3.3 Genotyping technologies for olive cultivar characterization and development of functional markers

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3.3.1 Introduction

To a very rich and complex germplasm, corresponds a great difficulty in identifying and characterizing each single genotype.

For the correct identification of the olive varieties, it is necessary to take into consideration some main aspects:

- the availability of reliable, precise and shared molecular markers;
- the possibility of accessing safe, credited and validated sources of plant material, currently represented by the institutional public varietal collections, where each variety has a known origin and a reliable and validated consensus molecular profile;
- the access to databases including the molecular info of varieties, as well as any other morphological and bio-agronomic data.

For this reason, many olive cultivar collections have been established at regional, national and international level, accessions of these collections have been genotyped and molecular profiles have been made available to the scientific and stakeholder community (Trujillo *et al.*, 2014; Ben Ayed *et al.*, 2016; El Bakkali *et al.*, 2018). To identify samples of unknown varieties, now it is possible to genotype them and compare their profile with those present in the databases and check for any matches.

3.3.2 Genotyping for cultivar identification

Since the early 1990s, various studies have been launched for the identification of olive varieties, using different types of molecular markers. These works have made it possible to draw an overall picture of the richness of the varietal heritage but, given the dominant nature, the lack of knowledge of the DNA sequence and the absence of reference molecular profiles for the main varieties, have contributed to the onset of further confusions, especially as regards intra-cultivar variability, sustained by some and denied by others.

For these reasons, we found it more useful to report only the markers that have demonstrated the greatest reliability and polymorphism. We then reported those most used today both for identification and discrimination works, for the study of the distribution of variability, the domestication process and for other purposes of great application relevance.

Simple sequence repeats – SSRs. SSRs represent the most popular markers for olive genotyping, due to the high polymorphism, particular abundance and fast transferability (Baldoni *et al.*, 2009; Belaj *et al.*, 2012; Díez *et al.*, 2015; Mousavi *et al.*, 2017a, b). They have been used to characterize most of the olive germplasm collections (Haouane *et al.*, 2011; Trujillo *et al.*, 2014; El Bakkali *et al.* 2019).
Other than for cultivar fingerprinting, SSRs have been used for many other purposes, including construction of linkage maps, traceability of olive oil cultivar composition, as well as for phylogenetic and domestication studies and population genomics (Dominguez-Garcia *et al.*, 2012; Kaniewski *et al.*, 2012; Díez *et al.,* 2015; Besnard *et al.*, 2018; Gomes *et al.*, 2018; Crawford *et al.*, 2019; Montemurro *et al.*, 2019; Mousavi *et al.*, 2019a; Mariotti *et al.*, 2020a).
About 100 SSR markers have been developed to date in olive, but only a small percentage of them, after a deep evaluation, have been selected and extensively used for cultivar identification and discrimination (Baldoni *et al.*, 2009). El Bakkali *et al.* (2019) have used 20 SSRs to study the molecular identity of the cultivars in common between the World Olive Germplasm Banks of Marrakech (Morocco) and Cordoba (Spain).
Most of the SSR markers used for fingerprinting contain dinucleotide repeats, which represent very short motifs that make it difficult to discriminate among alleles that differ only for two bases. To overcome this problem, it should be preferable the use of polynucleotide SSRs, differing for 3-4-5-6 or more bases. Recent advances in olive transcriptomics and genome sequencing, have enabled the access to sequence repositories, such as ESTs and untranscribed sequences, as a source of long core repeat SSRs (Muñoz-Mérida *et al.*, 2013; Mariotti *et al.*, 2016; Arbeiter *et al.*, 2017) (Figure 3.3.1). Even if long repeat SSRs are easier to analyze, their variation has revealed to be lower compared to dinucleotide markers, possibly because they are mainly developed from expressed gene sequences,and their application for cultivar discrimination still remains rarely utilized (Mousavi *et al.*, 2017a; Li *et al.*, 2020).

Fig. 3.3.1.

