Breeding For Resistance against Pest and Diseases in Tomatoes: A Review

Abstract

Diseases and pests have a substantial effect on tomato production, greatly affecting both the quantity and quality of this crucial vegetable crop. Although fungicides and insecticideshave been important in controlling plant diseases and pests, their excessive usage raises significant environmental issues. Vegetable breeders are increasingly concentrating on developing cultivars with natural tolerance to biotic stresses to promote sustainability and environmental friendliness. The change in focus is intended to cultivate tomato cultivars with inherent resistance to diseases and pests, hence decreasing the need for chemical treatments. Advancements in creating high-yielding genetically resistant tomato cultivars are a result of detailed study on the genetic basis of pest and disease resistance in tomato crops, as well as the complex interactions between the host plant and pathogens. For effective breeding programs and pre-breeding activities, scientists and breeders must have access to sources of resistance and a thorough grasp of the genetic complexities involved. This requires examining the genetic composition of both the tomato plants and the different infections that are impacting them. Breeders may generate tomato cultivars with strong resistance to common diseases and pests by using the inherent defensive mechanisms found in certain tomato types via selective crossing. Continuing to study how hosts and pathogens interact and the molecular processes involved in resistance is crucial. This information offers vital insights on how to improve and expand resistance, leading to the creation of cultivars with long-lasting and wide-ranging resistance. Currently, the emphasis on breeding is a proactive and sustainable strategy for transfer of resistances in high yielding tomato cultivars. Researchers aim to develop tomato cultivars that provide high yield and demonstrate tolerance to changing disease and pest stresses by integrating genetic knowledge with sophisticated breeding methods. This comprehensive method protects tomato crops and encourages environmental sustainability by decreasing the need on chemical inputs in agriculture.

Keywords: Tomato, biotic stresses**,** inheritance of resistance, biotechnological approaches, molecular marker and grafting.

Introduction

One of the most important vegetable crops is tomato, *Solanum lycopersicum* L. (Solanaceae).The origin of tomatoes is located in South America, particularly Peru(Mueller *et al.* 2005). However, the major domestication of tomatoes took place in Mexico due to the availability of several cultivated and wild species of the tomato that originated in this region (Rick 1969) (Fig1). Concerning the matter of human nutrition, it has developed into a significant commercial crop in recent years. The flavonoids, beta-carotene, lycopene, and vitamin C that it contains are among the nutrients that it offers. Furthermore, the anti-oxidative and anti-cancer capabilities of lycopene have contributed to the rise in popularity of tomatoes, particularly in contemporary times (Fentik 2017).

A paucity of genetic diversity is seen in conventionally produced tomatoes. As a result, it has been proposed that the required resistance features should be transmitted from their wild type species (Dhall 2015) (Fig2). For the purpose of regulating the expression of their target genes and orchestrating the biochemical and physiological adjustments that are essential for stress tolerance and the modulation of plant development, transcription factors (TFs) attach themselves to their target genes upon the detection of stress(Rick and Chetelat1995). The most important problem is the high number of instances of diseases and pests that come up during tomato production. The use of pesticides without discrimination in order to control diseases, nematodes and insect-pests, is harmful to both the environment and human health. In contrast, there has been virtually little progress made in the development of insect resistance over the years. Host plant resistance is the most cost-effective strategy; nevertheless, this sort of resistance against insect pests is not at all durable because of the population pressure that insects exert on the host. As a result, there is development of new biotypes and a breakdown of resistance (Hichri et al., 2014).

Varieties that have been launched up to this point have been connected with one or more traitsthat are not desired, and as a result, they have not earned the popularity that they deserve. Vegetable yields have decreased by around 40% due to the presence of insect pests (Singh et al., 2000).

The tomato, *S. lycopersicum* L., an economically significant crop was the first vegetable to be produced anywhere in the world. It is a model plant species due to its diploid, relatively compact, and recently sequenced genome as well as its large genetic and genomic resources(Ranjan et al, 2012).

Table1: Majorinsect-pestsanddiseases of tomato in India.

Diseases	**Insect-Pests**	**Reference**
ToLCV, CMV, earlyblight, lateblight, nematodes, root-knot, bacterialwilt(BW), tomatospotted wilt virus (ToSWV) and septorialeaf spot.	Aphid, Fruitborer and whitefly	Dhall, 2015

Several related wild species of tomato, including *S. pennellii* and S. *habrochaites*, have been found to possess resistance to major insect pests. Among these species, *S. habrochaites* is particularly noteworthy as it serves as a significant source of arthropod resistance. Two distinct forms of *S. habrochaites*, namely *S. habrochaites* f. *glabratum* and *S. habrochaites* f. *typicum*, exhibit resistance to at least 16 pest species, as indicated in Table 1. Similarly, *S. pennellii* demonstrates resistance to a minimum of nine insect species, such as carmine, greenhouse whitefly, the potato aphid, and spider mites. Additional wild species, including *L. esculentum* var. *cerasiforme*, *S. cheesmanii*, *S. pimpinellifolium*, *S. chmielewskii*, *S. chilense*, and *S. peruvianum* exhibit different levels of resistance to insects (Dhall 2015). Although these wild tomato species provide a wide range of resources for pest resistance, their whole potential has not been completely used in insect resistance breeding projects. Although there has been some research on inheritance, most of these genetic resources are not being fully used and lack proper characterization.

