



REVIEW ARTICLE

Chili: Breeding and Genomics

Madhavi Reddy K^{1*}, Rajesh Kumar², Naresh Ponnamm¹, Indivar Prasad², Satya P. Barik³, Roshini Pydi¹, Sai Timmarao¹, Pavani Narigapalli¹, Maheeb Shaik¹ and Karishma Pasupula¹

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.

¹Division of Vegetable Crops, ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India.

²Division of Crop Improvement, ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India.

³Department of Agriculture and Allied Sciences, CV Raman Global University, Bhubaneswar, Odisha, India.

*Division of Vegetable Crops, Indian Institute of Horticultural Research, Bengaluru, Karnataka, India.

*Corresponding author; Email: kmreddy14@gmail.com

Citation: Reddy, M.K., Kumar, R., Ponnamm, 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. annum* 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. annum*, *C. chinense*, *C. frutescens* (*C. annum* 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%),

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)

<i>Disease/Pest</i>	<i>Resistant sources</i>
Viral Diseases	
Begomoviruses	
Pepper golden mosaic virus (PepGMV) and Pepper huasteco yellow vein virus (PHYVV)	BG-3821 (<i>C. chinense</i>) (Anaya-Lopez <i>et al.</i> , 2005)
ChiLCV	Bhut Jolokia 001 (Adluri <i>et al.</i> , 2017).
PepLCV	GKC-29, EC-497636, BS-35 (Kumar <i>et al.</i> , 2006) VI012005, PBC495, PBC144, PBC143, PBC149 (Kenyon <i>et al.</i> , 2014) Kalyanpur Chanchal (Singh <i>et al.</i> , 2016)
Pepper yellow leaf curl Thailand virus	9852-123 (Barchenger <i>et al.</i> , 2019)
Tomato leaf curl New Delhi virus & ChiLCV	DLS-Sel-10, PBC142, PBC145, WBC-Sel-5, PBC345 (Srivastava <i>et al.</i> , 2015; 2017)
Chili leaf curl virus	IHR4615, IHR4630, and IHR4517 (Yadav <i>et al.</i> , 2022)
Cucumber mosaic virus (CMV)	Sapporo-oonaga, Nanbu-onaga (Suzuki <i>et al.</i> , 2003) Bukang (Kang <i>et al.</i> , 2010) LS1839-2-4 (Suzuki <i>et al.</i> , 2003) IHR2451, IHR4503 (Naresh <i>et al.</i> , 2016) PI439381-1-3 (<i>C. baccatum</i>) (Suzuki <i>et al.</i> , 2003) PBC688 (<i>C. frutescens</i>) (Guo <i>et al.</i> , 2017)
Poty viruses	
TEV, PVY (0), PepMoV	PI 159236, PI 152225 (<i>C. chinense</i>) (Murphy <i>et al.</i> , 1998)
PVY (0)	Yolo Y (Kang <i>et al.</i> , 2005)
TEVT, PVY (0, 1)	<i>C. annuum</i> Florida VR2 (Kang <i>et al.</i> , 2005)
PepMoV	Avelar (Guerini and Murphy, 1999) CM334 (Caranta <i>et al.</i> , 1999)
PVMV	Perennial (Caranta <i>et al.</i> , 1996)
ChiVMV	NW4 (Lee <i>et al.</i> , 2013) IHR2451 and IHR4503 (Naresh <i>et al.</i> , 2016) CV3, CV4, CV8, and CV9 (Lee <i>et al.</i> , 2017)
Tospoviruses (TSWV)	PI152225, PI159234 (<i>C. chinense</i>) (Jahn <i>et al.</i> , 2000) CNPH 275, PI-15, ECU-973, C00943 (Cebolla-Cornejo <i>et al.</i> , 2003) AC09-207 (<i>C. chinense</i>)
GBNV	EC631810, IHR4360, IHR4577, IHR4578, IHR4582, IHR4585, IHR4587, IHR4588 (Pavithra <i>et al.</i> , 2019)
Fungal diseases	
Phytophthora root rot	CM334 (Kim <i>et al.</i> , 2008) PI201232 and PI201234 (Silvar <i>et al.</i> , 2006)
Anthraxnose fruit rot	PBC80, PBC81, PI594137 (<i>C. baccatum</i>) and PBC932 (<i>C. chinense</i>) (Gniffke <i>et al.</i> , 2013)
Powdery Mildew	H3 ((Daubeze <i>et al.</i> , 1995; Lefebvre <i>et al.</i> , 2003) Pimenta Cheiro and PI 152225 (Blat <i>et al.</i> , 2005) VK515R (Jo <i>et al.</i> , 2017)
Bacterial diseases	
Bacterial wilt	IHR-B-HP-130 (Naveena <i>et al.</i> , 2020) Perennial, Narval, PI 322719, LS2341, YCM334 (<i>C. annuum</i>), Heiser 6240, LS 2390 (<i>C. frutescens</i>), LS1716, PBC385, PBC066, CNPH145 (HC10) (<i>C. baccatum</i>) (Parisi <i>et al.</i> , 2020) CNPH 3800, Dedo-de-moca 1, 2, 3 (<i>Capsicum baccatum</i>), Pimento-de-Bode red 2, Pimento-de-Bode red 4, Pimento-de-Bode yellow 1, (<i>Capsicum chinense</i>), Malagueta 4, Malagueta 5 (<i>Capsicum frutescens</i>) (Rossato <i>et al.</i> , 2018) PCWR-1-3-08, PCWR-Cap-4-08, PCWR-33-1-3-08 and PCWR-33-3-1-08 (Singh <i>et al.</i> , 2018)

