



Perspectives and recent progress of genome-wide association studies (GWAS) in fruits

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Abstract

Background Earlier next-generation sequencing technologies are being vastly used to explore, administer, and investigate the gene space with accurate profiling of nucleotide variations in the germplasm.

Overview and Progress Recently, novel advancements in high-throughput sequencing technologies allow a genotyping-by-sequencing approach that has opened up new horizons for extensive genotyping exploiting single-nucleotide-polymorphisms (SNPs). This method acts as a bridge to support and minimize a genotype to phenotype gap allowing genetic selection at the genome-wide level, named genomic selection that could facilitate the selection of traits also in the pomology sector. In addition to this, genome-wide genotyping is a prerequisite for genome-wide association studies that have been used successfully to discover the genes, which control polygenic traits including the genetic loci, associated with the trait of interest in fruit crops.

Aims and Prospects This review article emphasizes the role of genome-wide approaches to unlock and explore the genetic potential along with the detection of SNPs affecting the phenotype of fruit crops and highlights the prospects of genome-wide association studies in fruits.

Keywords Fruits · Next-generation sequencing (NGS) · Genotyping-by-sequencing (GBS) · Single-nucleotide polymorphisms (SNPs) · Genome-wide association studies (GWAS) · Genomic selection (GS)

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

Introduction

The topmost priority of fruit breeders and researchers is to enhance the yield and maintain the durability of key fruit crops to ensure food security for the rapidly growing population. Various biotic and abiotic factors are the key hurdles towards the genetic improvement of fruits and besides this, these factors can also hinder the quality and quantity of fruits particularly during their pre and post-harvest period [1]. To cope with the challenge, advanced plant-breeding techniques, improved genetic designs, agro-biotechnology, and genomics are expected. The economically significant traits in fruit trees like yield and quality of fruits are specifically controlled by polygenes or multi-allelic genes [2] located in quantitative trait loci (QTLs) interacting with each other and with the environment. Two mapping approaches like linkage mapping and association mapping are widely used to dissect complex traits and identify genetic variants associated with these traits [3, 4]. Both strategies are based on the co-inheritance of functional polymorphisms (genes that control trait) and DNA variants (molecular markers) and can be useful to identify QTL linked to fruit quality and

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yield. In this review, we summarize these two approaches and discuss the results and applications in fruit species.

Linkage mapping vs GWAS approaches

Linkage mapping (also known as linkage analysis or bi-parental mapping) uses artificial segregating populations, derived from initial crossbreeding of bi-parental (F_2 , BC_1 , and RIL). The availability of a genetic map with several molecular markers distributed across the genome is a prerequisite to carry out this approach in which the association between each marker and a QTL is tested. Many methods like single marker analysis, simple interval mapping, composite interval mapping, and different statistical analyses can be used. Subsequently, if statistical tests confirm that the phenotypic means of the two groups differ significantly, the association between marker and QTL is confirmed [5].

Depending on the specific procedure used, at the end of linkage analysis QTL position on the map, the number of QTL affecting the trait of interest and the genetic effect of every single QTL on phenotypic variability can be obtained. Furthermore, with this method the QTLs have localized at intervals up to 10–20 cM leading to a low-resolution mapping due to (1) few generations occurring in artificial population and consequently few possible recombination events that can be exploited (2) the limited number of offspring that can be analyzed due to the costs of their propagation and genotypic and phenotypic evaluation. Despite hundreds of linkage studies, only a few QTLs have been identified and cloned at the gene level [6, 7].

Instead, association mapping, also known as linkage disequilibrium (LD) mapping or Genome-wide association studies (GWAS), exploits historical and evolutionary recombination events, coming from many generations of random mating occurring in a natural population or extensive germplasm pool as multi-parental advanced generation intercrosses [8] and nested association-mapping strategies [9] that are becoming popular for LD based association mapping. GWAS approaches have progressed immensely and currently are an incredible asset particularly for the screening of traits controlled by genes with additive effects like quantitative traits. GWAS takes advances in genome-wide characterization of genetic variability exploiting high throughput sequencing technologies, enabling higher resolution and cost-effective mapping of QTLs [3, 10] linked to complex traits along with the detection of genes responsible for controlling various phenotypic variations within cultivars and accessions [11]. As for linkage analysis, the essential methodology in GWAS is to assess the relationship between each genotyped marker and a phenotype of interest that has been scored over countless individuals [12]. However, the main advantages of GWAS over linkage mapping

are resolution power and accommodation of multiple alleles at the same locus to be tested for associations.

