

Chicories Genome-Wide Datasets for Marker-Assisted Crop Breeding Applications

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Cichorium intybus L. is the most economically important species of its genus and among the most important of the Asteraceae family. In chicory, many linkage maps have been produced, several sets of mapped and unmapped markers have been developed, and dozens of genes linked to traits of agronomic interest have been investigated. This treasure trove of information, properly cataloged and organized, is of pivotal importance for the development of superior commercial products with valuable agronomic potential in terms of yield and quality, including reduced bitter taste and increased inulin production, as well as resistance or tolerance to pathogens and resilience to environmental stresses.

chicory

molecular markers

genetic maps

marker-assisted breeding

marker-assisted selection

1. Introduction

Chicories ($2n = 2x = 18$) are economically important dicot species belonging to the Asteraceae family. The *Cichorium* genus contains six main species, of which four are exclusively wild (*Cichorium bota*e Deflers., *Cichorium spinosum* L., *Cichorium calvum* Sch. Bip. ex Asch., and *Cichorium pumilum* Jacq.), one is exclusively cultivated (*Cichorium endivia* L.), and one contains both cultivated and wild individuals (*Cichorium intybus* L.) ^[1]. The main botanical variety in terms of economic impact is *Cichorium intybus* var. *foliosum*, widely appreciated for its leaves, which are eaten raw or cooked, and characterized by a distinctive bitter taste and crispiness. This variety includes 'Witloof Chicory' or 'Belgian Endive', commonly known in Europe for its typical etiolated buds named 'chicon', and Red Chicory, known as 'Radicchio', mostly distributed in northeastern Italy ^{[2][3][4][5]}. Apart from leaf chicory, mainly known for its nutritional and health-beneficial properties, an upsurge of interest has been observed in 'industrial' or 'root' chicory (*C. intybus* var. *sativum*), which is mostly used for inulin extraction and as a coffee substitute ^{[6][7][8]}. Inulin, as a carbohydrate reserve, accumulates during the first year's growing season in taproot chicory and is used for food and nonfood applications ^{[9][10]}.

The other economically relevant species from the same genus is *C. endivia*, whose curly and smooth leaves (var. *crispum* and var. *latifolium*, respectively) are consumed worldwide in fresh salads, with Spain, France, and Italy as major EU producers ^[9].

From a reproductive point of view, *Cichorium intybus* is a diploid plant species that is prevalently allogamous due to its efficient sporophytic self-incompatibility system [3][11][12]. Male sterility represents another efficient sexual barrier widely used in chicory to promote outcrossing and to facilitate the exploitation of heterosis through the production of F1 hybrids. In contrast, endive is an autogamous species with a rate of outcrossing of approximately 1% [13]. Chicory and endive, as closely related but distinct species, are completely interfertile and offer a vast genetic pool that, through cross-breeding schemes, might be exploited to obtain progeny with wide genetic diversity [3][4].

One of the main goals in chicory breeding programs is to achieve the best selections with valuable agronomic potential, such as yield, reduced bitter taste, increased inulin production, and resistance to both biotic and abiotic stressors. Molecular markers are fully addressed to assess genetic information on parental genotypes, heterozygosity evaluation and prediction, population uniformity and distinctiveness [13][14]. Moreover, these tools are employed not only in phylogenetic studies and genetic linkage map construction but also for the genetic traceability of the final commercial product [15][16]. As a result, the aim of generating a superior commercial product in accordance with market acceptance could be facilitated through the efficient implementation of marker-assisted breeding (MAB) and marker-assisted selection (MAS) programs [17][18][19].