Breeding for insect resistance in tomatoes has indeed posed more challenges compared to breeding for disease resistance. One significant obstacle that breeders face is what's known as "linkage drag." This refers to the tendency for genes controlling desirable traits, like insect resistance, to be physically close to genes that control undesirable traits or have negative effects on plant performance. The presence of linkage drag complicates the development of insect-resistant tomato cultivars because breeders must navigate through a genetic landscape where improving one trait may inadvertently introduce or perpetuate unwanted traits. This can slow down the progress of breeding programs and make it challenging to produce commercially viable insect-resistant tomato varieties.

Tomato leaf curl New Delhi virus (ToLCNDV) is a kind of bipartite begomovirus that belongs to the genus Begomovirus and the family Geminiviridae. The isolates of the virus are naturally transmitted by the whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae). This transmission happens in a cyclical and uninterrupted manner(Brown et al, 2001). Research has shown that ToLCNDV, a begomovirus, has significant economic implications since it inflicts substantial damage on tomato (*Solanum lycopersicum*) cultivation. The prevalence of this begomovirus is higher in northern India, as reported by King et al. (2012), Varma and Malathi (2003), Zaidi et al. (2016), and Chakraborty (2008). Tomato wilt infections may be caused by several pathogens, including as nematodes, fungus, bacteria, viruses, and other biotic factors. *Fusarium oxysporum* is a diverse fungus that exists in more than one hundred various variations, each of which is often linked to a specific host and capable of causing disease. There are around one hundred distinct species of *F. oxysporum* that cause vascular wilts in flowering plants (Mansoor et al., 1997). This specific fungus is a hyphomycete that is found in the soil. A variety of insects, including whiteflies*(Bemisia tabaci*),mites*(etranychus spp.),*aphids*(Aphisgossypii*), Lepidoptera (such as, beet armyworm (*Spodoptera exigua*), tomato fruitworm (*Helicoverpa zea*), cotton bollworm (*Helicoverpa armigera*), Coleoptera (such as tobacco flea beetle (*Epitrix hirtipennis*) and colorado potato beetle (*Leptinotarsa decemlineata*), Diptera (such as fruit fly (*Neoceratitis cyanescens*) and leafminers (*Tuta absoluta*), cutworms (*Peridroma saucia*), thrips (*Frankliniella occidentalis*)and sinkbugs (*Arvelius albopunctatus*) are responsible for causing damage to tomato plants (Table2).

Table2: Resistance sources for bioticstressesintomato.

Resistantgenes	**Resistance against diseases**	**Resistance Sources**	**References**
Asc-1	*Alternariaalternata*f.sp.*lycopersici*	*S.lycopersicum*	Domsch et al., 1980
Am	Alfalfamosaicvirus	*S.habrochaites*	Brandwagt et al., 2002
Bs4	*Xanthomonas campestris*	*S.lycopersicum*	Parrella et al., 2004
Cmv	Cucumbermosaicvirus	*S. chilense*	Schornack et al., 2004
Cf-1	*Cladosporiumfulvum*	*S.lycopersicum*varcerasiforme	Stamova and Chetelat 2000
Cf-2	*C.fulvum*	*S. pimpinellifolium*	Langford 1937
Cf-3	*C. fulvum*	*S. pimpinellifolium*	Dixon et al., 1996
Frl	*Fusariumoxysporum*f.sp.*radicis-lycopersici*		Hammond-Kosack and Jones 1993
Hero	*Globodera rostochiensis*	*S. pimpinellifolium*	Vakalounalus et al., 1997
I	*Fusariumoxysporumformae* speciales*lycopersici*	*S. pimpinellifolium*	Ernst et al., 2002
Mi-1.2	*Meloidogyne*spp	*S.peruvianum*	Sela-Buurlage et al., 2001
Ph-1	*Phytophthora infestans*	*S. pimpinellifolium*	Milligan et al., 1998
Sw-5	Tomatospottedwilt virus	*S.peruvianum*	Bonde and

	(ToSWV) and tomato chloroticspotvirus (ToCSV)		Murphy 1952
Sw-7	ToSWV	*S. chilense*	Brommenschenkel and Tankslet 1997
Ve1	*Verticilliumdahliae*	*S.lycopersicum*	Dockter et al., 2009
Ty-1	ToYLCV	*S. chilense*	Hammond-Kosack and Jones 1993
Ty-2	ToYLCV	*S.habrochaites*	Zamir et al., 1994
Ty-3	ToYLCV,ToMV	*S. chilense*	Ji et al., 2009
Ty-4	ToYLCV	*S. chilense*	Ji et al., 2007
	ToYLCV	*S.peruvianum*	Ji et al., 2009
ol-1	*Oidium neolycopersici*	*S.habrochaites*	Anbinder et al., 2009
ol-2	*O.neolycopersici*	*S.lycopersicum*var *cerasiforme*	Huang et al., 2000
ol-3	*O.neolycopersici*	*S.habrochaites*	De Giovanni et al.,2004

S.chilense *S.pennellii* *S.cheesmanii*

S.peruvianum *S.pimpinellifolium* *S.habrochaites*

Fig.1. Different wild tomato species for different resistant sources.

