Chapter 3
Genomic Designing for Breeding Biotic Stress Resistant Pepper Crop

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Abstract Pepper is one of the most important spice crops in the world today with an enormous economic value. The pepper fruits are rich in pharmaceutically important compounds such as carotenoids and capsaicinoids. Over the years, crops of pepper have suffered significant losses in terms of yield and quality due to a myriad of pathogen infections including fungi, viruses and bacteria. More often, broad host ranges, novel pathogen strains and simultaneous infections due to multiple pathogens lead to resistance breakdown of host plants. An increased virulence of pathogens also results in exacerbated disease symptoms and yield losses. Coevolution of pathogens and crops allows them to harden each other's defense responses, however the whole process remains skewed in favor of the pathogens. Genomic designing of Capsicum genotypes which are more resilient to the imminent threats of rapid climatic changes and biotic stresses is now the major focus of current research. Hence, it becomes critical to understand the pathogens and their pathogenic properties in details to incorporate this knowledge into future breeding programs on disease resistance. Traditional breeding programs have met with little success due to the polygenic control of resistance, wide variability in the pathogen range along with complex pathogenicity mechanisms. Marker-assisted selection allows indirect selection of desired resistance alleles in the early stages of life cycle of the plant. The development of resistant commercial pepper varieties and host plant resistance are the permanent, effective and eco-friendly substitutes to the chemical and physical control methods and cultural practices for management of various biotic stresses. The multiplicity of abiotic and biotic stresses are the warning signs to initiate serious and concerted efforts towards making the crops more resilient and resistant to these stresses and

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to achieve desired crop breeding goals. Present chapter assembles the recommendations, details of the resistance sources, genes, QTLs and other resources available to diminish the effects of different biotic stresses towards genetic improvement of *Capsicum* species with modern, time critical and scalable scientific methods.

Keywords *Capsicum* · Fungi · Virus · Bacteria · Resistance genes · QTLs

3.1 Introduction

Pepper (*Capsicum* species) belongs to the Solanaceae family and is one of the most important horticultural crops grown worldwide which is used both as a spice and vegetable. In the past years, pepper has suffered major yield losses due to pathogen infections and related diseases. This could be attributed due to many reasons such as advancement and expansion of pepper cultivation around the world, increasing globalization and trade of fresh pepper produce, all of which serve as carriers for a range of pathogens and vectors and introduce them to new geographical locations. Climate change also remains a key factor leading to expansion of geographic ranges of the pathogens. The world produced approximately 38–42 million tons of green and dry chili pepper, with India being the top producer with a production of 1.74 million tons of chili pepper (FAOSTAT 2019). Pepper however needs urgent attention from the plant researchers and breeders in order to reduce current crop losses (Chhapekar et al. 2018). The range of pathogens infecting pepper species is very broad and includes bacteria, fungi, viruses and insects (Parisi et al. 2020). The broad and overlapping host ranges along with an unpredictability of the pathogen outbreaks pose serious challenges in the process of designing and implementing disease management programs. Novel pathogen strains elevate the chances of co-infection, which in turn leads to exacerbated disease symptoms and the resulting yield losses. This is often accompanied by resistance breakdown of host plants and increased virulence of pathogens. In addition, the indiscriminate use of insecticides in the fields for controlling vector organisms has raised concerns over the irreversible consequences on the environment and overall well-being of both the cultivators and the consumers. Also, for most of the pathogen organisms no chemical control methods exist which are highly effective in reducing the yield losses. Despite these challenges, notable progress has been made in the fields of molecular biology to decipher host–pathogen and pathogen-vector interactions, identification of risk factors that lead to increased vulnerability to diseases, and several disease management strategies and control measures are currently in practice to alleviate the impact of biotic stresses. Tangible and pragmatic solutions that integrate traditional practices, sustainable use of insecticides, application of natural biochemical products and target gene resistance should therefore be employed for prevention and control of pathogen infections.

Conventional breeding programs have met with little success due to the polygenic nature of resistance, wide variability of pathogen range and complex pathogenicity

mechanisms. Thus, development of resistant commercial pepper varieties and host-plant resistance are a permanent, effective and eco-friendly source in management of biotic stresses. Techniques like ecotype target induced local lesions in genomes (EcoTILLING) and gene pyramiding can help analyze multiple accessions of pepper for identifying allelic polymorphisms in the candidate resistance genes in the natural germplasm, and to impart durable resistance against diverse pathogens. Eventually, marker-assisted selection (MAS) will allow selection of desired traits especially when the traits show recessive or polygenic inheritance. Molecular markers also offer a cost-effective, time saving and rapid way to detect the desired resistance alleles in the early stages of life cycle of a plant. Codominant markers can even detect homozygous and heterozygous resistant plants without phenotypic assessment.

3.1.1 Economic Importance of Pepper

Pepper is an important crop in the Indian subcontinent being used both as a vegetable and spice, and also has many important metabolic compounds. As a crop whose center of origin is believed to be Mexico, pepper is currently grown in different parts of the globe. The maximum diversity, however, is reported to exist in Peru and Bolivia, the primary center of diversity for the cultivated genotypes of pepper (Zonneveld et al. 2015).

India is the largest producer of dry chillies, with a production of around 2 million tons annually. Pepper plants easily adapt to a wide range of climatic conditions and exhibit remarkable diversity in plant architecture, fruiting flavors and ornamental appeal. The pepper crop has high economic importance as a great ornamental crop, due to ample variegation in foliage, flowers, diversity in fruits and the unique flavors ranging from sweet to fiery hot forming a continuous gradient. Several interesting variations in fruit shape have been observed in pepper such as erect, habanero type, cherry, pendant type, jalapeños, conical, and blocky, among the many other classified fruit morphologies. The commonly marketed forms of pepper include fresh fruits, dried whole fruits, powdered form, paste and sauces. Globally, pepper farmers fetch good revenue due to the growing food processing industry and rising awareness towards nutraceuticals, which have consequently led to an expansion in the crop area. Beneficial metabolites found in pepper, such as vitamin C and E, carotenoids (provitamin A), flavonoids and capsaicinoids are recognized for their health benefits and their nutraceutical applications. Studies undertaken in mice with direct administration of Ghost chili extracts have also indicated its antioxidant, genotoxic and apoptotic activities (Sarpras et al. 2018).

3.1.2 Reduction in Yield and Quality Due to Biotic Stresses

Although pepper plants have high adaptability and general resilience to most stresses yet the crop is susceptible to several biotic stresses that ultimately impact the overall quality as well as net yield, and significant damages have been reported even at post-production and storage stages (Lownds et al. 1994; Samira et al. 2013). Biotic stresses are much more persistent than abiotic stresses under cropping systems, and heavy yield and quality losses are reported with prolonged exposure, as a result productivity and quality downfall. Reduction in yields due to damages in vital tissues are very common with effects such as leaf discoloration, chlorosis, curling, insect damages, which are therefore the most common causes of yield losses. The yield losses can be incurred in many forms, even before the crop grows in field conditions; there are early losses in nursery stages such as root rot, stem rot, etc. Frequent encounters with biotic stresses at the seedling stage itself lead to significant crop management and economic issues particularly for the exotic seeds or rare genotypes. Assessment of quality of the consumption-ready fruits is an important point of active research along with the molecular assessment of pesticide residues, both of which are of great interest to the pepper breeders. It is an acceptable realization that varietal resistance may not be durable, and therefore external measures of stress management will become inevitable to achieve the end goals of better-quality pepper fruits. Golge et al. (2018) conducted health risk assessment of residual pesticides in peppers and cucumber, and made startling revelations that 12.9% of peppers and 13.5% of the cucumbers sampled had at least one detectable chemical residue from among the 170 pesticides used for screening 725 vegetable samples.

Pepper is known to be a highly responsive crop to greenhouses, surpassing yield thresholds of many other comparable crops due to good response to nutrients and ambient growth conditions, yet yield losses have been reported of higher orders (Parisi et al. 2020). Under greenhouse conditions, pest infestations such as due to whiteflies, aphids and thrips, all lead to increased viral attacks. High humid conditions even for brief periods are also conducive for many fungal and bacterial infections which often are more severe than those in the open fields. An outbreak of powdery mildew on peppers resulted in a loss of 100% plants in six out of the 12 fields evaluated in Ontario in 2005 (Cerkauskas et al. 2011), and upto 40% loss in the Pacific Northwest in 2009 (Glawe 2008; Glawe et al. 2018a, b). Direct damage to fruits accrues a considerable loss to their market value by compromising their quality.

Anthracnose disease lesions appearing as black concentric rings also cause serious damages to pepper production worldwide. The lesions, starting as sunset yellow and ultimately turning as gray spots cause considerable quality loss, as well as transitions to several other severe infections. Frog eye spots due to *Cercospora* species (spp.) are prevalent across tropical and subtropical climates appearing on leaf, stem, petiole and peduncles, as circular spots with water-soaked appearance which ultimately dry out to look as frog eyes causing passive losses attributed to reduced photosynthesis, while also serving as gateway to multiple successive infections.

Wilts are major diseases of peppers caused by multiple organisms, and unforeseen crop losses due to wilts have become common sightings across pepper fields. Wilts are soil-borne infections, mostly manifested under warm days with a sudden drop of all leaves and eventually the whole plant, sometimes leaving only a single chili if the fruiting stage has already been attained. Wilt caused by the fungus *Verticillium dahliae* characterized under field conditions of the central coast of California reported a mean incidence rate of 6.3–97.8% wilted plants per field with Anaheim, jalapeño, paprika or bell peppers (Bhat et al. 2003). The economic yield losses due to *Fusarium* spp. have been estimated to be 68–71% (Gabrekiristos and Demiyo 2020). Growing conditions of warm soil temperature, low soil moisture, susceptible host and pH in the range of 5–6, were ideal factors leading to massive losses attributed to Fusarium wilt. *Ralstonia solanacearum* is another major wilt causing bacteria, and is described as the most destructive disease-causing pathogen of not only the peppers, but rather whole of the Solanaceous crops which therefore suffer great yield losses worldwide (Mamphogoro et al. 2020; Thakur et al. 2021). Waxy skin of peppers lacks lenticels or stomata, and hence is relatively resistant to water loss, but a loss of 5% or more becomes evidently visible. In a study, a total loss of 28.6% in weight was observed under dry season, while 38.7% under humid conditions in Trinidad (Mohammed et al. 1992). Accompanied losses in quality were also incurred during prolonged storage in peppers including fresh weight loss, increased acidity, vitamin C content degradation and loss of fruit firmness under ambient conditions.

3.2 Description of Different Biotic Stresses

Extensive cultivation of pepper as a crop along with its expansion to wide geographical conditions exposes the pepper plants to many biotic stresses not encountered before. There is a great degree of sharing of pathogen profiles among the species belonging to Solanaceae and interspecies infections via the same pathogen are frequently observed. It also makes research results greatly exchangeable and translatable among members. In plants, resistance to most of the potential invaders is attained through an integrated transcriptional activation of pathogenesis related (PR) genes followed by a hypersensitive response (HR) and systemic acquired resistance (SAR) (Ryals et al. 1996; Dangl and Jones 2001). In brief, whenever a pathogen attacks, specific receptors trigger the warning signals to prevent the spread of the infection by inducing HR and programmed cell death (PCD). But sometimes, pathogens bypass these systems by releasing chemicals that inhibit these receptors or circumvent the membrane system by using a vector host (Liu et al. 2020). Upon recognizing the pathogen, plants activate numerous defense related genes, produce reactive oxygen species (ROS), undergo phosphorylation of proteins and change their ionic flux to induce SAR (Knogge 1996).

Diseases are molecular level disturbances, often having genetic manifestations, while disorders are physiological in nature, manifested at genetic levels after a certain condition persists for long. Emerging environmental patterns and projected changes

over the years have made a profound impact on the future of our crops. Pepper being distributed all across the globe is exposed to widely contrasting climatic conditions, and hence there is a greater challenge as well as the accompanying opportunity to get real insights on the dynamic influence of climate over disease resistance.

3.2.1 Range of Pathogens and Insects Afflicting Peppers

3.2.1.1 Fungi

Peppers encounter various fungal pathogens in nature. Pepper fungal pathogens are devastating in nature and directly attack internal tissues, thus affecting the physiology and growth of plants. The mycotoxins released by fungi affect the seed germination, viability and root growth. This physiological impairment is accelerated by prevailing environmental factors viz. nutritional substrate, water mismanagement, temperature and pH of the soil (Costa et al. 2019). Fungi spread among plants by contamination through wind, harvesting and mechanical pruning, besides being also carried by insects. They enter the plant tissues through the stomata or through exposed physical injury sites and directly affect the foliar tissues, roots, stems, fruits, vascular systems, causing physiological stress and serious impairment in the normal growth of plants. Plants normally respond to the biotic stress upon recognition of appropriate stimuli.

Peppers suffer infection from many common fungi present in the soil (Mandeel 2005). Species of *Aspergillus, Mucor* and *Rhizopus* mainly affect the organoleptic properties of processed pepper and create risk to the consumer's health (Costa et al. 2019). In fields, fungal pathogens mainly include, *Phytophthora, Fusarium* and several others (Table 3.1). A severe outbreak of *Choanephora cucurbitarum* was observed for the first time in bell pepper (*C. annuum* cvs. Aristotle, Crusader and Sentry) in Southwestern and Northern Florida, with an incidence of 40% and substantial fruit infection predominantly around the calyx (Roberts et al. 2003). The list of important diseases caused by fungal pathogens includes powdery mildew, fruit rots, root rot, necrotic spots, vascular wilt and leaf spots.

Fruit Rot of Pepper

Powdery mildew in peppers is caused by *Leveillula* spp. which affect many other crops also including cereals, legumes, onions and model organisms such as Arabidopsis and tobacco. The disease is characterized by the leaf underside turning grayish white in patches and appearance of yellowish green lesions on the opposite sides of leaves. Main causative agent is *Leveillula taurica* or *Oidiopsis taurica* (asexual stage). Powdery mildew in pepper was first reported in Florida in 1971 (Blazquez 1976), Puerto Rico in 1992 (Ruíz Giraldo and Rodríguez 1992), Idaho (in greenhouse grown pepper) in 1998 (Ocamb et al. 2007), in Canada (Cerkauskas and Buonassisi 2003), Bolivia (Correll et al. 2005), Oklahoma (Damicone and Sutherland 1999) and Maryland (Jones et al. 2009). *C. annuum* L. infected with *L. taurica*

Table 3.1 The common fungal diseases, causative organisms and symptoms in *Capsicum* spp.

Fungal disease	Pathogen	Symptoms	References
Powdery mildew	*Leveillula taurica*	White patches and lesions on adaxial as well as abaxial surface of leaves	Smith et al. (1999), Jones et al. (2009)
Anthracnose fruit rot	*Colletotrichum* spp.	Stem and leaf drooping, softening and rotting of fruits	Sun et al. (2015), Mongkolporn and Taylor (2018)
Verticillium wilt	*Verticillium* spp.	Browning of vascular tissues, wilting of leaves and stem, necrosis, foliar epinasty	González-Salán and Bosland (1991)
Fusarium wilt	*Fusarium* spp.	Drooping and yellowing of leaves, stunted growth, wilting of flowers	Lomas-Cano et al. (2014)
Pepper canker	*Rhizoctonia solani*	Root and stem rot, fruit canker	Muhyi and Bosland (1995), Mannai et al. (2018)
Necrotic root rot	*Pythium* spp.	Crown rot, Necrotic rot of root tips	Chellemi et al. (2000)
Pepper gray mold	*Botrytis cinerea*	Gray mould in fruits resulting in rot	Kamara et al. (2016)

(Lév.) G. Arnaud was reported for the first time in western New York in 1999 and Long Island, New York in August 2000 (McGrath et al. 2001).

L. taurica is an obligate biotrophic ascomycete, with mycelia spanning on the whole epiphytic surface, as well as haustorial structures exclusively in epidermal layers feeding on mesophyll cells. The visible infection occurs as powdery white patches on the leaves mainly stemming from the lower undersides of the abaxial surface. Eventually, infection progresses and affects the whole leaves and other parts of the plant. The fungus prefers to grow in leaves that are in moderate temperatures, high humidity and a moist environment. Affected leaves turn brown and defoliate, affecting the photosynthetic rate of the plants that results in a slow growth. PCR assays have been developed for the rapid and exact detection of damage and spread pertaining to the early and late stages of infection of *L. taurica* in peppers using primers from the rRNA internal transcribed spacer (ITS) regions of *L. taurica* (Zheng et al. 2013a). This relative quantification was done for rapid experimentation and assessment in the plant–microbe interaction domain.

Capsicum germplasm resistant to *Leveillula* has been reviewed by Parisi et al. (2020). Resistant varieties include *C. annuum*—H3, H-V-12 ['H3' x 'Vania' (susceptible)]; *C. baccatum*—CNPH36, CNPH38, CNPH50, CNPH52, CNPH279,

CNPH288, KC604, KC605 and KC608; *C. frutescens*—IHR 703; *C. chinense*—KH616; and *C. pubescens*—KC638, KC640, KC641, KC642, KC643, KC644 and CNPH279 (Anand et al. 1987; Daubeze et al. 1995; Souza and Café-Filho 2003).

Anthracnose of Chili

Anthracnose in chili is caused by the *Colletotrichum* spp. *Colletotrichum* is responsible for major crop losses and its pathogenicity is extremely diverse across different crop plants of Solanaceae, Malvaceae, Fabaceae and Brassicaceae (Jayawardena et al. 2016).

Worldwide, *Colletotrichum* affects up to 80% of crops in various countries viz. Vietnam (Don et al. 2007), Korea (Kim et al. 2008a, b; Park Sook-Young; Choi 2008), Thailand (Than et al. 2008), India (Ramachandran and Rathnamma 2006), Pakistan (Tariq et al. 2017), Brazil (Almeida et al. 2017), Australia (De Silva et al. 2017) and China (Diao et al. 2017) etc. Among the species, *C. truncatum* (previously known as *C. capsici*), *C. acutatum* and *C. gloeosporioides* are common in chili and are the most virulent. Highly virulent *C. truncatum* isolate (UOM-02) has reportedly caused severe losses under favorable conditions (Naveen et al. 2021). *C. javanense* and *C. scovillei* show great damages compared to other species after inoculation on intact fruits (De Silva et al. 2021). Infected plants suffer from sunken necrotic lesions resulting in both pre- and post-harvest rotting of fruits (Rao and Nandineni 2017). The pathogen is seed-borne and therefore can infect the next generation of plants also (Singh et al. 2018). The pathogen can be detected by loop mediated isothermal amplification assay (LAMP) (Aravindaram et al. 2016) or can be characterized using sequence characterized amplified regions (SCAR) (Srinivasan et al. 2014).