2. Toward a Genetic Genomic Map of Chicory Useful for Marker-Assisted Breeding

Linkage maps lay the groundwork for marker-assisted breeding. In chicory, the assembly of the first linkage map based on 371 markers (16 RAPDs, 72 SAMPLs and 283 AFLPs; 1201 cM) was reported in 1997 using an interspecific hybrid cross between *C. intybus* L. and an inbred line of *C. endivia* L. [20]. Similarly, Van Stallen et al. built a genetic linkage map based on an intraspecific cross between two inbred lines of witloof chicory (129 RAPD, 609.6 cM) [21]. A further RAPD-based genetic map was focused on the characterization of QTLs for the length and browning of pith [22]. Cassan et al. constructed a RAPD- and SSR-based genetic map (987 cM) to identify QTLs controlling physiological and agronomical traits under two levels of nitrogen fertilization during the vegetative phase of witloof chicory [23]. Unfortunately, all the above-mentioned maps, due to the type of markers (i.e., dominant markers), cannot be used for comparative studies. A turning point was the development by Cadalen et al. of a consensus genetic map from two industrial chicory progenies and one witloof chicory progeny, containing 472 SSR markers and covering 878 cM [24]. This study was further deepened by Gonthier et al. for the identification of markers associated with nuclear male sterility (NMS) and sporophytic self-incompatibility (SSI) loci [12]. Starting from the data produced in the two previous studies, Ghedina et al. developed an efficient multiplex assay for genotyping elite breeding stocks developed from old landraces of Radicchio di Chioggia [25]. This assay, composed of 27 SSR markers selected according to the polymorphism index and distribution, was further integrated with two additional SSR markers and successfully applied by Patella et al., 2019 [13]. Muys et al. produced a genetic map for industrial chicory that included 237 marker loci and spanned a total length of 1208 cM [26]. The map was built combining AFLPs, SSRs, SNPs, and 26 coding sequences. Finally, a high-density linkage map of leaf chicory was constructed using genotyping-by-sequencing (GBS) technology [27]. The map contained 727 SNP markers,

covering a total length of 1413 cM. Most importantly, the map was pivotal for the identification of the putative locus responsible for male sterility. All the genetic maps produced in chicory are summarized in **Table 1**.

Table 1. Genetic and physical maps developed over the years for *Cichorium intybus*. When available, for each map, the researchers report the correspondence between each linkage group (LG) and the chromosome (Chr) of the consensus map (from Fan et al., 2022 [28]), the number and type of markers employed, the length of each map, and the taxonomy of the sample used for map construction.

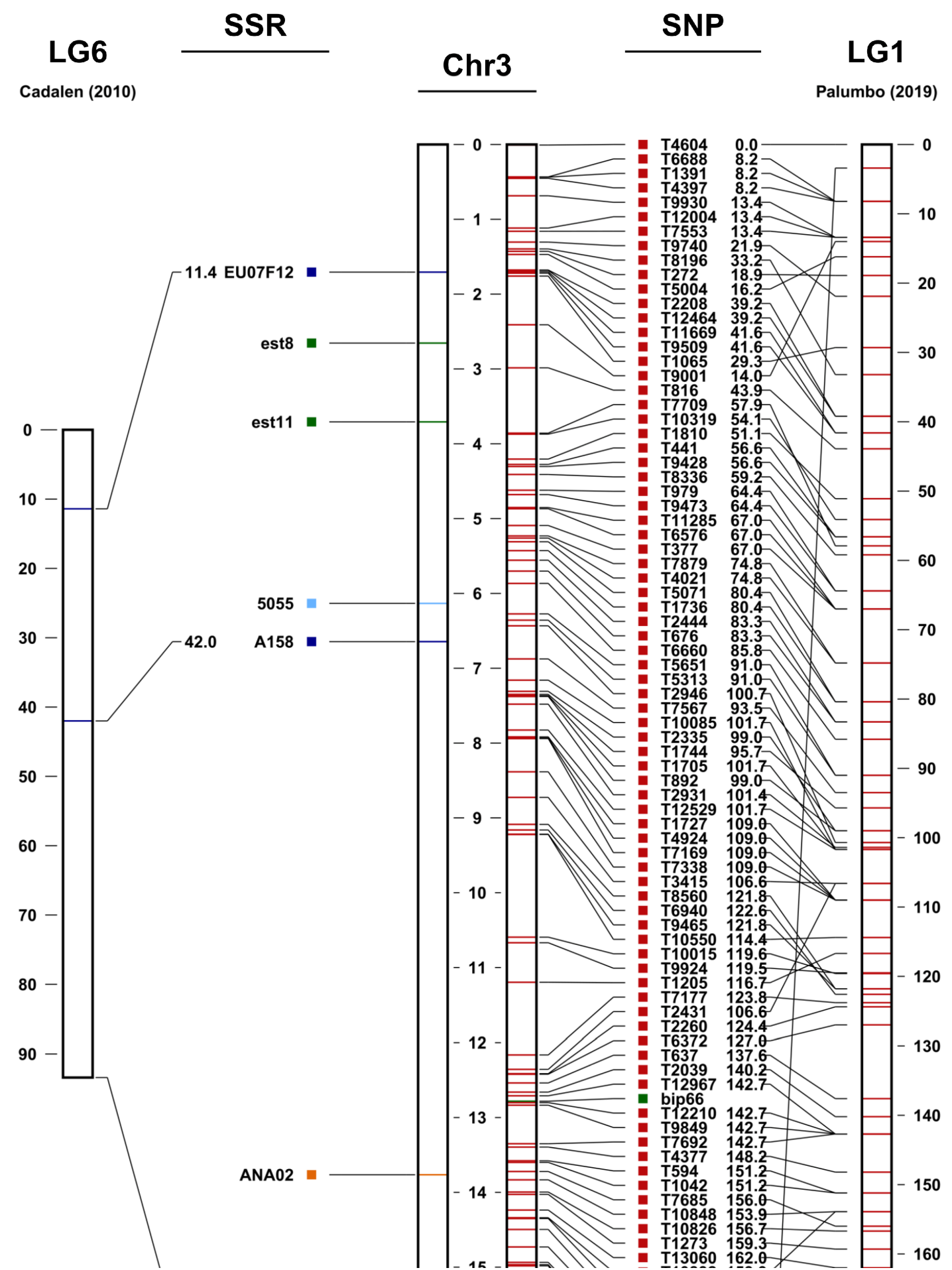
References	De Simone et al. [20]	Van Stallen et al. [21]	Van Stallen et al. [22]	Cassan et al. [23]	Cadalen et al. [24]	Gonthier et al. [12]	Muys et al. [26]	Palumbo et al. [27]	Consensus Map (from Fan et al. [28])
LG ↔ Chr	N.a.	N.a.	N.a.	N.a.	LG8	LG8	LG5	LG2	Chr1
					LG3	LG3	LG6	LG3	Chr2
					LG6	LG6	LG8	LG1	Chr3
					LG1	LG1	LG3	LG6	Chr4
					LG2	LG2	LG9	LG5	Chr5
					LG9	LG9	LG4	LG8	Chr6
					LG5	LG5	LG1	LG7	Chr7
					LG7	LG7	LG2	LG4	Chr8
					LG4	LG4	LG7	LG9	Chr9
Markers	16 RAPDs;	129 RAPDs	RAPDs	73 RAPDs;	472 SSRs	SSRs;	170 AFLPs;	727 SNPs	579 SNPs;