(GWAS) is an effective method in so many ways as it is a low-cost and precise method of genotyping with the potential to pinpoint the genes of interest exploiting the detection of phenotypic variations among large samples and populations and the power of statistical analyses. Four main elements are required in GWAS; (1) large population samples that could provide effective genetic information about the research, (2) polymorphic alleles that can be efficiently genotyped, inexpensive, and adequately cover the whole genome as Single-Nucleotide Polymorphism (SNP), (3) phenotypic data collection from a relatively large number of diverse accessions, with adequate replications across multiple years and multiple locations and (4) appropriate statistical methods to locate the genetic associations. These statistical methods used in GWAS are logistic regression particularly for fruits having dichotomous traits and linear regression used for continuous traits [13]. In addition to this, several other statistical tools such as descriptive statistics, analysis of variance, multiple linear stepwise regression, principal component analysis, and correlation analysis have been used specifically in GWAS for phenotypic traits with the help of statistics softwares (R, SPSS, JMP etc.). Another software named Trait Analysis by association, Evolution, and Linkage (Tassel) software has been frequently used to identify the marker-trait association in complex traits, exploiting high-quality SNPs and phenotypic data [14]. SNPs are widely used as a genetic marker in GWAS studies precisely to pinpoint the variation within the genome and this variation can be easily distinguished by different individuals [15]. Furthermore, SNP is the key to accessing the genotypes and handy to explore and investigate the associations, relationships, and linkage among the various plant species including fruits. With GWAS, millions of SNPs can be analyzed to search variants linked to traits of interest, enabling scientists to design novel molecular markers and pinpoint the trait variants in fruit trees. These associations information are mighty helpful for researchers and breeders to examine the domestication history of fruit species along with the identification of significant traits for domestication and eventually beneficial to analyze the potential genetic loci for selection [16]. An important aspect of mapping by association is the level of LD that is the level of non-random assortment of alleles in different loci: certain allelic combinations are inherited together over the generations, few crossing over between them occur. It is the net result of all the recombination events that occurred in a population since the origin of an allele by mutation. Thus, it is a specific characteristic of a population and of its history. This parameter is affected by association between alleles located in the same chromosome, can be a consequence of the reproduction mode (LD extends to a much longer distance in self-pollinated crops,

than in cross-pollinated species), genetic drift, not random mating due to breeding procedures or, geographical origin of samples for which natural selection would have favored certain allele combinations.

Populations with low LD (LD decays within a short distance) mapping resolution is expected to be high, cloning of QTL is possible but a large number of markers is required (high marker density). In this case, if a high-density map is not available, a candidate gene approach can be carried out where the research of polymorphisms is not performed at genome-wide level but is limited to known genes potentially linked to the trait of interest. On the other hand, if LD is high (LD extends a long distance (several cM) mapping resolutions will be low, cloning of QTL is not possible but a relatively small number of markers is required [3].

Association mapping (GWAS) starts from existing collections, such as varieties or wild accessions, without the costly production of artificial populations. Choice of germplasm is critical to the success of association analysis because genetic diversity and relatedness within the population affect the extent of genome-wide LD and mapping resolution [17, 18]. Samples with population structure and/or familial relationships due to local adaptation, selection, and breeding history strongly limit association analyses leading to abnormal LD increase, generating false associations between genetic variants and traits of interest (Type I error). If structured populations are used, specific statistic analyses can be used to avoid type I error. For example, Atwell et al. (2010) [19] carried out a genome-wide-association (GWA) study and analyzed about 200 lines of 107 genotypes in *Arabidopsis thaliana* with Affymetrix chip containing 200,000 SNPs, searching for possible association with 107 phenotypes related to flowering, development, the defense mechanism of plants, and various physiological characters. Efficient mixed-model association [20] was used in the study due to population being heavily structured involving patterns of relatedness on all scales, and thus there was every reason to expect an increased false-positive rate. This allowed controlling for an association between individuals at various levels and minimized the chances of bogus associations among markers and phenotypes [19].