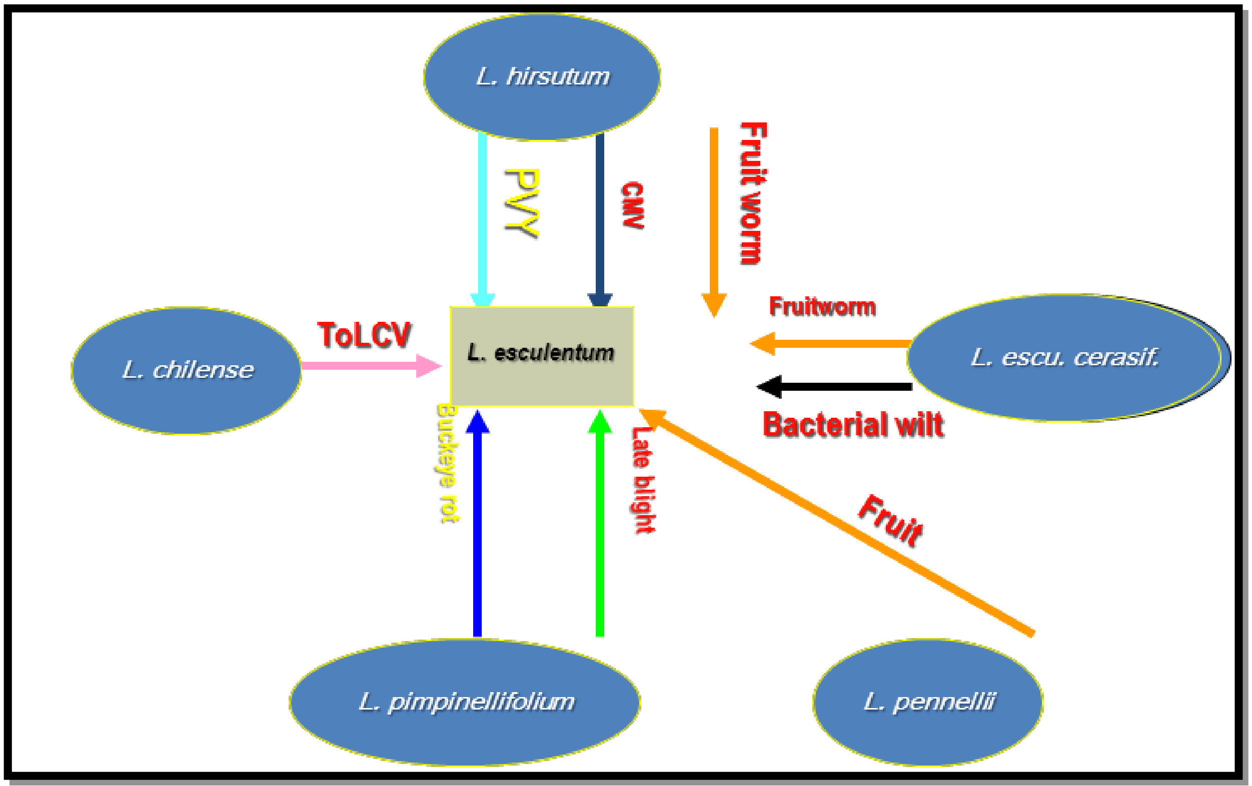

Fig.2. Process of introgression of wild species in cultivated tomato

BiotechnologicalInterventions

Tomatoes have long served as a model in plant research due to their genomic characteristics and growth habits, as noted by Ranjan et al, (2012). However, despite their high diversity and genetic variability, much of the potential of tomato landraces remains untapped, primarily due to limited genetic background information and performance data across diverse climates (Carelli et al. 2006). This scarcity of information hinders the effective utilization of these varieties in breeding programs.

Traditional breeding methods for quantitative and qualitative tomato traits are known to be time taking, often taking around five years for market commercialization (ResistanttoViralDiseases; Panthee and Gardner 2011; Bai and Carbonell et al, 2018 Lindhout 2007). This lengthy process highlights the need for more efficient breeding techniques to accelerate the development of improved tomato cultivars.Recent advancements in tomato tissue culture, mutagenesis, recombinant DNA technologies, transformation protocols, and transient expression assays offer promising avenues for enhancing tomato cultivars (Wolters et al. 1994; Chaudhary et al. 2019; Gosal et al. 2009; Fernandez et al. 2009). These technologies provide alternative means to traditional breeding methods and can significantly contribute to the improvement of tomato cultivars.One notable obstacle in tomato breeding is the incompatibility between wild and cultivated tomatoes, which can impede the process of crossing and introgressing desirable traits. However, tissue culture technologies offer solutions to overcome such barriers. Techniques like embryo rescue, in vitro cultivation, protoplast fusion, and somatic hybridization can facilitate the successful transfer of beneficial traits from wild tomato species to cultivated varieties (Wolters et al. 1994).