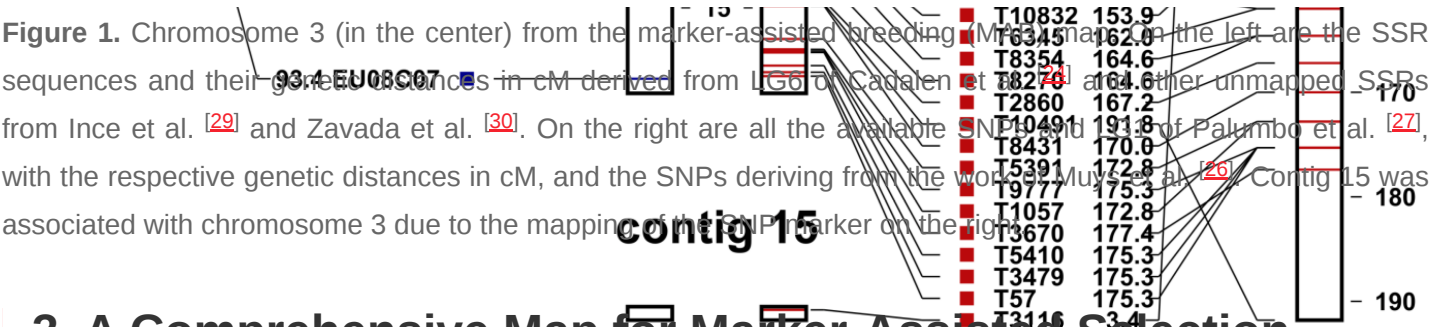
References	De Simone et al. [20]	Van Stallen et al. [21]	Van Stallen et al. [22]	Cassan et al. [23]	Cadalen et al. [24]	Gonthier et al. [12]	Muys et al. [26]	Palumbo et al. [27]	Consensus Map (from Fan et al. [28])
	72 SAMPLs; 283 AFLPs			9 SSRs		AFLPs	28 SSRs; 27 EST-SNPs; 12 EST-SSRs		60 SSRs
Length	1201 cM	609.6 cM	N.a.	987 cM	878 cM	N.a.	1208 cM	1413 cM	1280 Mb
Source	<i>C. intybus</i> (radicchio) × <i>C. endivia</i> (escarole)	<i>C. intybus</i> (witloof)	<i>C. intybus</i> (witloof)	<i>C. intybus</i> (witloof)	<i>C. intybus</i> (industrial); <i>C. intybus</i> (witloof)	<i>C. intybus</i> (industrial)	<i>C. intybus</i> (industrial);	<i>C. intybus</i> (radicchio)	<i>C. intybus</i> (Grassland Puna)

