be mainly associated chili leaf curl disease (ChiLCD). Thakur *et al*. (2019) identified S-343 as a resistant source through natural and artificial screening for Chili leaf curl disease where the virus species associated was *Tomato leaf* curl *Joydebpur virus* (ToLCJoV) and they also reported a monogenic dominant nature of resistance. PAU-LC-343-1 and CA 516044 were reported as linked markers for chili leaf curl disease resistance which were located on chromosome 6 of the pepper genome at a genetic distance of 6.8 cM and 8.9 cM, respectively, from the resistant gene (Thakur *et al*., 2020). Recently, three sources IHR4615, IHR4630, and IHR4517 resistant to *Chili leaf curl virus*- Raichur isolates were identified at ICAR-IIHR and genetic studies showed monogenic dominant nature of resistance (Yadav *et al*., 2022). Further using these accessions, chili F_1 hybrids viz., Arka Tejasvi, Arka Tanvi, Arka Saanvi, Arka Yashasvi and Arka Gagan with *Chili leaf curl virus* resistance in different market segments were developed at ICAR-IIHR for commercial cultivation (IIHR Annual Report, 2021).

Molecular genetic studies have reported many potyvirus resistance loci (*pvrs*), most of which are recessive in nature (e.g. *pvr1, pvr2,* and *pvr6*). *Pvr4* is the dominant gene reported so far, which is allelic to *Pvr7* on chromosome 10 (Venkatesh *et al*., 2018). Apart from the previously mentioned resistance genes, *pvr1*^{2} and *pvr6* (recessive) (Hwang *et al*., 2009), additionally *pvr2* (Moury *et al*., 2005) showed resistance to ChiVMV. Dominant genes such as *Cvr1* and associated molecular markers were reported on chromosome 6 (Lee *et*

Table 4: Molecular markers availability in *Capsicum sps*

Type of molecular markers developed	*Method/data used for development*	*Reference*
SSR markers	Enriched genomic and cDNA libraries	Sugita *et al*., (2005)
626 SSRs	SSR-enriched genomic DNA libraries	Minamiyama *et al*., (2005)
1,201 SSRs	10,232 non-redundant ESTs of transcriptome sequencing	Yi *et al*., (2006)
2,869 COSII-markers	Orthologous sequences of multiple plant species	Wu *et al*., (2006)
783 SSRs	576 non-redundant EST sequences	Portis *et al*., (2007)
First chili pepper EST database with 122,582 sequenced ESTs	21 pepper EST libraries of transcriptomic sequencing	Kim *et al*., (2008)
755 SSR markers	EST sequences	Huan-huan *et al*., (2011)
11,849 SNPs and 853 SSRs	NGS data	Nicola *et al*., (2012)
26,000 SNPs, and 12,398 SSRs	Two datasets of NGS	Ashrafi *et al*., (2012)
5,751 SSR primer pairs	118,060 publicly available ESTs	Shirasawa *et al*., (2013)

al., 2013). Further two QTLs (*Cvr2-1* and *CVr2-2*) were reported for resistance against ChiVMV (Lee *et al*., 2017). Recently through GBS approach, recessive loci on chromosome 9 was mapped (Naresh *et al*., 2022).

The *Cucumber mosaic virus* (CMV) is one of the widely occurring menace of peppers. Several studies till date have given us a brief knowledge on the inheritance of CMV resistance, single dominant in Bukang (Kang *et al*., 2010), dominant gene cluster (Grube *et al*., 2000), and polygenic in Perennial (Naresh *et al*., 2016). Additionally, a few QTLs (Caranta *et al*., 2002) and two major QTLs in BJ0747–1–3-1-1 have also been reported (Yao *et al*., 2013). A CAPS marker was developed for the dominant resistant gene *Cmr1*, located on the centromeric region of LG2, in the genotype Bukang for CMV resistance. Two main QTLs, *qCmr2.1* and *qCmr11.1* were identified in PBC688 for CMV resistance. Moreover, *CA02g19570* was acknowledged as a possible candidate gene of *qCmr2.1* (Guo *et al*., 2017).