Such GWAS can exploit also natural population, and existing cultivars or lines so that, no preparation of the segregation populations is requested, this method is very useful especially when studies concern tree species that have long life cycles [2]. The availability of genomic resources like high-density maps or long genomic sequences is very important for obtaining reliable GWAS results. In a recent study SNP identification in multiple melon botanical groups allowed marker-anchoring to the whole genome sequence (WGS), which enables the scientist a complete understanding of genetic control of domestication and diversification [21]. For producing reliable genotyping data, researchers considered only SNPs that mapped the

whole genome sequence draft of melon, denying the bogus LD, thus reducing errors in GWAS. Genome-wide marker data can also be used to predict genetic values and therefore predict unobserved phenotypes for complex traits [22].

Integration/limitation among linkage mapping and GWAS approaches

GWAS are frequently integral to QTL mapping and, when operating together, they alleviate each other's constraints [11]. Population-based methodologies, for example, GWAS uses the population of random individuals to screen the genome-wide relationship between SNPs and phenotypes. On the contrary, bi-parental mapping is a family-based approach, using crosses between parents contrasting for the trait of interest (tolerant vs susceptible) and then analyzing phenotypes and genotypes (with molecular markers) in progeny populations to determine marker-trait associations, thus it is onerous and expensive and can be applied for complex pedigrees having crosses among various genotypes [23]. With this approach association between marker and QTL could be limited to a specific population while with GWAS associations have a more universal value [24]. However, association studies require extensive knowledge of SNPs within the genome of the organism of interest and are therefore difficult to perform in species that have not been well studied or do not have well-annotated genomes.

In linkage mapping associations with rare alleles can be found since an artificial population with positive versus negative alleles with numerous individuals with rare alleles can be created, while in the natural ones there is a more pronounced "dilution" effect so in GWAS, that use natural population, it is more difficult to identify rare alleles and only rare major genes with great effect on the phenotype can be identified [25]. On the other hand, association studies allow identifying multiple QTLs for the same trait and associations of traits with alleles with low effect on the phenotype, and common variants. Hence, the genomic selection (GS) is effective in fruitsbi-parental populations using the genomic best linear unbiased predictor (GBLUP) approach [26]. In addition to this, association mapping studies like GWAS present greater fine-scale perspectives than QTL mapping to recognize small distinctive markers in linkage disequilibrium with traits of interests. The bi-parental approach suffers from a low mapping resolution and adverse effects of linkage drag. Hence, they are based on a few generations, so there are only a few opportunities for recombination to occur within families with known ancestry [3].

GWAS in fruits

Genome-wide characterization of genetic variation may have immense potential for the exploitation of natural genetic resources in fruit species as observed in grapes [27]. Robust and equally distributed genome-wide SNP markers linked with reference genetic linkage maps, help us to utilize new genomic-based approaches like GWAS and GS [28] which are currently developing as effective tools in various fruit tree breeding programs like apple, pear, and forest tree [29]. Most of the significant fruit traits like fruit quality are quantitative and restrained by multiple genes and GWAS is more accomplished for the detection of QTLs in fruit crops because it does not involve bi-parental populations [30]. Despite this, there are few studies conducted so far on the versatility and diversity of GWAS in various fruit crops: some examples are summarized in (Table 1).

Table 1 shows the traits that have been studied recently, including the genetic variability and varietal identification, evaluation of fruit quality traits like color and firmness, disease resistance genes and qualitative traits identification, sex determinants detection, fruit hindrance genes investigation, development of novel markers and identification of SNPs using genome-wide based approaches (GWAS, GBS, and SNPs) in various fruits (*Prunus* fruit species, melon, apple, fig, citrus, jujube, and olive cultivars). By utilizing these genome-based approaches they identified the candidate genes or new pathways that are particularly associated with the traits they are looking for.

Role of next-generation sequencing in fruits genotyping

Next-generation sequencing (NGS) technologies enable the researchers to sequence the whole genome of a species rendering a comprehensive gene catalog along with the transcriptome to permit the study of the expression scheme of entire genes at the whole genome level. Various scientific studies depict the genome sequence of different fruit crops with the number of coding genes (Table 2).