Ideally, plant breeders draw on genetic maps and markers to mine information useful for MAB purposes [32]. However, as in the case of chicory, the availability of multiple linkage maps (each based on single and independent populations) and unmapped markers makes the interpretation and exploitation of the data very challenging. This challenge can be overcome through the production of consensus maps.

The observed discrepancy between the number of markers actually used for the consensus map and the total number of markers developed over the years essentially relies on two factors. The first, which is far from negligible, is that in many cases, the authors of the maps have not made (completely or partially) available the markers used. The second is that some of the available markers did not map. This last aspect is not surprising at all considering that almost all the markers were derived from extragenic and therefore less-conserved regions. This observation assumes particular relevance if we take into account that the different genetic maps and marker sets have been developed using interspecific hybrids (*C. endivia* × *C. intybus*) or different botanical varieties (*C. intybus* var. *sativum* and var. *foliosum*). The consensus map allowed us to anchor to specific chromosome positions those markers that until now lacked a position (i.e., all the unmapped markers), such as those from Ince and Zavada et al. [29][30]. Furthermore, the consensus map enabled us to establish the correspondences between the linkage groups of the genetic maps produced by Cadalen et al., Muys et al., and Palumbo et al., and the chromosomes assembled by Fan et al. (Table 1) [24][26][27][28]. An example is provided in Figure 1, where chromosome 3 (JAKNSD010000003.1) was found to correspond to LG6 of Cadalen et al. and LG1 of Palumbo et al. [24][27][28]. Within each linkage group/chromosome, most of the markers showed full collinearity. The cases in which

collinearity was not observed could be the result of species/variety-specific rearrangements, errors in the construction of the genetic maps, or errors during genome assembly [\[32\]](#). Finally, it should be noted that, thanks to the integration between the genetic maps and the physical map, it was possible to improve the latter by assigning some of the 199 unassembled contigs (JAKNSD010000010.1-JAKNSD010000208.1) to specific chromosomes.





3. A Comprehensive Map for Marker-Assisted Selection Purposes

cM **1e7 bp** **cM**

Linkage maps based on molecular markers also have the potential to bridge the gap between a given genotype and the resulting phenotype [33]. The basic principle of MAS is to identify a tight linkage between a marker and a gene controlling a trait of interest (e.g., disease resistance, plant cycle length, flowering time, or the reproductive system). This association can be used for practical purposes, including the preliminary screening of plant materials or to verify the introgression of a given gene. Thus, knowing the association with the gene of interest, traditional breeding methods, such as hybridization, backcrossing, self-pollination, and selection, are facilitated in the constitution of new varieties [34]. In this section, the researchers first reviewed the scientific literature dealing with the identification of genes underlying ten topics of interest in *C. intybus*, as summarized in **Table 2**.

■ Palumbo (2019) ■ Cadalen (2010) ■ Muys (2014) ■ Ince (2012) ■ Zavada (2017)

Table 2. The most relevant traits/features investigated in chicory, the responsible genes and/or the associated markers, and the methods used for their identification are reported. The superscript numbers (from 1 to 10) reported for each trait/topic were used to facilitate the correspondence with the genes shown in **Figure 2** (for chromosome 6).