Bacterial spot	Global (Cherry type) (Palotás, 2016) UENF 1381 (Moreira <i>et al.</i> , 2012) KC01617, KC01760, KC01779, KC01137, KC01777, KC00939 (Byeon <i>et al.</i> , 2016)
Root knot Nematodes	
Root-knot nematodes	UFGFR 05 (<i>C. frutescens</i>) (Marques <i>et al.</i> , 2019) UFGCCH 24 – ‘Bode Roxa’ (<i>Capsicum chinense</i>) (Marques <i>et al.</i> , 2020)
Insect pests	
Thrips	X-1068, X-743, X-1047, NP-46A, Caleapin Red, Chamatkar, BG-4 (Dhall, 2015) RU27, RU32 and RU28 (<i>Capsicum chinense</i>) (Visschers, 2020) AC 1979, Bisbas, Keystone Resistant Giant CM 331 (<i>C. annuum</i>), No. 1553, Aji Blanco Christal (<i>C. baccatum</i>) (Maharajaya <i>et al.</i> , 2011; 2015) EC378630, EC391082, EC378633, IC214991 (Sarath Babu <i>et al.</i> , 2002) IC572492, IC342390, IC337281 (Rameash <i>et al.</i> , 2015).\nCGN16795 (Pauline van Haperen <i>et al.</i> , 2021)
Mites	Navsari Jwala, RHRC Erect and ACG-77 (Desai <i>et al.</i> , 2006) IC572481, EC596952 (Rameash <i>et al.</i> , 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 <i>et al.</i> , 2014) Monogenic dominant (Yadav <i>et al.</i> , 2022)
Cucumber mosaic virus (CMV)	Partially dominant (Pochard and Daubeze, 1989) Single dominant (Kang <i>et al.</i> , 2010) Polygenic recessive (Naresh <i>et al.</i> , 2016)
Poty viruses	
TEV, PVY (0), PepMoV	<i>pvr1</i> , Recessive (Yeam <i>et al.</i> , 2005)
PVY (0)	<i>pvr2</i> (<i>pvr2</i> ¹ = <i>pvr1</i> ¹) Recessive (Ruffel <i>et al.</i> , 2002)
TEVT, PVY (0, 1)	<i>pvr2</i> (<i>pvr2</i> ¹ = <i>pvr1</i> ¹) Recessive (Ruffel <i>et al.</i> , 2002)
PepMoV	<i>pvr3</i> Recessive (Parrella <i>et al.</i> , 2002) <i>Pvr4</i> , Dominant (Grube <i>et al.</i> , 2000) <i>Pvr7</i> , Dominant (Grube <i>et al.</i> , 2000)
PVMV	<i>pvr6</i> - <i>pvr1</i> ¹ or <i>pvr1</i> ² Recessive (Ruffel <i>et al.</i> , 2006)
ChiVMV	Monogenic dominant (Lee <i>et al.</i> , 2013 and Lee <i>et al.</i> , 2017) Monogenic recessive (Naresh <i>et al.</i> , 2016)
Tospoviruses (TSWV)	Single dominant gene (Boiteux <i>et al.</i> , 1993). Monogenic dominant gene and non-allelic gene action in PI159236 and PI152225 (Hoang <i>et al.</i> , 2013)
Fungal diseases	
Phytophthora root rot	Recessive to dominant nature (Reifschneider <i>et al.</i> , 1992) Polygenic (Thabuis <i>et al.</i> , 2003) Polygenic in nature with additive and epistatic effects (Lefbrve <i>et al.</i> , 1996) Monogenic dominant (Manish <i>et al.</i> , 2022)
Anthracoese fruit rot	Monogenic recessive (Mahasuk <i>et al.</i> , 2009) Duplicate gene action (Lin <i>et al.</i> , 2007) Polygenic (Lee <i>et al.</i> , 2010)

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

Table 3: Publicly available pepper genomes

Cultivar/Species	Method of sequencing	Genome size	Database	Reference
CM334 (<i>Capsicum annuum</i>)	Illumina sequencing	3.48	http://peppergenome.snu.ac.kr	Kim <i>et al.</i> , 2014
PBC81 (<i>C. baccatum</i>)	Illumina Hiseq 2500 system	3.9	http://peppergenome.snu.ac.kr	Kim <i>et al.</i> , 2017
PI159236 (<i>C. chinense</i>)	Illumina Hiseq 2500 system	3.2	http://peppergenome.snu.ac.kr	Kim <i>et al.</i> , 2017
Zunla-1 (<i>C. annuum</i>)	Illumina sequencing	3.26	http://peppersequence.genomics.cn	Qin <i>et al.</i> , 2014
Chiltepin (<i>C. annuum</i> var. <i>glabrusculum</i>)	Illumina sequencing	3.07	http://peppersequence.genomics.cn	Qin <i>et al.</i> , 2014
UCD-10X-F1 (CM334 x blocky pepper-breeding line)	Illumina HiSeq X Ten	3.5	https://solgenomics.net	Amanda M Hulse-Kemp <i>et al.</i> , 2018
Takanotsume (<i>Capsicum annuum</i>)	HiFi long-read sequencing technology.	3.058	https://plantgarden.jp	Kenta Shirasawa <i>et al.</i> , 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 F₁ 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 (*pvr*s), 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 <i>et al.</i> , (2005)
626 SSRs	SSR-enriched genomic DNA libraries	Minamiyama <i>et al.</i> , (2005)
1,201 SSRs	10,232 non-redundant ESTs of transcriptome sequencing	Yi <i>et al.</i> , (2006)
2,869 COSII-markers	Orthologous sequences of multiple plant species	Wu <i>et al.</i> , (2006)
783 SSRs	576 non-redundant EST sequences	Portis <i>et al.</i> , (2007)
First chili pepper EST database with 122,582 sequenced ESTs	21 pepper EST libraries of transcriptomic sequencing	Kim <i>et al.</i> , (2008)
755 SSR markers	EST sequences	Huan-huan <i>et al.</i> , (2011)
11,849 SNPs and 853 SSRs	NGS data	Nicola <i>et al.</i> , (2012)
26,000 SNPs, and 12,398 SSRs	Two datasets of NGS	Ashrafi <i>et al.</i> , (2012)
5,751 SSR primer pairs	118,060 publicly available ESTs	Shirasawa <i>et al.</i> , (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 *Ralstonia 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 (*EcoACT+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-1QTL* (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 and insertion–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 (*Scirtothrips 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 F₂ 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, IHR 4338 and IHR 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. IHR 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 'Pl 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.