Several *Capsicum* spp. resistant varieties are reported that include *C. annuum* resistant against *C. truncatum* and *C. siamense* viz. Jinda, Bangchang, 83–168, Acchar lanka, CA-4, Pant C-1, Punjab Lal and Bhut Jolokia BS-35 (Mongkolporn et al. 2010; Mishra et al. 2018); *C. frutescens* against *C. siamense* viz. Khee Noo and Karen (Mongkolporn et al. 2010); *C. chinense* against *C. truncatum*, *C. scovillei* and *C. siamense* viz. PBC932, CO4714, PRI95030, CO4714 (Montri et al. 2009); *C. baccatum* against *C. truncatum* and *C. scovillei* viz. PBC80, PBC81, CA1422 (Montri et al. 2009) and *C. baccatum* var. *pendulum* against *C. scovillei* viz. UENF 1718, UENF 1797 (Silva et al. 2014).

Pepper Gray Mold

Pepper gray mold disease is caused by a polyphagus fungal pathogen *Botrytis cinerea.* This pathogen has a broad range of distribution affecting vegetable and crop plants viz. tomato, chickpea, strawberry, castor, tulips and ornamental plants like chrysanthemum, rose and lily (Pande et al. 2006; Petrasch et al. 2019; Kumar et al. 2020). *Botrytis* affecting peppers was reported in some Middle East and Asian countries viz. Taiwan (Huang and Sung 2017) and Pakistan (Naz et al. 2018). In India, the gray mold caused by *B. cineria* Pers. Fr. in *C. annuum* var. *grossum* was first reported in Jammu and Kashmir (Kamara et al. 2016). The fungus develops both in warm and cold temperatures and remains latent in the fruits and later affects post-harvest produce which makes it difficult to control the infection rate (Droby and Lichter

2007). Pathogenicity of *B. cinerea* is partially attributed to a phytotoxin Botrydial, however its role as a primary determinant is not established. Highest concentration of botrydial on the ripe fruit samples and open wounds with induced inoculation, correlates with strain's overall virulence (Deighton et al. 2001).

Genetic diversity present in *B. cinerea* among isolates studied from Southern Turkey revealed two distinct gene pools and five genetic clusters indicating that presence of the ample diversity can be exploited to design gray mold disease management breeding strategies (Polat et al. 2018).

White mold

Fungus *Sclerotinia sclerotiorum* was first observed in Korea infecting peppers (*Capsicum annuum* var. *grossum*) and was identified using ITS rDNA regions ITS1, ITS2 and 5.8S sequences which were 100% similar to the ones that infected lettuce (Jeon et al. 2006). Twelve commercial pepper cultivars and 110 *Capsicum* accessions were tested for their resistance to *S. sclerotiorum* (Lib.) de Bary out of which 58 showed some resistance (Yanar and Miller 2003). The results indicated that the Sclerotinia stem rot resistance existing among the *Capsicum* spp. could be used to transfer resistance to commercial pepper cultivars.

Root rot of pepper

Fusarium spp. cause decaying of roots, stems and leaves along with brown sunken cankers visible at the base of the plant. *Fusarium oxysporum* induced crown and root rot was first reported in Italy on sweet pepper plants (Gilardi et al. 2019), while *F. semitectum* was first reported in China affecting greenhouse pepper (*C. annuum*) (Li et al. 2018). Several other isolates of *Fusarium* have been reported in pepper viz. *F. solani* (Ramdial and Rampersad 2010), *F. oxysporum* f. sp. *vasinfectum*, *F. redolens*, *F. oxysporum* f. sp. *capsici*, *F. verticillioides* and *F. pallidoroseum* (Lomas-Cano et al. 2014). *Fusarium* strains are more complex and are pathogenic to many plants. *F. oxysporum*, the main pathogenic species, impacts onion in Japan and Indonesia (Dissanayake et al. 2009; Sasaki et al. 2015), cotton (Cianchetta and Davis 2015) and melon (Imazaki and Kadota 2019) etc. Among Solanaceae, it affects tomatoes (Srinivas et al. 2019), potatoes (Du et al. 2012), eggplant (Ishaq et al. 2019) and peppers (Gabrekiristos and Demiyo 2020). However, not all *Fusarium* are pathogenic with some of them being beneficial endophytes or soil saprophytes, and even antagonists of other fungus like *Verticillium*. In *Fusarium* spp. molecular characterization was carried out using ITS of the fungus ribosomal region in the affected pepper (*C. annuum*) (dos Anjos et al. 2019). Earlier, protein profiles of a resistant (Mae Ping 80) and susceptible (Long Chili 455) cultivars identified NADPH HC toxin reductase, serine/threonine protein kinase and 1-aminocyclopropane-1-carboxylate synthase 3 that were involved in plant defense mechanism (Wongpia and Lomthaisong 2010).

Necrotic spot and Vascular wilt

Verticillium affects plants viz. cotton, alfalfa, watermelons, chili and some ornamental plants like petunia, chrysanthemum and rose. *Verticillium* causes stunting and yellowing of leaves leading to leaf shedding, permanent wilt and plant death.

The epidemic was first reported in 1937 in California in pepper fields with about 20% crop losses (Bhat et al. 2003). *V. dahliae* is cross pathogenic and infects crops during rotational cycle of growth.

V. dahliae usually affects the temperate crops. The leaf and vascular wilt in pepper caused by *V. dahliae* leads to dropping of the leaves as a result of dehydration or increased transpiration exceeding water intake by plants. *V. dahliae* is restricted to the infection of the vascular tissues of plants and plugs the xylem and phloem tissues, thus resulting in leaf wilt as the plant is unable to transport water to its sink (Reusche et al. 2012).

Early studies in pepper have uncovered 125 novel accessions of *C. annuum* and *C. baccatum* and identified 27 *Capsicum* accessions that were resistant to *Verticillium* wilt. Plant introductions (P.I.) PI215699 and PI 535616 that included *C. baccatum* var. *microcarpum* and *C. annuum* showed the highest resistance (González-Salán and Bosland 1991). Later on, 397 *Capsicum* accessions were screened for resistance against two isolates Vdca59 and VdCf45. These accessions included *C. annuum, C. chinense* and *C. frutescens* varieties. Eight accessions, namely, Grif 9073, PI 281396, PI 281397, PI 438666, PI 439292, PI 439297, PI 555616 and PI 594125 were resistant to *V. dahliae* (Gurung et al. 2015). In another study, a total of 97 pepper accessions from Bulgaria, Serbia and Romania were studied, of which 12 were reported to be resistant to *V. dahliae*. Among these breeding lines, Buketen 3, Buketen 50, Gorogled 6, IZK Rubin and, IZK Kalin were found to be highly resistant (Vasileva et al. 2019). Changes observed in lignin composition and higher deposition of bound phenolics in infected stems seem to contribute to the reinforcement of cell walls and the impairment of *V. dahliae* colonization, and hydroxycinnamic acidamide N-feruloyltyramine was reported in response to *V. dahliae* infection (Novo et al. 2017).

Damping off and Root Rot

Pythium spp. cause a disease in plants known as "damping off" where the newly emerging seedlings wilt and die (Sutton et al. 2006). They constitute a range of species including *Pythium aphanidermatum, P. myriotylum, P. helicoides* and *P. splendens*, reported to cause significant root rot and reductions in root biomass of bell pepper, with *P. aphanidermatum* and *P. myriotylum* being the most severe (Chellemi et al. 2000). They commonly affect plants grown in greenhouses. They are generalists and unspecific in their range of hosts and are more dangerous than *Phytophthora* or *Rhizoctonia* which prefer specific hosts (Owen-Going et al. 2003). Their spores are motile and therefore commonly affect waterlogged or hydroponically grown plants. *Pythium* also causes serious losses in agricultural production worldwide. *Pythium* does not influence the photosynthetic activity of the plants but rather directly reduces the biomass (Wu et al. 2020). Damping off can result in heavy losses in crop yields as has been shown in a study where 5–80% of the seedlings were affected, and caused serious economic losses to the farmers (Lamichhane et al. 2017).

Rhizoctonia is a soil-borne pathogen responsible for causing root rot, collar rot and damping off related to stem wilt in various crops including Capsicum (Mannai et al. 2018). It was first observed in potato tubers in 1858 and was named *Rhizoctonia*

solani. In *Capsicum*, *R. solani* affects multiple growth stages and causes seedling damping off, necrotic spots at the hypocotyl and tap roots and root rot (López-Arredondo and Herrera-Estrella 2012). Genetic resources in pepper showing resistance against this pathogen are rare. Pepper accessions that develop resistance to *R. solani* have been found in *C. annuum, C. baccatum, C. chinense and C. frutescens* against a virulent strain of Mexican PWB-25 isolate (Anaya-López et al. 2011). Screening of 74 *Capsicum* accessions representing these four species for resistance against *R. solani* identified 19 accessions that were resistant (Muhyi and Bosland 1995).

Chili leaf spot/Gray leaf spot

Stemphylium solani (or *Stemphylium lycopersici* for the ones that infect tomatoes) first described by G. F. Weber in 1930, is a pathogenic ascomycete that causes gray leaf spot in plants. Its distribution varies, with *S. lycopersici* reported in Japan causing fruit rot even in peppers (Tomioka and Sato 2011), *S. solani* reported in Malaysia (Nasehi et al. 2012), and *S. lycopersici* in China (Xie et al. 2016). Infected plants have white spots and sunken red or purple lesions on leaves that finally necrose. The pathogen severely affects important vegetable crops like tomato, brinjal, chili, potato, onion, cotton etc. (Zheng et al. 2008). It causes secondary infections among the cycle of rotational crops and spreads through wind or air, and is even transmitted through seeds (Zheng et al. 2010).

Chili leaf spot caused by *Cercospora capsici* is prevalent in the tropics. Optimal conditions for infection are a relative humidity of 77–85% and temperatures close to 23°C. Assessment of the survival ability of the fungus on soil surface, infected debris and in refrigerator (4°C) showed their broad adaptability (Swamy et al. 2012). Infected leaves turn dark brown with a distinctive sporulating gray center, hence called the "frog eye" spot. It was first isolated from bell peppers and described by Heald and Wolf (1911). Later, sightings of *Cercospora* were studied in peppers for their virulence and pathogenicity by Meon (1990) in Malaysia. The *C. capsici* isolate reduced the photosynthetic ability of the infected plants resulting in consequent yield losses.

Resistant varieties have not been reported as yet for *C. capsici*. But, the responses of different *Capsicum* genotypes viz. *C. chinense* (Jacq.) cv. Rodo, *C. frutescens* L. cv. Ata wewe, *C. frutescens* cv. NHVI-AB and *C. frutescens* cv. Sombo were observed to be moderately resistant in field experiments conducted under tropical conditions to assess the effects of genotype, season and the genotype × season interaction (Afolabi and Oduola 2017). Some variants of the species infect peppers viz. *C. apii* affecting *C. chinense* grown in Brazil (Nicoli et al. 2011) and *C. tezpurensis* affecting Naga king chili in north-eastern states of India (Meghvansi et al. 2013).

3.2.1.2 Bacteria

Bacterial spot

Bacterial spot (BS) initially observed on tomato in South Africa in 1914, is a condition caused by a gram-negative bacterium formerly called *Xanthomonas campestris* pv. *vesicatoria* (*Xcv*), which is presently classified into *X. euvesicatoria*, *X. vesicatoria*, *X. gardneri*, and *X. perforans* on the basis of homology of DNA sequences and the phenotypes (Obradovic et al. 2004; Jones et al. 2005; Hamza et al. 2010). The occurrence of BS has been reported all over the world, such as the USA, north-western Nigeria and Saudi Arabia (Jones et al. 2005; Ibrahim and Al-Saleh 2012; Jibrin et al. 2014).

The bacteria have a short life span in the soil, but can persist for longer periods in association with infected debris or diseased plants or weed species. Bacteria can gain entry through stomata on the surfaces of the leaves and injured leaves and fruits. Extended spells of high humidity intensify the infection and disease development. Bacteria infect the stems and fruits, forming lesions on fruit and the peduncle, adversely affecting the crop productivity due to shedding of blossoms and developing fruits, while the fruits that remain lose commercial value because of poor quality.

Bacterial wilt

Bacterial wilt is one of the most common diseases in members of the Solanaceae family. It is caused by a soilborne, aerobic gram-negative bacteria named *Ralstonia solanacearum*. The disease is also known as 'Green wilt' because even though the infected plant wilts, the leaves remain green. Symptoms are usually seen on the young foliage and include necrosis and browning of vascular tissues. Use of resistant varieties remains the most effective, economical and environmentally safe method to control the disease (Yuliar et al. 2015).

3.2.1.3 Viruses

The number of incidences of viral diseases has increased considerably in pepper producing areas over the last few years. Earlier catalogues suggested some 35 viruses affecting pepper species (Green and Kim 1994). Till date, more than 45 viruses have been reported to infect chili peppers causing severe losses in production and quality (Arogundade et al. 2020). Of the viruses that threaten pepper over the past are—*Potato virus Y* (PVY), *Tomato spotted wilt virus* (TSWV) and *Pepper mild mottle virus* (PMMov), and among these, PVY and TSWV fall under top ten in the list of most detrimental plant viruses (Scholthof et al. 2011).

Most of the virus infections result in distortion of foliar tissues, chlorosis and necrotic spots, and sometimes these spots appear on other tissues such as of fruits. A comprehensive study on incidences of viral diseases in *C. chinense* var. Bhut Jolokia from Assam concluded that most of these were infected with Potyvirus, followed by Cucumovirus, Tospovirus and Begomovirus (Talukdar et al. 2017). PVY

is distributed worldwide and is transmitted by a large number of aphid species that cause global yield losses in Solanaceae members including pepper (Janzac et al. 2008). Several leaf curl begomoviruses associated with beta satellites were reported in chili pepper plants in Pakistan (Yasmin et al. 2017). A serological survey conducted in different altitude zones of Rwanda confirmed the presence of at least one virus from among—*Cucumber mosaic virus* (CMV), *Pepper veinal mottle virus* (PVMV), PVY, *Tobacco mosaic virus* (TMV), PMMoV and *Pepper vein yellows viruses* (PeVYV) (high to low incidence), in 73% of Capsicum plants (Waweru et al. 2021).

Most of the pepper-infecting viruses are transmitted by vector groups belonging to aphids, thrips and whiteflies (Kenyon et al. 2014). More often than not, the synergistic effects of more than one virus infection are seen in plants that further increase disease severity (Murphy and Bowen 2006). Aphids transmit nearly 30% of plant viral species known till date (Brault et al. 2010). Whiteflies are very resistant to most insecticides and also cover long distances over foliage and spread many viruses. Poleroviruses (Luteovirideae) is a phloem-restricted RNA plant virus exclusively transmitted by aphids, while *Pepper whitefly-borne vein yellows virus* (PeWBVYV) is *Bemisia tabaci*-transmitted polerovirus or whitefly-borne vein yellows virus (Ghosh et al. 2019).

Orthotospoviruses

***Tomato spotted wilt virus* (TSWV)**

Tospoviruses pose a major constraint in the production of vegetable crops, including pepper in various parts of the world due to their wide host range and propagative transmission by thrips (Pappu et al. 2009). Since the end of the 20th century, the spread of the invasive western flower thrips (*Frankliniella occidentalis*) from the western United States and local reemergence have led to major TSWV outbreaks worldwide (Moury and Verdin 2012). Temperatures greater than 30°C promote the incidences of TSWV infections (Llamas-Llamas et al. 1998; Roggero et al. 1999). The typical symptoms in in *Capsicum* spp. include stunting and yellowing or browning of leaves or of the whole plant, mosaic or necrotic ringspots on leaves and fruits, necrotic streaks on stems and curling of the leaves. Deformed fruits exhibit necrotic ring patterns along with discolored arabesque-like areas.

***Tomato chlorotic spot virus* (TCSV)**

TCSV was first reported to infect bell pepper in Spain but it could not be transmitted experimentally to healthy plants (Lozano et al. 2004; Wintermantel and Wisler 2006). TCSV causes irregular chlorotic, interveinal yellowing, mild leaf curl, necrotic ring spots and stunting along with deformed leaves as the common symptoms. Out of the four thrips species—*F. kelliae*, *F. schultzei*, *F. bruneri* and *Thrips palmi* that were detected in pepper growing areas (Webster et al. 2013), *F. schultzei* was an efficient vector for TCSV (Nagata et al. 2004).

***Capsicum chlorosis virus* (CaCV)**

It is a serogroup IV virus species infecting *Capsicum* and was first reported in 2000 in Queensland, Australia (McMichael et al. 2002). In the same year, CaCV was first detected in chili pepper fields in Karnataka, India (Krishnareddy et al. 2008). Recently, incidences of CaCV were also reported in glasshouse grown *C. annuum* var. *annuum* in Greece (Orfanidou et al. 2019). Symptoms include mottling and distortion of leaves, chlorotic and necrotic ring spots on leaves and apical necrosis.

***Groundnut ringspot virus* (GRSV)**

Distortion of leaves and fruits, chlorotic and necrotic spots on newly developed leaves, terminal necrosis and mottle were observed in GRSV infected *C. annuum* L. (Webster et al. 2011). *F. schultzei* is observed to be a better vector for GRSV than *F. occidentalis* and has contributed to recent outbreaks in Brazil and North America (Webster et al. 2013).

Potyvirus

***Chili veinal mottle virus* (ChiVMV)**

ChiVMV is a destructive potyvirus found mostly in Asia and causes systemic mosaic, vein-banding and leaf mottling and chlorosis (Tsai et al. 2008). The concurrent double recessive mutations—$pvr1^2$ in *eIF4E* and *pvr6* in *eIF(iso)4E*, respectively, provide resistance to ChiVMV, and double silenced plants showed reduced viral accumulation (Hwang et al. 2009). Recombination events and geographical locations drive most of the genetic variations, diversity and environment adaptability among the ChiVMV isolates as studied in China (Rao et al. 2020).

***Pepper veinal mottle virus* (PVMV)**

PVMV is mostly common in Africa and Asia causing major setbacks in chili pepper yield and quality. Recently, PVMV was reported in Rwanda along with Pepper Yellow Virus (PeYV) (Skelton et al. 2018). The prevalent symptoms observed for PVMV infected chili plants are mosaic, vein mottling and stunted growth. Aphid species like *Aphis gossypii* are the potential insect vectors for non-persistent transmission of PVMV (Shah et al. 2009). Six Japanese isolates of PVMV in *C. annuum* were characterized by whole genome sequencing and found to have similar molecular and pathological impacts (Laina et al. 2019). The cDNA clone used to study the molecular etiology of PVMV in *C. chinense* cv. Yellow Lantern was associated with floral chlorosis and rugosity (Hu et al. 2020).