Traits/Topic	Gene or Marker Locus	Methods	Citation
Reproductive barriers ¹	<i>NMS-related (NMS1, NMS2)</i>	Genetic mapping (AFLP-based SCARs)	[12]
	<i>ms1 (MYB103-like)</i>	Genetic mapping (SSR; SNP)	[24] [27] [35]
	<i>S-related (S1-S4), MIK2</i>	Genetic mapping (AFLP-based SCARs)	[12] [36]
Sesquiterpene lactone biosynthesis (STL) ²	<i>GASlo, GASsh</i>	cDNA library construction; expression analysis in <i>E. coli</i>	[37]

Traits/Topic	Gene or Marker Locus	Methods	Citation
	GAO	Analyses of the metabolites from transgenic yeast; immunoblot analysis; in vitro enzyme assay; GC—MS enzyme assay	[38]
	CYP71AV8	Isolation; cloning; coexpression in yeasts; GC—MS analysis	[39]
	GASsh2, GAS1, GAO, COS	RNA sequencing, transcriptome assembly, functional annotation, gene expression analyses, qPCR	[40]
Hydroxycinnamates (HCAs) ³	HCT1, HCT2, HQT1, HQT2, HQT3	In vitro assays of recombinant proteins in <i>E. coli</i> , transient expression in <i>N. benthamiana</i> , SDS—PAGE and immunoblot analysis	[41]
Inulin metabolism ⁴	1-FEH I	Cloning, MALDI-TOF and Q-TOF analyses, and expression in transgenic potato tubers	[42]
	1-FEH IIa, 1-FEH IIb	Sequencing, Q-TOF analyses, RNA isolation, RT—PCR, and subcloning	[43]
	1-FEH IIa2	Northern blot hybridization, Transient expression analysis, Promoter analysis	[44]
	1-FEH IIb2, CiMYB17, SUT1, SUT2, SUT3, 1-SST, 1-FFT	RNAseq, yeast one-hybrid assay, transfection experiments, transient expression in grapevine (<i>Vitis vinifera</i>), and qPCR	[10] [45]
Stress response ⁵	nia gene	Northern blot analysis, In-situ hybridization, cloning, and sequencing	[46]

Traits/Topic	Gene or Marker Locus	Methods	Citation
	<i>PPX1</i>	Ion exchange chromatography, construction of a cDNA library, cloning, Expression analysis in <i>E. coli</i> , and ProTox assay	[47]
	<i>CAld5H (bip41)</i>	Genetic mapping (SNP)	[26]
	<i>DHN1, DHN2</i>	Southern blot analysis, Northern blot analysis, cloning, and transcription promoter analysis	[48]
	<i>CiNHX1</i>	Cloning of <i>CiDREB1</i> , transformation in <i>E. coli</i> , qPCR, and subcellular localization	[49]
	<i>DREB1A, DREB1B</i>	Subcloning, sequencing, qPCR, protein localization, and functional expression in a yeast mutant	[50]
Blue-lilac color ⁶	<i>F3'H, F3'5'H</i>	Extraction of anthocyanins, cloning of F3'H and F3 5 H cDNAs, and expression analysis in yeast	[51]
Flowering time ⁷	<i>FL1 gene</i>	Cloning, qPCR, construction of transgenics, and transformation in Arabidopsis via floral dip method	[52]
Somatic embryogenesis ⁸	<i>nsHb</i>	Construction of cDNA library in a phage lambda and integration in <i>E. coli</i> , differential screening of the cDNA library, and Northern blot analysis	[53]
	<i>chi-GST1</i>	RT—PCR, Northern blot analysis, and	[54]

Traits/Topic	Gene or Marker Locus	Methods	Citation
Red discoloration ⁹		expression of the protein in <i>E. coli</i> ,	
	<i>CG1</i>	qPCR, RACE PCR, in vivo expression of cDNAs in <i>Escherichia coli</i> , Southern blot analysis, and Northern blot analysis	[55]
	<i>GTP1/2</i>	Cloning, library construction and screening, Northern blot analysis, (RACE) PCR, RT—PCR, and expression analysis in BL21 bacterial cells	[56]
Red discoloration ⁹	<i>PAL1</i> , <i>PAL2</i>	Color analysis, RNA extraction, cDNA synthesis, and qPCR	[57]
Gene normalization ¹⁰	<i>βTUB</i> , <i>UBQ10</i> , <i>SAND</i> , <i>Clath</i> , <i>TIP41</i> , <i>PP2AA3</i> , <i>CYP5</i> , <i>ACT2</i> , <i>PROF</i> , <i>ACT7</i>	Determination of reference gene expression stability using geNorm, NormFinder and BestKeeper	[58]
	<i>ACT</i> , <i>EF-1αM</i> , <i>NADHD</i> , <i>His-H3</i> , <i>rRNA</i> , <i>TUB</i>	Determination of reference gene expression stability using geNorm, NormFinder and BestKeeper	[59]