References

- Adluri, P. K., Baldoldiya, G. M. and Nath, P. D. (2017). Screening of Bhut Jolokia (*Capsicum chinense* Jacq.) germplasm of North East India against chili leaf curl virus. *Int J Pure Appl Biosci*, 5(4), 1189-1196.
- Aguilar-Melendez, A., Morrell, P. L., Roose, M. L., *et al.* (2009). Genetic diversity and structure in semiwild and domesticated chilles (*Capsicum annuum*; Solanaceae) from Mexico. *Am J Bot*, 96(6), 1190-1202.
- Aitken, E., Mc Coll, G. & Kingsmore, D. (2017). The role of Qutenza (topical capsaicin 8%) in treating neuropathic pain from critical ischemia in patients with end-stage renal disease: An observational cohort study. *Pain Medicine (United States)*, 18(2), 330-340. <https://doi.org/10.1093/pm/pnw139>.
- Anand, N., Deshpande, A. A. & Sridhar, T. S. (1987). Resistance to powdery mildew in an accession of *Capsicum frutescens* and its inheritance pattern. *Capsicum Eggplant Newsletter*, 6, 77-78.
- Anaya-Lopez, J. L., Perez-Mora, E., Torres-Pacheco, I., *et al.* (2005). Inducible gene expression by Pepper huasteco virus in *Capsicum chinense* plants with resistance to geminivirus infections. *Canadian J. Plant Pathol.* 27(2), 276-282.