Additionally, since high-throughput genotyping is a prerequisite for GWAS, providing data about population structure [61, 62] and fine mapping, NGS technology has made attainable the prompt affinity of phenotypes with genotypes in various fruit and crop species, thereby accelerating the accuracy of crop improvement [63]. Furthermore, NGS technologies have been successfully introduced and used for SNP genotyping through (GBS), [64] and restriction site-associated DNA sequencing [65]. These strategies are based on the reduction of genome complexity before sequencing, through restriction enzyme digestion. Regarding the

whole-genome shotgun sequencing, with these approaches only a low percentage of the genome is sequenced and the sequenced fragments are normally well distributed among chromosomes ensuring a uniform distribution of SNP across the genome. Genome complexity reduction is an important aspect to nullify the eminent proportion of DNA repeats occurring in the majority of fruit tree genomes. GBS is a rapid, specific, and cheap sequencing method also for creating high-density maps that can be used both in natural population genetic variability studies and for SNP discovery among the parents and between the RILs [64], being useful both for GWAS and for bi-parental mapping of QTL [4, 66].

NGS technologies have refined the output and made sequencing attainable of variable samples with the ability to develop high-density genetic maps [4]. The advancement in genome sequencing through NGS technologies administer the chances to identify millions of innovative markers, as well as the determination of agronomically significant genes [67] also in fruit species [68]. GBS provides data also for GS that predicts the breeding values of lines in a population by analyzing their phenotypes and high-density marker scores, allowing marker-assisted selection (MAS) at the genomic level, also for quantitative traits [30, 69]. Many recent studies using GBS have been carried out in fruit species. Thurow [36] investigated the genetic variability, population structure, and patterns of linkage disequilibrium in 220 peach genotypes. Finally, Kishor [32] obtained high-quality SNP markers by using (GBS) to differentiate among Korean melon cultivars. Breeding in stone fruits particularly in (*Prunus species*) where (MAS) is difficult to execute as a result of the polygenic effects for the tricky characters associated with the quality of fruits. In these species, GBS has supplied a large amount of profitable data which have been highly beneficial for fine SNP mapping as in the case of Japanese plum (*Prunus salicina* Lindl.) where molecular information is not available or limited [70]. Furthermore, the role of GBS in peach cultivars has been significant for the identification of QTLs associated with low-temperature requirements and blooming periods, respectively [71].

QTL cloning in fruits

Mapping and cloning of QTLs are the key approaches that have started to recognize the variation among the genes [72] as well as the evolutionary elements that maintain the quantitative variation in populations [73]. In different studies, QTLs linked to genes involved in various fruit crops diseases and pests are reported (Table 3), and QTLs are related to fruit quality traits (Table 4).

Table 3 shows the studies which led to the identification of multiple QTL on genes against various fruit diseases, including the fruit rot resistance in cranberry and brown

Table 1 A summary of genome-wide association studies (GWAS) in various fruit crops