Numerous identification and characterization campaigns have been undertaken in all countries and at regional level by the use of SSR markers, allowing a detailed analysis of the large variability of olive cultivars (Cantini *et al.*, 2008; Corrado *et al.*, 2011; Abdessemed *et al.*, 2015; Belaj *et al.*, 2010; Beghè *et al.*, 2011; Marra *et al.*, 2013; Hosseini-Mazinani *et al.*, 2014; i Martí *et al.*, 2015; Lazović *et al.*, 2016; Hmmam *et al.*, 2018; Ninot et all., 2018; Avramidou *et al.*, 2020; Li *et al.*, 2020; Gómez-Rodríguez *et al.*, 2021; Saddoud Debbabi *et al.*, 2021; Yadav *et al.*, 2021).
SSR markers are successfully applied for paternity tests in order to identify cultivars, progenies or embryo parents (Seifi *et al.*, 2012; Dridi *et al.*, 2018; Mariotti *et al.*, 2020a; Vuletin Selak *et al.*, 2021).
Few efforts have been devoted to the identification of nursery plant material for true-to-type stock certification, while markers are being developed to detect the presence of

dangerous pathogens for propagated plants, such as *Xylella fastidiosa* (Loconsole *et al.*, 2021), or *Verticillium dahliae* (Altaae, 2019).

Single nucleotide polymorphisms – SNPs. SNPs are point mutations on single nucleotides, generally biallelic and very frequent along the genomic sequence, particularly in olive where a SNP frequency of 1/53 bp or 1/19.5 bp were detected within gene sequences (Cultrera *et al.*, 2019; Salimonti *et al.*, 2020). They are randomly distributed along the entire genome, are less mutable than SSRs and readily assayed using high-throughput genotyping protocols and automated data analysis.

Based on transcriptome and genome sequence data made available for many cultivars, wide sets of SNP markers are being identified and used for genotyping purposes (Kaya *et al.*, 2013; Biton *et al.*, 2015; D'Agostino *et al.*, 2018; Mariotti *et al.*, 2020b).

Sequences related to expressed tags developed from transcript collections contributed to evaluate gene variations among different olive cultivars, highlighting the possible functional effect of these polymorphisms. Thanks to a wide set of EST–SNPs, the study of functional polymorphisms in olive is finally having a boost.

Among the strategies for SNP analysis, genotyping-by-sequencing (GBS) technology is a method based on next-generation sequencing, that enables multi-sample, high-throughput parallel sequencing.

SNP genotyping has been successfully applied for olive cultivar discrimination (Hakim *et al.*, 2010; Zhu *et al.*, 2019; Friel *et al.*, 2021; Islam *et al.*, 2021). Kaya *et al.* (2013) analyzed 2,987 SNPs and characterized high levels of genetic variation in Turkish olive genotypes. Belaj *et al.* (2018) reported the clear cutoff between inter- and intra-cultivar variation in olive by using 1,043 EST-SNPs on a representative number of accessions from 20 olive growing countries (Figure 3.3.2). Using 22,088 GBS SNP data, a wide set of Italian cultivars was analyzed, detecting unexpected molecular diversity (D'Agostino *et al.*, 2018).

Works have been carried out also to develop SNP markers able to distinguish between cultivated and wild forms of olive (Kaya *et al.*, 2013; Kyriakopoulou *et al.*, 2020; Mariotti *et al.* 2020) (Figure 3.3.3).

Figure 3.3.2.

Figure 3.3.3.

3.3.3 Functional markers

In order to develop new functional markers useful for discriminating among plant functions rather than among genotypes, SNP markers have been largely used for genetic mapping and for genome-wide association studies (GWAS), the most powerful strategies to detect marker-phenotype linkage, that is the association between a molecular marker and an agronomic or qualitive character of the tree. The so-called functional markers developed by these approaches allow to screen many individuals (varieties, cross progenies, etc.) for a certain character by doing a simple molecular analysis rather than complex and long in vivo evaluations.

Transcriptomics. The most widely used approach to capture genes putatively involved in specific characters (biosynthetic metabolic pathways, resistance to pathogens and pests, tolerance to environmental stress, etc.), refers to the identification of gene transcripts differentially (over or under) expressed under the conditions of interest (i.e. flowering, oil accumulation, plant response to pathogen attack or to drought stress, etc.).

Works have focused on many aspects of olive plant development, production and stress response. Transcriptomics has allowed to identify differentially expressed sequences involved in tolerance to *Verticillium dahliae* (Leyva-Pérez*et al.*, 2018), or in response to the olive fruit fly *Bactrocera oleae* attack (Grasso *et al.*, 2017), or transcripts differentially expressed under salt stress and cold acclimation (Bazakos *et al.*, 2015; Guerra *et al.*, 2015).

Muñoz-Merida *et al.* (2013) got information about genes determining oil content and composition in fruit mesocarp of cvs. Picual and Arbequina, and numerous transcripts differentially transcribed during fruit fatty acid synthesis were identified by Niu *et al.* (2022).