- Ashrafi, H., Hill, T., Stoffel, K., *et al.* (2012). *De novo* assembly of the pepper transcriptome (*Capsicum annuum*): a benchmark for *in silico* discovery of SNPs, SSRs and candidate genes. *BMC Genomics*, 13, 571.
- Baenas Nieves, *et al.* (2019). Industrial use of pepper (*Capsicum annuum* L.) derived products: Technological benefits and biological advantages. *Food Chem.* 274, 872-885
- Baral, J. B & Bosland, P. W. (2004). Unraveling the species dilemma in *Capsicum frutescens* and *C. chinense* (Solanaceae): a multiple evidence approach using morphology, molecular analysis, and sexual compatibility. *J. Am. Soc. Hortic.* 129 (6), 826-832.
- Barchenger, D. W., Yule, S., Jeeatid, N., *et al.* (2019). A novel source of resistance to Pepper yellow leaf curl Thailand virus (PepYLCThV) (Begomovirus) in chile pepper. *HortSci.* 54(12), 2146-2149.
- Barik, S., *et al.* (2022). Breeding peppers for industrial uses: Progress and prospects. *Ind Crops Prod*, 178, 114626.
- Bartoszewski, G., Waszczak, C., Gawronski, P., *et al.* (2012). Mapping of the ms8 male sterility gene in sweet pepper (*Capsicum annuum* L.) on the chromosome P4 using PCR-based markers useful for breeding programmes. *Euphytica*, 186 (2), 453-461. <http://link.springer.com/article/10.1007%2Fs10681-012-0637-9>.
- Berke, T., *et al.* (2005). Suggested cultural practices for chili pepper. *Int. CoOperator's Guide*.
- Blat, S. F., Costa, C. P. D., Vencovsky, R., *et al.* (2005). Inheritance of reaction to *Leveillula taurica* (Lev.) Arn. in *Capsicum annuum* L. *Sci Agric*, 62, 40-44.
- Boiteux, L. S., Nagata, T., Dutra, W. P., *et al.* (1993). Sources of resistance to *tomato spotted wilt virus* (TSWV) in cultivated and wild species of *Capsicum*. *Euphytica*, 67:89-94
- Bosland, P. W. & Baral, J. B. (2007). 'Bhut Jolokia'—The world's hottest known chile pepper is a putative naturally occurring interspecific hybrid. *Hort Science*, 42 (2), 222-224.
- Byeon, S., Mekuriaw, A., Jegal, Y., *et al.* (2016). Characterization of Sources of Resistance to Bacterial Spot in *Capsicum* Peppers. *Hortic. Sci. Tech*, 34, 779-789. 10.12972/kjhst.20160082.
- Caranta, C., *et al.* (2002). QTLs involved in the restriction of Cucumber mosaic virus (CMV) long-distance movement in pepper. *Theor Appl Genet*, 104:586-591
- Caranta, C., Palloix, A. (1996). Both common and specific genetic factors are involved in polygenic resistance of pepper to several potyviruses. *Theor. Appl. Genetics*, 92, 15-20 <https://doi.org/10.1007/BF00222946>
- Caranta, C., Thabuis, A., Palloix, A. (1999). Development of a CAPS marker for the *Pvr4* locus: a tool for pyramiding potyvirus resistance genes in pepper. *Genome*, 42, 1111-6.
- Cebolla Cornejo, J., Soler, S., Gomar, B., *et al.* (2003). Screening *Capsicum* germplasm for resistance to tomato spotted wilt virus (TSWV). *Ann. Appl. Biol.*, 143(2), 143-152.
- Chaim, B. A., Grube, R. C., *et al.* (2000). Identification of quantitative trait loci associated with resistance to Cucumber mosaic virus in *Capsicum annuum*. *Theor Appl Genet*, 102:1213-1220
- Daubeze, A. M., Hennart, J. W. and Palloix, A. (1995). Resistance to *Leveillula taurica* in pepper (*Capsicum annuum*) is oligogenically controlled and stable in Mediterranean regions. *Plant Breed*, 114, 327-332.
- De, S., Cafe, V. L. & Filho, A. C. (2003). Effect of chemical control on the progress of sweet pepper powdery mildew under greenhouse conditions. *Summa Phytopathol (Brazil)*, 29(4), 317-322
- Desai, H., Bandhanja, K. A., Rai, A., *et al.* (2006). Assessment of yield loss and resistance to yellow mite *Polyphagotarsonemus latus* banks in chili. *Vegetable Science*, 36. 46-50.
- Dhall, R. K. (2015). Breeding for biotic stresses resistance in vegetable crops: A Review. *Research & Reviews: J Crop Sci & Tech*, 4, 13-27.
- Djian-Caporalino, C. (2007). Root-knot nematode (*Meloidogyne* spp.) *Me* resistance genes in pepper (*Capsicum annuum* L.) are clustered on the P9 chromosome. *Theor. Appl. Genet.*, 114, 473-486.
- Du, H. (2019). Identification of a Major QTL (*qRRs-10.1*) that Confers Resistance to *Ralstonia solanacearum* in Pepper (*Capsicum annuum*) using SLAF-BSA and QTL Mapping. *Int. J. Mol. Sci.*, 20, 5887.
- Fazari, A., Palloix, A., Wang, L., *et al.* (2012). The root-knot nematode resistance *N*-gene co-localizes in the *Me*-genes cluster on the pepper (*Capsicum annuum* L.) P9 chromosome. *Plant Breed*, 131:665-673.
- Gajanayake, B., Trader B. W., Reddy K. R., *et al.* (2011). Screening ornamental pepper cultivars for temperature tolerance using pollen and physiological parameters. *Hort Sci.*, 46(6), 878-884.
- Gangarde, S., Patil, B. T., Bachkar, C. B., *et al.*, (2018). Genotypic response to heat stress tolerance in Chili (*Capsicum annuum* L.). *J. pharmacogn. phytochem.* 7(3),1551-1554.
- Gaur, R., Sharma, V., Chhapekar, S. S., *et al.* (2016). Comparative analysis of fruit metabolites and pungency candidate genes expression between Bhut Jolokia and other *Capsicum* species. *PLoS One*, 11(12), p.e0167791. <https://doi.org/10.1371/journal.pone.0167791>
- Giorno, F., Wolters-Arts, M., Mariana, C., *et al.* (2013). Ensuring reproduction at high temperatures: the heat stress response during anther and pollen development. *Plants*, 2, 489-506.
- Gniffke, P. A., Shieh, S. C., Lin, S. W., *et al.* (2013). Pepper research and breeding at AVRDC—The World Vegetable Center. In *XV EUCARPIA Meeting on Genetics and Breeding of Capsicum and Eggplant (2-4 September)*, Turin, Italy (pp. 305-311).
- Guerini, M. N. and Murphy, J. F. (1999). Resistance of *Capsicum annuum* 'Avelar' to pepper mottle potyvirus and alleviation of this resistance by co-infection with cucumber mosaic cucumovirus are associated with virus movement. *J Gen. Virol.*, 80, 2785-2792. <https://doi.org/10.1099/0022-1317-80-10-2785>.
- Guo, G., Wang, S. and Liu, J., *et al.* (2017). Rapid identification of QTLs underlying resistance to Cucumber mosaic virus in pepper (*Capsicum frutescens*). *Theor Appl Genet.*, 130. 10.1007/s00122-016-2790-3.
- Guzman, I., Hamby, S., Romero, J., *et al.* (2010). Variability of carotenoid biosynthesis in orange colored *Capsicum* spp. *Plant Sci.*, 179 (1-2), 49-59
- Hernandez-Verdugo, S., *et al.*, (2001). Genetic structure and differentiation of wild and domesticated populations of *Capsicum annuum* (Solanaceae) from Mexico. *Plant Syst Evol*, 226(3),129-142.
- Hoang, N. H., Yang, H. B. & Kang, B. C. (2013). Identification and inheritance of a new source of resistance against *Tomato spotted wilt virus* (TSWV) in *Capsicum*. *Sci Hort*, 161,8-14.
- Hulse-Kemp, A. M., Maheshwari, S., Stoffel, K., *et al.* (2018). Reference quality assembly of the 3.5-Gb genome of *Capsicum annuum*