No.	Fruit cultivars	Aim of study	Techniques used	Results of the study	References
01	Pear (<i>Pyrus pyrifolia</i>) accessions	Gene identification and Molecular breeding	GWAS	<i>PbrSTONE</i> candidate gene was identified as responsible for the regulation of stone cell formation in Pear	[31]
02	48 Oriental melon varieties	To detect the genetic diversity, varietal identification “and marker-assisted selection (MAS)	GBS, SNPs, and GWAS	SNP markers were identified which are linked with morphological traits particularly two of them were novel for sex expression	[32]
03	192 Apple germplasm	To locate the genes responsible for causing (AMB ^h) disease	GWAS	A candidate gene linked with (AMB ^h) disease resistance was successfully identified	[33]
04	386 Grapevine genotypes	To locate the genes, which are responsible for creating resistance in certain grapefruit diseases, include white rot	RAD-Seq and GWAS	6 SNP markers were identified along with eight candidate genes linked with white rot resistance	[34]
05	Red raspberry genotypes	To locate the genomic region linked with prickly development	GBS, SNPs, and GWAS	Identified prickly-free significant markers comprising of four SNPs were detected on chromosome 4	[35]
06	220 Peach genotypes	Studied the genetic variability, population structure, and linkage disequilibrium in Brazilian peach	GBS-SNPs and GWAS	Successfully identified the population genetic structure along with the significant value of SNP trait linkage were observed as predicted by linkage mapping	[36]
07	180 Jujube accessions	To locate the various SNPs linked with nine fruit quality traits	GWAS	45 Candidate genes were identified particularly related to fruit size quality, stone size, and fruit cracking-related traits of Jujube	[37]
08	183 Olive accessions	Identification of candidate genes along with the development of markers	GWAS	Accessions were genotyped by the GBS method, GWAS was conducted with the help of 24,977 SNPs, and 19 candidate genes were identified	[38]
09	109 Grape genotype was studied	Fruit color traits were examined	GWAS	Successfully determined the genetic determinants of grape berry-related traits	[39]
10	Total of 86 pear parental lines were studied	To investigate the hindrance of fruit breeding due to long juvenile period	GWAS and GS	The phenotypic and genome-wide marker data of pear fruit cultivars were collected	[40]
11	A total of 1575 southern highbush blueberry individuals were examined	Explore the genetic association in traits linked with fruits and identification of candidate genes which affects the phenotypic variation	SNPs and GWAS	117 Full-sib families were genotyped by NGS. Results depicted that novel SNPs were observed within and around biologically credible candidate genes	[41]
12	110 Japanese citrus accessions were examined	8 Fruit quality traits were evaluated	GBS, SNPs, and GWAS	Successfully figure out LD ^b in 110 accessions, enough SNPs gathered to conduct GWAS, along with this seven QTLs were identified four of them are novel	[42]

Table 1 (continued)

No.	Fruit cultivars	Aim of study	Techniques used	Results of the study	References
13	A total of 785 genotypes of citrus were examined	Identification of association among 17 various fruit quality traits	GS, SNPs, and GWAS	1841 SNPs were identified, 17 fruit quality traits were phenotyped. The gathered results confirm the accuracy and validation of GWAS and GS for genetic improvement in fruit traits related to <i>Citrus</i>	[43]
14	Fig cultivars	Identification of sex determinants	QTL mapping, (RAD-seq) ^c , SNPs and GWAS	Successfully discovered a candidate gene <i>RESPONSIVE-TO-ANTAGONISTIC (RANI)</i>	[44]
15	129 Peach accessions	Qualitative traits were investigated	GWAS	The candidate's genes were identified for two qualitative traits regarding cell death and auxin-efflux associated with fruit shape	[45]
16	Apricot	Identification of pathogen resistance	GWAS ^d	The candidate's genes were identified for pathogen resistance	[46]
17	120 Melon accessions	Identification of variation for fruit firmness	QTL, SNPs ^e , GWAS and Bi-parental mapping	13,789 SNP markers were developed by (GBS) ^f . The recombination rate of chromosomes was identified along with genome-wide segregation distortion. QTLs ^g levels were classified and showed high to moderate linked with fruit firmness	[47]
18	104 Peach landraces were studied	Identification of 10 fruit quality traits	SSR markers, QTL, and association mapping were used	Successfully identified the associated markers with the help of peach association mapping	[48]
19	1120 Seedlings of Apple were examined	6 fruit quality traits were evaluated	SNPs and GS	Selection for fruit quality traits was successfully done by Genomic selection	[49]

AMB apple Marssonina blotch; GWAS genome-wide association study; RAD-seq restriction site associated DNA sequencing; SNPs single-nucleotide polymorphisms; GBS genotyping-by-sequencing; QTL quantitative trait locus; NGS next generation sequencing; GS genomic selection; LD linkage disequilibrium