Transcripts putatively involved in phenolic synthesis have been identified by comparative large-scale transcriptome analysis performed on fruits of high- and low-phenolic cultivars at different developmental stages (Alagna *et al.* 2009; Guodong *et al.*, 2019), as well as those controlling flavonoid and anthocyanin metabolism in cultivars producing white and black drupes (Iaria *et al.* 2016).

Transcriptome analysis revealed insights into hormonal and vesicle trafficking regulation among fruit tissues (Briegas *et al.*, 2020) and changes in gene expression were observed in drupes of cv. Carolea at different maturation stages and cultivation areas (Bruno *et al.*, 2019).

After the release of wide transcriptome data on pollen and pistil at different developmental stages (Carmona *et al.* 2015), transcripts potentially involved in flower development, pollen/pistil interaction or ovary abortion were investigated by comparing different cultivars (Alagna *et al.*, 2016).

Finally, transcriptome analysis has allowed to identify miRNAs (non-coding RNAs that play important roles in regulating gene expression) involved in alternate bearing (Yanik *et al.*, 2013), or in fruit ripening (Carbone *et al.*, 2019).

Genetic mapping. The generation of high-resolution linkage maps represents a powerful way to identify markers linked to characters of interest, a prerequisite for gene positional identification. For example, a cross progeny segregating for fruit color, putatively controlled by a single locus, may be used for a deep SNP genotyping in order to identify SNP markers tightly linked to fruit color. If the character of interest is controlled by multiple genes, as is the case for most agronomic traits, it is possible at least to identify major quantitative trait loci (QTL).

Linkage analysis can be performed on biparental population families derived from the cross, backcross or selfing of homozygous or heterozygous lines. In olive, the use of these progenies is hindered by the long generation time and the lack of homozygous genotypes, thus, only full-sib F1 families derived from intervarietal crosses of highly heterozygous genotypes have been used for olive mapping, and linkage analysis is separately conducted for each parent.

Dense maps have been produced using AFLP, DArT, SSR and SNP markers on cross progenies of different cultivars and with the aim to identify markers for specific traits (de la Rosa *et al.*, 2003; Sadok *et al.*, 2013; Atienza *et al.*, 2014; Biton *et al.*, 2015;

Baldoni *et al.*, 2016; Ipek *et al.*, 2016, 2017; Kaya *et al.*, 2016; Marchese *et al.*, 2016; İpek *et al.*, 2017; Unver *et al.*, 2017; Mariotti *et al.*, 2020c) (Figure 3.3.4).

Figure 3.3.4.

Genome-wide association studies. GWAS, based on the SNP analysis on unrelated individuals from natural or cultivated populations, requires whole genome scans with large sets of markers directly applied on phenotypically characterized genotypes, to detect linkage between markers and traits. It mostly provides a high resolution and does not need segregating populations. The development of this kind of markers requires a high level of genome sequence information, it is therefore not surprising if only a few GWA studies were reported in olive before the release of sound and informative genome sequences of numerous varieties (Khadari *et al.*, 2014; Kaya *et al.*, 2019). Another limitation for the application of GWAS refers to the need of precise, deep and climate-referenced phenotyping of as many cultivars as possible.

Epigenetic studies. In addition to genetic diversity in olive, the first studies on the epigenetic changes were also recently carried out, taking into account the increasing knowledge on how epigenetics may affect the way genes work. The methylation status of the olive genome during fruit ripening has been revealed through methylated DNA immuno-precipitation sequencing (MeDIP-seq) approach, profiling leaves and fruits during fruit development in wild and cultivated olives (Badad *et al.*, 2021) and differentially methylated gene sequences under salt stress were identified distinguishing tolerant and susceptible cultivars (Mousavi *et al.*, 2019c).

Genes and gene polymorphisms involved in plant performance. Massive EST and genomic sequence data have made available data on annotated gene sequences, their organization and distribution on the genome and their allele differences, representing an unprecedented information that should be fully exploited in the coming years.

Numerous works have focused on the evaluation of gene sequence polymorphisms, in order to detect potential markers linked to agronomical traits of interest, for germplasm screening and for breeding purposes.

Great advancements have been reached on the identification of genes involved in the biosynthetic pathways leading to the most important secondary metabolites of olive, such as phenolics, sterols, triterpenes and tocopherols (Alagna *et al.*, 2016; Koudounas *et al.*, 2017; Georgiadou *et al.*, 2019; Inês *et al.*, 2019; Volk *et al.*, 2019; García-Vico *et al.*, 2021; Rodríguez-López *et al.*, 2021; Wang *et al.*, 2022).