- from a single linked-read library. *Hortic. Res.*, 5.
- Hwang, J., Li, J., Liu, W. Y., *et al.* (2009). Double mutations in eIF4E and eIFiso4E confer recessive resistance to Chili veinal mottle virus in pepper. *Mol. Cells*, 27, 329-336.
- Jahn, M., Paran, I., Hoffmann, K., *et al.* (2000). Genetic Mapping of the *Tsw* Locus for resistance to the *Tospovirus* tomato spotted wilt virus in *Capsicum* spp. and its relationship to the *Sw-5* gene for resistance to the same pathogen in tomato. *Mol Plant-Microb Interact*, 13, 673-82.
- Jarret, R. L. & Dang, P. (2004). Revisiting the waxy locus and the *Capsicum annuum* L. complex. *Georgia Journal of Science*, 62(3), 118.
- Jeong, H. B., *et al.* (2019). Single-molecule real-time sequencing reveals diverse allelic variations in carotenoid biosynthetic genes in pepper (*Capsicum spp.*). *Plant Biotechnol. J.*, 17(6):1081-1093.
- Jeyarani, S. & Chandrasekaran, M. (2006). Bioefficacy of certain acaricides against chili mite, *Polyphagotarsonemus latus* (Banks). *Agric. Sci. Digest.*, 26(2),132-34.
- Jo, J., *et al.* (2017). Molecular mapping of PMR1, a novel locus conferring resistance to powdery mildew in pepper (*Capsicum annuum*). *Front. Plant Sci.*, 8, 2090.
- Jones, D. R. (2005). Plant viruses transmitted by thrips. *Eur. J. Plant Pathol.*, 113, 119–157.
- Kang, B. C., Yeam, I., Frantz, J. D., *et al.* (2005). The *pvr1* locus in *Capsicum* encodes a translation initiation factor eIF4E that interacts with *Tobacco etch virus* VPg. *Plant J.*, 42, 392-405.
- Kang, W. H., Hoang, N. H., Yang, H. B., *et al.* (2010). Molecular mapping and characterization of a single dominant gene controlling CMV resistance in peppers (*Capsicum annuum* L.). *Theor Appl. Genet.*, 120 (8), 1587–1596. <https://doi.org/10.1007/s00122-010-1278-9>.
- Kenyon, L., Kumar, S., Tsai, W. S. and Hughes, J. D. A. (2014). Virus diseases of peppers (*Capsicum* spp.) and their control. In: G. Loebeinstein and N. Katis (eds.). *Advances in virus research.*, Vol. 90. Academic Press p. 297-254.
- Kim, D. H. & Kim, B. D. (2005). Development of SCAR markers for early identification of cytoplasmic male sterility genotype in chili pepper (*Capsicum annuum* L.). *Mol. Cells*, 20(3), 416–422.
- Kim, D.H., Kang, J.G. & Kim, B. D. (2007). Isolation and characterization of the cytoplasmic male sterility-associated orf456 gene of chili pepper (*Capsicum annuum* L.). *Plant Mol. Biol.*, 63(4), 519–532. <https://doi.org/10.1007/s11103-006-9106-y>
- Kim, H. J., Baek, K. H., Lee, S. W., *et al.* (2008). Pepper EST database: comprehensive in silico tool for analyzing the chili pepper (*Capsicum annuum*) transcriptome. *BMC Plant Biol.*, 8(1), 1-7.
- Kim, H. J., Nahm, S. H., Lee, H. R., *et al.* (2008). BAC-derived markers converted from RFLP linked to *Phytophthora capsici* resistance in pepper (*Capsicum annuum*). *Theor Appl Genet*, 118, 15-27.
- Kim, H., Lee, J. H. & Na, S. H. (2017). Predictor-estimator using multilevel task learning with stack propagation for neural quality estimation. In *Proceedings of the Second Conference on Machine Translation* (pp. 562-568).
- Kim, O. R., Cho, M. C., Kim, B. D., *et al.* (2010). A splicing mutation in the gene encoding phytoene synthase causes orange coloration in Habanero pepper fruits. *Mol. Cells*, 30(6), 569-574. <https://doi.org/10.1007/s10059-010-0154-4>.
- Kim, S., Park, M., Yeom, S. I., *et al.* (2014). Genome sequence of the hot pepper provides insights into the evolution of pungency in *Capsicum* species. *Nat Genet*, 46, 270–278. <https://doi.org/10.1038/ng.2877>
