An Outlook on GWAS with a Special Focus on Solanaceous Vegetable Crops – A Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

Review Article

ABSTRACT

The commercial solanaceous group of vegetables *viz.,* Tomato, Brinjal, Peppers, and Potatoes hold a prime position among all other vegetables in terms of cultivation and consumption worldwide. These vegetables are consumed fresh by all strata of people and are also used as raw materials in the processing industries. Hence, most plant breeders have a keen interest in the crop improvement of these crops emphasizing yield improvement, quality and nutraceuticals enrichment and imparting resistance to various biotic and abiotic stresses in accordance with climate change. Most of the desirable traits are polygenic in nature which may have a complex inheritance pattern. It is essential to have clear-cut knowledge of the expression frequencies of multiple genes/alleles governing a particular quantitative trait/phenotype, the methods employed to examine and comprehend the candidate genes governing one or various characteristics in plants are quantitative trait loci mapping and genome-wide association studies. In This review, we have discussed GWAS and its future perspectives and made efforts to tabulate the recent past works done in solanaceous

vegetable crops using this approach. GWAS is a attractive strategy that constitutes an important advancement in genetic analysis and has unquestionably proven to be a useful tool in identifying candidate genes, which is justified in this article.

ABBREVIATIONS

QTLs	*- Quantitative Trait Loci*
RIL	*- Recombinant Inbred Line*
LD	*- Linkage Disequilibrium*
GWAS	*- Genome-Wide Association Study*
SNP	*- Single-Nucleotide Polymorphism*
WGS	*- Whole Genome Sequencing*
GS	*- Genomic Selection*
NGS	*- Next-Generation Sequencing*
MAS	*- Marker-Assisted Selection*
GBS	*- Genotyping-by-Sequencing*
GLM	*- Generalised Linear Model*
SSR	*- Single Sequence Repeats*
RADseq	*- Restriction Site-Associated DNA Sequencing*
ddRAD-seq	*- Double Digest Restriction-Site Associated DNA Sequencing*

1. INTRODUCTION

Vegetable breeders' and researchers' key priorities are to increase yield, quality, and impart resistance to various biotic and abiotic challenges in order to ensure food and nutritional security for the fast-expanding population and to reduce the problem of hidden hunger. Vegetable genetic improvement is hampered by several biotic and abiotic variables, and these factors may also reduce the quantity and quality of vegetables, especially before and after harvest [1]. It is anticipated that enhanced genetic designs, agro-biotechnology, advanced plant breeding methods and genomics will be used to meet the problem. The features like yield and quality in vegetable crops that are economically important and are primarily regulated via multi-allelic or polygenic genes found using quantitative trait loci (QTLs) that interact with one another and the surroundings [2]. To break down complicated variables and find genetic variations linked to these traits, two mapping techniques, linkage mapping/QTL mapping and association mapping are frequently utilized [3,4]. Since both approaches lay foundation on the co-inheritance of functional polymorphisms (genes which alter phenotype) and DNA modifications (molecular markers), they can be used to locate QTL associated with vegetable yield and quality [5].

As previously mentioned, the techniques used to investigate and comprehend various characteristics of plants include quantitative trait loci (QTL) mapping and genome-wide association studies (GWAS). A statistical approach known as QTL mapping makes it easier to link multiple genotypes and phenotypes [6,7]. Molecular markers including single nucleotide polymorphisms (SNPs) and amplified fragment length polymorphisms (AFLPs) are used to link mapped QTLs to reported phenotypic information. Multiple types of investigations employing QTL mapping have been reported for plant species to examine several attributes associated to production, quality, and various biotic and abiotic stresses [8,9,10]. QTL mapping has the benefit that it enables the mapping of trait variation in F_2 RIL populations. The same benefit revealed QTL mapping's shortcomings, wherein only RIL populations can be mapped and allelic variation among parents can be measured at an F2 hybrid [11]. GWAS outperforms QTL mapping's shortcomings. In this review, we made an effort to discuss the GWAS approach and the past few years' works were highlighted along with the future perspective of GWAS in solanaceous vegetable crops. We believe that this information will provide an overall outlook on GWAS and help researchers to find out the research gaps in the improvement of these crops.