***Pepper severe mottle virus* (PepSMoV)**

The symptoms of PepSMoV infection include deformed leaves and stunted growth. The coat protein gene from PepSMoV was isolated from chili pepper plants in

Colombia that showed high sequence similarity with the PepSMoV strain from Venezuela (Rivera-Toro et al. 2021).

Cucumovirus

***Cucumber mosaic virus* (CMV)**

Symptoms include curling, mosaic, vein banding, leaf mottling and malformation. Monogenic recessive resistance was found in a multiple disease resistant pepper variety, Punjab Lal, against CMV and other mosaic tobamoviruses (Bal et al. 1995). The gene expression analysis could confirm the presence of CMV causing disease symptoms in pepper plants in Malaysia (Azizan et al. 2017). The viral coat protein gene of 800 bp was isolated from leaf tissues of CMV infected chili peppers in Tamil Nadu also showed high sequence similarity with other Indian CMV isolates (Rajamanickam and Nakkeeran 2020). Higher incidences of CMV in various accessions of king chili in Manipur were reported alongside mixed infection with ChiVMV (Chanu et al. 2004).

Tobamovirus

The Tobamovirus pathotypes are named by the type of *L-gene* mediated resistance they break, for example, P_0, P_1, $P_{1.2}$ and $P_{1.2.3}$. The *L4* HR mediated resistance, which previously had the broadest resistance spectra, was overcome by a new PMMoV pathotype $P_{1.2.3.4}$ in *C. annuum* (Genda et al. 2007). Susceptible allele L^0 carrying *Capsicum* plants are infected by any Tobamovirus pathotype.

***Pepper mild mottle virus* (PMMoV)**

PMMoV has been found to be transmitted through hydroponic systems in pepper with 100% incidence (Choi et al. 2004). The infection cycle of PMMoV was traced in developing seedlings of infected *C. annuum* cv. Shosuke up to the seed development stage, and in seeds to cotyledon stage via immunofluorescence of viral coat protein (Genda et al. 2011). PMMoV specific virus screening tests were developed based on double antibody (Anti-PMMoV) sandwich enzyme-linked immunosorbent assay (DAS-ELISA) for advanced detection of soilborne PMMoV, which allows preventing possible damage to the crops (Ikegashira et al. 2004).

Geminivirus

Geminiviruses, being the largest family of plant viruses, pose a major threat to economically important crops throughout the world especially in developing countries (Boulton 2003). Among all, *Begomovirus* is the most notorious genus of the family Geminiviridae which affects a wide range of host plants. Geminiviruses are

mostly transmitted by the B-biotype of the polyphagous whitefly vector. Recently, *Pepper yellow leaf curl virus* (PepYLCV) and PeVYV were reported for the first time in Malaysia with serious implications in pepper production (Sau et al. 2020). Several attempts to characterize the chili plants infected with *Pepper leaf curl virus* (PepLCV) at the molecular level have been carried out to isolate the viral amplicons (Nigam et al. 2015). In India, the viral genome sequence of chili infecting Begomoviruses like *Tomato leaf curl Joydebpur virus* (ToLCJV), *Chili leaf curl Vellanad virus* and *Chilli leaf curl Gonda virus* have been successfully characterized (Kumar et al. 2012; Shih et al. 2007; Khan and Khan 2017). *Cotton leaf curl Multan virus* (CLCuMuv) and *Tomato leaf curl beta satellite* (ToLCPaB) with genetic recombination sites were found to be associated with ChiLCV disease in Bhut Jolokia accessions from Manipur state of north-east India (Yogindran et al. 2021).

***Pepper leaf curl virus* (PepLCV)**

PepLCV is also one among the most destructive viruses affecting chili peppers and causes heavy yield losses in pepper production in India and globally. New variants of *Chilli leaf curl virus* (ChiLCV) were reported from districts of Uttar Pradesh in North India (Rai et al. 2010). The histopathological characterization of ChiLCV and associated *Tomato leaf curl Bangladesh betasatellite* (ToLCBDB), revealed elevated levels of stress-related biological compounds like proline and polyphenols and defense enzymes like Superoxide dismutase (SOD) along with overall deterioration of fruit quality in sweet pepper plants (Kumar et al. 2018).

***Tomato yellow leaf curl virus* (TYLCV)**

Pepper is an asymptomatic host to TYLCV, which is primarily a tomato pathogen, and may act as an alternative host and a natural reservoir for acquisition and transmission of TYLCV (Kil et al. 2014). Some reports suggest that pepper is a dead-end host in the epidemiological cycle of TYLCV, while others speculate that it may serve as a source of TYLCV for healthy tomato plants via whitefly (Morilla et al. 2005; Polston et al. 2006). The acquisition, path of translocation in vector body, transmission between vector organisms and to host plants, and retention of pathogen components in the vector organisms have been studied for TYLCV that offer alternative solutions to resistance gene breeding (Czosnek et al. 2002). In a remarkable incidence of synergistic interaction of four viral components—ChiLCV, ToLCBDB, *Tomato leaf curl New Delhi virus* (ToLCNDV) and *Tomato leaf curl Gujarat virus* (ToLCGV) were found to be associated with severe leaf curl disease, increased viral DNA and suppression of NBS-LRR gene expression in resistant *C. annuum* cv. Kalyanpur Chanchal (Singh et al. 2016). Recently, ToLCNDV was reported to infect sweet peppers for the first time in Europe which may thus affect the genetic variability and virus prevalence (Luigi et al. 2019).

***Tobacco mosaic virus* (TMV)**

TMV, the first ever virus to be identified infects more than 350 plant species, including tobacco, tomato, pepper, eggplant, potato and cucumber (Kumar et al. 2011). The virus subsists in diseased plants for a long duration. It can reproduce in living plant

tissues but remains inactive in dead tissues, retaining without any loss in its ability to infect (Damiri et al. 2017). TMV propagates mostly through contact among plants, infested seeds and by mechanical means. Typical symptoms include leaf chlorosis, mosaic leaves, leaf distortion and arrested growth accompanied with small-sized fruits.

3.3 Management Strategies—Cultural, Chemical, Biocontrol and Integrated Pest Management

Different cultural, chemical, biocontrol and Integrated Pest Management (IPM) practices are currently being used by farmers to control pathogens and pests of peppers. The pre-sowing cultural practices include deep summer ploughing, fallow, crop rotation with non-host crops and destruction of the alternate host plants. Timely sowing of the pepper crop should be ensured at the seed sowing/transplanting stage, cultivation with resistant/tolerant varieties, and use of healthy, certified and weed free seeds are some important approaches to minimize yield losses. Other practices implemented at this stage include removal and destruction of infected plants, growing pest repellent plants like Ocimum/Basil, and crop rotation with a non-host cereal, cucurbit, or cruciferous vegetable crop. Common cultural management practices at the vegetative stage of the pepper crop include adoption of the recommended spacing for adequate air circulation, judicious use of fertilizers, collection and destruction of crop debris, sufficient irrigation at critical stages of the crop, ensuring minimal waterlogging and other field sanitation methods. Some of the common cultural and traditional methods for controlling disease organisms and their vectors are listed in Table 3.2.

Table 3.2 Common cultural methods of control of disease pathogens and vector organisms in *Capsicum* spp.

Method	Effective against	Remarks	References
Leaf pruning	Aphididae	Leaf pruning coupled with application of natural predator *Macrolophus pygmaeus* effectively controls aphids in sweet pepper	Brenard et al. (2020)
Yellow sticky traps	*Trialeurodes vaporariorum*	Significant reduction in oviposition of greenhouse whitefly in *C. annuum*	Moreau and Isman (2011)
Vegetable extracts	*Cercospora*	*Momordica charantia* and garlic-pepper sprays were significantly effective in reducing the green peach aphid abundance on pepper	Oke et al. (2010)

Chemical methods of control like soil fumigants were used in the early days viz. MeBr (Methyl Bromide), to control the rate of epidemic, which was observed to be biocidal and cost-effective, but was not practical (Xie et al. 2015). Prolonged ozone exposure was sufficient to prevent PepMOV infection at lower PepMOV concentrations, but chemical treatments like trisodium phosphate (TSP) were more efficacious at higher concentrations (Stommel et al. 2021). Treatment with fungicide seems to ameliorate their growth; however, growing concerns of using synthetic chemicals have prompted the use of a natural resistance approach. Some chemical methods of control are summarised in Table 3.3.

The biological control or biocontrol methods for defending the pepper crop from various phytopathogens are progressively eliciting interest among the farmers because it is environment-friendly. In a study on biocontrol of pepper seedling wilt disease, three natural substances called lipopeptides, with antifungal properties—surfactin, iturin and fengycin produced post *B. subtilis* infection in the host were shown to be effective against *R. solani* infection (Wu et al. 2019). The results

Table 3.3 The chemicals effective against pathogen organisms and their vectors along with their working mechansims

Chemical	Effective against	Remarks	References
Spinosad, indoxacarb, methoxyfenozide	*Ostrinia nubilalis* (European corn borer)	–	Chapman et al. (2009)
Thiamethoxam (TMX)	*Bemisia tabaci*	Assessed optimal application of doses	Mei et al. (2019)
Novaluron	*Liriomyza trifolii*	Effective against leafminer	Hernández et al. (2011)
Spiromesifen	*Bactericera cockerelli*	Reduction in oviposition and egg hatching against tomato-potato Psyllid	Tucuch-Haas et al. (2010)
Spiromesifen	mites and whiteflies	Foliar application of Oberon/spiromesifen shows effective control against whiteflies in *C. annuum* even after 36 days with no residual phytotoxicity	Fanigliulo et al. (2010)
Azadirachtin and methoxyfenozide	*Spodoptera littoralis*	Reduction in adult longevity by 2.3 d at high concentration; significant impact on population dynamics of pest by oviposition deterrence on *C. annuum* plants pretreated with Azadirachtin	Pineda et al. (2009)

obtained in the study also indicated that *B. subtilis* SL-44 triggered the induced systemic resistance in the seedlings against *R. solani* wilt through the jasmonic acid-dependent signaling pathway. Moreover, *B. subtilis* SL-44 also produced antifungal compounds—lipopeptides, which could further inhibit or even damage the mycelial growth of *R. solani*. Biotrophic bacteria and arbuscular mycorrhiza are other alternatives to control fungal pathogens. They are natural and their effect is permanent. Some Arbuscular mycorrhizal fungi (AMF) have shown the potential in providing resistance against *V. dahliae* in *C. annuum* L. pepper cv. Piquillo by delaying the disease symptoms buildup by improving a balanced antioxidant metabolism in leaves during early inoculation, and reducing the photosynthesis in *Verticillium* inoculated tissue to conserve resources, adding up to final yield outcomes. Biocontrol is also a practical approach for mitigation of the blight of *Rhizoctonia* like several others (Huang et al. 2017). Some biotrophic fungi like *Trichoderma*, *Gliocladium* and *Rhizobacteria*, *Pseudomonas* and *Bacillus* are natural bio-antagonist of *R. solani* (Mannai et al. 2018). Antagonistic rhizobacterial and epiphytic species viz. *B. cereus*, *P. putida*, *B. subtilis*, *Paenibacillus macerans*, *Serratia marcescens*, *B. pumilus* and *P. fluorescens*, compete with and inhibit the growth of *R. solani* (Mamphogoro et al. 2020).

Some fungi viz. *Trichoderma harzianum*, *T. viride* and *Gliocladium virens* control damping off caused by *P. aphanidermatum* and *P. ultimum* in pepper seedlings, showing improved seedling emergence and length up to 25% relative to control, respectively (Sivan et al. 1984; Lumsden and Locke 1989; Mannai et al. 2020). The rhizobacteria, *P. aureofaciens, P. fluorescens*, *P. putida* and *B. pumilus* have been shown to increase the length of the seedlings and biomass in pepper (Hahm et al. 2012). Control of *Pythium* root rot was mostly based on fungicides in the early days (Cook et al. 2009), but there is a growing concern for health issues and ethical considerations. Some of the *Pythium* species themselves have received interest as potential biocontrol agents and include *P. oligandrum*, *P. nunn*, *P. periplocum* and *P. acanthicum*. Different biocontrol measures have been summarized in Table 3.4.

The IPM approach relies on the optimal usage of every applicable management solution to achieve pest management goals with ecologically sustainable goals in mind. A mixed application of cultural, biocontrol and chemical means at minimal levels, often provides much better results than individual applications of each of these crop practices. Usage of chemical controls is discouraged in IPM approaches till necessary. Even in the least preference cases, all reliance is held upon the use of biorational pesticides, with low toxicity, easy degradation and consumption safe doses. Efficacy of such pesticides in most cases is really insufficient to moderate pest populations, but in mixed proportions with other milder pesticides or conventional one, achieves the goals sustainably.

3.4 Genetic Sources of Resistance to Biotic Stresses

Among the 35 characterized species of the genus *Capsicum*, only *C. annuum*, *C. chinense*, *C. frutescens*, *C. baccatum* and *C. pubescens* are widely domesticated.

Table 3.4 The biocontrol methods adopted and their molecular mechanisms in *Capsicum* spp.

Species	Biocontrol species/bioactive compounds	Summary	References
B. cinerea	*B. licheniformis*	–	Márquez et al. (2020)
B. cinerea	*F. oxysporum* f. sp. *lycopersici* (FOL) insoluble protein free fraction	Induction of defense related genes such as chitinase (*CACHI2*), a peroxidase (*CAPO1*), sesquiterpene cyclase (*CASC1*) and basic *PR1* (*CABPR1*)	Veloso and Díaz (2012)
B. cinerea	*Beauveria bassiana*	Antifungal properties against *B. cinerea* infection	Barra-Bucarei et al. (2019)
B. cinerea	Capsaicinoid–N-Vanillylnonanamide	Lateral chain of capsaicinoids has more inhibitory activity than the phenolic part; confers systemic protection to the upper leaves of pepper	Veloso et al. (2014)
Leveillula taurica	Bicarbonate, sulphates and phosphates-KH_2PO_4, $KHCO_3$, $MgSO_4$, $MnSO_4$	Salts control the growth and infection rate probably by disrupting the osmotic balance for the growth of fungus	Dik et al. (2003)
Colletotrichum gloeosporioides	Antimicrobial peptides (AMPs)	Inhibition of trypsin and α-amylase activity of fungi	da Silva Pereira et al. (2021)

(continued)

Major evolutionary and historical events often lead to loss or gain of desired allele copies from domesticated populations. To incorporate novel alleles for disease resistance, breeders have to regularly survey the crop wild relatives (CWRs). Expansion of crop germplasm resources with CWRs is crucial for development of varieties suitable for climate change affected production systems (FAO 2015).

Table 3.4 (continued)

Species	Biocontrol species/bioactive compounds	Summary	References
Colletotrichum coccodes	Compost water extracts (CWEs)	In vitro inhibition of conidial germination and appressorium formation and enhanced expression of PR proteins CaBPR1, CaBGLU, CaCHI2, CaPR-4, CaPO1, CaPR-10	Sang and Kim (2011)
Rhizoctonia solani	*B. subtilis*	Production of fungicidal compounds surfactin, iturin and fengycin	Wu et al. (2019)
F. oxysporum, *F. culmorum*, and *F. moniliforme*	*Beauveria bassiana* (strain NATURALIS) and *Metarhizium brunneum* (strain BIPESCO5)	Antagonize the persistence of crown and root rot	Jaber (2018)
Verticillium dahliae	*Arbuscular Mycorrhizal Fungi (AMFs)*	Balanced antioxidant metabolism in leaves, deposition of higher lignin, induction of new isoforms of chitinases and superoxide dismutases and enhanced *PAL* expression in roots	Goicoechea et al. (2010)
Verticillium dahliae	*B. chitinosporus, B. megaterium, B. pumilus, B. subtilis, B. thuringiensis, P. fluorescens* and *P. putida* induced by Chemicals (IRCs) Bion (BTH), chitosan and salicylic acid	Increase in photosynthetic pigment and Vitamin C	Abada et al. (2018)
Stemphylium solani	*Kluyvera cryocrescens* and *Brevibacterium iodinum*	Activation of defense related *CaPR* and *CaChi2* genes and induction of SAR (Systemic Acquired Resistance) by the whole plant	Son et al. (2014)

(continued)

Table 3.4 (continued)

Species	Biocontrol species/bioactive compounds	Summary	References
Xanthomonas campestris pv. *vesicatoria*	*Ascophyllum nodosum*	Foliar applications of 0.5% *A. nodosum* extract (AN) at 10-day intervals resulted in significant ($p < 0.05$) increase in plant growth parameters, including plant height (40%), leaf number (50%), plant dry biomass (52%), root length (59%) and chlorophyll content (20%) compared to control	Ali et al. (2019)

Table 3.5 summarizes the various viral pathogens affecting *Capsicum* spp. under broad classes along with their symptoms and the available sources of resistance against each viral organism. In Florida, the asexual stage of *S. solani* was used to infect 33 breeding lines of pepper in order to study their pathogenicity, and it was found that all plants were susceptible (Blazquez 1971). Early screening for pepper resistant varieties were done in Korea where 467 accessions of peppers were screened for their resistance to *S. solani* and *S. lycopersici* (isolated separately). Accessions KC320, KC220, KC208, KC47 (PI244670), KC43 (PI241670), KC380 and KC319 showed highest resistance to both the pathogens (Cho et al. 2001). *S. solani* and *S. lycopersici* (Enjoji) Yamamoto were identified in the northern provinces of Korea, Gyoengbuk and Gangwon (Kim et al. 2004), and were reported to be prevalent since 1994.