Tospoviruses are mainly transmitted by thrips. The *C. chinense,* lines PI152225 and PI159236 have been reported to be predominant sources for *Tospoviruses* (ssRNA) resistance. The dominant gene *Tsw* was reported in the same on chromosome 10 (Moury *et al*., 2000). In an individual study conducted by Hoang *et al*., (2013), a monogenic dominant gene that is non-allelic to PI152225 and PI159236 was identified in AC09-207. In *C. baccatum* line PIM26-1, Soler *et al*. (2015) observed, resistance against highly virulent TSWV isolate.

Breeding for Bacterial wilt Disease Resistance

Bacterial wilt caused by *Ralastonia solanacearum* is a serious threat, mainly in tropics and sub-tropics. It causes irrecoverable damage to the plants and ultimately leads to their death. A major QTL *(Bw1)* was reported in LS2451 (Mimura *et al.,* 2009). Recently, Du *et al*. (2019) identified a major QTL, qRRs-10.1 that accounted for 19.01% phenotypic variation in BVRC 25 (susceptible) x BVRC-1 (Bacterial wilt resistant) F2 population and a cluster of five predicted R genes and three defense-related genes were reported to be candidate genes for bacterial wilt resistance in chili. In NIL population of Anugraha and Pusa Jwala, an AFLP marker (*Eco*ACT+*Mse* CAC) associated with this resistant recessive allele has been identified (Thakur *et al*., 2014).

Breeding for Fungal Diseases Resistance

Phytophthora capsici L. is a soil-borne fungal disease that causes root rot. Criollo de Morelos-334 (CM334) was reported as a reliable source of resistance against wide and virulent strains of *Phytophthora capsici* (Sy *et al*., 2005). INRA pepper maps (YW X CM334, H3 X Vania and Perennial X YW) were utilized and a major QTL *Pc 5.1* (chromosome 5) was discovered which confers 55 to 70% of resistance (Mallard *et al*., 2013). The meta-analyses studies on *Phytophthora* resistance revealed three major meta QTLs on chromosome 5 *viz. Meta Pc5.1,Meta Pc5.2* and *Meta Pc5.3*. The *Meta Pc5.1* included *Pc 5.1* QTL (Mallard *et al*., 2013), *Phyt-1*QTL (Sugita *et al*., 2006), three QTLs detected by Truong *et al*. (2012) and a QTL detected by Minamiyama *et al*. (2007).

Resistant sources against prevailing spp. of *Colletotrichum* (Chili anthracnose disease) have been identified mainly in *C. chinense* (PBC932) and *C. baccatum* (PI594137, PBC81 and PBC80) (Gniffke *et al*., 2013). Resistance is reported to be governed by recessive genes (Mahasuk *et al*., 2009), duplicate gene action (Lin *et al*., 2007) and polygenic (Lee *et al*., 2010). *SSR-HpmsE032* and *SCAR-Indel* markers associated with resistance were used to transfer resistance from PBC 80 to *C. annuum* background (Suwor *et al*., 2017). QTLs were reported in Bangchang x PBC932, and PBC80 x CA1316 (Mahasuk *et al*., 2016). *Colletotrichum scovillei* is another species that affects green fruits. PBC 932 was reported to be resistant against this species and through whole genome resequencing, Kompetitive allele-specific PCR (KASPar) markers andinsertion–deletion (InDel) markers linked to AnRGO5 at the green mature fruit stage were developed.

Powdery mildew is caused by an obligate ascomycete's plant fungus, *Leveillula taurica*. *C. chinense*, *C. frutescens* and *C. baccatum* species are most often resistant, while the majority of *C. annuum* are susceptible to powdery mildew (De Souza and Café-Filho, 2003). "HV-12", "H3" and "4638","IHR 703", KC 604,605,608 (*C. baccatum*), KC 616 (*C. chinense*), KC 638,640,641,642,643,644 (*C. pubescens)* are reported resistant sources to *L. taurica* (De Souza and Café-Filho, 2003). Inheritance studies found that powdery mildew resistance is a major dominant to polygenic nature (Blat *et al*., 2005). The *C. frutescens* line 'IHR 703' is thought to have three pairs of incompletely dominant genes for resistance (Anand *et al*., 1987). Recently *PMR1,* major dominant gene on chromosome 4, harbouring two potential NBS-LRR-type disease resistance genes were identified in VK515R resistant line (Jo *et al*., 2017).