2. GENOME-WIDE ASSOCIATION STUDY

A study of genome-wide association, commonly referred to as whole genome association studies, evaluate a collection of genetic changes over the entire genome to see whether any variation is linked to a trait [12]. The focus of GWAS is frequently on the connections among characteristics and SNPs, for instance, DNA from diverse plant species is when related to varied phenotypes for a specific character. GWAS, despite being hypothesis-free, can generate hypotheses. GWAS are used for association result analysis, replication, interpretation, and follow-up based on designs, genotyping technologies, and statistical principles [13].

2.1 GWAS Design

An effective study needs a consistent approach or design. The DNA of several plants with various phenotypes for a given characteristic is frequently compared in case versus control, or quantitative, GWAS designs [13]. Studies that are trait-focused can employ case vs. control research, whereas studies that are trait-measurement oriented can use quantitative research with a quantitative design. When comparing a case to a control, the variety could be the case itself, another variety like it without any modifiable traits, or a variety with different phenotypes of the same trait. Every variation is often classified as either a case or a control. In some situations, it may be straightforward to quantify a measurable characteristic that is included in a statistical design since the study can take genetic variations into consideration [13]. The efficiency of the GWAS design for gathering SNP (single nucleotide polymorphism) data will determine the outcome of the investigation.

2.2 Mapping SNPs

SNPs are the current genetic diversity units evidenced in the genomes of all organisms. They are DNA mutations that affect only one base pair. Utilizing genotyping technologies such as tailored, chip-based microarray technology [14], Illumina (San Diego, California), Affymetrix (Santa Clara, California) [15], or other next-generation sequencing technologies, more than a million SNPs can be detected [16]. Based on GWAS design, these collected SNPs can be examined or linked to phenotypes or traits.

2.3 GWAS Assessment

The linkage (collection of genes/alleles) of the heritable unit for a population's character is transmitted from parent to offspring. A assessment of changes in the linkage that can be linked to mutations, linkage breaks, or SNPs is called linkage disequilibrium (LD). Evaluation of SNPs in the genome that affects phenotype is the aim of GWAS. There are two methods for evaluating SNPs that affect phenotypes: both direct and indirect associations [13]. Indirect association happens whenever the SNP is not genotyped directly but is correlated statistically with the phenotype. Direct association occurs when the trait's SNP is precisely genotyped and analytically connected to the SNP affecting trait [13]. For single-locus or multi-locus analyses, the association of alleles and SNP in a sample is performed [17-19]. An analysis of the independent connections between each SNP and phenotype is known as single-locus statistical analysis. When the Each SNP's relationship to a phenotype or trait is investigated, multi-locus analysis takes place [17-19,13].

Logistic regression will be used to analyse traits whenever the quantitative approach is used in the GWAS study. When the GWAS investigation is for a case vs control design, a generalised linear model (GLM) and analysis of variance (ANOVA) will be utilized to assess traits. The null hypotheses or assumptions that govern the three techniques of GLM, ANOVA, and logistic regression when the attribute follows normal distribution, the trait variance within each group is the same, and the groups are independent [13]. Even while there are benefits to utilising GWAS to relate SNPs to traits or qualities, there are also some disadvantages. Population stratification makes it more likely for SNPs to be linked to traits during GWAS analysis. Typically, genetic analysis acts as a sign of substructure of the population [13]. The segmentation of the population can be avoided by investigating population structures and using PCA (Principal component analysis) to eliminate influences among the information [13].

2.4 GWAS Replication

The influence of genetics applies to various groups, and a replication leads to generalization of the link between SNPs and characteristics. To validate the results of the population, repetition experiments must be carried out using separate datasets, as with GWAS, generated from comparable samples [13]. The link of SNPs associated with characteristics is supported if the findings hold up throughout case studies and replication studies [20].

2.5 Meta-analysis of GWAS

Since the first successful publication in 2005, innumerable case studies on GWAS have already been reported. On a common hypothesis, scientific articles typically concur or disagree. Publications employ meta-analysis to clarify this misunderstanding. To explore the similar assumption and determine the usual result of integrated study, meta-analysis is a potent statistical technique that brings together GWAS data from multiple published studies

[13,20]. The data from merged studies should be imputed before being used in meta-analysis because they were collected from different genome sequence platforms and in the study, no SNPs were genotyped directly [13,20].