- Kumar, S., Kumar, S., Singh, M., *et al.* (2006). Identification of host plant resistance to pepper leaf curl virus in chili (*Capsicum* species). *Sci. Hort.*, 110(4), 359-361.
- Kumar S., Singh V., Singh M., *et al.* (2007). Genetics and distribution of fertility restoration associated RAPD markers in inbreds of pepper (*Capsicum annuum* L.). *Sci. Hort.*, 111, 197-202.
- Lang, Y., *et al.* (2009). Functional loss of pAMT results in biosynthesis of capsinoids, capsaicinoid analogs, in *Capsicum annuum* cv. CH19 Sweet. *Plant J*, 59(6), 953-961.
- Lapidot, M., *et al.* (1997). Tolerance to Cucumber mosaic virus in pepper: development of advanced breeding lines and evaluation of virus level. *Plant Dis*, 81,185–188.
- Latha, S. & Hunumanthraya, L. (2018). Screening of chili genotypes against chili thrips, *Scirtothrips dorsalis* (Hood) and yellow mite, *Polyphagotarsonemus latus* (Banks). *J. Entomol. Zool. Stud.*, 6, 2739-44.
- Lee, D. H. (2001). Studies on unstable fertility of CGMS (cytoplasmic-genic male sterility) in *Capsicum annuum* L. Dissertation, Seoul National University.
- Lee, H. R., *et al.* (2013). Development of a novel codominant molecular marker for Chili veinal mottle virus resistance in *Capsicum annuum* L. *Euphytica*, 193, 197–205.
- Lee, J., Hong, J. H., Do, J. W., *et al.* (2010). Identification of QTLs for resistance to anthracnose to two *Colletotrichum* species in pepper. *J Crop Sci Biotechnol*, 13, 227–233.
- Lee, J.H., *et al.* (2017). Identification and molecular genetic mapping of Chili veinal mottle virus (ChiVMV) resistance genes in pepper (*Capsicum annuum*). *Mol Breed*, 37, 121.
- Lee, J., Han, J. H., An, C. G., *et al.* (2010). A CAPS marker linked to a genic male-sterile gene in the colored sweet pepper, 'Paprika' (*Capsicum annuum* L.). *Breed. Sci.*, 60(1), 93-98.
- Lee, J., Yoon, J. B. & Park, H. G. (2008). A CAPS marker associated with the partial restoration of cytoplasmic male sterility in chili pepper (*Capsicum annuum* L.). *Mol. Breed.*, 21, 95-104.
- Lee, J., Yoon, J. B., Han, J. H., *et al.* (2010). A codominant SCAR marker linked to the genic male sterility gene (*ms₁*) in chili pepper (*Capsicum annuum*). *Plant Breed.*, 129, 35-38.
- Lee, J., Yoon, J. & Park H. (2008). Linkage analysis between the partial restoration (*pr*) and the restorer-of-fertility (*Rf*) loci in pepper cytoplasmic male sterility. *Theor. Appl. Genet.*, 117, 383-9.
- Lefebvre, V., Daubeze, A. M., Voort, J., *et al.* (2003). QTLs for resistance to powdery mildew in pepper under natural and artificial infections. *Theor. Appl. Genet.*, 107, 661-6.
- Lefebvre, V., Kuntz, M., Camara, B., *et al.* (1998). The capsanthin-capsorubin synthase gene: a candidate gene for the *y* locus controlling the red fruit color in pepper. *Plant Mol. Biol.*, 36 (5), 785–789. <https://doi.org/10.1023/A:1005966313415>.
- Lin, S. W., Gniffke, P. A. and Wang, T. C. (2007). Inheritance of resistance to pepper anthracnose by *Colletotrichum acutatum*. *Acta Hort*, 760, 329–334.
- Lin, S. W., Lin, Y. W., Wang, *et al.* (2020). High throughput pollen phenotyping using impedance flow cytometry for heat tolerance selection in pepper (*Capsicum spp.*). *Hort Sci*, 55(9):S156 (abstr.).
- Lin, S. W., *et al.* (2022). Impedance Flow Cytometry for Selection of Pollen Traits Under High Temperature Stress in Pepper. *Hort Sci*, 57(2), 181-190.