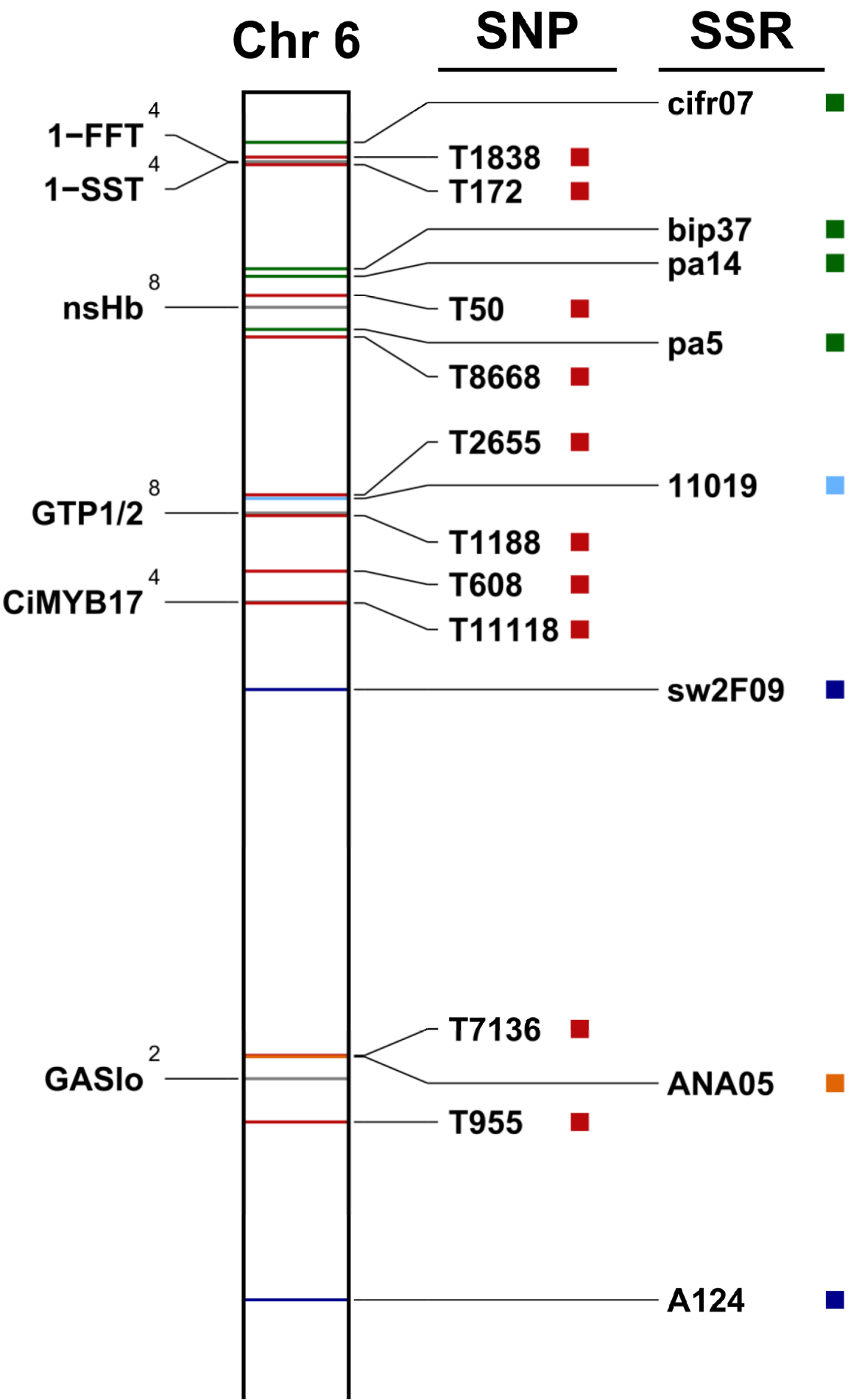


Figure 2. Chromosome 6 from the marker-assisted selection (MAS) map. On the left are the genes with their trait identity number (in the form of an apex: 2: sesquiterpene lactone biosynthesis (STL); 4: inulin metabolism; 8: somatic embryogenesis). On the right are reported the markers (SSRs or SNPs) closest to each gene and retrieved from Cadalen et al. [24], Muys et al. [26], Palumbo et al. [27], Ince et al. [29] and Zavada et al. [30]. Each gene is also described in detail in Table 2.



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