This strategy has a number of benefits, such as the ability to generalise the study's findings to a larger group. Techniques can increase precision and accuracy of the estimations. Comparing and contrasting the results of various GWAS reports is possible. To test the hypothesis, the meta-analysis may use, for example, an overview of the findings of a GWAS study [13].

3. GWAS IN SOLANACEOUS VEGETABLES

The Solanaceae contain many horticultural species of economic importance known for their food and medicinal values, among which the most common and commercial vegetable crops include tomato (*Solanum lycopersicum*), eggplant (*Solanum melongena*), pepper (*Capsicum spp.*) and potato (*Solanum tuberosum*). All these four vegetables are the most important vegetables throughout the world among different strata of people. Most of the yield and quality characteristics of these vegetables are mostly governed by polygenes. As we discussed earlier genome-wide association studies along with linkage disequilibrium are one of the best techniques to dissect complex traits. Hence for effective crop improvement of these crops many researchers are focusing more on research employing GWAS. So far only countable work has been done in this area concerning these vegetable crops and a lot more is yet to be explored. We attempted to tabulate some recent works done in solanaceous vegetable crops using GWAS approaches are given below:

Tomato

Sl. No	Aim of study	Techniques used	Results	References
1	To study the genomic diversity and population structure analysis	ddRAD-seq	In the Mediterranean 'da serbo' gene pool, 2297 new genes with harboring SNPs were identified which can be subjected to further study using GWAS	Esposito, S [21]
2	To find QTLs for eight tomato fruit attributes	SNPs (51K Axiom® tomato array)	A number of traits were linked to two SNP markers on chromosome 1 and 2, demonstrating the pleiotropic effects of QTL. Furthermore, eight fruit attribute potential new QTLs are offered by 16 of 30 MTAs (marker-trait associations).	Kim, M [22]
3	determining the genetic influences on agronomical qualities in contemporary breeding lines, and assessing their genetic diversity	GWAS, Illumina	• Over 11,000 SNPs were discovered. • Along with numerous new loci important for tomato breeding, the genetic architecture and connections for fruit weight, plant development, and earliness were discovered.	Bauchet, G., [23]
4	To identify genomic regions for four fruit characteristics they are fruit weight (FW), soluble solid content (SSC), fruit shape, and fruit color and to find associations between them.	GWAS, 547 InDel markers	A group of 102 markers that were substantially (p < 1.19–1.30 × 10−4) linked with SSC, FW, fruit morphology, and fruit colour was discovered on 11 of the 12 chromosomes. The findings showed that association mapping utilising a small population and a limited range of InDel markers might not only supplement and improve prior QTL data but also uncover new loci enabling marker-assisted selection of tomato fruit characteristics.	Liu, X., [24]
5	To assess the genetic differentiation and linkage disequilibrium in *Solanum pimpinellifolium*	GWAS, RADseq	• In order to account for population stratification, SNP genotypic data consistently verified the genetic differentiation. • When markers are saturated in GWAS, the 18-Kb linkage disequilibrium decay does in fact show the possibility for single-gene resolution.	Lin, Y. P., [25]