Additionally, the process of introgression, which involves the introduction of desirable genes from wild relatives into domesticated species, may be accomplished via the use of marker-assisted breeding (Table 3). On account of the fact that the desired gene is only present in a single or a few locations across the genome, it is possible to choose against markers that indicate other regions of the wild type chromosomes. This will result in the deletion of those genes, which are often undesirable, from the offspring. There have been attempts made to generate plants that are resistant to a variety of biotic stressors, including viruses, bacteria, fungi, and insect pests, via the use of genetic engineering. Researchers have successfully developed a strong defense against Tomato mosaic virus (ToMV) infection by expressing solely the coat protein. This approach has also shown positive results in transgenic tomato plants, providing protection against several plant viruses such as Cucumber mosaic virus (CMV) and alfalfa mosaic virus (Huang et al, 2000). Progress in engineering insect resistance in transgenic tomato has been achieved (Shukla et al, 1998 and Fischhoffet al, 1987) (Table 4). Overall, the integration of modern biotechnological tools with traditional breeding methods holds immense potential for advancing tomato cultivars with improved traits, addressing challenges related to genetic diversity, climate adaptation, and pest/disease resistance.

Table3: Molecularmarkersused intomato.

Sr.No.	Markers type	References
1	SNP	Babu et al, 2003; Jiménez-Gómez and Maloof 2009; Sim et al, 2011; Hamilton et al, 2011; Sim et al, 2012; Iquebal et al, 2013 and Víquez-Zamora et al, 2013
2	CAPS	Kevei et al, 2015
3	SSR	He et al, 2003; Ruiz et al, 2005; Grushetskaya et al, 2007; Sim et al, 2011 Ning et al, 2012and Yang et al, 2014
4	AFLP	Todorovska et al,2014
5	RFLP	Ning et al, 2012
6	SRAP	Tanksley et al,1992 and Ruiz et al,2005

7	SCAR	Al Shaye et al,2018

Table4: Transgenes intomatocrop for resistancetoviraldiseases.

Transgenes	**Resistantto**	**Reference**
*Cp*gene	ToMV	Dhall R.K(2015)
*Cp*gene	ToYLCV	
Antisense RNA	ToMV	
Satellite RNA	CMV	
*N*gene	ToSWV	
Truncated C1gene	CMV	
Two*Cp* genes	CMV	

Grafting

The production of grafted seedling vegetables was created in Japan and Korea with the intention of minimizing the amount of main crop loss that was brought about by the infection of soil-born illnesses that were made worse by recurrent cropping. This was done with the intention of lowering the amount of main crop loss. The strong roots of the rootstock that was selected have the ability to display an unusual degree of resistance to severe soil-borne illnesses. These diseases include those that are caused by *Pseudomonas*, *Fusarium*, *Verticillium*, and *Phytophthora*. despite the fact that the degree of tolerance varies substantially depending on the rootstocks, the plant is able to tolerate nematodes, *Monosporascus cannonballus*, and *Didymellabryoniae* (Yang et al, 2014 and Edelstein et al, 1999). Depending on the level of resistance that is present in both the scion and the rootstocks, it is feasible that virus-resistant rootstocks might have a major influence on the scion infection of some viral infections (ToMV races). This would be the case if their presence was sufficient. There is a chance that the disease resistance of grafted seedlings is purely attributed to the rootstock roots' capacity to endure infections of this sort. This is a possibility. According to the agreement that has been achieved (Hanson et al, 2000 and Ji et al, 2007), the disease-prone features of the scion are not passed to the rootstock. On the other hand, the rootstock does not inherit the trait of being susceptible to disease.

Table 5: Resistance source of rootstock used in tomato grafting.

Resistance Source	**Resistance to**	**References**
Solanum pennelli	*Alternariaalternata*f.sp. *lycopersici*	Wanget al., 2006[65]
S.habrochaites	*Pseudomonassyringe*pv. tomato race 1	Van der Biezen et al,1995
S. chilense	CMV, ToYLCV	Thapa et al,2015
S.neorickii	*Botrytiscinerea*	Zamir et al,1994

S.pimpinellifolium	Colour,quality,resistancetoBWLB	Finkers et al, 2008
S. lycopersicum	Fungi and root rot	Danesh et al,1994
S.peruvianum	ToSWVand RKN	Pierce et al,1971 ; Balint-Kurti et al,1994 and Williamson et al,1994