Two *C. annuum* lines 'Perennial' and 'Vania' showed no symptoms upon CMV inoculation but the yield and specific infectivity of the virus was lower when extracted from Perennial than from Vania (Nono-Womdim et al. 1993). The Indian hot pepper accession Perennial was used to develop CMV resistant pepper varieties which were able to recover from high viral titers (Lapidot et al. 1997). The inheritance was found to be polygenic and incompletely dominant. A *C. frutescens* accession, BG2814-6, represented incomplete penetrance of resistance towards six isolates of CMV via at least two recessive genes (Grube et al. 2000a). The resistance to CMV_{KOREAN} and CMV_{FNY} strains is controlled by a single dominant gene *Cucumber mosaic resistance 1* (*Cmr1*) in *C. annuum* with three single nucleotide polymorphisms (SNP) markers linked to this gene (Kang et al. 2010). Hybrids—PBC1354 and PBC378 were crossed

Table 3.5 The various viral pathogens under broad classes affecting *Capsicum* spp. along with their symptoms. The available sources of resistance against each viral organism in *Capsicum* germplasm have also been listed

Virus	Symptoms	Sources of resistance		
		Accession	Species	Reference(s)
Thrips trasmitted orthotospovirus				
Tomato spotted wilt virus (TSWV)	Chlorotic and necrotic rings on leaves, stunting	PI 159,236 (CNPH 679) x Magda (CNPH 192), PI 152,225, Panca, AC09-207, ECU-973, PIM261, AVRDC C00943	*C. chinense* x *C. annuum, C. baccatum*	Boiteux and de Ávila (1994), Cebolla-Cornejo et al. (2003), Sherwood et al. (2003), Hoang et al. (2013), Soler et al. (2015)
Tomato chlorotic spot virus (TCSV)	Chlorosis, necrosis, mottle/mosaic, bronzing	–	–	Batuman et al. (2014)
Capsicum chlorosis virus (CaCV)	Necrotic ringspot, leaf mottling	–	–	–
Groundnut bud necrosis virus (GBNV)	Mosaic with ringspots and necrosis	IIHR4360, IIHR4577, IIHR4578, IIHR4582, IIHR4585, IIHR4587, IIHR4588 and EC631810	*C. annuum*	Pavithra et al. (2020)
Groundnut ringspot virus (GRSV)	Ringspots, chlorotic and necrotic areas	–	–	–
Aphid trasmitted potyvirus				
Potato virus Y (PVY)	Mosaic, mottling	PI2664281, SC46252	*C. annuum*	Kyle and Palloix (1997)
Tobacco etch virus (TEV)	Vein clearing, chlorotic and necrotic spots	–	–	–
Pepper yellow mosaic virus (PepYMV)	Leaf curling, yellow green mosaic, fruit deformation	UENF 1616 × UENF 1732	*C. baccatum*	Bento et al. (2013)
Chilli veinal mottle virus (ChiVMV)	Leaf mottling, mosaic, mottle, yellow vein banding	CV3, CV8 and CV9	*C. annuum*	Shah et al. (2009), Tsai et al. (2008), Lee et al. (2017)

(continued)

Table 3.5 (continued)

Virus	Symptoms	Sources of resistance		
		Accession	Species	Reference(s)
Pepper veinal mottle virus (PVMV)	Foliar chlorosis, rugosity, mosaic, vein banding	–	–	–
Aphid trasmitted cucumovirus				
Cucumber mosaic virus (CMV)	Mosaic-mottling, necrosis, yellow ringspots, leaf deformation, stunting	Punjab Lal, Perennial, BG-2814–6	*C. annuum, C. frutescens*	Bal et al. (1995), Nono-Womdim et al. (1993)
Contact trasmitted tobamoviruses				
Pepper mild mottle virus (PMMoV)	Mottling, chlorosis, curling, stunting	PI159236, CM334, 9093	*C. chinense*, *C. annuum*	Venkatesh et al. (2018)
Paprika mild mottle virus (PaMMV)	Yellowing, light and dark green mottling	–	–	–
Pepper severe mottle virus (PepSMoV)	Mosaic, leaf deformation	–	–	–
Tobacco mosaic virus (TMV)	Mosaic, mottle, necrosis, yellowing, stunting	PI315008, PI315023, PI315024	*C. chinense*	Boukema (1980), Scholthof (1997)
Whitefly transmitted geminivirus				
Pepper leaf curl virus (PepLCV)	Stunted growth, upward leaf curling, crowding of leaves, swelling of veins, puckering of intervenous regions, blistering	GKC-29, BS-35, Bhut Jolokia, EC-497636, Japani Longi, Punjab Lal, Pant C-1, S-343, SL 456, SL 475, DLS-Sel-10, WBC-Sel-5, PBC-142, BJ001	*C. chinense, C. annuum*	Kumar et al. (2006), Rai et al. (2014), Srivastava et al. (2017), Thakur et al. (2018, 2019, 2020)
Tomato yellow leaf curl virus (TYLCV)	Curling and yellowing	–	–	–
Pepper golden mosaic virus (PepGMV)	Interveinal chlorosis of young leaves, apical necrosis	BG3821, BG3820, BG3819	*C. chinense, C. annuum*	Anaya-López et al. (2003), Holguín-Peña et al. (2008), García-Neria and Rivera-Bustamante (2011)

(continued)

Table 3.5 (continued)

Virus	Symptoms	Sources of resistance		
		Accession	Species	Reference(s)
Pepper huasteco yellow vein virus (PHYVV)	Yellowing of veins, mosaic, leaf curl, stunting	BG3821, BG3820, BG3819, UAS12, El Reparo, Yecorato	*C. chinense, C. annuum*	Hernández-Verdugo et al. (2001), Holguín-Peña et al. (2008), García-Neria and Rivera-Bustamante (2011)

with CMV tolerant parents to generate fifteen backcross populations, which were characterized for morphological traits and CMV resistance. Nine genotypes including B3A29-13, B3A24-20, B3A29-22, B3B12-13, B3B12-25, B3B37-9, B3C16-16, B3C16-5 and B3C16-5, and six genotypes including B3D11-17, B3D11-8, B3D12-17, B3D38-5, B3E31-19 and B3E20-22 resembled the two parents, PBC378 and PBC1354 in tolerance to CMV, respectively (Herison et al. 2012). A single recessive *CMV resistance gene 2* (*cmr2*) was identified which provides resistance to CMV-P1 along with other pathotypes (Choi et al. 2018).

Eight *C. annuum* genotypes from Karnataka (India) showed a HR to *Groundnut bud necrosis virus* (GBNV) without systemic infection and can be utilized as natural sources of resistance in breeding programs (Pavithra et al. 2020). The wild *C. annuum* populations from El Reparo and Yecorato region of Northwest Mexico showed neither the presence of viral DNA nor any symptoms upon mechanical and biolistic inoculation of *Pepper huasteco virus* (PHV) (Hernández-Verdugo et al. 2001).

Genes that provide broad spectrum resistance to viruses in *Capsicum* have been studied using genetic analysis. Two genes—*Pr4* (dominant) and *pr5* (recessive) provide resistance to all the known and common strains of PVY, respectively, in *C. annuum* variety 'Serrano Criollo de Morelos 334' (SCM334), while another dominant gene *Pn1* is involved in systemic necrotic response (Dogimont et al. 1996). Afterwards, the potyvirus resistance genes were designated by the symbol *pvr* followed by chronological order of the identified locus, and alleles at the locus were differentiated using subscripts (Kyle and Palloix 1997). The recessive allele *pvr2* provides resistance to PVY strains—$pvr2^1$ to PVY-0 and $pvr2^2$ to PVY-0 and PVY-1, respectively, and encodes a translation eukaryotic initiation factor 4E (*eIF4E*) in pepper (Ruffel et al. 2002). It was reported that *eIF4E* interacts with the potyviral genome-linked protein (VPg) to cause viral production and breaking of resistance during potyvirus infection (Léonard et al. 2000). Mutations in the *eIF4E* lead to incompatibility in host-virus interaction, without compromising the plant life cycle and resistance systems against several RNA viruses (Lellis et al. 2002).

3.5 Breeding Objectives and Methods

Chili pepper is becoming an increasingly important crop for being both a vegetable and a spice crop with diverse applications and considerable socio-economic importance. Keeping these points in mind a comprehensive strategy must be evolved which has a guided purpose to serve the objectives of pepper breeding in order to obtain genotypes that meet the demands of the growers and consumers. While briefly touching upon its use as a flavoring agent, as a reservoir of antioxidants and nutraceuticals, a vegetable and many other uses due to its great therapeutic value, the principal focus of this chapter is on the aspect of breeding for biotic stress resistance.

The highly versatile nature of pepper crop makes it adapted to very divergent conditions of cultivation as well as cultural practices, leading to entirely exclusive preferences in terms of end usage. Preferences of the pepper growing countries and assorted cultures for hot or sweet pepper varies, leading to totally isolated domestication paths; hence, a suitable breeding strategy has to be accountable to address those specific needs by choosing most acceptable parental pools.

Resistance breeding has been emphasized for the need of *Capsicum* breeding. Identifying the suitable resistant hosts as well as focusing on pathogens is extremely important in *Capsicum* as there is a very broad spectrum of choices to make owing to very rich and diverse morphologies. Some earlier work on the classification of major *Capsicum* pathogens is discussed in details in Sect. 3.2. Identifying and understanding the genetics and crossability of novel (wild sources) or established (characterized lines) resistance sources with host is a very vital step to achieve effective introgression of desired characters.

Several diseases of interest in the present scenario have been successfully addressed by utilization of wild resistance sources. Many viral, fungal and bacterial diseases, and pests such as whiteflies, thrips, mites and nematodes have been characterized for their source of plant resistance genes involved in important defense complexes. Two important aspects need to be clearly established before designing a resistance breeding program, by making a distinction between the qualitative as well quantitative nature of trait of interest, and to understand linked traits by sourcing inputs from genetic mapping and verification with suitable markers, as undesirable traits are also very likely to introgress, especially when the source is a wild relative. Further, it should be equally important to have continuous efforts to track resistance breaking pathogens along with a constant search for novel resistance sources.

Other major objectives with indirect relationship to biotic stresses are yield, marketability traits such as colour, aroma, flavour etc., desired chemicals, pungency, oleoresin, flavonoids etc. However, the major breeding objective of *Capsicum* breeding is to increase overall productivity by increasing yields and secondary morphological traits such as branching habits, height, nutrient use efficiency and stress tolerance. Heterosis breeding programs are gaining popularity in *Capsicum* breeding as a targeted solution to multiple end goals. Targeted efforts made in the identification of male sterility-based hybrid development systems will be very useful in saving time as well as labour. For hybrid seed development, both kind of

male sterility systems—genetic (GMS) and cytoplasmic (CMS) have been utilized in *Capsicum* breeding. The CMS system which is being widely explored in *Capsicum* breeding is mainly dependent on the well characterized maintainers as well as diversified germplasm. Priority areas in the development of CMS based hybrids will consist of identification of suitable restorer lines with good general and specific combining ability, and exploiting them by introgressing resistance genes for easy transferability.

Capsicum is a vegetable crop also revered for its ornamental properties, and accessory features such as fruit colour, fruit length, and overall glossiness also play an important role in marketability and consumer preferences. Along with the features promoting the economic value, there are several other horticultural and biochemical traits demanding a breeder's attention, e.g., pungency, which is an important commercial attribute in peppers and is mainly governed by capsaicinoid complexes. Most abundant capsaicinoids are capsaicin and dihydrocapsaicin, while 71% of pungency in all varieties is a manifestation of capsaicin alone (Kosuge and Furuta 1970). Total capsaicin content is an important quality parameter of breeder's interest in the development of new commercial varieties.

Effective breeding for fruit dry matter content refers to improvement in the powder formation qualities as well as color and pungency. Major characteristics desirable for export quality produce include high dry matter content, but in practice there is no positive correlation between the capsaicin levels and dry matter obtained (Dhall 2008). The thin pericarp of fruits assures quicker drying times, while thick skin fruits are severely shriveled and dull upon visual inspection after drying. A growing trade among countries enforces certain quality standards, which are always to be met with locally available and adapted germplasm for inclusive growth of all stakeholders. Genomic designing along with improved breeding practices can assure uniformity and desired throughput in emerging climate change scenarios, and stresses.

Blocky fruit shape and colour variations at unripe stages of sweet peppers are also a desired objective of *Capsicum* breeding. Sweet peppers are primarily consumed for their high levels of antioxidants and vitamins, such as ascorbic acid, flavonoids and phenolic compounds, carotenoids including vitamin A precursor like alpha and beta-carotene, beta-cryptoxanthin (Tomlekova et al. 2009). Sweet pepper breeding traits of secondary importance include stability and sustainability of carotenoids content unaffected by the photooxidation damages and varied storage conditions. Multiple pathogens infecting the sweet peppers include *Phytophthora*, anthracnose, viruses, and bacteria under field conditions. Therefore, breeding for genotypes with wider adaptability is highly desirable for cold as well as tropical climates to ensure the survival of crop in areas with excessive biotic and abiotic stresses, and also for the expansion of pepper crop to non-traditional areas. Under protected and curated conditions, many of the field stresses become obsolete, and traits including indeterminate growth habits, manageability to training and pruning, marketable fruit shapes such as blocky, and resistance to soil borne pests such as nematodes are therefore the major goals (de Swart 2007).

3.5.1 Traditional Breeding Methods

Mendelian principles of heredity and inheritance have been the leading concepts in resistance breeding throughout the past century. Acknowledging critical limitations of classical breeding methods is however the need of hour under changing climatic conditions and biotic factors outpacing our crops. Traditional breeding is the art and science of aggregating all favorable traits in a plant from two compatible parents. Mass selection, pedigree selection, single seed descent, recurrent selection and backcrossing are the common breeding methods. Selection is the most vital and distinguishing aspect of conventional versus modern breeding methods. Few notable limitations to conventional methods while breeding for biotic stress resistance are as follows: (1) a disconnect of genotype vs. phenotype: conventional breeding selection cycles heavily depend upon the major traits where, gene x environment interactions govern the final phenotypes, but environment components are nearly impossible to account for without compromising significant error margins and thus create a lot of inherent selection bias, thus allowing undesired genes; (2) hybridization to achieve heterosis is the common goal with expectation of a fair introgression of desired traits, particularly sexually incompatible crosses give undesirable results due to linkage drag, disrupting the Mendelian assumptions, and therefore very limited control on the process can be achieved via conventional means; (3) lack of control over the expression in crossed progenies is also a major concern with conventional approaches, in resistance breeding it is often desirable to completely express an introgressed gene complex.

The major objectives in breeding of pepper genotypes focus on yield, earliness and vigor, superior fruit quality, resistance against pathogens, and high stress tolerance. Classical plant breeding techniques have proven to be very useful for improvement of pepper crop for yield and quality traits as well as enhancing disease resistance properties. Traditional breeding involving the use of various crossing schemes and periodic selection of suitable plants reflecting traits of interest, is mostly based upon easily recognizable morphological characters.

Among some of the classical methods exploited in *Capsicum* breeding, mass selection which is based on phenotype of traits with high heritability has been used by some breeding groups in Portugal and Brazil. In comparison, the pedigree method based on hybridization was used to breed the cultivars, BRS Sarakura and BRS Garça, adapted to Central Brazil (Carvalho et al. 2009). The backcross method was used to transfer virus resistance from *C. chinense* to *C. frutescens* (Greenleaf 1986). Recurrent selection, which can be used to select traits of low heritability was used by Palloix et al. (1990a, b) in the development *C. annuum* genotypes showing resistance against *V. dahliae* and *P. capsici*. The single seed descent method for the development of recombinant inbred lines (RILs) was employed by Moreira et al. (2013) to obtain *Capsicum* lines resistant to bacterial spot, and by Villalon (1986) to fix recessive genes conferring resistance to potyvirus.

Of the several plant breeding procedures, heterosis breeding is expected to play a crucial role in increasing the yield of pepper crop and improving other important

traits with commercial value. In heterosis breeding, genetically diverse inbred lines of chili showing good combining ability are utilized. Two cultivars, Branang (resistant) and Lembang1 (susceptible) were crossed and their F_1 hybrid was analyzed for *CaChi2* gene expression patterns after infection with *F. oxysporum*. Results showed an increased expression in the F_1 hybrid by qRT-PCR (Ferniah et al. 2018). JNA2 × ACB1 × 9608D and Rajaput × P3 hybrid lines were obtained by Maruti et al. (2014) against *F. solani*. Monogenic and dominant resistant lines were also observed in the hybrids—SNK × P3, KA2 × P3, and RAJPUT × P3 (Manu et al. 2014). Good sources of resistance against *F. verticillioides* and *F. pallidoroseum* viz. Masalawadi, SC-120, Phule C-5, SC-335, SC-415, SC-1 07, SC-348, SC-108, LCA-304, Arka Lohit, Pusa Jwala and Pant C-2 for *C. annuum* are also available (Khan et al. 2018).

3.5.2 *Limitations of Traditional Breeding and Rationale for Molecular Breeding*

Traditional breeding methods have generated many useful results in terms of better varieties and a knowledge-base of mapping information. However, there are some major limitations of these methods. Classical plant breeding methods require longer periods and several generations for identifying useful genotypes. The basis of selection in traditional breeding is always on major phenotypic traits, which as they allow rapid visual selections, but on the other hand they fail badly for identification of undesirable genes, which in later cycles of selection may reappear or even remain unidentified for whole breeding cycles. Another important issue relates to the problematic incompatible crosses, e.g., across genera. Such morphological as well physiological barriers are hard to overcome.

In contrast, molecular breeding allows selection for both qualitative and quantitative traits at all stages of plant's life cycle and thus reduces the time required for accurate phenotyping of a plant. It also allows identification of undesirable genotypes, which can be easily eliminated by marker-assisted selection (MAS). Furthermore, as molecular markers are not affected by the environment, selection can be undertaken in all types of environmental settings—greenhouses, nurseries or field conditions. Thus, traits that are conditional upon favorable conditions of a particular environment, e.g., disease/pest resistance and stress tolerance, can also be selected with precision. Genomic designing of modern stress resistant crops involves precise selection with the help of genetic markers and genetic maps. Polygenic traits with known linkages can be efficiently mapped and targeted via simple and accessible genetic markers. Genetic maps of fine details are nowadays a reality achieved via incremental steps of progress, and a vast body of work generated with markers such as RFLP, RAPD (as low resolution), SSRs as (mid-resolution) and SNP markers with the finest resolutions to aid in the screening and selection stages of breeding programs. Robust genotyping possibilities allow efficient and guided understanding of linkage patterns at genome wide scales and help find associations such as QTLs

and/or through association mapping of traits of interest. Genomic designing is therefore the way forward for *Capsicum* crops with modern biotechnological tools such as restriction enzymes-based engineering, transgenics as well as pyramiding of genes of interest.