^aAMB, apple Marssonina blotch

^bLD, linkage disequilibrium

^cRAD-seq, restriction site associated DNA sequencing

^dGWAS, genome-wide association study

^eSNPs, single-nucleotide polymorphisms

^fGBS, genotyping-by-sequencing

^gQTL, quantitative trait locus

Table 2 Fruit crops with their genome information

No.	Fruit Trees	Size of genome in Mb (mega-byte)/Mbp (megabit)	Decoded genes	Sequencing methodology	References
01	Star fruit	470.51 Mb	24,726	BLAST ^a , BUSCO ^b	[50]
02	Mango	392.9 Mb	41,251	WGD ^c , NGS ^d	[51]
03	Black raspberry	290 Mb	34,545	Single-molecule real-time Pacific Biosciences sequencing	[52]
04	Common fig	356 Mb	27,995	Illumina GAIIx, MiSeq and HiSeq 2000	[44]
05	Sweet cherry	272.4 Mb	10,148	NGS	[53]
06	Sweet orange	320.5 Mb	29,445	Whole-genome shotgun, tag sequence reads, Illumina GAII sequencer	[54]
07	Pear	512.0 Mb	42,812	NGS	[55]
08	Peach	265 Mbp	27,852	Sanger whole-genome shotgun	[56]
09	Strawberry	240 Mbp	34,809	Roche/454 illumina	[57]
10	Apple	742.3 Mbp	57,386	Whole-genome short gun	[58]
11	Papaya	372 Mbp	28,629	Whole-genome shotgun	[59]
12	Grapevine	504.96 Mb	29,585	Sanger whole-genome shotgun	[60]

BLAST basic local alignment search tool; *BUSCO* benchmarking universal single-copy orthologs; *WGD* whole genome development; *NGS* next generation sequencing

^aBLAST, basic local alignment search tool

^bBUSCO, benchmarking universal single-copy orthologs

^cWGD, whole genome development

^dNGS, next generation sequencing

Table 3 Fruit crops with their QTLs genes reported against pest/diseases

No.	Fruit crop	QTLs or genes reported against pest/diseases	References
01	Orange	Disease resistance	[74]
02	Cranberry	Fruit rot resistance	[75]
03	Peach	Brown rot resistance	[76]
04	Grapevine	Downy and powdery mildew resistance	[77]
05	Apple	Scab resistance	[78]
06	Pear	Scab resistance	[79]
07	Apricot	Plum pox virus resistance	[80]

rot resistance genes in peach, downy and powdery mildew resistance in grapevine, scab resistance in apple and pear, and plum pox virus resistance in apricot. Furthermore, various fruit developmental factors have been a key focus in modern breeding programs for many fruit tree species. Likewise, in Table 4. Significant fruit development factors such as fruit skin color, fruit firmness, fruit yield, and other phenological traits that affect fruit maturation were investigated in various fruit cultivars for the identification of candidate loci associated with above-mentioned factors. Therefore, besides these findings, a few studies have reported QTL cloning in fruits. In the future, with GWAS, we expect to increase the number of QTL clones.

Table 4 Fruit crops with their QTLs controlling fruit quality traits

No.	Fruit crop	QTLs (fruit quality traits)	References
01	Blueberry	Fruit firmness	[81]
02	Mandarin	Fruit yield	[82]
03	Orange	Cold tolerance	[74]
04	Melon	Fruit skin color, sugar content, fruit weight, and harvest time	[68]
05	Pear	Fruit skin color, sugar content, fruit weight, and harvest time	[83]
06	Apple	Fruit skin color, sugar content, fruit weight, and harvest time	[84]
07	Grapevine	Fruit skin color, sugar content, fruit weight, and harvest time	[85]
08	Peach	Fruit skin color, sugar content, fruit weight, and harvest time	[86]