Future Strategies

Developing cultivars with resistance or tolerance to diseases and insects is crucial for reducing losses caused by these biotic stressors. While chemical control methods are effective, they are often costly and can have long-lasting environmental impacts. Therefore, active research programs are essential to tap into the genetic diversity of existing germplasm, especially wild relatives, to create pre-bred lines with potential resistance traits. Efficient techniques for artificial inoculation of plantlets can greatly enhance the breeding process for disease and pest resistance. Gene pyramiding, combining multiple resistance genes into hybrids or varieties, is another important strategy to combat a range of biotic stressors effectively. Priority should be given to breeding efforts targeting integrated diseases and insect pests, such as TMV and leaf curl in tomatoes, to achieve optimal outcomes. Collaborative efforts between breeders and plant pathologists or entomologists are crucial for addressing these challenges effectively.

Conclusion

As a conclusion, the process of developing resistance to pests and diseases in tomatoes involves a comprehensive and integrated strategy. By combining conventional breeding methods with advanced biotechnological tools, substantial advancements have been achieved in the development of tomato varieties with improved resistance characteristics. The incorporation of genetic diversity from wild tomato species has played a crucial role in transferring new resistance genes into cultivated variants. In addition, progress in molecular breeding techniques, such as marker-assisted selection and genetic engineering, has accelerated the creation of cultivars that are resistant to diseases or pests. Nevertheless, there are ongoing difficulties that need to be addressed, such as the appearance of novel pest and disease strains, the genetic diversity within pathogen populations, and the need for sustainable and ecologically sound remedies. To overcome these issues and ensure the long-term success of tomato resistance breeding programs, it is necessary to continue research efforts that concentrate on understanding plant-pathogen interactions, improving breeding procedures, and fostering genetic diversity.

References

Al Shaye N, Migdadi H, Charbaji A, Alsayegh S, Daoud S, Wala AA *et al*. Genetic variation among saudi tomato (*Solanum lycopersicum* L.) landraces studied using sds- page and srap markers. *Saudi journal of biological sciences.* 2018;25(6):1007-1015.

Anbinder I, Reuveni M, Azari R, Paran I, Nahon S *et al*. Molecular dissection of Tomato leaf curl virus resistance in tomato line TY172 derived from *Solanum peruvianum*. *Theor Appl Genet*. 2009;119:519-530.

Babu RM, Sajeena A, Seetharaman K *et al*. Advances in Genetically Engineered (Transgenic) Plants in Pest Management An Overview. *Crop Protection*. 2003;22:1071-1086.

Balint-Kurti PJ, Dixon MS, Jones DA, Norcott KA, Jones JDG. RFLP linkage analysis of the Cf-4 and Cf-9 genes for resistance to Cladosporium fulvum in tomato. *Theoretical and Applied Genetics.* 1994;88:691-700.

Bonde R, Murphy EF. Resistance of certain tomato varieties and crosses to late blight. *Maine Agr Exp Sta Bull.* 1952;497:5-15

Brandwagt BF, Kneppers TJ, Nijkamp HJ, Hille J. Overexpression of the tomatoAsc-1 gene mediates high insensitivity to AAL toxins and fumonisin B1 in tomato hairy roots andconfers resistance to *Alternaria alternata* f. sp. *lycopersici* in *Nicotiana umbratica* plants. *Mol Plant Microbe Interact*. 2002;15:35-42.

Brommenschenkel SH, Tankslet SD. Map-based cloning of the tomato genomic region that spans the Sw-5 tospovirus resistance gene in tomato. *Mol Genet Genomics*. 1997;256:121-126.

Brown JK, Fauquet CM, Briddon RW, Zerbini FM, Moriones E, Navas-Castillo J. Family *Geminiviridae*. In Virus Taxonomy 9th Report, *Proceedings of the International Committee on Taxonomy of Viruses*, 2001.

Carbonell P, Alonso A, Grau A et al Twenty years of tomato breeding at EPSO-UMH: transfer resistance from wild types to local landraces from the frst molecular markers to genotyping by sequencing (GBS). *Diversity* 2018;10:12

Carelli BP, Gerald LT, Grazziotin F, Echeverrigaray S Genetic diversity among brazilian cultivars and landraces of tomato *Lycopersicon esculentum* Mill. revealed by RAPD markers. Gen Res Crop Evol 2006;53:395–400

Chakraborty S. Tomato leaf curl viruses from India (*Geminiviridae*). In *Enciclopedia of Virology*; Mahy, B.W.J., Van Regenmortel, M.H.V., Eds.; Elsevier: London, UK, 2008,124-133p. [Google Scholar]

Chaudhary J, Alisha A, Bhatt V et al Mutation breeding in tomato: advances, applicability and challenges. *Plan Theory* 2019;8(5):128. https://doi.org/10.3390/plants8050128

Danesh D, Aarons S, McGill GE, Young ND. Genetic dissection of oligogenic resistance to bacterial wilt in tomato. *Molecular Plant-Microbe Interactions*. 1994;7:464-471.