Breeding for Root-knot Nematode Resistance

Various studies on root-knot nematode resistance revealed the dominant nature of resistance. Till date, nine resistance genes (*N, Me1, Me2, Me3, Me4, Me5, Me7, Mech1 and Mech2*) have been reported (Wang and Bosland, 2006). Majorly the genes *Me1, Me3, Me7* have been found to show resistance for wide range of *Meloidoyne spp* (Djian-Caporalino *et al*., 2007). Among the identified genes, six genes *i.e.Me1, Me3, Me4, Me7, Mech1* and *Mech2* were reported as a cluster on chromosome P9 at interval of 28 cM. *N* gene is co-localized to the *Me* gene cluster that is located on ch9 and is also allelic to *Me7* gene (Fazari *et al*., 2012).

Breeding for Insect Pest Resistance

Thrips (*Scritothrips dorsalis*) and mites (*Polyphagotarsonemus latus*) are damaging pests to chili production worldwide. Approximately 21% of crop losses due to mite infestation and 30-50% due to thrips have been reported (Jeyarani and Chandrasekaran, 2006). Thrips can also cause indirect damage by serving as vectors for virus transmission through saliva during feeding (Jones, 2005), with members of *Tospovirus* being among the most devastating for chili production (Ullman *et al*., 1992). Due to the tremendous damage caused by thrips and mites on a global scale, several tolerant lines have been identified such as EC-596952, EC-390033, EC391082, GCh 3, GCh 2, Navsari Jwala, RHRC Errect, ACG-77, PDG-1 A, Taiwan-2, DC-28, IC572481, EC596952, EC378688, IC344366, IC337281, IC572492, and IC34239 (Desai *et al*.,2006; Singh and Pandey, 2015; Rameash *et al*., 2015; Rameash *et al*.,2017; Rajput *et al*.,2017; Gopal *et al*., 2019). Resistance to *Thrips palmi* has been identified by Saeko *et al*. (2020) in the F_2 population derived from AC 1979 (highly resistant) x *C. annuum* Berceo (highly susceptible). A QTL in linkage Group 1 was located on the M238 SNP marker with about 12.2% phenotypic variance. The highly significant QTL in linkage Group 2 was located on the M171 SNP marker with 8.9% phenotypic variance. Recently, farmers incurred huge crop losses (>6000 crores in Telangana state alone) due to outbreak of black thrips *T. parvispinus* in India. No resistance source for *T. parvispinus* was identified so far.

Mites (*Polyphagotarsonemus latus)* is another serious pest causing huge economic losses. There are no reports of the genetic inheritance of mites resistance in chili. Few accessions such as DCC-109, DCC-185, DCC-3 and DCC-89 reported as potential donors (Latha and Hunumanthraya, 2018). Against whitefly resistance, IIHR 4338 and IIHR 4300 were reported to be potential donors (Yadav *et al*., 2022). Some other reported resistant sources are CM331 and California Wonder 300 (Firdaus *et al*., 2011) and CA 9, CA 28, and ACC 05 (Jeevanandham *et al.,* 2018). There are no reports of genetic inheritance studies against whitefly resistance.

Breeding for Abiotic Stresses Tolerance

The current climate change scenario demands the exploitation of tolerance to high temperatures in cultivated crops for sustainable crop production. High temperature is major abiotic stress affecting crop yields in chili (Lin *et al*., 2022). A temperature range of 18 to 30°C is ideal for the optimum growth and development of chili and a drastic reduction in vigor and yield of the crop occurs when the mean temperature exceeds 30°C (Berke *et al*., 2005). Reduction in fruit set occurs due to the high sensitivity of pollen to elevated temperature (Giorno *et al*., 2013).