- Lin, T. H., *et al.* (2021). Growing environment and heat treatment effects on intra-and interspecific pollination in chili pepper (*Capsicum spp.*). *Agronomy*, 11(7),1275.
- Macel, M., Visschers, I. G. S., Peters, J. L., *et al.* (2020). High Concentrations of Very Long Chain Leaf Wax Alkanes of Thrips Susceptible Pepper Accessions (*Capsicum spp.*). *J. Chem. Ecol.*, 46 (11-12), 1082–1089. <https://doi.org/10.1007/s10886-020-01226-x>
- Mahasuk, P., Struss, D., Mongkolporn, O. (2016). QTLs for resistance to anthracnose identified in two *Capsicum* sources. *Mol Breed*, 36, 10. <https://doi.org/10.1007/s11032-016-0435-5>.
- Mahasuk, P., Taylor, P. W. J., Mongkolporn, O. (2009) Identification of two new genes conferring resistance to *Colletotrichum acutatum* in *Capsicum baccatum*. *Phytopathology*, 99, 1100–1104.
- Mallard, S., *et al.* (2013). A key QTL cluster is conserved among accessions and exhibits broad-spectrum resistance to *Phytophthora capsici*: a valuable locus for pepper breeding. *Mol Breed*, 32, 349–364.
- Marques, M., Chadud J., Oliveira, M., *et al.* (2019). Identification of Chili Pepper Genotypes (*Capsicum spp.*) Resistant to *Meloidogyne enterolobii*. *J. Agric. Sci.*, 11, 165. 10.5539/jas.v11n8p165.
- Marques, M., Oliveira, M. F., Pereira, P. S., *et al.* (2020). Penetration and development of *Meloidogyne enterolobii* in resistant and susceptible *Capsicum spp.* *Eur. J. Hort. Sci.*, 85, 86-91. 10.17660/eJHS.2020/85.2.2.
- Mathur, R., Dangi, R. S., Dass, S. C., *et al.* (2000). The hottest chili variety in India. *Curr. Sci.*, 79 (3), 287-288.
- Mimura, Y., Yoshikawa, M., Hirai, M. (2009). Property of resistance to bacterial wilt in *Capsicum* line LS2341. *Hortic. Res.*, 1,231.
- Minamiyama, Y., Tsuru, M., Kubo, T., *et al.* (2007). QTL analysis for resistance to *Phytophthora capsici* in pepper using a high density SSR-based map. *Breed Sci*, 57, 129–134.
- Minamiyama, Y., Kinoshita, S., Inaba, K., *et al.* (2005). Development of a cleaved amplified polymorphic sequence (CAPS) marker linked to pungency in pepper. *Plant Breed.*, 124, 288–291. <https://doi.org/10.1111/j.1439-0523.2005.01101.x>.
- Mishra, S., Laxman, R. H., Reddy, K. M., *et al.* (2020). TIR approach and stress tolerance indices to identify donor for high-temperature stress tolerance in pepper (*Capsicum annum L.*). *Plant Genet. Res.*, 18(1), 19-27.
- Moury, B., Palloix, A., Caranta, C., *et al.* (2005). Serological, molecular, and pathotype diversity of Pepper veinal mottle virus and Chili veinal mottle virus. *Phytopathology*, 95(3), 227-232.
- Murphy, J., Blauth, J., Livingstone, K., *et al.* (1998). Genetic mapping of the pvr1 locus in *Capsicum spp.* and evidence that distinct potyvirus resistance loci control responses that differ at the whole plant and cellular levels. *Mol. Plant Microbe Interact.*, 11, 943-951. 10.1094/MPMI.1998.11.10.943.
- Naresh, P., *et al.* (2022). Molecular mapping of Chili veinal mottle virus (ChiVMV) resistance in hot pepper (*Capsicum annum L.*). *Plant Gene*, 33, 100396..
- Naresh, P., Rao, V. K., Reddy, L., *et al.* (2016). Genetic analysis for fruit biochemical traits (capsaicinoids and carotenoids) and dry fruit yield in chili (*Capsicum annum L.*). *Ind Crops Prod*, 94, 920-931.
- Naresh, P., Reddy, M. K., Reddy, P. H. C., *et al.* (2016). Screening chili (*Capsicum spp.*) germplasm against Cucumber mosaic virus and Chili veinal mottle virus and inheritance of resistance. *Eur. J. Plant Pathol.* 146(3), 451–464.
- Naresh, P., Reddy, K. M., Reddy, M. K., *et al.* (2012). Allelic variation at capsanthin capsorubin synthase gene for ripening fruit color in chili (*Capsicum annum L.*). *Indian J Genet Plant Breed.*,72(01), 72-78.
- Ogundiwin, E. A., *et al.* (2005). Construction of 2 intraspecific linkage maps and identification of resistance QTL for *Phytophthora capsici* root-rot and foliar-blight diseases of pepper (*Capsicum annum L.*). *Genome*, 48, 698–711.
- Ou, L., Li, D., Lv, J., *et al.* (2018). Pan-genome of cultivated pepper (*Capsicum*) and its use in gene presence–absence variation analyses. *New Phytol.*, 220(2), 360-363.
- Padayatty, S. J., Katz, A., Wang, Y., *et al.* (2003). Vitamin C as an antioxidant: evaluation of its role in disease prevention. *J Am Coll Nutr.* 22(1), 18-35. <https://doi.org/10.1080/0731572.4.2003.10719272>.
- Panda, R. C., Kumar, O. A. & Rao, K. G. R. (2004). Cytogenetic Studies of Some F1 Hybrids between Wild and Cultivated Taxa of *Capsicum L.* *Cytologia*, 69 (2), 203-208.
- Parisi, M., Alioto, D., Tripodi, P. (2020). Overview of Biotic Stresses in Pepper (*Capsicum spp.*): Sources of Genetic Resistance, Molecular Breeding and Genomics. *Int. J. Mol. Sci.*, 21(7), 2587.
- Pavithra, B. S., Reddy, K., Kedarnath, G. and Krishna Reddy, M. (2019). Identification of resistant sources in chili (*Capsicum sp.*) genotypes to Groundnut bud necrosis virus (GBNV). *Australasian Plant Pathology*, 49. 10.1007/s13313-019-00672-w.
- Peterson, P. A. (1958) Cytoplasmically inherited male sterility in capsicum. *Am Nat.*, 92, 111–119.
- Pochard, E. & Daubeze, A. M. (1989). Progressive construction of a polygenic resistance to cucumber mosaic virus in the pepper. *In: Proc 7th Eucarpia Meet Genet Breed Capsicum Eggplant*, pp. 189–192.
- Pongjareankit, S., Saeko, A., Lithanatudom, S. K., *et al.* (2020). QTL mapping specific to *Thrips palmi* resistance in *Capsicum annum*. *Asia-Pac. J. Sci. Technol.*, 25(03), APST-25. <https://doi.org/10.14456/apst.2020.29>
- Portis, E., Nagy, I., Sasvari, Z., *et al.* (2007). The design of *Capsicum spp.* SSR assays via analysis of in silico DNA sequence, and their potential utility for genetic mapping. *Plant Sci.*, 172(3), 640-648.
- Purkayastha, J., Alam, S. I., Gogoi, H. K., *et al.* (2012). Molecular characterization of 'Bhut Jolokia' the hottest chili. *J. Biosci.*, 37, 757-768.
- Qin, C., *et al.* (2014). Whole-genome sequencing of cultivated and wild peppers provides insights into *Capsicum* domestication and specialization. *Proceedings of the National Academy of Sciences of the United States of America*, 111 (14), 5135-5140. 10.1073/pnas.1400975111.
- Rossato, M., Santiago, T., Lopes, C. (2018). Reaction of *Capsicum* peppers commercialized in the Federal District to bacterial wilt. *Hortic. Bras.*, 36, 173-177.
- Sanwen, H., Baoxi, Z., Milbourne, D., *et al.* (2001). Development of pepper SSR markers from sequence databases. *Euphytica*, 117(2), 163–167.
- Sarwa, K. K., Mazumder, B., Rudrapal, M., *et al.* (2013). Capsaicinoids content of some indigenous capsicum varieties of Assam, India. *J. Nat. Sci.*, 3(4), 112-116.
- Shirasawa, K., Ishii, K., Kim, C., *et al.* (2013). Development of *Capsicum* EST-SSR markers for species identification and