3.6 Molecular Genetics and Breeding of Biotic Stresses Related Traits

The *L* locus genes (*L3* and *L4*) which provide resistance to PMMoV in *Capsicum* spp. have been widely used in breeding programs. Several DNA markers closely linked to the *L4* genes have been screened for their applications in cost and time effective selection of markers in the PMMoV-resistance breeding (Kim et al. 2008a; Matsunaga et al. 2003). Resistance allele *L1a* was found to be involved in PaMMV (Japanese strain) resistance in bell pepper (Sawada et al. 2004). Unlike the other *L* alleles, *L1a* is temperature insensitive and is elicited by the viral coat protein of the P_0 pathotype of tobamoviruses (Matsumoto et al. 2008). *Pr4* (*Pvr4*) gene also provides resistance to all the known pathotypes of PeMV (Dogimont et al. 1996). Cleaved amplified polymorphic sequence (CAPS) markers for three recessive alleles of *pvr* locus—*pvr*, $pvr1^1$ and $pvr1^2$ on chromosome 3, were developed for selection of potyvirus resistance in *Capsicum* (Yeam et al. 2005).

Salicylic acid accumulation and reactive oxygen species (ROS) production were induced in PepGMV and PHYVV resistant BG3821 pepper plants carrying at least two genes with recessive epistatic effects (García-Neria and Rivera-Bustamante 2011). Three *C. annuum* varieties—DLS-Sel-10, WBC-Sel-5 and PBC-142 were found to be resistant to leaf curl causing begomoviruses (Srivastava et al. 2017). Genetic inheritance of PHYVV resistance in three wild pepper varieties from Mexico—UAS12, UAS13 and UAS10 showed that at least two genes govern the PHYVV resistance (Retes-Manjarrez et al. 2017). The *C. annuum* line, UAS12 showed high resistance towards PHYVV with lesser symptoms, longer incubation time, lower viral DNA levels and stable inheritance, and therefore can be a promising genetic resource for pepper improvement programs against begomoviruses (Retes-Manjarrez et al. 2018). Resistance for LCVD in a population developed from a cross between resistant DLS-Sel-10 and susceptible Phule Mukta pepper varieties was found to be monogenic recessive (Maurya et al. 2019). The phenolic content and peroxidase (POD) activity in resistant pepper variety 9853–123 was observed to be higher than the susceptible variety (KKU-P31118) upon PepYLCThV inoculation (Thailand) (Kingkampang et al. 2020). At least 7 genes, including *Pvr4* control the resistance to PepYMV in *C. baccatum* (Bento et al. 2013). Sixteen RILs in the F_6 population of the *C. baccatum* var. *pendulum* were resistant for PepYMV when tested via phenotyping and agronomic performance. A highly resistant line did not give good agronomic performance, while four other lines were resistant and productive, and suitable for field tests in resistance breeding programs (da Costa et al. 2021).

3.6.1 *Genetic Mapping in* Capsicum *Spp.*

Interspecific variability among 21 accessions of cultivated and wild pepper (*C. annuum*, *C. baccatum*, *C. chacoense*, *C. chinense* and *C. frutescens*) and later on intraspecific variability was examined among four *C. annuum* cultivars (NuMex R Naky, Jupiter, Perennial and Criollo de Morelos 334) to study DNA polymorphisms utilizing restriction fragment length polymorphism (RFLP) and random amplified polymorphic DNA (RAPD) markers. Important findings suggested that any two pepper accessions can be utilized as parents to create a good segregating population for RFLP analysis (Prince et al. 1995).

A genetic map of *Capsicum* spp. based on an intra specific cross was developed with a total length of 720 cM. The map was based on 192 molecular markers consisting of RFLP and isozymes, and comprised of 19 linkage groups. At least a genetic distance of 228 cM (31.7%) covered by the markers reflected a high level of conservation with respect to the tomato genome in terms of order (Prince et al. 1993) (Table 3.6). Authors also concluded that the mechanism for genome evolution in Solanaceae is primarily via centric fusions and resulting chromosome breakage events.

RFLP and RAPD markers were also utilized to construct an intraspecific linkage map of segregating doubled haploid (DH) progenies. Spanning an approximate length of 820 cM, a total of 85 markers were mapped on to 18 linkage groups which were assigned to 4 chromosomes eventually (Lefebvre et al. 1995). Genes responsible for fruit pungency were precisely located; meanwhile segregation data also labelled the genomic regions with evident segregation ratios favouring particularly big fruited parents, suggesting available selection of DH progenies for mapping. Also, two new genes of breeder's interest for controlling hypersensitive resistance to TMV and controlling the erect growth of fruits were located (Lefebvre et al. 1995).

Tomato specific probes were utilized to create a genetic linkage map from an interspecific F_2 population in *Capsicum*, with a total coverage of 1,245.7 cM. Eleven large (76.2–192.3 cM) and two small (19.1 and 12.5 cM) linkage groups were identified. Comparisons with genetic maps of tomato reflected a high degree of conservation, and 18 homologous linkage blocks covered 98.1% of tomato and 95.0% of the pepper genome (Livingstone et al. 1999).

An intraspecific consensus map of *C. annuum* was constructed using three populations comprising 215 DH lines and 151 F_2 individuals. Each individual map comprised 16 to 20 linkage groups with lengths ranging from 685 to 1,668 cM. The consensus map contained 100 known functional gene markers as well as loci of plant breeder's interest such as disease resistance locus *L*, *pvr2*, *pvr4* and *C* locus determining capsaicin content and the erect fruit locus. Additional linked loci related to disease resistance such as *Tsw*, *Me3*, *Bs3* and *Y* locus for fruit color were also identified in the same study (Lefebvre et al. 2002).

RILs of PSP11 (susceptible) crossed with PI201234 (resistant), and F_2 lines of Joe E. Parker (susceptible) × CM334 (resistant) were used to create two independent linkage maps. The RIL map spanning a distance of 1,466.1 cM consisted of a total

Table 3.6 The mapping populations and genetic markers used for the development of genetic maps*Capsicum* spp

Population	Markers	References
Interspecific F_2 Hybrid from *C. annuum* (CA133) X *C. chinense* (CA4)	RFLP and Isozymes (192)	Prince et al. (1993)
Three intrapsecific *C. annuum* DH populations	RFLP and RAPD (85)	Lefebvre et al. (1995)
(*C. annuum*) BG 2816 (*frutescens*) derived Interspecific BC2 population constructed by crossing the C. annuum cv. Maor (recurrent parent) with A C. frutescens wild accession BG 2816	RFLP (92)	Rao et al. (2003)
Intrapsecific C. annuum F_2 *population derived from* CM334/Chilsungcho cross	RFLP (202), WRKY (6), SSR (1)	Kim et al. (2008a)
Populations derived from cross between ChiVMV resistant and susceptible varieties	SNP (1466)	Lee et al. (2017)
C. annuum (DLS-Sel-10 x Phule Mukta)	–	Maurya et al. (2019)
Intraspecific C. baccatum F_2 *population derived from a cross between UENF 1616 (female parent) and UENF 1732*	SSR (42), ISSR (85), RAPD (56)	Moulin et al. (2015)
Interspecific F_2 *population derived from crossing C. annuum (TF68) and C. chinense (Habanero)*	EST-SSR (150)	Yi et al. (2006)
Doubled haploid C. annuum population derived from crossing California Wonder and LS2341	SSR (106), AFLP (253)	Mimura et al. (2009, 2010)
F_2 mapping population derived from a cross between the inbred lines BA3 (*C. annuum*)and YNXML (*C. frutescens*)	SSR (95)	Tan et al. (2015)
F_2 mapping population developed by selfing the F_1 hybrid of the inbred lines FL201 (*C. annuum*) and TC 07245 (*C. galapagoense*)	SSR (400)	Arjun et al. (2018)

of 144 markers including 91 Amplified fragment length polymorphism (AFLPs), 34 RAPDs, 15 SSRs, 1 SCAR and 3 morphological markers (erect fruit habit, elongated fruit shape, and fasciculate fruit clusters) across 17 linkage groups. Meanwhile, F_2 map covered a total of 1,089.2 cM with 113 markers (51 AFLPs, 45 RAPDs, 14 SSRs and 3 SCAR) distributed across 16 linkage groups (Ogundiwin et al. 2005).

A linkage map with a total genetic length of 54.1 cM was constructed with 7 AFLP and one CAPS marker. AFLP markers detected by bulked segregant analysis of 8 markers were linked to fertility restorer locus (Rf), while one AFLP marker (AFRF8) was converted to CAPS marker in this study. The AFRF8 CAPS marker was located close to the *Rf* locus within a genetic distance of 1.8 cM (Kim et al. 2006a, b).

A RIL population consisting of 297 individuals was used to construct a high-resolution intra-specific linkage map of *C. annuum* using the parents 'Yolo Wonder' and CM334 as source of resistance to a number of diseases. A total of 587 markers (507 AFLP, 40 SSR, 19 RFLP, 17 sequence-specific amplified polymorphisms, and 4 sequence tagged sites) were used, which assembled into 49 linkage groups. With an average inter-marker distance of 5.71 cM, spanning over 1,857 cM, 69% markers covering 1,553 cM were assigned to 1–12 chromosomes, while 26 LGs remained unassigned (Barchi et al. 2007).

An integrated map developed from four genetic maps of two interspecific (*C. annuum* 'TF68' and *C. chinense* 'Habanero') and two intraspecific (*C. annuum* 'CM334' and *C. annuum* 'Chilsungcho') populations of pepper, was construed using 169 SSR, 354 RFLP, 23 STS from BAC-end sequences, 6 STS from RFLP, 152 AFLP, 51 WRKY, and 99 rRAMP markers on 12 chromosomes of *Capsicum.* A total map distance of 1,858 cM with 805 markers for interspecific population, and a total map distance of 1,892 cM with 745 markers were covered in the intraspecific population (Lee et al. 2009a, b).

A total of 288 conserved orthologous set II (COSII) markers spanning 12 linkage groups which corresponded to 12 chromosomes were characterized. Aforementioned map represented genomes of cultivated *C. annuum* and wild *C. annuum* as well as other related *Capsicum* spp. differing by reciprocal chromosome translocations. This high resolution COSII map identified 35 conserved syntenic segments (CSSs) between tomato and pepper, wherein gene/marker order was well-preserved (Wu et al. 2009).

The *C. baccatum* genetic map of the F_2 population (203 progenies) was constructed based on 42 SSR, 85 inter-simple sequence repeat and 56 RAPD markers. A total of 12 major and 4 minor linkage groups covering a total genome distance of 2,547.5 cM, with an average distance of 14.25 cM in between markers were inferred from the map. Sixty-two SSR markers out of 152 already available for *C. annuum* were successfully transferred to *C. baccatum*, generating polymorphisms of which 42 were directly mapped, allowing further studies with other members of the genus *Capsicum* (Moulin et al. 2015).

3.6.2 Molecular Mapping of Biotic Stress Related Loci

Marker-assisted selection (MAS) has proved to be a very useful technique in classical as well as the post genomic era. Breeding objectives turn towards finer traits as molecular information about traits of interest stack up. The ability to do so for selection even before plants see the field saves a lot of screening time and personal human biases while evaluating major morphological traits. In *Capsicum,* MAS has been successfully utilized for biotic stress resistance breeding. Available marker resources can be effectively utilized in MAS since well-characterized and markers tightly linked with the locus of interest are very effective at narrowing down selection and screening efforts.

In Solanaceae, resistant genes were found only for tomatoes at the *Ve* locus. The linked genes, *Ve1* and *Ve2* in the locus cause H_2O_2, peroxidase and *PAL* expression in the roots of inoculated plants (Gayoso et al. 2010). Further, in *Capsicum* (New Mexico variety), an ORF (open reading frame) was identified by WGS (whole genome sequencing) with homology to the *Ve* locus of tomato. Sixteen SNPs were identified between the resistant and the susceptible cultivars (Barchenger et al. 2017). A CAPS marker developed from the coding region of *CaVe* was used to screen diverse germplasm that was resistant to Verticillium wilt. The CAPS marker could identify accessions with resistance against the New Mexico *V. dahliae* isolate with 48% accuracy.

A partially dominant gene *L* has been identified, isolated and employed for broad resistance to Tobamoviruses like TMV, ToMV and PMMoV in pepper breeding programs. Different alleles of the *L* locus on chromosome 11 determine the resistance for TMV strains in five *C. chinense* accessions (Boukema 1980). The major alleles at the *L* locus—L^1, L^{1a}, L^{1c}, L^2, L^{2b}, L^3 and L^4 have different resistance spectra determined by multiple sub-regions of the leucine rich repeats (LRR) domain of the L proteins in *Capsicum* spp. (Tomita et al. 2011). The *L3* and *L4* were suggested to be closely linked genes instead of different alleles based on SNP markers (Yang et al. 2009). The mutation studies demonstrated that the functional coat protein, and not the viral RNA is required to induce the L^2 allele mediated HR in resistant *Capsicum* varieties (de la Cruz et al. 1997). L^3 gene was able to provide resistance to most of the Tobamoviruses including PMMV-S isolate, to which a local hypersensitive response is induced in *Capsicum* plants (Berzal-Herranz et al. 1995). *L* allele specific markers like L4segF&R have been developed based on the LRR region of the L^4 allele, which however did not completely segregate with the L^4 allele (Yang et al. 2012).

The *Pvr4* from *C. annuum* CM334 and *Pvr7* from *C. chinense* variety PI159236 provide completely dominant resistance to PepMoV. Eight AFLP markers linked to the *Pvr4* gene were mapped and a tightly linked codominant marker was converted into CAPS marker using sequence alignment of the allelic sequences (Caranta et al. 1999). The molecular mapping of *Pvr7* gene from *C. annuum* resistant variety '9093' using SNP markers of *Pvr4* region and further sequence analysis revealed that *Pvr4* and *Pvr7* are the same genes on chromosome 10 (Venkatesh et al. 2018).

The dominant, additive and epistatic effects were observed for the genes responsible for ChiLCV resistance in the F_1 and F_2 population of a cross between *C. annuum* L. and *C. frutescens* L. (Anandhi and Khader 2011). Pepper genotypes were screened using artificial inoculation in a microarray and a recessive monogenic inheritance pattern against PepLCV was revealed in Bhut Jolokia (*C. chinense*) (Rai et al. 2014). Three *C. annuum* genotypes—S-343, SL 456 and SL 475 were tested for ChiLCV resistance using natural and artificial inoculation that was found to be controlled by a single dominant gene (Thakur et al. 2019). Two SSR markers, *Ca516044* and *PAU-LC-343–1* were found to be linked to the ChiLCV resistance gene on chromosome 6 of the pepper genome (Thakur et al. 2020). *Solanum pseudocapsicum* was found to be a symptomless carrier of ChiLCV when field tested for ChiLCV resistance via inoculation challenge and could therefore serve as a source of resistance for pepper species (Srivastava et al. 2021). Nine *Capsicum* genotypes were screened for ChiLCV resistance and three genotypes exhibited lower viral incidences—Punjab Lal, Pant C-1 and Japani Longi (Singh et al. 2021). The combination of two recessive alleles—*pvr6* and *pvr2*[2] provided complete resistance to PVMV (Caranta 1997).

A new source of resistance in the form of a single dominant resistance gene at the ChiVMV locus was discovered linked to two AFLP and one CAPS marker on chromosome 6 in *Capsicum* spp. (Lee et al. 2013). Further, three ChiVMV resistance genes—single dominant gene *Cvr1* on chromosome 6, single recessive gene *cvr4* and one oligogenic resistance gene—*Cvr2-1* and /*Cvr2-2* on chromosomes 6 and 10, respectively, were identified using population analysis in four *Capsicum* varieties from Hong Kong (Lee et al. 2017).

A RFLP based linkage map derived from F_2 generation (100 lines) of a cross of *C. annuum* cv. CM334 and *C. annuum* cv. Chilsungcho detected a QTL associated with *Phytophthora capsici* resistance (Kim et al. 2008b). Bulked segregant analysis performed with 400 RAPD markers identified three capsaicinoid content related loci that could distinguish the two bulks in *Capsicum.* QTL mapping for individual and total capsaicinoid content detected a major QTL, which could explain more than 30% of the phenotypic variation for this trait (Blum et al. 2003). Four disputed *C. annuum* samples were differentiated with 17 Inter-simple sequence repeat (ISSR) markers (Kumar et al. 2001). An intraspecific F_2 population of *C. baccatum* var. pendulum and *C. baccatum* 'Golden-aji' was used for QTL identification for anthracnose resistance with 175 AFLP markers (Kim et al. 2010). A total of 197 AFLP markers were developed in the introgression population of *C. annuum* cv. SP26 and *C. baccatum* cv. PBC81 to identify QTLs for resistance against anthracnose caused by *C. scovillei* and *C. dematium* (Lee et al. 2010). Genetic variability was studied in six *Capsicum* spp. with the help of 8 ISSR markers (Thul et al. 2012).

A total of 95 SSR markers were validated against a genetic map developed using *C. annuum* cv. BA3 and *C. frutescens* cv. YNXML. The map was used to identify the QTLs for initiation of flower primordia (Tan et al. 2015). A total of 28 SSR markers were mapped in the F_2 population of a cross between *C. annuum* cv. FL201 and *C. galapagoense* cv. TC07245, from a survey panel of 400 SSR markers (Arjun et al. 2018). The molecular markers developed in pepper populations are summarized in Table 3.7. To effectively characterize the potyvirus resistance locus recessive alleles

Table 3.7 The molecular markers and their respective linked loci in *Capsicum* mapping populations for viral resistance

Population	Marker	Linked locus	Derived from	References
F_2 progenies developed from a cross between *C. annuum* L. cv. 'Yolo Wonder' and an accession Criollo de Morelos 334 (CM334)	AFLP and CAPS	*Pvr4*	AFLP (E41/M49-645)	Caranta et al. (1999)
F_2 progenies developed from a cross between a *C. frutescens* accession (PI 195301) and a *C. chinense* accession (PI 152225)	RAPD and CAPS	*TsW*	RAPD ($OPAC10_{593}$)	Moury et al. (2000)
F_2 population derived from a cross between *C. annuum* inbred variety (Maor) and a *C. frutescens* line (BG 2816)	RFLP and CAPS	*C* locus	RFLP (TG 205)	Blum et al. (2002)
Germplasm representing C. annuum and C. chinense	CAPS	*Pvr1* + , *pvr1*, $pvr1^1$, $pvr1^2$	Sequences of exon1, exon2, and intron1 at the *Capsicum pvr1* locus	Yeam et al. (2005)
F_2 segregating population of *C. annuum* developed from a cross of TS502 (CMS line) and HK6T (Restorer line)	AFLP and CAPS	*Rf*	AFLP (AFRF8)	Kim et al. (2006a)
F_2 mapping population consisting developed by crossing PepMoV-resistant *C. annuum* '9093' and the PepMoV-susceptible *C. annuum* 'Jeju'	SNPs	*Pvr7*	SNP-H2.3 and SNP-H1.7	Venkatesh et al. (2018)
F_2 population derived from pepper CMS line BA3 and restorer line B702	SNPs	*Rf*	SNP-H2.3 and SNP-H1.7	Venkatesh et al. (2018)

$^{+}$*pvr1*, *pvr1*^{1} and *pvr1*^{2}, three CAPS markers viz. *Pvr1-S*, *pvr1-R1*, and *pvr1-R2* were developed in *Capsicum* spp. (Yeam et al. 2005). Among eight AFLP markers used for mapping the *Rf* locus, the closest marker at 1.8 cM, AFRF8 was converted to a CAPS marker named as AFRF8CAPS in *C. annuum* L. (Kim et al. 2006a). AFLP maker E-AGC/M-GCA112 positioned at 1.8 cM from partial restorer (pr) locus was used to develop CAPS marker PR-CAPS in pepper (Lee et al. 2008). RFLP marker CT211, linked to *P. capsici* resistance has also been converted to a CAPS marker in *C. annuum* (Kim et al. 2008b).