For the efficient evaluation of pollen activity under heat stress conditions, the World Vegetable Center, Taiwan recently developed a standardized protocol utilizing an impedance flow cytometer (IFC). By using this methodology, significant progress has been made in phenotyping for pollen traits in *Capsicum,* including using IFC to evaluate pollen activity in 500 breeding lines and gene bank accessions, leading to the identification of 20 high-performing heat tolerance lines (Lin *et al*., 2020). Pollen is the most heat-sensitive tissue in many crops, and fruit set is reduced or entirely impeded in the absence of viable pollen. The wild progenitor *C. annuum* var *glabriusculum*, PBC 831, PBC 507, PBC 1970 and PBC 1969 have been identified as potential sources for heat tolerance (Lin *et al*., 2021, 2022). Genetic studies were carried out and good to excellent heat tolerant lines have been identified *i.e* AVPP9905, AVPP0105, AVPP9812, AVPP0514, AVPP0201, AVPP0307 AVPP0805, AVPP0803, AVPP0702, AVPP0506, AVPP0513, AVPP9805, AVPP0705, AVPP0907, Treasures Red, Ember, Medusa, Explosive, and Thai Ho (Gajanayake *et al*., 2011). Recently, Usman *et al*. (2020) successfully incorporated the heat-tolerant genes (*Hsps*) into 'Kulai' cultivar from donor parent 'AVPP0702' through MABC. Highest fruit setting percentage, fruits/plant and yield /plant were recorded by genotype RHRC-216, and because of its high pollen viability and tolerance to high temperature, it can be a potential donor for heat tolerance (Gangarde *et al*., 2018). Recent screening of germplasm through Temperature Induction Response and field screening; Punjab Guchhedar and Ajeet-1 were reported as heat-tolerant donors in chili (Mishra *et al.*, 2020). Though moisture stress is major production constraint in the present climate change scenario, however, there is not much focus on breeding for moisture stress tolerance in chili. IIHR 4502 has been reported to be deep-rooted and drought-tolerant. Genetic analysis showed that root traits are mainly controlled by the dominance component (Naresh *et al.*, 2017).

Breeding for Fruit Quality Traits

Chili fruits are rich sources of health-promoting capsaicinoids, tocopherols, carotenoids, and ascorbic acid. Several attempts have been taken to understand the interrelationship between morphological variability and genes governing carotenoid biosynthesis in ripe fruits of *Capsicum sp*. (Lefebvre *et al.*, 1998). Hyo-Bong Jeong *et al.* (2019) reported that six candidate genes are involved in a carotenoid biosynthetic pathway in chili and among these two genes *Psy* and *Ccs* contribute to ripe fruit color. Allelic variations associated with the carotenoid biosynthesis genes in pepper have been documented by several workers (Guzman *et al.*, 2010, Kim *et al.*, 2010, Naresh *et al.*, 2012 and Bong Jeong *et al.*, 2019).

The alkaloid compound capsaicinoids are only found in the genus "Capsicum". In order of importance, capsaicin, dihydrocapsaicin, nor-dihydrocapsaicin, homodihydrocapsaicin, and homocapsaicin constitute peppers (Mueller-Seitz *et al.*, 2008). The vanillylamine and 8-methyl-6-nonenoyl-CoA condensed into capsaicin is governed by the capsaicin synthase (*CS* and *Pun1*) gene. These genes, which produce an acyltransferase homolog, are highly expressed in hot peppers during placenta development in comparison with non-pungent peppers (Kim *et al.*, 2014). Several molecular markers have been identified associated with the pungency trait in pepper (Blum *et al.*, 2003; Tanaka *et al.*, 2018; Lee *et al.*, 2016; Tanaka *et al.*, 2014; Wyatt *et al.*, 2012; Stellari *et al.*, 2010).

Male Sterility

Male sterility can help in the reduction of hybrid seed production cost up to 50 %. Both Cytoplasmic Male sterility (CMS) and genic or nuclear male sterility (GMS) have been successfully exploited in pepper. Martin and Crawford (1951) first documented GMS in *C. frutescens* pepper, after which 20 such independently inherited *ms* genes have been reported (Shifriss, 1997; Dhaliwal and Jindal, 2014). Markers associated with genic male sterile genes have been reported for *ms1* (Lee *et al.*, 2010), *ms8* (Bartoszewski *et al.*, 2012), *ms3* (Lee *et al.*, 2018 and Naresh *et al.*, 2018), *ms10* (Aulakh *et al.*, 2016) and ms_w (Naresh *et al.*, 2018).