- in silico* mapping onto the tomato genome sequence. *Mol Breed*, 31, 101–110.
- Silvar, C., Merino, F. & Diaz, J. (2006). Diversity of *Phytophthora capsici* in Northwest Spain: analysis of virulence, metalaxyl response, and molecular characterization. *Plant Dis.*, 90, 1135–1142. 10.1094/PD-90-1135.
- Singh, Y., Thakur, R. & Sekhon, B. S. (2018). Genetic variability among bacterial wilt resistant genotypes of sweet pepper for yield and morpho-physiological traits under mid hill conditions of North Western Himalayas. *Vegetable Science*, 45(1), 109–115.
- Singh, A. K., Kushwaha, N. & Chakraborty, S. (2016). Synergistic interaction among begomoviruses leads to suppression of host defense-related gene expression and breakdown of resistance in chili. *Appl. Microbiol. Biotechnol.*, 100, 4035–4049.
- Soler, S., Debreczeni, D. E., Vidal, E., *et al.* (2015) A new *Capsicum baccatum* accession shows tolerance to wild-type and resistance-breaking isolates of *Tomato spotted wilt virus*. *Ann Appl Biol*, 167, 343–353.
- Srivastava, A., Mangal, M., Saritha, R. K., *et al.* (2017). Screening of chili pepper (*Capsicum* spp.) lines for resistance to the *Begomovirus* causing chili leaf curl disease in India. *Crop Prot.*, 100, 177–185.
- Srivastava, A., Mangal, M., Saritha, R. K., *et al.* (2015). Natural epiphytotic screening of chili germplasm lines against leaf curl virus complex. *Intl. J. Trop. Agr.*, 33, 3581–3586.
- Sugita, T., *et al.* (2006). QTL analysis for resistance to *Phytophthora* blight (*Phytophthora capsici* Leon.) using an intraspecific doubled-haploid population of *Capsicum annuum*. *Breed. Sci.*, 56 (2), 137–145.
- Sugita, T., Kinoshita, T., Kawano, T., *et al.* (2005). Rapid construction of a linkage map using high-efficiency genome scanning/AFLP and RAPD, based on an intraspecific, doubled-haploid population of *Capsicum annuum*. *Breed. sci.*, 55(3), 287–295.
- Sunil, K. P. & Rasheed, A. (1998) Cross compatibility in five species of *Capsicum*. *J. Spices Aromat.*, 7(1), 35–38
- Suwor, P., Sanitchon, J., Thummabenjapone, P., *et al.* (2017). Inheritance analysis of anthracnose resistance and marker-assisted selection in introgression populations of chili (*Capsicum annuum* L.). *Sci Hort.*, 220, 20–26.
- Suzuki, K., Kuroda, T., Miura, Y., *et al.* (2003). Screening and Field Trials of Virus Resistant Sources in *Capsicum* spp. *Plant Dis.*, 87, 779–783. 10.1094/PDIS.2003.87.7.779.
- Thakur, H., Jindal, S. K., Sharma, A., *et al.* (2019). A monogenic dominant resistance for leaf curl virus disease in chili pepper (*Capsicum annuum* L.). *Crop Prot.* 116, 115–120.
- Thakur, H., Jindal, S. K., Sharma, A., *et al.* (2020). Molecular mapping of dominant gene responsible for leaf curl virus resistance in chili pepper (*Capsicum annuum* L.). *3 Biotech*, 10, 1–10.
- Thakur, P. P., Mathew, D., Nazeem, P. A., *et al.* (2014). Identification of allele specific AFLP markers linked with bacterial wilt [*Ralstonia solanacearum* (Smith) Yabuuchi *et al.*] resistance in hot peppers (*Capsicum annuum* L.). *Physiol. Mol. Plant Pathol.*, 87, 19–24.
- Truong, H. T. H., *et al.* (2012). Identification of isolate-specific resistance QTLs to *Phytophthora* root rot using an intraspecific recombinant inbred line population of pepper (*Capsicum annuum*). *Plant Pathol. J.* 61 (1), 48–56.
- Ullman, D. E., Cho, J. J., Mau, R. F. L., *et al.* (1992). Thrips-tomato spotted wilt virus interactions: Morphological, behavioral and cellular components influencing thrips transmission. In: Harris KF (Ed), *Advances in disease vector research*. Springer-Verlag, New York, Vol. 9, pp. 195–240.
- Usman, M. G., *et al.* (2020). Molecular confirmation of candidate Hsp70 gene associated with heat tolerance in BC3F2 advanced backcross lines and their phenotypic resemblance with recurrent chili Kulai. *Acta Agric Scand B Soil Plant Sci.*, 70(3), 252–264.
- Van, H., Voorrips, P., Van, R. E., *et al.* (2021). Fine mapping of a thrips resistance QTL in *Capsicum* and the role of diterpene glycosides in the underlying mechanism. *Theor Appl Genet*, 134, 1557–1573. <https://doi.org/10.1007/s00122-021-03790-6>
- Venkatesh, J., *et al.* (2018) Fine mapping of the dominant potyvirus resistance gene *Pvr7* reveals a relationship with *Pvr4* in *Capsicum annuum*. *Phytopathology*, 108,142–148.
- Wang, D. & Bosland, P.W. (2006). The Genes of *Capsicum*. *Hort Sci*, 41, 1169–1187.
- Wu, F.N., Mueller, L.A., Cruzillat, D., *et al.* (2006). Combining bioinformatics and phylogenetics to identify large sets of single-copy orthologous genes (COSII) for comparative, evolutionary and systematic studies: a test case in the euasterid plant clade. *Genetics*, 174, 1407–1420.
- Yadav, R., *et al.* (2022). Evaluation of chili genotypes and understanding biochemical basis of whitefly (*Bemisia tabaci* Genn.) resistance. *S. Afr. J. Bot.*, 151, 433–444.
- Yadav, R., Reddy, K., Ashwathappa, V., *et al.* (2022). Screening of *Capsicum* germplasm and inheritance of resistance to chili leaf curl virus. *Indian Phytopathology*, 75. <https://doi.org/10.1007/s42360-022-00530-8>.
- Yao, M., Li, N., Wang, F., *et al.* (2013). Genetic analysis and identification of QTLs for resistance to Cucumber mosaic virus in chili pepper (*Capsicum annuum* L.). *Euphytica*, 193,135–145
- Yi, G., Lee, J. M., Lee, S., *et al.* (2006). Exploitation of pepper EST-SSRs and an SSR-based linkage map. *Theor. Appl. Genet.*, 114, 113–130.

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 कैप्सेन्थिन, कैप्सेसिनोइड्स और कैप्सेनोइड्स कैप्सिकम जीनस के विशिष्ट गुण हैं। इस जीनस में बड़ी मात्रा में जैव-विविधता 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/किस्मों/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 हैं। प्रजनन कार्यक्रमों में तेजी लाने के लिए जीनोमिक संसाधनों में उन्नति और नेक्स्ट जनरेशन सिक्वेसिंग तकनीकों का प्रयोग किया जा सकता है।