Sl. No	Aim of study	Techniques used	Results	References
6	To detect quantitative trait loci (QTL) for fruit traits in tomato	GWAS	A total of 41 loci associated with the six fruit traits *viz,* fruit shape, fruit color, pericarp thickness, fruit weight, fruit height, and fruit width were identified	Phan, N. T., [26]
7	To study the genetic mapping for earliness-related traits in cultivated tomato	Molecular markers (SNPs, InDels, and SSRs)	The study found 23 associations for variables linked to earliness, confirmed some prior QTLs, and found several possibly new loci that regulate earliness in tomato.	Wang, T., [27]
8	To locate key genetic loci and regions that regulate the acid and volatile content of tomato fruit	GWAS	• In the study, 10000 SNP markers were detected, and 79 relationships that had significant impacts at high resolution on 13 major and 19 secondary metabolites were discovered. • The study also identified potential genes that could alter the metabolite content.	Bauchet et al., [28]
9	To describe the genetics of malate synthesis	GWAS	A quantitative trait locus responsible for variation in fruit malate accumulation was identified i.e, TFM6 (tomato fruit malate 6), which corresponds to Al-ACTIVATED MALATE TRANSPORTER9 (Sl-ALMT9 in tomato).	Ye et al., [29]
10	To locate the QTL in organic agriculture conditions for agronomic, fruit quality, and root architectural traits.	Phenotyping and GWAS (dd‑RADseq)	• High heritability was observed among different characters under study. • On chromosome 11, a single member of the SUN family (SLSUN31) was linked to six flower and fruit characteristics.	Tripodi et al., [30]
11	To look into the quantitative trait loci (QTL) for resistance to bacterial wilt.	GWAS (51 K Axiom® tomato array)	Three genes pertaining to bacterial wilt resistance were identified *viz., Bwr-4, Bwr-12 and Bwr-6* on chromosome 4, 12 and 6 respectively.	Nguyen et al., [31]
12	To study the regulation and formation of multicellular trichomes in tomato	GWAS	The study revealed the key gene controlling trichome formation i.e, *Hair (H)* along with its three alleles.	Chang et al., [32]
13	To identify the genetic factors that contribute to the buildup of tocochromanol in tomato fruits	GWAS and mapping	The study identified a total of 25 quantitative trait loci pinpointing the chorismate–tyrosine pathway.	Burgos et al., [33]
14	To recognise the lipase gene and its relationship to flavour volatiles produced from short-chain fatty acids in tomato fruits.	GWAS and mapping	The analysis identified a gene *Sl-LIP8*, which is connected to the buildup of volatile organic molecules produced from short-chain fatty acids in tomato fruit hence contributing to the flavor of the tomato fruits.	Li et al., [34]

Brinjal

Sl. No	Aim of study	Techniques used	Results	References
1	To comprehend the process through which the eggplant fruit peel produces chlorophylls	GWAS	The results showed that the genes *APRR2* and *SmAPRR2* were found having association with the fruit peel colour in brinjal	Arrones et al [35]
2	To determine the QTLs in aubergine that control anthocyanin pigmentation and fruit colour	GWAS	56 SNP locus/phenotype relationships were discovered by the study, and the genomic areas carrying these loci were dispersed over nine of the 12 chromosomes of eggplant	Cericola et al [36]
3	To detect the candidate genes for anthocyanin pigmentation in MAGIC population of Brinjal	GWAS, Phenotyping and Genotyping (5k probes SPET platform)	Strong connections between MYB113 and two myeloblastosis (MYB) genes involved in the anthocyanin biosynthesis pathway were found.	Mangino et al [37]

SI. No	Aim of study	Techniques used	Results	References
4	To generate high resolution genetic map and to locate the QTL for anthocyanin pigmentation and Seed vigour	GWAS	For each characteristic, the study found 7 to 17 QTLs (at least one significant QTL). And the outcomes showed that the newly established map offers useful information for brinjal crop improvement.	Toppino et al [38]
5	To uncover the genetic structure and diversity by studying the selection based on fruit shape	GWAS, Genotyping	Five related SNPs around the SUN and OVATE homologs were found by a study based on the 219 SNPs, and they had a conserved function in regulating the form of the fruit.	Liu et al [39]