De Giovanni C, Dell'orco P, Bruno A, Ciccarese F, Lotti C *et al*. Identification of PCR-based markers (RAPD, AFLP) linked to a novel mildew resistance gene (ol-2) in tomato. *Plant Sci*. 2004;166:41-8.

Dhall RK. Breeding for biotic stresses resistance in vegetable crops: a review. *Journal of Crop Science Technology*. 2015;4:13-27.

Dixon MS, Jones DA, Keddie JS, Thomas CM, Harrison K, Jones JDG. The tomatoCf-2 disease resistance locus comprises two functional genes encoding leucine-rich repeat proteins. *Cell*. 1996;84:451-60.

Dockter KG, O'neil DS, Price DL, Scott J, Stevens MR. Molecular Mapping of the tomato spotted wilt virus resistance gene Sw-7 in tomato. *In. American Society for Horticultural Science*. St. Louis, MO, 2009.

Domsch KH, Gams W, Anderson TH. Compendium of soil fungi, Academic Press, New York, USA, 1980.

Edelstein M, Cohen R, Burger Y *et al*. Integrated Management of Sudden Wilt of Melons, Caused by Monosporascus cannonballus, Using Grafting and Reduced Rate of Methyl Bromide. *Plant Dis*. 1999;83:1142-1145.

Ernst K, Kumar A, Kriseleit D, Kloos DU, Phillips MS *et al*. The broadspectrum potato cyst nematode resistance gene (Hero) from tomato is the only member of a large gene family of NBS-LRR genes with an unusual amino acid repeat in the LRR region. *Plant J*. 2002;31:127-36.22

Fentik DA. Review on Genetics and Breeding of Tomato (*Lycopersicon esculentum* Mill.). *Advances in crop Science and Technology*. 2017;5:5.

Fernandez AI, Viron N, Alhagdow M et al Flexible tools for gene expression and silencing in tomato. *Plant Phys* 2009;151(4):1729–1740.

Finkers R, Bai Y, van den Berg P, van Berloo R, Meijer- Dekens F, ten Have A *et al*. Quantitative resistance to Botrytis cinerea from Solanum neorickii. *Euphytica*. 2008;159:83-92.

Fischhoff DA, Bowdish KS, Perlak FJ *et al*. Insect Tolerant Transgenic Tomato Plants. *Biotechnology*. 1987;5:807-813.

Gosal S, Wani SH, Kang M Biotechnology and drought tolerance. *J Crop Improv* 2009;23(1):19–54

Grushetskaya ZE, Lemesh VA, Poliksenova VD, Khotyleva LV. Mapping of the Cf-6 tomato leaf mould resistance locus using SSR markers. *Russian Journal of Genetics*. 2007;43(11):1266-1270.

Hamilton JP, Hansey CN, Whitty BR, Stoffel K, Massa AN, Van Deynze A *et al*. Single nucleotide polymorphism discovery in elite North American potato germplasm. *BMC Genomics*. 2011;12(1):302.

Hammond-Kosack KE, Jones JDG. Incomplete dominance of tomato Cf genes for resistance to Cladosporium fulvum. *Mol Plant Microbe Interact*. 1993;7:58-70.

Hanson PM, Bernacchi D, Green S *et al*. Mapping of a Wild Tomato Introgression Associated with Tomato Yellow Leaf Curl Virus Resistance in a Cultivated Tomato Line. *J Amer Soc Hort Sci.* 2000;125:15-20.

He C, Poysa V, Yu K. Development and characterization of simple sequence repeat (SSR) markers and their use in determining relationships among Lycopersicon esculentum cultivars. *Theoretical and Applied Genetics.* 2003;106(2):363-373.

Hichri I, Muhovski Y, Zizkova E, Dobrev PI, Franco- Zorrilla JM, Solano R, *et al*. The *Solanum lycopersicum* zinc finger 2 cysteine-2/histidine-2 repressor-like transcription factor regulates development and tolerance to salinity in tomato and Arabidopsis. *Plant Physiol.* 2014;164:1967-1990. doi: 10.1104/pp.113.225920

Huang CC, Cui YY, Weng CR, Zabel P, Lindhout P. Development of diagnostic PCR markers closely linked to the tomato powdery mildew resistance gene Ol-1 onchromosome 6 of tomato. *Theor Appl Genet*. 2000;101:918-24.

Huang CC, Cui YY, Weng CR, Zabel P, Lindhout P. Development of diagnostic PCR markers closely linked to the tomato powdery mildew resistance gene Ol-1 onchromosome 6 of tomato. *Theor Appl Genet*. 2000;101:918-24.

Iquebal MA, Arora V, Verma N, Rai A, Kumar D. First whole genome based microsatellite DNA marker database of tomato for mapping and variety identification. *BMC Plant Biology.* 2013;13(1):197.

Ji Y, Schuster DJ, Scott JW. Ty-3, a begomovirus resistance locus near the Tomatoyellow leaf curl virus resistance locus Ty-1 on chromosome 6 of tomato. *Mol Breed*. 2007;20:271-284.