Powdery mildew sensitive (Saengryeg) and resistant (PRH1) were sequenced to develop 6,840,889 and 6,213,009 SNP markers respectively (Ahn et al. 2018). Additionally, 6281 SNPs associated with 46 resistance genes that were related to the NBS-LRR family were mapped to chromosomes 4 and 5, respectively, in the PRH1 line, and were validated using high-resolution melting (HRM) assay in 45 F_4 populations, and correlated with the phenotypic disease index (Ahn et al. 2018).

Genotyping by sequencing (GBS) identified 2,831,791 SNP markers from a panel of 142 *Capsicum* genotypes from Ethiopia. A total of 509 were significantly associated with fruit, stem and leaf related traits (Solomon et al. 2019). A total of 10,307 SNPs were observed in a core collection panel (256) of pepper accession upon GBS (Tamisier et al. 2020). A high-density genetic map was constructed with 7,566 SNP markers from the F_2 population to study the pepper restorer-of-fertility (*CaRf*) gene in *Capscium* spp. (Cheng et al. 2020). A total of 35 different *C. annuum* lines were sequenced to identify 92 perfectly polymorphic SNPs (Du et al. 2019). F_5 population of 188 plants derived from AR1 (powdery mildew resistant) × TF68 (powdery mildew susceptible) was subjected to GBS, generating a total of 41,111 polymorphic SNP markers, of which a filtered set of 1,841 markers was further used for linkage map construction (Manivannan et al. 2021). A total of 66,750 high-quality SNPs with homogenous distribution among 12 chromosomes were identified using GBS in *Capsicum* spp. for the purpose of a diversity study (Lozada et al. 2021).

Other markers linked to resistance were identified in different studies viz. SCAR, SNPs and InDels that were tightly linked to the *PMR1* (Powdery mildew resistance) region on chromosome 4 (Lee et al. 2001; Jones et al. 2009; Rajesh and Madhukar 2018). The powdery mildew resistance locus, *PMR1*, was identified in the 4 Mbp region between two markers, CZ2_11628 and HRM4.1.6 in the pepper genome (Jo et al. 2017). GBS analysis revealed one SCAR and 5 SNP markers to be closely linked to *PMR1*. The comparative analysis of *C. baccatum* specific markers and SNP markers linked to *PMR1* locus revealed that the resistant variety 'VK515R' may have the alien resistance source from *C. baccatum*. In addition to *PMR1* on chromosome 4, QTL *Lt6.1* on chromosome 6 (Lefebvre et al. 2003) was reported to confer resistance against powdery mildew.

Several QTLs have been identified for peppers that resist *C. truncatum* and *C. gloeosporioides* using interspecific populations derived from varieties of *C. annuum* and *C. chinense* (Voorrips et al. 2004). Pepper accession PBC932 (*C. chinense*), PBC80 and PBC81 (*C. baccatum*) with resistance against *Colletotrichum* were used to introgress anthracnose resistance (Yoon et al. 2009). The PBC932 (*C. chinense*) showing resistance in green and mature fruits against *C. acutatum* is associated with

QTLs on the P5 chromosome (Sun et al. 2015). Two pepper populations—Bangchang (*C. annuum*) × PBC932 (*C. chinense*), and PBC80 (*C. baccatum*) × CA1316 (*C. baccatum*), were used for the identification of two and three major anthracnose resistance QTLs flanked by SNP markers on LG2 and LG4, respectively (Mahasuk et al. 2016). Two anthracnose resistant *C. annuum* introgression lines derived from PBC932 and PBC80 were crossed to a susceptible parent, and the resistance was found to be individually controlled by a major recessive gene. The resistance genes were selected by SCAR-InDel and SSR-HpmsE032 with a combined efficiency of 77% (Suwor et al. 2017).

Pvr4 locus provides resistance to PVY and PepMoV. Eight AFLP markers in an interval of 2.1 ± 0.8 to 13.8 ± 2.9 cM were mapped in pepper, followed by shortlisting of one co-dominant AFLP marker, with verified polymorphic sequence converted into CAPS marker, based on two related allele sequences (Caranta et al. 1999). A total of 78 *C. annuum* var. *annuum* L. genotypes were studied for gene effects for six generations, prior total genetic variability estimation with variance analysis of half-diallel crosses for over-dominance genes and their distribution along chromosomes. Progeny generations F_1, F_2, B_1 and B_2 outperformed for fruit traits, and were much better than parents P1 and P2. This direct application of screening and selection for significant gene pairs among diverse choices of breeding populations resulting from heterosis, backcrossing, multiple crossing and pedigree breeding greatly facilitates exploitation of desired gene effects and genetic components to develop new varieties (Marame et al. 2009).

A RAPD marker linked to *Pvr4* was transformed into a SCAR marker ($SCUBC19_{1432}$) to facilitate its use in developing PVY resistant pepper varieties (Arnedo-Andrés et al. 2002). Besides *Pn1*, *Pvr4* and *pvr5*, two more PVY resistance genes were identified at the *pvr2* locus in SCM334, a recessive gene *pvr8* and a codominant gene which expressed only in the absence of *Pvr4*. The genetic analysis revealed that the *pvr2*/*pvr5* locus for resistance to PVY and TEV in the pepper genome shares orthology with the *pot-1* gene for resistance to both potyviruses on chromosome 3 of tomato (Parrella et al. 2002). The SNPs in four different alleles of *pvr2* locus were detected using tetra-primer ARMS-PCR procedure to make them useful in breeding for potyvirus resistance (Rubio et al. 2008). Single gene resistance by $pvr2^3$ was defeated in a susceptible genetic background without the partial resistance QTL which suggested that polygenic host resistance will be more durable than monogenic resistance and should be favorably incorporated in breeding strategies (Palloix et al. 2009). EcoTILLING analysis of variability in the coding sequence (CDS) of *eIF4E* and *eIF/(iso)/4E* led to identification of five new mutants at the *pvr* locus—$pvr2^{10}$, $pvr2^{11}$, $pvr2^{12}$, $pvr2^{13}$ and $pvr2^{14}$ related to PVY resistance in *Capsicum* spp. (Ibiza et al. 2010).

QTL mapping in *Capsicum* also identified 84 RAPD and 51 RFLP markers on three linkage groups significantly associated with partial resistance to CMVY in *Capsicum* lines (Caranta et al. 1997). The population obtained from the cross between susceptible 'Maor' and resistant 'Perennial' varieties of *C. annuum* led to the identification of four QTLs governing CMV resistance, out of which *cmv11.1* was also

linked to the *L* locus for TMV resistance, indicating some association between CMV resistance and TMV susceptibility (Chaim et al. 2001).

A functional codominant marker—*PR-Bs3* was established, which allowed the identification of bacterial spot resistance *Bs3* lines by detecting nucleotide polymorphism, and was thus considered to be useful for marker assisted selection of *Bs3* resistant lines in resistance breeding programs (Römer et al. 2010).

Chili genotypes that were resistant to *Fusarium* were screened using RAPD markers to identify mutants in M_2 and M_3 generation that included P3 T1 1–26, P3 T2 1–26 and P3 T3 1–14 (Tembhurne et al. 2017).

3.6.3 Gene Pyramiding

Gene pyramiding involves the aggregation of related alleles governing the same trait from multiple parental lines. Gene pyramiding has been an effective tool to aggregate multiple alleles or complete QTLs for traits of interest in *Capsicum.* Availability of quality genetic maps enriched with multiple markers including classical and next generation markers can be an integrated approach for improved Genomic selection (GS) and pyramiding of resistance traits in *Capsicum.* Additionally, gene pyramiding offers the recycling of the broken genes as well as introduction of new alleles.

In case of breeding for resistance traits, it is desirable to have broad spectrum resistance against all subsequent mutations of the pathogen, which on the plant's side is mostly governed by the effective recognition by the resistance complexes. Gene pyramiding can thus assist to have multiple allelic variants of all major or minor associated QTLs for increasing the range of response. Gene pyramiding has also been a useful approach to introduce multiple gene pairs in a single breeding cycle. It has thus helped to develop several resistant phenotypes with great yield and quality traits. Prior characterization of interactions among alleles and genes of many polygenic as well as traits with complex linkage patterns is helpful to achieve successful screening and selection with carefully designed markers.

Tamisier et al. (2020) observed natural gene pyramiding in *C. annuum* against PVY accumulation at systemic levels. By using 10,307 SNPs, generated from GBS (256 genotypes), GWAS was performed and crucial observations were made on resistance alleles found at different loci stacking up together with unlikely frequency indicating pyramiding events.

A marker assisted backcrossing (MABC) scheme was proposed for introgression of new traits into elite lines by using 412 evenly spread locus specific SNP markers in *Capsicum* on a diversity panel of 27 accessions. The SNP markers were able to clearly distinguish each accession suggesting that these SNP loci will be useful for MABC, genetic mapping and comparative genome analysis in *Capsicum* spp.

3.7 Association Mapping Studies

Linkage disequilibrium (LD) is an important measure to understand genetic variability of the population. Confounded by the inherent limitations of size of the experimental populations and captured allelic diversity which tend to be really limited in terms of power of resolution, LD mapping is an improved and scalable direct sampling approach from the populations. Association mapping helps to identify significant marker-trait associations by exploiting the naturally present high genetic diversity of the population under equilibrium state compared to observed disequilibrium (Flint-Garcia et al. 2003; Myles et al. 2009). A wide range of resistance genes or factors are highly conserved as well as distributed across the Solanaceae, one such locus *P11* showing linkage to *L* locus confers resistance to TMV (Lefebvre et al. 1995; Thabuis et al. 2003).

In contrast to linkage mapping based approaches, association mapping directly probes the available polymorphisms, and the simple marker-trait associations give important insights to effectively target polygenic traits, and thus a limited representative set of makers is sufficient to select relevant traits.

Under ideal conditions, linkage operates proportionately to physical distance on chromosomes, which has been the basis of many assumptions in genetics. While in practice, linkage never exists in equilibrium state, hence called LD. It is an important metric to study the composition of populations and individual members, reflected as arbitrary grouping sharing common allele frequency profiles, called haplotypes. Genetic drift, mating system, high levels of selfing and selection history are important factors influencing the LD in plants (Flint-Garcia et al. 2003).

Transcriptome sequencing of progenies of *C. annuum* cv. YCM344 (*P. capsici,* resistant) and Teaen (*P. capsici,* susceptible), labeled as TF68, revealed many polymorphic linked loci, and 7 resistance related genes were identified by putative locus SLch11. A total of 1,500 high confidence SNPs, validated against NCBI dbEST (ID: 23,667) were also identified (Lu et al. 2011).

Sharp differences in the distribution patterns of crossover points were observed for *L3* locus in two mapping populations, viz. NK and YB. NK reflected a selfed F_1 of an intraspecific cross between two *C. annuum* genotypes (KOS and NDN), while YB reflected an interspecific cross of *C. chinense* (PI159236) and *C. frutescens* (LS1838-2–4); a high discrepancy among the number of recombinants among NK and YB, for respective markers suggested a presence of strong LD (Tomita et al. 2008).

Fruit mass gene in tomato, encoding for ortholog KLUH, SIKLUH, a P450 enzyme of CYP78A subfamily, regulates enlarged pericarp and septum tissue size by increasing cell numbers. Role of SIKLUH is also ascertained in plant architecture traits, such as side shoots, and ripening time. Down-regulation of SIKLUH dramatically reduces fruit mass. Association mapping has been successfully applied to find a polymorphic SNP locus in the promoter of the fruit mass gene, indicating an important regulatory mutation. This association has been observed in *C. annuum*, emphasizing on the idea of fruit mass gene orthologs to be generated in an independent domestication event (Chakrabarti et al. 2013). An association was also found

among six promoter region SNPs of the *Pun1* gene among *Pun1, CCR, KAS and HCT* with capsaicin metabolite levels. Candidate gene *Pun1* can therefore be an effective design target for resistance breeding.

3.7.1 Genomewide LD Studies

Covering a physical distance of 2,265.9 Mb from the 3.48-Gb hot-pepper genome, SSR markers were used to model population structure and LD of *C. annuum* cultivars. Five population clusters were identified and cross-confirmed by diversity analysis based on SSR dataset covering the hot pepper genome. Seventeen LD blocks were characterized across chromosomes with spans ranging from 0.154 Kb to 126.8 Mb. Significant association of *CAMS-142* was reported with capsaicin (CA) and dihydrocapsaicin (DCA) levels. A fairly large LD (98.18 Mb) encasing the *CAMS-142* gene was observed, with alleles of 244, 268, 283 and 326 bp. Among all, alleles with band sizes of 268 and 283 bp were found to have positive effects on CA (R^2 = 12.5%) and DCA (R^2 = 12.3%) levels. Eight markers across seven chromosomes were also shown to be significantly associated with fruit weight, with three major QTLs, CAMS-199 (chromosome 8), HpmsE082 (chromosome 9) and CAMS-190 (chromosome 10) from data across two years (Nimmakayala et al. 2014).

Population structure was characterized by utilizing the 36,621 polymorphic SNPs for *C. annuum* and *C. baccatum*. A population bottleneck was identified among both populations based on the estimated mean nucleotide diversity (π) and Tajima's D, observed as a biased distribution towards negative values across all but chromosome 4 in *C. baccatum*, while for *C. annuum* the same measures showed a bias towards positive values except chromosome 8, indicating that domestication events at multiple sites have contributed to its wider genetic base (Nimmakayala et al. 2016).

It was noted that selection for different goals within domesticated *C. annuum* types might have fragmented the genetic diversity into narrow pools (Pickersgill 1997). Despite the great economic and cultural importance of *C. annuum*, the population structure of worldwide collections is little known (Aguilar-Meléndez et al. 2009).

3.7.2 Future Potential for the Application of Association Studies

High-throughput genotyping and low-cost marker generation with the help of modern sequencing-based technologies have enabled genomewide association studies (GWAS) in plants. Novel genes and alleles identified with GWAS greatly facilitate modern crop breeding for pathogen resistant and climate resilient traits. One common inference from above-mentioned studies can be derived as, choice of and number of markers (SSRs, AFLP, RFLPs) heavily influence scope of final outcome,

classical markers prepared by laborious screening processes present an inherent limitation of scalability. Modern NGS-based marker development has greatly accelerated the population level marker-trait association studies.

3.8 Genomics-Aided Breeding for Resistance Traits

Intensified crop production and better stress management is the new realization for crop breeders owing to rapidly evolving priorities of feeding a massive human population in the coming years. An integrated and combinatorial approach using modern OMICS tools such as genomics, transcriptomics, proteomics, and metabolomics have proven to be effective. Successful genomic designing of crops revolves around two fundamental aspects, (1) identify and discover available resources such as diversity and novel alleles in the population; (2) maximize the efficiency of breeders with information, and scalable modern technologies. Recent genomic scale approaches have shifted the focus on the second aspect, which was severely lagging behind since decades. Now with novel resources such as high-density genomic scale maps, whole genome sequences, annotated resources and data services, and modern tools to scale up the data, analysis capabilities have greatly enabled genomic designing in crops. Low-cost GBS led marker development has not only accelerated the discovery process but scaled it towards whole population. Pangenomic scale experimental planning has enabled discovery of novel alleles from large populations, while the genomewide association studies have helped in providing an unparalleled support to stress tolerant crops breeding (Scheben et al. 2017).

Transcriptomics

Underlying mechanisms of biological processes, excluding the regular housekeeping processes, are mostly condition-specific such as growth stages, stress response, response against external inputs such as pesticides, and resistance responses which all are very contrasting with mean housekeeping expression. Transcriptome analysis enables the study of expression differences in a robust way to understand such phenomena, in an empirical manner (Ashrafi et al. 2012). These techniques employ absolute/relative quantification of RNA present in the sample, primarily by means of hybridization e.g., microarrays or by a variety of sequencing techniques which later on can be compared by simple counts e.g., RNAseq.

The merits of RNA sequencing of whole transcriptomes using next-generation-sequencing (NGS) approaches have been emphasized enabling coverage of all expressed transcripts, without any prior knowledge of any sequence information (Wang et al. 2009). RNA-seq has been effectively extended to capture quantitative as well as qualitative expression of almost all kinds of RNA species observed in a cell, such as mRNAs, miRNAs, LncRNAs, and small interfering RNAs (Marioni et al. 2008). Recently, isolates of *Bacillus spp.* LBF-01 in pepper indicated resistance against *F. oxysporum* (Silvar et al. 2009). Besides quantitative profiling in temporal and spatial dimensions, across various developmental stages, ecological

influences, treatments and tissues, RNA-seq is also very helpful to identify intron–exon structures, full transcripts diversity and annotation of structural as well as functional features of genomes. These insights are directly useful in genome annotation and refinement of gene definitions as well as variant identification and marker development.

Genotyping By Sequencing

NGS-based approaches also allow marker generation, and multiple in silico prior quality checks on polymorphisms and potency of markers can be applied on such datasets. Classical markers are however based on random probing of genomic locations and are characterized to be useful only after showing some linkage to recognizable traits, but coverage cannot be assured to be homogeneous across the whole genome, while the costly and labour-intensive nature can be excused however in modern age of lab automation. Sequencing based marker development and genotyping allows surpassing many abovementioned limitations of classical markers, such as RFLP, AFLP, ISSR and SSR etc., by allowing more targeted marker development with good reproducibility and very high coverage. Genotyping by such markers enables full population scale mining of genomic patterns such as linkage, LD and most consistent haplotypes, at very low cost but with high accuracy.