Peppers

SI. No	Aim of study	Techniques used	Results	References
1	To investigate the population structure, genetic diversity and links among the landrace varieties of pepper (*Capsicum spp.*) from the Spanish Center of Diversity.	Genotyping by-sequencing (GBS)	• The population under study was divided into seven clusters by using discriminant analysis of principal components (DAPC) • A tight relationship between Mexican and Spanish accessions was revealed via phylogenetic analyses.	Pereira-Dias et al [40]
2	To understand the underlying genetics of Chile pepper's yield and agronomic characteristics (*Capsicum spp.*) by employing multi-locus association mapping.	GWAS	Eight SNP markers spread over six chromosomes were discovered to be associated with a number of traits.	Lozada et al [41]
3	To investigate the genetic variation and population dynamics of Ethiopian Bell pepper accessions.	GBS	• Two different genetic populations made up of nine *C. frutescens* accessions and 132 *C. annuum* accessions respectively made up the 142 capsicum collections. • 509 SNP markers were found by GWAS analysis to be strongly correlated with characteristics related to fruit, stems, and leaves.	Solomon et al [42]
4	To identify the potential genes responsible for features connected to fruit	GWAS & QTL Mapping	The GWAS results revealed that 16 casual genes were believed to be connected to characteristics linked to fruit morphology.	Lee et al [43]
5	To investigate genetic resistance and generate Phytophthora blight disease markers.	GWAS, GBS	The findings showed an SNP marker termed Chr02-1126, which is positioned at 112 Mb on Chr.02 and exhibits *P. capsici* resistance with 78.5% accuracy.	Ro et al [44]
6	To identify genomic loci and alleles responsible for resistance to bacterial wilt	GBS	The QTL analysis showed that the gene *pBWR-1* was found on chromosome 01 reported to be involved in imparting resistance against bacterial wilt	Chae et al [45]
7	To investigate the correlations between 36 agronomic traits throughout the genomes of 287 pepper accessions.	GWAS, specific-locus amplified fragment sequencing (SLAF-seq)	The results revealed that 109 correlation peaks were significantly associated with the 26 agronomic characteristics *via* GWAS, which can be further studied for the crop improvement of pepper	Wu et al [46]
8	To evaluate the genetic diversity and relationship between the amount of capsaicinoids in Thai chilli landraces	GWAS, Diversity array genotype-by-sequencing (DArTseq)	• With a dissimilarity score ranging from 0.0092 to 0.841, cluster analysis separated the chilli landraces into two distinct groups based on their species, *Capsicum annuum* and *C. frutescens*. • GWAS analysis revealed significant association between seven SNPs with the capsaicinoids content.	Kethom et al [47]
9	To locate and catalogue the gene in mature peppers that	GWAS, Mapping and Sequencing	Using a map-based cloning method, the anthocyanin biosynthesis gene *Ca3GT*	Liu et al [48]

Sl. No	Aim of study	Techniques used	Results	References
	regulates anthocyanin production		was precisely mapped in a 110.5 kb region and the strong candidate gene *Capana10g001978* was confirmed.	
10	To identify and locate the gene responsible for producing light-green immature peppers.	GWAS, BSA (bulked segregant analysis)	The study identified a 35.07 kbp region on chromosome 10 as the LG locus affecting light-green immature pepper fruits. In this region, *CaPP2C35*, a potent candidate gene, was discovered.	Wu et al [49]
11	To study the genomic diversity of fruit morphology in capsicum	GWAS	The fruit morphology phenotypes were linked to four unique loci, including a non-synonymous mutation in the Longifolia 1-like (*CA03g16080*) gene of the pepper plant.	Colonna et al [50]

Potato

Sl. No	Aim of study	Techniques used	Results	References
1	To investigate the roles and functions of MYB genes in anthocyanin biosynthesis in potato.	GWAS and transcriptomic analysis	The findings showed that the two MYB TFs (StMYB88 and StMYB89) on chromosome 10 were connected to the development of anthocyanin.	Li et al [51]
2	To identify potential genes associated with potato late blight resistance	GWAS	According to the whole genome association study, there were 18 candidate genes in lesion diameter and 22 candidate genes for disease resistance grade (late blight).	Wang et al [52]
3	The study sought to discover genomic areas associated with the morphology of potato starch granules in *Solanum tuberosum* L.	GWAS	The study demonstrated genetic diversity for starch granule morphology. Significant SNPs were found on chromosomes 2, 4, 7, and 11. With this candidate genes can be found in the future.	Erst et al [53]
4	The study was carried out to reveal genetic variations and genentic architecture associated with Chip Processing clones	GWAS & Sweeps analysis	The Sweeps analysis and GWAS results identified the related genetic variations in chromosome 10, along with variants under selection throughout the genome.	Jo et al [54]
5	The study sought to investigate the phenotypic diversity and genetic basis of essential floral traits in potatoes.	GWAS, GBS	The results revealed a total of 15 significant SNPs for stamen length, pistil length, and pistil length above stamen across both years. The identified candidate genes from this study might be useful to the potato breeders.	Zia et al [55]
6	To investigate genetic variation in response to water deprivation in a panel of diploid potatoes and find the QTL that governs this feature.	GWAS	The findings indicated nine QTL on chromosomes 2, 3, 5, 8, 10, and 12, as well as three candidate genes with a possible function in water deprivation response.	Diaz et al [56]
7	To identify genomic regions associated with starch granule morphology and to increase number of known genome loci associated with potato starch yield.	GWAS	The study discovered 53 new SNPs on chromosomes 1, 2, 4, 5, 6, 7, 9, 11, and 12 that are linked to tuber starch preparative yields and starch granules morphology.	Khlestkin et al [57]
8	To find QTLs and potential candidate genes linked to protein levels in a sample of tetraploid potatoes.	GWAS	The study explored and pinpointed potential genes. QTLs have been discovered on chromosomes 3, 5, 7, and 12.	Klaassen et al [58]
9	To find loci those are strongly linked to common scab disease resistance in a Canadian potato germplasm.	GWAS	The study found significant SNPs for potato common scab resistance on potato chromosomes 2, 4, and 12.	Yuan et al [59]
10	To identify novel QTLs for common scab resistance in potato	GWAS	This resulted in the discovery of an unique QTL for common scab resistance that accounted at the most 14.7% of the total variance; this QTL was located on potato chromosome 1 in the 640 kb gap between 0.43 Mb and 1.07 Mb.	Koizumi et al [60]