Ji Y, Scott JW, Hanson P *et al*. Sources of Resistance, Inheritance, and Location of Genetic Loci Conferring Resistance to Members of the Tomato Infecting Begomoviruses. In: Tomato Yellow Leaf Curl Virus Disease: Management, Molecular Biology, Breeding for Resistance (Ed. Czosnek H). Springer, The Netherlands, 2007,343-362p.

Ji Y, Scott JW, Schuster DJ. Toward Fine Mapping of the Tomato Yellow Leaf Curl Virus Resistance Gene Ty-2 on Chromosome 11 of Tomato. *Hort Science*. 2009;44:614-8

Jiménez-Gómez JM, Maloof JN. Sequence diversity in three tomato species: SNPs, markers, and molecular evolution. *BMC Plant Biology*. 2009;9(1):85.

Kevei Z, King RC, Mohareb F, Sergeant MJ, Awan SZ, Thompson AJ. Resequencing at≥ 40-

fold depth of the parental genomes of a Solanum lycopersicum × S. pimpinellifolium recombinant inbred line population and characterization of frame-shift In Dels that are highly likely to perturb protein function. *G3: Genes, Genomes, Genetics*. 2015;5(5):971-981.

King AMQ, Adams MJ, Carstens EB, Lefkowitz EJ. Eds., Elsevier Academic Press: London, UK, 2012, 351- 373p. [Google Scholar]

Langford AN. The parasitism of Cladosporium fulvum Cooke and the genetics of resistance to it. Can J Res. 1937;15:10828

Mansoor S, Khan SH, Saeed M, Bashir A, Zafar Y, Malik KA. Evidence for the association of a bipartite geminivirus with tomato leaf curl disease in Pakistan. *Plant Dis.* 1997;81:958. [Google Scholar] [CrossRef]

Milligan SB, Bodeau J, Yaghoobi J, Kaloshian I, Zabel P *et al*. The root knot nematode resistance gene Mi from tomato is a member of the leucine zipper, nucleotide binding, leucine-rich repeat family of plant genes. *Plant Cell*. 1998;10:1307-1319

Mueller LA, Tanksley SD, Giovannoni JJ, van Eck J, Stack S, Choi D, *et al*. The tomato sequencing project, the first cornerstone of the international Solanaceae Project (SOL). Comp. Funct. Genomics. 2005;6:153-158. doi: 10.1002/cfg.468.

Ning L, Jing-Bin J, Jing-Fu L, Xiang-Yang X. Development of molecular marker linked to Cf-10 gene using SSR and AFLP method in tomato. *Journal of Northeast Agricultural University*. 2012;19(4):30-36.

Panthee DR, Gardner RG Genetic improvement of fresh market tomatoes for yield and fruit quality over 35 years in North Carolina: a review. *Int J Veget Sci*2011;17(3):259–273

Parrella G, Moretti A, Gognalons P, Lesage ML, Marchoux G *et al*. The Am Gene Controlling Resistance to Alfalfa mosaic virus in Tomato Is Located in the Cluster of Dominant Resistance Genes on Chromosome 6. *Phytopathol*. 2004;94:345-350.

Pierce LC. Linkage tests with Ph conditioning resistance to race O, Phytophthora infestans. *Report of the Tomato Genetics Cooperative*. 1971;21:30.

Ranjan A, Ichihashi Y, Sinha NR. The tomato genome: implications for plant breeding, genomics and evolution. *Genome Biol*. 2012;13:167

Rick CM, Chetelat RT. Utilization of related wild species for tomato improvement. *Acta Horticulturae*. 1995;412:21-38.

Rick CM. Origin of cultivated tomato, current status and the problem. International Botanical Congress, 1969,180p.

Rossi M, Goggin FL, Milligan SB, Kaloshian I, Ullman DE, Williamson VM. The nematode resistance gene Mi of tomato confers resistance against the potato aphid. *Proceedings of National Academy of Sciences USA.* 1998;95:9750-9754.

Ruiz JJ, GarcíaMartínez S, Picó B, Gao M, Quiros CF. Genetic variability and relationship of closely related Spanish traditional cultivars of tomato as detected by SRAP and SSR markers. *Journal of the American Society for Horticultural Science*. 2005;130(1):88-94.

Schornack S, Ballvora A, Gurlebeck D, Peart J, Baulcombe D *et al*. The tomato resistance protein Bs4 is a predicted non-nuclear TIR-NB-LRR protein that mediates defense responses to severely truncated derivatives of AvrBs4 and overexpressed AvrBs3. *Plant J*. 2004;37:46-60.

Sela-Buurlage MB, Budai-Hadrian O, Pan Q, Carmel- Goren L, Vunsch R *et al*. Genome-wide dissection of Fusarium resistance in tomato reveals multiple complex loci. *Mol Genet Genomics*. 2001;265:1104-1111.