Role of genomic selection (GS) in fruits

DNA-based selection approaches are amongst the latest breeding strategies, which are successfully implemented for the enhancement of crop yield. The selection at the genome-wide level, GS, is a reliable and vastly improved method practiced in crop breeding programs precisely for the selection of tricky traits like yield by monitoring and detecting the role of candidate genes particularly genes of interest within a genome [87]. Generally, the use of genomic-based methods such as GWAS and GS allows breeders to enhance productivity and uplifts efficiency precisely in the tree sector including forest and tree fruits [30, 88]. Genomic selection can use genome-wide markers for the accurate prediction and measurement of the effect of loci in target traits within the genome [28]. GS is adventitious because it exploits markers like SNPs accompanied by high LD values to grab a considerable amount of genetic variance [89]. Grattapaglia & Resende (2011) compared the role of GS and MAS in their study and they revealed that GS is immensely effective than MAS when phenotypic selection of tricky traits is concerned [90]. Furthermore, GS is superior than MAS since marker-assisted selection is only comprised of those markers which are closely linked with the trait of interest and on the whole not proven to be so effective on complex traits [30]. On the other hand, GS exploits those molecular markers having an ability to detect an ample amount of genetic variation among various polygenic fruit traits [89]. Hence, GS prevents the effect of biases on the marker and generates a measured correlation among the phenotypically predicted breeding values [69]. GS has the immense potential to boost the breeding process in the horticulture sector with improved genetic attainability [91]. For improved fruit cultivars GS is highly beneficial in perennial fruit crops over annual fruit crops to speed up the yield and overall genetic gain [92]. Apart from this, GS may be a handy approach to minimize the overall cost of the fruit breeding program with improved orchard management [93].

Future perspectives of GWAS in fruit trees

For many years, designing and developing markers precisely for eminent commercial value fruit crops have proved to be costly due to the high expense of their genotyping and sequencing. Besides this, to counter this hurdle recently there is a new advancement of sequencing known as “next-generation sequencing technology” (NGS) which has had an immense impact on the economic perspectives and efforts for whole-genome sequencing [16] allowing the development of GWAS and GS. As far as the credibility and specificity of these two approaches are concerned, they

will evolve as significant methods for future fruit breeding programs accompanied by their effective use in the field of genetics. This will be possible due to the accurate prediction of genetic worth and values of untested lines and genotypes by establishing genome-wide marker data, which could be handy by the combination of high throughput and low-cost genotyping techniques. This could be achieved by genome-wide SNPs accompanied by enhanced precision and effective use of statistical methods. Researchers are working currently on the mission towards the genetic improvement of fruit trees through genomics-assisted breeding and genomics-based techniques. The advancements in genome-wide association approaches will be useful and convenient to improve the genetic improvement specifically in fruit trees despite the obstacles that still prevails and it's a challenge for plant breeders to design the fruit breeding programs in such a way that they will take a maximum benefit from these genomics-based approaches because each fruit species is unique [94]. The yield and quality of the fruits and traits like shelf life, harvesting time, firmness, ripening time, skin color, fruit weight, shape, flesh color, and chlorophyll index can be examined through GWAS to decide whether any of the identified markers are linked with each trait [95]. Genomics resources coming from a combination of the latest advancement on whole-genome sequencing, genome-wide SNPs, and traditional SSR markers will provide the development of high-density reference genetic linkage maps that, accompanied by synteny studies, will assist fruit breeders in developing new cultivars with desirable characters using genome-wide molecular assisted selection as observed in Rosaceae fruit trees [96].

Without any doubt, genome-wide association studies have had an immense impact on crop and fruit breeding programs. Fruit breeders and researchers have been contrived to discover novel genetic risk elements for common fruit diseases. For example, Khadgi & Weber (2020) [35] discovered the gene that controls the prickle production in Red raspberry fruit, likewise Noh et al. (2020) [33] identified the gene causing Apple Marssonina Blotch (AMB) disease in the Apple germplasm. The credibility and efficiency of GWAS will be expected to increase immensely in fruit crops once the genome sequence of all the fruits is acquired. This association study approach is significant in a way that it does not require any prior information to measure out the associations among the variation in genetics and the diversity of phenotypes. Along with this, GWAS can dissect the previously unexplored valuable genetic variation in fruit trees germplasm resources, providing new genetic variability to be exploited in future breeding programs. In addition, after QTL mapping and cloning of candidate genes, GWAS can allow transgenesis and target mutagenesis approaches like genome editing [97] to assay whether identified genes are involved in the phenotypic variation of traits of interest.

Finally most importantly, if fruit breeders can gather the phenotypic and genotypic data, this subsequent collection of data will eventually expand the horizons for detection of the strength of GWAS and the precision of GS. Furthermore, the use of brisk development in NGS technologies is awaited to endorse yield benefits in all major fruit crops. Collaborative efforts are currently proceeding relatively in every major fruit species, and we await the outcomes from these findings that would eventually refine our perspective and advocate the development and improvement of potent avenues [98].

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