Detailed analyses on the sequence of genes involved in lipid synthesis and fatty acid desaturation have allowed the identification of SNPs and indels (insertions/deletions) putatively controlling oil content and fatty acid composition in olive fruits (Cultrera *et al.*, 2019; Hernández *et al.*, 2019, 2020; Vatansever *et al.*, 2022).

A gene involved in the juvenile-to-adult transition in olive cultivars has been identified (Fernández-Ocaña *et al.*, 2010). Nucleotide diversity observed in candidate genes for Verticillium wilt resistance in olive has been reported as responsible for plant response to pathogen attack (Cardoni *et al.*, 2022; Serrano *et al.*, 2020). Differentially methylated and regulated genes in tolerant and susceptible olive cultivars under salt stress have been identified (Mousavi *et al.*, 2019c; Skodra *et al.*, 2021).

3.3.4 DNA tracking of olive products, olive oil and table olives

An important application of molecular analysis refers to the evaluation of food products derived from the olive crop: olive oil and table olives, that represent main targets of food fraud in Europe, including mislabeling of origin and composition. Oil and table olives contain traces of DNA that can be amplified and analysed. It represents ~~an~~ *a posteriori* analysis, an alternative to documentary traceability, also applicable to products on the shelf, able to detect the raw materials from which they were obtained. But, while the markers used for tree-derived samples can be directly applied to olives, in the case of oil, the analysis of molecular markers is complicated by the small quantity of DNA, by its degradation level and, above all, by the fact that oils are generally extracted not from a single variety but from blends of several cultivars, in unpredictable proportions. For this reason, the application of standard markers on oils has proved difficult to apply to commercial oils. Many efforts have been dedicated to improve methods of DNA extraction from olive oil (Baldoni *et al.*, 2013; Raieta *et al.*, 2015), as well as to identify suitable and reliable markers to distinguish different cultivars in a blended oil and thus revealing its varietal composition (Pereira *et al.*, 2018; Chedid *et al.*, 2020; Ben Ayed *et al.*, 2022).

Other works have demonstrated the possibility to identify the cultivars of table olives (Crawford *et al.*, 2020; Sion *et al.*, 2021), also through the identification of the microbial flora of the processed fruits (Benítez-Cabello *et al.*, 2020).

For DNA barcoding, chloroplast markers represent an ideal system and some chloroplast regions have been used for DNA food tracking and forensic studies on olive cultivars and olive oil composition (Uncu *et al.*, 2017; Partovi *et al.*, 2021).

3.3.5 Population genomics and olive domestication

Through genome sequence data on a number of cultivated and wild olives, it became possible to establish genomic evidence for recurrent genetic admixture during the domestication of Mediterranean olive trees (Julca *et al.*, 2020), and evolutionary transcriptomics has revealed the genomic changes associated with olive domestication (Gros-Balthazard *et al.*, M. 2019).

Cytoplasm markers, represented by the polymorphisms of chloroplast and mitochondrial genomes, have been used in olive for different purposes. Since these organelles pass to offspring from the female parent also in olive, as in many other plant species (Besnard *et al.*, 2000), they are able to specifically trace the maternal lineage, allowing for reconstructing the routes of olive diversification along the time and the space.

Chloroplast markers thus represent a valuable tool in population genomic analysis, phylogenesis, domestication and cultivar-wild discrimination (Mariotti *et al.*, 2010; Besnard *et al.*, 2016; Van de Paer *et al.*, 2018). A strong genetic differentiation for chloroplast markers was observed between eastern and western Mediterranean olives (Besnard *et al.*, 2011; 2018), and phylogenetic studies in cultivated and wild olives showed three sublineages E1, E2 and E3 and about 40 chlorotypes (Besnard *et al.*, 2007). Meanwhile, nuclear markers are quite uniformly distributed between varieties and wild olives and the discrimination between the two forms on the basis of these markers is more difficult~~,~~; chlorotypes are strongly geographically structured in the wild olive populations, while most of the varieties belong to a single chlorotype (E1.1), typical of the eastern

Mediterranean and only a small percentage of them show polymorphisms typical of the wild populations of central and western Mediterranean (Besnard *et al.*, 2013, 2018).

The mitochondrial genome of olive has been recently sequenced, but the evaluation of its polymorphisms among cultivars and other olive taxa is still ongoing (Van de Paer *et al.*, 2018).

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