4. FUTURE PERSPECTIVES OF GWAS IN VEGETABLE CROPS

Precision marker design and development for significant vegetable crops with high economic value have proven to be costly for many years because of the significant expense of sequencing and genotyping. In addition, a recent development in sequencing dubbed as "next generation sequencing technology" (NGS) has significantly impacted the costs and efforts associated with whole-genome sequencing [61, 62], enabling the creation of GWAS and GS (Genomic Selection). Regarding the accuracy and uniqueness of these two methods, they are going to become important tools for next vegetable breeding programmes as well as effective genetics applications. It will be possible to accurately estimate the genetic value and worth of untested lines and genotypes through the generation of genome-wide marker data that could be advantageous by combining low-cost and high-throughput genotyping techniques. This might be accomplished using genome-wide SNPs with better statistical measures with high precision and efficacy [62]. The genetics of vegetable crops are constantly being worked on by researchers using genomics-based breeding and genomics-assisted selection. By analyzing the yield and quality of the vegetables as well as characteristics such as storability, firmness, weight, shape, colour, maturity time, size, nutrient content, and chlorophyll index through GWAS, it is possible to ascertain whether any of the found markers are associated with particular traits [63]. Vegetable breeders can create novel cultivars with favorable characteristics using genome-wide molecular assisted selection by creating high-density reference genetic linkage maps using genomic resources from the most recent advancements in whole-genome sequencing, genome-wide SNPs, and conventional SSR markers [64].

Without a doubt, breeding efforts for crops and vegetables have greatly benefited from genome-wide association analyses. Researchers and vegetable breeders have devised new genetic risk factors for prevalent crop illnesses. Once the entire vegetable genome has been sequenced, it is anticipated that the legitimacy and effectiveness of GWAS in vegetable crops would greatly rise. This association study methodology is noteworthy in that it may measure relationships between genetic variation and a variety of phenotypes without requiring any prior knowledge. Additionally, GWAS can analyze the

hitherto untapped genetic variety in vegetable germplasm supplies, revealing fresh genetic variability that can be used in upcoming breeding initiatives. Additionally, GWAS can enable transgenesis and target mutagenesis techniques like genome editing [65,62] to assess whether discovered genes are responsible for the phenotypic variance of traits of interest after QTL mapping and gene cloning of candidate genes [62].

5. CONCLUSION

Finally, and perhaps most crucially, collecting phenotypic and genotypic data from vegetable breeders will eventually broaden the possibilities for detecting the potency of GWAS and the accuracy of GS. Furthermore, it is anticipated that the application of NGS technologies would advance yield advantages in all significant vegetable crops. Every major vegetable species is currently the subject of collaborative efforts, and we anticipate the results of these efforts, which will eventually sharpen our viewpoint and support the creation and enhancement of effective routes [66,62].

CONFERENCE DISCLAIMER

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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