Shukla DD, Ward CW, Brunt AA *et al*. Potyviridae. AAB Descriptions of Plant Viruses, No. 366, 1998.

Sim SC, Durstewitz G, Plieske J, Wieseke R, Ganal MW, Van Deynze A *et al*. Development of a large SNP genotyping array and generation of high-density genetic maps in tomato. *PloS one*, 2012,7(7).

Sim SC, Robbins MD, Van Deynze A, Michel AP, Francis DM. Population structure and genetic differentiation associated with breeding history and selection in tomato (*Solanum lycopersicum* L.). *Heredity*. 2011;106(6):927-935.

Sim SC, Robbins MD, Van Deynze A, Michel AP, Francis DM. Population structure and genetic differentiation associated with breeding history and selection in tomato (*Solanum lycopersicum* L.). *Heredity*. 2011;106(6):927-935.

Singh M, Chakraborty S, Kumar S, *et al*. Genetic Engineering for Insect Resistance in Vegetable Crops. *Veg Sci*. 2000;27(2):105-16p.

Stamova BS, Chetelat RT. Inheritance and genetic mapping of cucumber mosaicvirus resistance introgressed from *Lycopersicon chilense* into tomato. *Theor Appl Genet*. 2000;101:527-537.

Tanksley SD, Ganal MW, Prince JP, De Vicente MC, Bonierbale MW, Broun P *et al*. High density molecular linkage maps of the tomato and potato genomes. *Genetics*. 1992;132(4):1141-1160.

Thapa SP, Miyao EM, Davis MR, Coaker G. Identification of QTLs controlling resistance to Pseudomonas syringae pv. tomato race 1 strains from the wild tomato, Solanum habrochaites LA1777. *Theoretical and Applied Genetics*. 2015;128(4):681-92.

Todorovska E, Ivanova A, Ganeva D, Pevicharova G, Molle E, Bojinov B *et al*., 2014.

Vakalounalus DJ, Laterrot H, Moretti A, Ligoxigakis EL, Smardas K. Link age between Frl (Fusarium oxysporum f.sp. radicis-lycopersici resistance) and Tm-2 (tobacco mosaicvirus resistance-2) loci in tomato (Lycopersicon esculentum). *Ann Appl Biol*. 1997;130:319-23.

Van der Biezen EA, Glagotskaya T, Overduin B, Nijkamp HJ, Hille J. Inheritance and genetic mapping of resistance to Alternaria alternate f. sp. lycopersici in Lycopersicon pennellii. *Molecular Genetics and Genomics*. 1995;247:453-461.

Varma A, Malathi VG. Emerging geminivirus problems: A serious threat to crop production. *Ann. Appl. Biol*. 2003;142:145-164. [Google Scholar] [CrossRef]

Víquez-Zamora M, Vosman B, van de Geest H, Bovy A, Visser RG, Finkers R *et al*. Tomato breeding in the genomics era: insights from a SNP array. *BMC Genomics*. 2013;14(1):354.

Wang D, Bosland PW. The Genes of Capsicum. *Hort Sci.* 2006;41:1169-1187p.

Williamson VM, Ho JY, Wu FF, Miller N, Kaloshian I. A PCR-based marker tightly linked to the nematode resistance gene, Mi in tomato. *Theoretical and Applied Genetics*. 1994;87:757-763.

Wolters A, Jacobsen E, O'Connell M et al Somatic hybridization as a tool for tomato breeding. *Euphytica*1994;79:265–277

Yaghoobi J, Kaloshian I, Wen Y, Williamson VM. Mapping a new nematode resistance locus in Lycopersicon peruvianum. *Theoretical and Applied Genetics*. 1995;91:457-464

Yang X, Caro M, Hutton SF, Scott JW, Guo Y, Wang X *et al*. Fine mapping of the tomato yellow leaf curl virus resistance gene Ty-2 on chromosome 11 of tomato. *Molecular Breeding*. 2014;34(2):749-760.

Yang X, Caro M, Hutton SF, Scott JW, Guo Y, Wang X *et al*. Fine mapping of the tomato yellow leaf curl virus resistance gene Ty-2 on chromosome 11 of tomato. *Molecular Breeding*. 2014;34(2):749-760.

Zaidi SSS, Martin DP, Amin I, Farooq M, Mansoor S. Tomato leaf curl New Delhi virus: A widespread bipartite begomovirus in the territory of monopartite begomoviruses. *Mol. Plant Pathol.* 2016;18:901-911.

Zamir D, Ekstein MI, Zakay Y, Navot N, Zeidan M, Sarfatti M *et al*. Mapping and introgression of a tomato yellow leaf curl virus tolerance gene, Ty1. *Theoretical and Applied Genetics*. 1994;88:141-146.

Zamir D, Ekstein-Michelson I, Zakay Y, Navot N, Zeidan M *et al*. Mapping and introgression of a tomato yellow leaf curl virus tolerance gene, TY-1. *Theor Appl Genet*. 1994;88:141-146.