Sequencing Based Trait Mapping

Studying and identifying trait introgression is an immensely useful approach to understand complex linkage behaviour of various alleles, while in practice designing effective markers using traditional approaches was an important bottleneck. Further, it suffered a huge reproducibility problem and overall number of candidate genes identified was also very less. Data repositories providing sequencing information such as reference genomes, BAC sequences, ESTs and RNA-seq data, serve as a valuable resource to design and refine high-density linkage maps, and after sufficient coverage these maps can also lead to candidate gene identification in *Capsicum.* However, GBS platforms have furthered these studies in terms of vast scale and reproducibility.

3.8.1 Genome Sequencing in Capsicum *Spp.*

Capsicum species have around nine genome assemblies available as of now, covering species such as *C. annuum*, *C. chinense* and *C. baccatum.* Early sequencing efforts in *Capsicum* were focused on assembling a reference quality genome, hence critical attention was paid towards quality control using the short-read sequencing datasets, cross-verified with BAC libraries with at least 99% match. However, since *Capsicum* spp. are too diverse, no single reference could qualify as best representative even when representing the same genera of plants under study. *Capsicum* genome is four-fold in terms of size, compared to its near relative members from the Solanaceae (tomato).

Majority of plants in Solanaceae share the same number of chromosomes (n = 12), yet considerably differ in size.

Early sequenced genotypes belonged to *C. annuum.* A Mexican landrace Criollo de Morelos 334 (CM334), characterized for its *Phytophthora* spp. resistance properties, was sequenced at 186.6X coverage (650.2 Gb), with an effective genome size estimated to be of 3.4 GB (based on 19-mer analysis), of which 80% region consisted of repetitive sequences, yet a fair number of genes (~35,000) were mapped in the first draft alone. Sequenced reads (GAIIx and HiSeq2000) were subjected to filtering and only good matches (identity >98%, coverage >50%) were used for assembly, discarding all low-quality reads, as well as potential duplications, along the pipeline. Assembled reads were anchored to genetic maps generated for this purpose exclusively. RILs from a cross between *C. annuum* cv. Perennial and *C. annuum* cv. Dempsey were used to generate high-density linkage and physical maps (Kim et al. 2014).

After a short interval, *C. annuum* cv. Zunla-1 and its progenitor and wild relative Chiltepin (*C. annuum* var. *glabrisculum*) were also sequenced. Zunla-1 is an inbred line (F_9 generation), from a cross of two *C. annuum* cultivars from China, while Chiltepin belongs to North-central Mexican wild selection landrace. Zunla-1 was sequenced at 146.43X coverage (477.37 Gb; 6PE and 5MP libraries) and Chiltepin to a 96.37X coverage (295.85 Gb), using the Illumina genome analyser platform II (Qin et al. 2014).

Another genome assembly was published based on F_1 progeny of CM334 (hot pepper) and a non-pungent blocky pepper using Illumina HiSeq10 sequencer (Hulse-Kemp et al. 2018). A single "pseudohap" composed of 83,391 scaffold sequences for 3.21 GB size demarcated a reference assembly. With 123 KB (contig), 3.69 Mb (scaffolds) and 227.2 Mb (pseudo-molecules) average N50 lengths, a total of 83% data (~2.67 GB) was anchored to 12 chromosomes, with only 541 Mb of unplaced sequences.

Resequencing is often done for refinement or gap filling in early drafts, sometimes with assistance of better BAC libraries, and assemblies are improved or coverage is extended for poorly represented genomic regions. In some cases, newer and latest technologies with better accuracy or longer read length are employed to address the repeat regions. These projects have led to identification of many novel genes as well as helped to improve the understanding of evolutionary lineage in *Capsicum* with sequencing of another genome *C. baccatum* cv. PBC81, known for broad spectrum resistance against multiple fungal and bacterial pathogens. Publication of reference assembly of the *Capsicum* genome has led to many other genetic and genomic scale studies. Several aspects of Capsicum research have been influenced by the downstream exploration of the genome by characterizing the architectural and functional aspects. Genomic scale understanding of genetic variation and regulations has enabled study of many comparative and evolutionary interrelations among related crops from Solanaceae and the genus Capsicum itself. Table 3.8 summarizes the sequence assemblies of the pepper genomes.

Table 3.8 Details of sequencing projects completed for *Capsicum* accessions

Assembly	Prot	Genes	Unplaced	Scaffolds/N50 (Mb)	Size (Mbp)	Cultivar	References
C. annuum							
Zunla 1 Ref_{v1}.0; GCA000710875.1	45,410	36,784	4,589	6,478/1,483	2,935	Zunla-1	Qin et al. (2014)
UCD10Xv1.0; GCA002878395.2	–	–	–	81,378/227,195	3,212	CM334 x Blocky; F1	Hulse-Kemp et al. (2018)
ASM51225v2; GCA000512255.2	35,845	31,600	4,245	35,797/250,930	3,064	CM334	Kim et al. (2014)
SNU_{ECW1}.0; GCA011745845.1	36,937	36,937	–	44,080/385	2,880	ECW	SAMN12612368 (NCBI)
SNU_{SF1}.0; GCA011745865.1	36,854	36,854	–	44,704/418	2,882	SF	SAMN12612367 (NCBI)
Chiltepin Ref_{v1}.0; GCA000950795.1	–	–	–	16,998/919	2,768	Chiltepin	Qin et al. (2014)
C. baccatum							
ASM227188v2; GCA002271885.2	35,853	29,592	6,261	23,261/58	3,216	PBC81	Kim et al. (2017a)
C. chinense							
ASM227189v2; GCA002271895.2	34,974	31,592	3,382	87,978/103	3,071	PI159236	Kim et al. (2017b)

3.8.2 Applications of Structural and Functional Genomics in Genomics-Assisted Breeding

Transcriptomes and Gene Discovery for Biotic stresses

Plants respond in a variety of manners when exposed to a biotic stress. An understanding of these responses by genomewide expression studies opens up a new and holistic outlook of the underlying processes. Stressed versus non-stress conditions when compared in terms of differentially expressed transcripts provide a fair understanding of the ongoing interactions based on principles of guilt by association. Those involved in the common processes are supposed to reflect common expression profiles. This sort of profiling helps to identify behavior in stressed vs. normal or controlled conditions. Functional genomics approaches are an important resource to identify and understand disease resistance mechanisms and to design successful breeding programs.

Earlier studies based on functional genomics and expression analysis of *Capsicum* have relied on microarrays. To elucidate the defense mechanisms in hot pepper (*C. annuum*), a total of 8,525 expressed sequence tags (ESTs) were generated for an in silico expression study (Lee et al. 2004). A total of 613 hot pepper genes were found to be responsive to non-host soybean pustule pathogen *Xanthomonas axonopodis* pv. *glycines* (*Xag*). Early infection of *Xag*, induced functional genes involved in cell wall modification/biosynthesis, transport, signalling pathways and many other diverse defense reactions, and revealed a clear contrast of expression of chloroplast biogenesis proteins, photosynthesis and carbohydrate metabolism genes to be downregulated in later stages of *Xag* infection. The expression profiles corroborated with almost similar profiles which are displayed when *Capsicum* suffers fungal, wounding, cold, drought and high salinity stresses. The authors also elucidated the role of gibberellin deactivation as a defense reaction in hot peppers.

Non-host resistance sources are also an important reservoir of knowledge to understand defense mechanisms (Lee et al. 2016). Microarray analysis also helped to identify the molecular mechanisms for induction of *cytosolic pyruvate kinase 1* (*CaPK(c)1*) gene after inoculation by TMV in *C. annuum.* Inoculated leaves of *C. annuum* cv. Bugang with TMV-P (0) showed upregulated response for HR genes. The expression of the cloned *CaPK(c)1* gene was also reported to increase, specifically in the incompatible interaction with TMV-P(0). *CaPK(c)1* also showed triggered response to hormones such as salicylic acid (SA), ethylene, methyl jasmonate (MeJA), and also to NaCl and wounding, indicating a role of (*CaPK(c)1*) as defense response under various TMV infection and many abiotic stresses (Kim et al. 2006b). The TMV resistance locus *L* in pepper is homologous to I2 in tomato in the *R*-like gene cluster region on chromosome 11 (Grube et al. 2000b). A WRKY transcription factor CaWRKYb is involved in positive regulation of immune response to TMV-P_0 pathotype infection by binding to the CaPR-10 promoter (Lim et al. 2011). Another transcription factor CaWRKYd was found to bind to the W-box containing promoters of *PR* genes and causes HR mediated cell death during TMV-P_0 infection (Huh et al. 2012a). *Capsicum annuum* basic transcription factor 3 (CaBtf3) also regulates the

expression of *PR* related genes during hypersensitive response upon TMV infection in *C. annuum* (Huh et al. 2012b). In high temperature conditions, the antiviral immune response in *C. annuum* is conferred via specific vsiRNAs based on RNA-i mediated resistance (Kim et al. 2021).

In another study, *C. annuum* cv. Bukang, inoculated with *X. axonopodis* pv. *glycines* 8ra showed increased expression of *C. annuum* cytochrome P450 (*CaCYP1*). Expression of *CaCYP1* has earlier been observed to increase under salicylic acid (SA) and abscisic acid responses; however, the authors established the role of *CaCYP1* under non-host defense response also, which was confirmed by gene silencing studies. The silencing of *CaCYP1* under the same inoculation results in a down-expression of defense-related genes such as *CaLTP1*, *CaSIG4* and *Cadhn* (Kim et al. 2006b). The transcriptomic profiling of the susceptible (IVPBC535) and resistant (BS-35) pepper varieties led to the identification of 234 genes that were upregulated during TYLCV resistance (Rai et al. 2016).

Pepper hypersensitive induced reaction protein gene (*CaHIR1*) is proposed to be a positive regulator of cell death in plants and has been functionally associated with non-specific basal disease response against multiple pathogens. *CaHIR1* was verified for involvement in defense response against *Pseudomonas syringae*, *Hyaloperonospora parasitica* and *B. cineria* as well as osmotic stress. Genomewide comparative expression profiling revealed 400 differentially expressed proteins, and 11 of them directly mapped to many key metabolic pathways (Jung et al. 2008).

Bacterial TALE proteins (*Xanthomonas* spp.) bind with host plant susceptibility genes to induce diseases, and many of the plant defense mechanisms revolve around the recognition of TALE and with the help of TALE binding sites often found in upstream regions of resistance (*R*) genes. They also comprise a hallmark expression pattern, with expression only invoked under the specific TALE binding events. RNA-seq based transcriptome profiling has been used to identify a candidate of *BS4C*, a resistance gene from peppers mediating the recognition of *Xanthomonas* TALE protein AvrBs4. RNA-seq was also effectively used to identify the major *Bs4C* transcripts and it's uniquely encoding *R* genes (Strauss et al. 2012). Negative regulation of *bcbrn1* and *bcpks13*, which encode polyketide synthase and tetrahydroxynaphthlane (THN) in *B. cinerea* can be utilized for regulating the overall virulence and melanization.

Virus induced gene silencing experiments with *Mildew Resistance Locus O* (*MLO*) established a new functional role for the loss of function of *CaMLO2* gene in *C. annuum*, which is transcriptionally induced in response to *X. campestris* pv. *vesicatoria* and salicylic acid. It is a membrane bound amphiphilic Ca^{2+}-dependent calmodulin binding protein known to accelerate cell-death and rapid bacterial growth, however, silenced allele conferred increased resistance by disrupting the downstream communications in pepper and Arabidopsis (Kim and Hwang 2012).

Disease Resistance

Resistance against a variety of plant pathogens and insect pests is among the major objectives of crop improvement. Constant exploration of sources of diversity against pathogen resistance is very useful to achieve durable resistance. Pathogens on

the other hand are also constantly under evolution towards having increased virulence. Therefore, for a future ready and successful breeding program, knowledge of available genetic variation in germplasm for resistance, evolutionary potential of pathogens, and a comprehensive application of modern methods are required. A large number of pathogens are known to impart biotic stresses in *Capsicum* plants by means of a variety of damages and cause quality loss impacting global productions.

A short-read genome assembly of *L. taurica* detected up to 92,881 transposable elements covering 55.5 Mbp from the total sequenced 187.2 Mbp assembly from a sweet pepper (*C. annuum*) in Hungary, and predicted the occurrence of 19,751 protein coding gene models (Kusch et al. 2020). Genomes of some species of *Colletotrichum* were comparatively sequenced to detect a class of pathogenesis related genes that affect chili (Rao and Nandineni 2017). A compendium of genomic resources is now available for several species in different stages of pathogenicity (Weir et al. 2012; Baroncelli et al. 2014; Zampounis et al. 2016).

Effectors like FAD oxidases, subtilisins, pectin lyases, metabolic enzymes like carbohydrate-active enzyme (CAZyme) family of pectinases and cutinases along with several proteases were key factors associated with *Colletotrichum* infection (Baroncelli et al. 2016). Many of the genes expressed under *Colletotrichum* infection are usually chemically induced, defense responsive, pathogenesis related proteins and transcription factors that relay signaling transduction to induce systemic acquired resistance. An expression analysis by qRT-PCR under infection in Bhut jolokia demonstrated the accumulation of jasmonic acid and ethylene responsive genes (Mishra et al. 2017). Expression of genes—*Lipoxygenase 3* (*Lox3*), *Allene oxide synthase* (*AOS*), *Plant defensins 1.2* (*PDF 1.2*) for JA biosynthesis, and *ACC synthase 2* (*ACS2*) for ethylene biosynthesis were associated with *C. truncatum.* Transcription factors, *WRKY33*, *CaMYB*, *CaNAC* and *bZIP10* were upregulated in response to *C. truncatum* infection (Mishra et al. 2017). With regard to mitigation, melatonin has been shown to increase transcription of *CcChiIII2* chitinase genes and confer resistance against anthracnose (Ali et al. 2021). Extracts of the common tropical plants *Eupatorium odoratum* L. also inhibit anthracnose and are shown to be more effective than synthetic biofungicides (Indrawati 2021). Antimicrobial peptides (AMPs) from pepper accession UENF1381 inhibit trypsin and amylase activity and significantly reduce the growth of *C. scovellei* (da Silva Pereira et al. 2021). Recently, 79 C_2H_2 Zinc Finger transcription factors were identified in *C. annuum* out of which 18 of them were differentially expressed in response to *C. truncatum* infection (Sharma et al. 2021).

A loss of function mutation in *SlMlo1* was reported in tomato to confer resistance against *Oidium neolycopersici,* another powdery mildew causing pathogen. The investigation was extended to study *C. annuum*, *CaMlo1* and *CaMlo2* genes which were isolated by a homology based cloning approach to study their relationship with *L. taurica* infection. Both *CaMlo1* and *CaMlo2* played a role in susceptibility of the plant when infected with the pathogen though *CaMlo2* was phylogenetically more related to *SlMlo2*, and overexpression of *Mlo* restored the susceptibility of the plant (Zheng et al. 2013b).

Increasing the disease resistance by a modified promoter pCaD has also been explored. Sesquiterpene phytoalexin capsidiol (produced as defense response to fungal pathogen attack) is catalyzed by two final-step enzymes—a sesquiterpene cyclase (EAS) and a hydroxylase (EAH), which are genetically linked and present in head-to-head orientation in the genome, and are governed by a common bidirectional promoter pCAD in *C. annuum.* Promoter deletion analysis showed that the 226 bp of the adjacent promoter region of EAS and GCC-box in EAH orientation were determined as critical regulatory elements for the induction of each gene (In et al. 2020). Pepper shows local resistance against *Botrytis* infection in response to wounding, but manifests systemic susceptibility (García et al. 2015). This was proved using inhibitors of hormonal regulators at the cotyledonary stage of the plant where differential expression of plant defense genes *CaBPR1* and *CaSC1* were observed locally but reduced systematically (García et al. 2015).

Pepper plants infected with *Botrytis* have reduced floral anthesis and the flowers drop automatically with increased inoculation (Le et al. 2013). The production of ethylene promotes the growth of *Botrytis,* and changes in cell wall composition reflected by polygalacturonase activity are associated with infection (Rha et al. 2001). The leaves of *C. annuum* form free radicals at positions remote from the site of infections (Muckenschnabel et al. 2001). Some cultivars of pepper grown in Egypt upon treatment with BC-3 isolate displayed both tolerance and susceptibility correspondingly; in turn upregulating defense related enzymes *PPO*, *POD* and *PAL* in response to salicylic acid, methyl jasmonate, abscisic acid and calcium chloride treatment (Kamara et al. 2016). Some extracts of *F. oxysporum* have also been shown to reduce the infection rate of *Botrytis* in peppers (de Lamo and Takken 2020). SAK1, a Stress-Activated Mitogen-Activated Protein Kinase is involved in vegetative differentiation and pathogenicity in response to *B. cinerea* infection (Segmüller et al. 2007). In *Arabidopsis,* the membrane anchored *BOTRYTIS-INDUCED KINASE1* (*BIK1*) plays a distinct role in resistance to necrotrophic and biotrophic pathogens and could also be reflected in *Capsicum* (Veronese et al. 2006).

Role of PdeR transcription factor in virulence of *B. cinerea* has been established by comparing expressions of deleted and complement strains of *B. cinerea.* Deleted strain showed impaired polysaccharide hydrolysis by reducing amylase and cellulase expression. Fungus grows normally yet without surface penetration in case of the deletion strain (Han et al. 2020). Vanillyl nonaoate (VNT) treatment imparts a systemic resistance to *B. cinerea*, both symptoms and colonization of pathogen are reduced via induction of two pathogenesis-related and another phytoalexin biosynthesis gene, and increased lignification via peroxidase gene's hyperexpression (García et al. 2018).

No genes for resistance to *Stemphylium* have been reported, but, a single dominant resistance gene *Sm* locus located on chromosome 11 in tomato has been mapped and reported to be responsible for conferring resistance to *S. lycopersici* (Su et al. 2019). The *Capsicum* pectin methylesterase inhibitor protein *CaPMEI1* provides basal disease resistance to pathogens including *P. syringae* pv. *tomato* (An et al. 2008).

Peppers infected with *C. coccodes* among other pathogens showed increased transcription predominantly in the phloem areas of vascular bundles in the stems and fruits (Cannon et al. 2012). *C. coccodes* was first reported causing chili anthracnose in India (Sharma et al. 2011). *CaChi2*, a pepper basic class II chitinase gene is constitutively expressed in leaf, stem, fruit and root endodermis of peppers infected with *C. coccodes* (Hong and Hwang 2002).