The investigation by Peterson (1958) on the line 'PI 164835' provided insight of Cytoplasmic male sterility being inherited maternally. Many molecular markers linked to sterile cytoplasm *viz., atp6-2* (Ji *et al.*, 2013), *orf456* (Kim *et al.*, 2005 and 2007) are conventionally employed in the hybrid seed production system. Restorer of fertility (*Rf*) genes are responsible for compensating the specific mitochondrial dysfunctions that are phenotypically expressed in pollen development, which ultimately lead to male sterility. Recently, a CAPS marker Co1Mod1-CAPS and an SNP-based CAPS marker *CaRf648* (Ortega *et al.*, 2020) have been developed for Rf genes on chromosome 6. Other developed molecular markers linked to *Rf* gene include two RAPD markers *i.e* OPP131400' and 'OPW19800' (Kumar *et al.*, 2007). Partial restorer genes also have been reported (Lee *et al.*, 2008) and a CAPS marker *i.e.,* E-TCT/M-CCG116 and E-AGC/M-GCA122 associated was developed for marker-assisted selection.

Conclusion

Chili being a highly commercial crop and its huge demand in various applications, there is a need to develop varieties/hybrids suitable for market segments with resistance/tolerance to biotic and abiotic stresses. *Capsicum* genetic resources have been widely explored and conserved at national and international gene banks with more than 5000 collections. Conventional crop improvement is very successful and genetic resources for various traits have been identified and explored. Due to the emergence of pests and diseases, there is a need to accelerate breeding programs with use of recent advancements in genomic resources. Wide hybridization and exploration of wild species need to be focused on utilizing novel genetic resources as donors for prioritized traits under the present climate change scenario. Advanced genomic technologies and precise marker discovery through the employment of next-generation techniques will enable marker-assisted selection.

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सारांश

मिर्च एक महत्वपूर्ण सब्जी एवं मसाला फसल है, जिसका भोजन, पोषण, दवा और कॉस्मेटिक उद्योगों में बड़े पैमाने पर व्यावसायिक अनुप्रयोग होता है। कैप्सिकम जीनस की उत्पत्ति लगभग 35 प्रजातियों के साथ मध्य अमेरिका में हुई, जिनमें से पांच प्रजातियाँ खेती के लिए प्रचलित हैं। रंग और तीखापन से संबंधित घटक जैसे कि कैप्सैन्थिन, कैप्सैसिनोइड्स और कैप्सिनोइड्स कैप्सिकम जीनस के विशिष्ट गुण हैं। इस जीनस में बड़ी मात्रा में जैव-विविधिता मौजूद है और फलों की गुणवत्ता में वृद्धि के साथ जैविक और अजैविक तनावों के प्रति प्रतिरोध/सहिष्णुता वाली किस्मों/संकरों के प्रजनन के लिए आनुवंशिक संसाधनों पर गहनता शोध किया गया है। वर्तमान जलवायु परिवर्तन परिदृश्य में, विभिन्न कीटों और बीमारियों का विकास हो रहा है, जिसके लिए नवीन जीन/एलील के लिए निकट संबंधी और जंगली प्रजातियों सहित सम्पूर्ण जननद्रव्य में निरंतर खोज की आवश्यकता होती है। पारंपरिक प्रजनन से उन्नत वंशावली/किस्में/संकरों का विकास हुआ है। मिर्च के संपूर्ण जीनोम अनुक्रम की जानकारी और पैन जीनोम सार्वजनिक रूप से उपलब्ध है, जो प्रमुख लक्षणों से जुड़े आणविक मार्करों के विकास में मदद कर सकते है। प्रजनन कार्यक्रमों में तेजी लाने के लिए जीनोमिक संसाधनों में उन्नति और नेक्स्ट जनरेशन सिक्वेंसिंग तकनीकों का प्रयोग किया जा सकता है।