MLO, primarily associated with powdery mildew susceptibility in plants is also known to be a positive regulator in response to high temperature and high humidity but negatively regulates *R. solanacearum* infection led damages, partially moderated by CaWRKY40 (Yang et al. 2021). A novel MYB transcription factor *CaPHL8* provided clues about evolution of pepper immunity against soil borne pathogens. *C. annuum HsfB2a* positively regulates the response to *R. solanacearum* infection or high temperature and high humidity forming transcriptional cascade with *CaWRKY6* and *CaWRKY40*. Three receptor-like proteins CaRLP264, CaRLP277 and CaRLP351 in *C. annuum* provide broad spectrum resistance to multiple biotic stresses like viruses and bacteria including *R. solanacearum* (Kang et al. 2021).

Multiple breeding programs for developing pepper varieties resistant to viruses have been undertaken and genes from resistant varieties have been introduced into commercial varieties. The *pvr1* locus in *Capsicum* lines is responsible for viral infection and susceptibility via complex interaction between elF4E and VPg. This locus has been used in breeding programs for more than 60 years for broad spectrum resistance to potyviruses including TEV. Two recessive alleles of the *pvr1* locus—*pvr11* and $pvr1^2$ with narrow resistance spectra were identified in *Capsicum* that encode elF4E homologs that failed to bind to the VPg and therefore resulted in resistance and reduced susceptibility (Kang et al. 2005).

Highly polymorphic and closely linked markers have assisted in the selection of resistance traits in pepper varieties. One of them led to the development of a superior pepper line resistant to three viruses-PVY, TSWV and PMMoV using molecular markers linked to *Pvr4*, *Tsw* and L^4 locus (Özkaynak et al. 2014). The markers associated with *Tsw*, L^4 and *Pvr4* genes have been assessed for useful selection of resistant *Capsicum* genotypes (Dato et al. 2015). *Capsicum* accessions have also been field tested for their resistance to viruses, for instance, five *Capsicum* accessions showed resistance to CMV-Y but were susceptible to TSWV (Suzuki et al. 2003). A detailed pepper linkage map located the three disease resistance loci—L, *pvr2* and *pvr4* using linked markers (Lefebvre et al. 2002). The survival mechanisms for plant viruses have been laid down in several studies. Incidences of transmission of CMV and PMMoV via contaminated soil with debris of previous crops have been reported in *Capsicum* plants grown in glasshouse conditions (Pares and Gunn 1989). Five NBS-LRR resistance gene analogues (RGAs) were characterized in a pepper multiple disease resistant variety 'IHR 2451' that provided helpful insights into the identification of other resistance genes for marker assisted breeding in pepper plants (Naresh et al. 2017). The evolutionary phenomenon of gene duplication and divergence has led to the emergence of a plethora of resistance genes in plant immune response that though sharing a common ancestral origin and high sequence similarity, differ in the effector viral targets and functional specificity (Kim et al. 2017a, b). Often

wild *Capsicum* varieties carry lower viral diversity than the commercial varieties under natural conditions, and are a potential resource for resistance genes (Vélez-Olmedo et al. 2021).

Three TSWV resistant lines belonging to *C. chinense*—PI 159236, PI 152225 and AVRDC C00943 showing concentric local necrosis were earlier identified (Black 1991; Black et al. 1996). A single dominant gene located at the *Tsw* locus that provides resistance to TSWV was identified using segregation and allelism studies in *C. chinense* accessions 'PI 159236', 'PI 152225' and 'Panca' (Boiteux and de Ávila 1994; Boiteux 1995). The *Tsw* gene codes for a *NB-LRR* (Nucleotide binding and leucine rich repeats) gene on chromosome 10 of the pepper genome for which the non-structural (NS) proteins encoded by S-RNA of the TSWV are the effector molecules. The resistance hypersensitive response was characterized by local necrotic lesions and premature leaf abscission in other *C. chinense* accessions (Moury et al. 1997). However, high temperatures and the heterozygosity at the *Tsw* locus increase the chances of systemic symptoms and decrease the resistance in the plants (Moury et al. 1998). The corresponding locus in tomato—*Sr-5* shares phenotypic and genetic similarity with *Tsw* in pepper, however, the genome segments responsible for overcoming *Tsw* and *Sr-5* resistance are different in TSWV (Grube et al. 2000b). When 29 *Capsicum* accessions were tested for TSWV resistance, a *C. chinense* accession ECU-973 showed 100% resistance upon inoculation and vector transmission (Cebolla-Cornejo et al. 2003). Often there is sympatric occurrence of TSWV, GRSV and TCSV due to common routes and concurrent introduction of these three viruses in peppers as reported in South Florida (Webster et al. 2011). However, the *Tsw* resistance is only effective against TSWV isolates and not against other tospoviruses (Boiteux 1995). A unique resistance gene at the *Tsw* locus was identified in *C. chinense* resistant variety, AC09-207, that showed highly different immune responses from the previously identified resistant varieties, PI152225, PI159236 and PI159234 (Hoang et al. 2013). A *C. baccatum* variety, PIM26-1 showed a similar level of resistance and very high tolerance to TSWV resistance breaking isolates as compared to PI159236 (Soler et al. 2015).

At the same time, resistance-breaking pathotypes of TSWV were isolated from a few *C. chinense* lines with systemic necrotic symptoms which posed fresh challenges for *Capsicum* breeding. Three resistance breaking isolates—TSWV-LE, TSWV-YN18 and TSWV-YN53 caused systemic necrosis, ring spot and chlorotic mottling, respectively, and could suppress RNA silencing in the *C. chinense* accession PI152225 (Jiang et al. 2017). Sometimes, the resistance breaking and non-resistance breaking TSWV isolates showed a synergistic infection characterized by systemic necrosis, stunting and chlorosis in resistant pepper varieties (Aramburu et al. 2015). The phylogenetic analysis of resistance breaking strains of TSWV reported in Hungary revealed the closest similarity with the wild type and no common mutations in the NS effector proteins with those of other resistance breaking strains indicating separate evolution (Almási et al. 2016). Another TSWV strain, RB-TSWV-CA-P-1 was reported to break *Tsw* resistance and caused stunting and mottling in resistant and susceptible commercial sweet pepper varieties in California, USA (Macedo

et al. 2019). Recently, a *Tsw* resistance breaking strain TSWV-P1 was isolated from a commercial *C. annuum* variety in South Korea (Yoon et al. 2021).

Certain isolates of PMMoV like PMMV-I were able to break the resistance by the L^3 gene in *C. chinense* which is due to a single amino acid substitution in the coat protein gene (Berzal-Herranz et al. 1995). Point mutation and deletion studies in the replicase (REP) gene and pseudoknots in the 3' non-coding region (NCR) could determine the major pathogenicity domains of PMMoV (Yoon et al. 2006). Two amino acid substitutions in the PMMoV coat protein reversed the L^3 mediated resistance in *C. annuum* (Hamada et al. 2002). Similarly, two amino acid substitutions in the coat protein of PMMoV pathotype $P_{1,2,3,4}$ enabled overcoming L^4 resistance in *Capsicum* varieties (Genda et al. 2007). Further characterization of $P_{1,2,3,4}$ revealed severe mosaic symptoms associated with it and unique restriction cleavage sites for its differentiation from other *L* gene resistance breaking PMMoV isolates (Antignus et al. 2008). Two Korean isolates—S47 and J-76 of PMMoV produced mild symptoms in *C. annuum* whereas very severe symptoms in *Nicotiana benthamiana* (Han et al. 2017). There has been an expansion of *Tsw* and L^3 resistance breaking pepper TSWV and PMMoV isolates over the years. As much as the resistance breaking virus isolates raise an alarm for agriculturists, they also serve as models for plant-virus interaction and coevolution studies.

Mature plant resistance or age-related resistance has been a well adopted mechanism against viruses and was demonstrated in bell pepper plants in response to CMV (Garcia-Ruiz and Murphy 2001). Therefore, the resistance in plants that are infected at an early growth stage can easily be overcome by evolution of resistance breaking isolates. A more dangerous CMV pathotype Ca-P1-CMV is able to break the resistance of the P0-CMV resistant pepper cultivar variety (Lee et al. 2006).

Transcriptome profiling of CaCV inoculated susceptible and resistant bell *Capsicum* varieties revealed several differentially expressed genes that were either upregulated or downregulated such as *PR* genes like *PR1* and thionins, disease resistance genes (*Rg*) like *NB-LRR* and Coiled-coil at N-terminal (CNL) and secondary metabolism-related genes like *5-epi-aristolochene synthase* (*EAS*) (Gamage et al. 2016). Polyclonal antibodies against the recombinant nucleocapsid proteins of CaCV were produced in rabbits that could successfully detect natural and artificial CaCV infection (Haokip et al. 2018).

3.9 Recent Concepts and Strategies Developed

3.9.1 Gene Editing

Recent advancements in gene editing have enabled targeted site-specific modifications in genomic regions. Engineered or bacterial nucleases have extended this to almost every type of eukaryotic cell and across organisms. Direct gene editing has

accelerated designing more resilient and resistant crops for the future. Choice of suitable vector, transformation mediator and protocol standardization are very crucial aspects of any cloning or point editing exercise. Rigorous optimizations are often conducted to achieve optimal and replicable results. Many such vectors and protocols have been standardized in *Capsicum* for resistance loci as well and have shown good applications in molecular characterization of pathogenicity mechanisms of various pathogens.

Gene editing mediated via *Agrobacterium tumefaciens* has been utilized in *C. annuum* cv. CM334 and bell pepper cultivar Dempsey. Efficacy of multiple *A. tumefaciens* strains such as AGL1, EHA101, and GV3101 has been investigated by assessing the number of calli induced by each strain in both *Capsicum* cultivars. The sweet pepper cultivar Dempsey reported the highest number of calli with GV3101, while no difference was observed in case of CM344 for any strain. Diligent screening of transformed calli with phosphinothricin (PPT) to select CRISPR/Cas9 binary vector (pBAtC) was done prior to screening. Target locus *C. annuum MLO* gene (*CaMLO2*) showed consistent 1-bp deletion at primary indel region, however all other screened calli reflected different indel frequencies from transformed calli. Sensitivity levels of CM334 and Dempsey against *A. tumefaciens* mediated callus induction with pBAtC binary vector are different and carefully accounted while designing future gene editing experiments (Park et al. 2021).

Soil grown leaf—or callus-derived protoplast for *Capsicum* gene editing has been utilized in CM344 and Dempsey cultivars to screen efficient guide RNAs for CRISPR/Cas9 or CRISPR/Cas12a (Cpf1). Purified ribonucleoproteins (RNPs) and endonuclease mixed complexes of CRISPR/Cas9 or Cpf1 and single guide RNA targeted towards conserved *CaMLO2* locus were delivered (PEG-mediated) to *C. annuum* cvs. CM334 Dempsey. Differential editing was observed in both cultivars upon targeted deep sequencing, depending on the applied CRISPR/RNPs (Kim et al. 2020). Alteration in susceptibility gene *CaERF28* (anthracnose resistance) was performed through CRISPR/Cas9 mediation (Mishra et al. 2021).

3.9.2 Nanotechnology

Nanotechnology has been a powerful tool in recent years and many novel products have been developed with the help of nanomolecular transformations to already potent compounds. Usage and application of nanotechnology in crop research is an underexplored area. Many potential areas are emerging for nanomolecules in *Capsicum* research, apart from effective transformation potential by effective delivery of DNA into protoplast, increasing pharmaceutical availability (Choi et al. 2013), many other alternate areas such as new product creation out of many nutraceuticals from *Capsicum*, novel pesticides against a variety of pathogens, quality assessment of *Capsicum* produce for residues of harmful chemicals, heavy metal contamination detection (Gupta et al. 2021) and fruit quality assessment (Vidak et al. 2021). Nanotechnology has the potential to enhance the industrial application of

the *Capsicum* crop, improving its already diversified usage profile, which might not be directly involved into biotic stress resistance itself, but this secondary usage allows, a novel kind of breeding approach leading to targeted breeding for desired molecules, such as capsaicin.

Cobalt and nickel ferrite nanoparticles ($CoFe_2O_4$ and $NiFe_2O_4$) have been successfully tested as potential fungicides for antimycotic activity against *F. oxysporum*, *C. gloeosporioides* and *Dematophora necatrix* (Sharma et al. 2017). Another important application of lecithin nanoemulsion of Oleoresin Capsicum (OC) extract has been characterized as a potential food grade surfactant effective against *Escherichia coli* and *Staphylococcus aureus* (Akbas et al. 2019).

Bioactive selenium nanoparticles (SeNPs) of mycogenic origin from *Trichoderma atroviride* displayed excellent in vitro antifungal activity against *Pyricularia grisea* and inhibited infection of *C. capsici* and *A. solani* on chili and tomato leaves at concentrations of 50 and 100 ppm, respectively. Also, an aggregation and binding with zoospore of *P. infestans* was reported at 100 ppm (Joshi et al. 2019). *B. licheniformis* encapsulated in alginate-chitosan nanoparticle (CNPs) beads supplemented with rice starch demonstrated antifungal activity against *Sclerotium rolfsii,* and also reflected plant growth promoting and biocontrol properties in *C. annuum* (Panichikkal et al. 2021).

3.9.3 Gene Stacking

Gene stacking is the practical solution to the problem of not finding desired genetic diversity to select suitable parents. In such cases, a breeder has to look out for external sources of available allelic diversity to bring desired genes into close linkage so that subsequent crosses do not lose the desired gene. Though the term is frequently used to indicate transgenic compilation of desired genes into a single plant, classical backcrossing to introduce more parental genes is also a valid example of gene stacking. Molecular gene stacking or more generic version of it is called gene pyramiding when targeting multiple genes into a single plant. Many pathogenic responses have evolved in specific plants based on evolutionary exposure towards it, many times the best resource for resistance lies outside the gene pool of the host plant in such cases. Stress response is more often governed by highly polygenic traits, showing disproportionate linkage patterns, which are also cumbersome to map and inherit; marker-assisted selection is a good solution in such cases. A few examples are listed in Table 3.9.

3.10 Future Perspectives

Global demand for *Capsicum* production has been steadily rising owing to rising awareness of health and nutrition. Besides being an excellent source of important

Table 3.9 Transgenic genes introduced into *Capsicum* varieties

Source	Host	Gene of interest	Effective against	Method	References
Solanum bulbocastanum	*C. annuum*	Broad host resistance gene *RB*	*Phytophthora capsici*	*Agrobacterium tumefaciens* mediated transformation	Bagga et al. (2019)
A. thaliana	*C. annuum* L	*AtEDT1/HDG11* and *Cry2Aa2*	*Prodenia litura*	*Agrobacterium tumefaciens* mediated transformation	Zhu et al. (2015)

metabolites, *Capsicum* is also an important culinary enhancement to most of the global cuisine. Compounds from *Capsicum* are finding their importance in cosmetics as well as nutrient supplement industry which is a rising phenomenon.

Fungal stress at the seedling stage influences growth potential and eventually lowers the resistance barrier of the plant leading to multiple attacks and significant plant mortality as well, emphasizing the development of fungal stress tolerant genotypes. Sources of biotic stress resistance have been identified through rigorous screening of available germplasm of *Capsicum* spp. *C. baccatum* has been identified as a great source of resistance genes against various fungal as well as bacterial attacks. Identified loci have been successfully transferred as well as expressed in other related *Capsicum* members to confer similar or enhanced resistance. Major challenge for the *Capsicum* producing nations is to mitigate the rising demand for nutraceuticals by achieving inexpensive and sufficient quantity as well as quality. Classical breeding methods severely fall short to meet the rising expectations of the industry, and hence a major overhaul in production capacity as well as quality is only achievable through modern biotechnological as well as bioinformatics-based interventions. Changes as well as frequent exposure to climate extremes is likely to decrease major crop yields and will simultaneously affect all dimensions of crop production.

There is an alarming realization that conventional breeding methods do not account for a sufficient amount of genetic variation and are incompetent to address rising biotic stresses and to compensate for quality and yield losses. Immediate incorporation of superior biotic stress traits should be prioritized to address climate change and its effects on the pathogenicity of biotic stress causing organisms. Crop improvement programs incorporating highly diverse parents can help to design widely resistant *Capsicum* varieties for the majority of biotic stresses through identification and integration of resistance associated QTLs utilizing marker-assisted selection in genetically adapted backgrounds.

3.10.1 Potential for Expansion of Productivity

Enhancing the disease resistance of *Capsicum* genotypes towards the most common pathogens can be prioritized for immediate increase in production as a major share of total yield is wasted while in field and also due to post-harvest losses. Current rising trends of adoption of polyhouses with precision nutrient delivery systems have played a major role in ensuring quality in urban areas. However, selling prices are not that competitive to sustain a major share of *Capsicum* production in such facilities. Multi-pronged approach with a general focus on productivity as well as disease management can be realized with efficient and improvised use of agricultural inputs and methods. Quality seed availability of resistant cultivars and adoption of better crop and nutrient management, resource conservation and precision farming coupled with crop contingency planning can be adopted. *Capsicum* has heavy yield losses on field as well as post-harvest, hence its production as well as marketing is a challenging task to be handled by marginalized farmers.

Climate change has been an important factor in deciding overall production cost, and adoption of high-quality germplasm has the potential to curtail overall pathogen loads on the pepper crop. Furthermore, a large number of rare *Capsicum* spp. germplasm can be utilized for screening of both biotic and abiotic stress resistance and identification of important genes with great yield potential and response to nutrients dosage.

3.11 Conclusions

The past three decades have seen massive losses in crop production, yield and quality due to plant disease causing organisms. The wide use of naturally occurring resistance genes for the improvement of plant varieties have also triggered the emergence of resistance breaking pathogen isolates which urge the discovery of new resistance genes (Turina et al. 2016). Genetic recombination and the presence of satellite DNA molecules have led to increasingly new epidemics due to emergence of resistance-breaking new strains and new species, altogether, of viruses and other pathogens that may prove detrimental to food and agricultural production. Vector management strategies, like, growing plants in vector-free periods and covering plants with row covers have long been used as sustainable solutions to plant diseases, but, breeding for resistance has always been a priority. To control the crop losses caused by biotic stresses, there is a rapid need to identify and characterize the causative organisms via extensive genetic mapping, transcriptome analysis and expression profiling, understand their epidemiology and etiology, and to develop effective integrated and practical solutions. Detailed characterization of receptor molecules in vector organisms will promote strategies like transgenic expression of receptor blocking molecules in plant hosts to avoid pathogen transmission. RNA-interference mediated gene silencing of viruses has several advantages over traditional pesticides such as zero crop-residue, minimum off-target effects and lower chances of resistance (Nilon et al. 2021). Innovative eco-friendly methods and biocontrol strategies are therefore urgently needed for sustainable management of diseases in *Capsicum* spp.

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