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The ancient olive trees of Capri Island renaissance of an abandoned treasure

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ABSTRACT

The ancient olive trees are the living proof of the very long tradition of cultivation, and, in most cases, their genotyping has revealed strong differences with the actual known olive varieties. Thus, in addition to their historical and cultural significance, old olives offer horticultural interest due to their genetic potential, constituting an un-exploited reservoir of olive diversity. Moreover, in the last decades several ancient orchards were abandoned generating dramatic scenarios at social, landscape and biodiversity levels. To highlight the importance of abandoned olive trees, a deep restoration was made in an Island well known for the tourism as Capri, which was important in the past for agropastoral activities. The different morphologies detected after orchards cleaning together with the huge dimensions of some olive trees, had open the possibility to seek for the ancient olive cultivation in the Capri Island. The molecular identification of both canopy and rootstock through SSR markers of 67 accessions, highlight the existence of twenty-one ancient genotypes in this island. Two of these were corresponded to the Italian and Greek known cultivars while the genetic identity of remained genotypes resulted unique, even have been compared genetically with more than 450 worldwide olive cultivars. Molecular identification has demonstrated that some of them were clonally propagated and only in two cases, the grafting scenario has been discovered. Age determination by radiocarbon (^{14}C) dating and specific algebraic formulas, shed light on the centennial age of analyzed trees, meaning that they probably represent remnants of ancient olive cultivations, since hundreds of years ago. The outstanding performance of these trees makes really promising their agronomical evaluation and possible use in future olive breeding programs. Their ongoing propagation will avoid losing this priceless olive germplasm and will re-constitute olive orchards with autochthonous and well-adapted varieties in the Capri Island restarting the extra virgin olive oil production after decades of abandonment.

1. Introduction

The olive (*Olea europaea* subsp. *europaea* var. *europaea*) counts a huge genetic diversity, represented by more than 1200 named cultivars and thousands of local/minor varieties, which includes pollinators, ecotypes, and monumental trees (Hosseini-Mazinani et al., 2014; S. Mousavi et al., 2017; El Bakkali et al., 2019). It is mandatory to increase the availability of genetically characterized and highly differentiated cultivated olive genotypes (Mariotti et al., 2023). These genotypes could be able to face new agronomical challenges (De Gennaro et al., 2012; Larbi et al., 2015) and future climatic constrains (Moriondo et al., 2013; Tanasijevic et al., 2014), increasing and diversifying the gene pools currently available (Bracci et al., 2011; Corrado et al., 2011; Klepo et al., 2013).

The extraordinary longevity of the species and its high adaptation to different environmental constraints have allowed the survival of numerous monumental olives sometimes covered by forest vegetation after being abandoned by the cultivation state. These trees surely hold genetic, landscape and historical importance (Valeri et al., 2022), but every year we are losing them due to numerous environmental and human threats as well as new biotic stresses such as *Xylella fastidiosa* (Pannelli et al., 2010; Diez et al. 2011; Barazani et al., 2014; Saponari et al., 2019). The study of monumental olives together with their rootstocks (Valeri et al., 2022; Mariotti et al., 2023) could help to find genomic traits correlated to strong adaption to environmental stresses as well as to re-discover paleo-varieties cultivated in the past and now abandoned. They could be valorized as local production at high regional value (Cicatelli et al., 2013), landscape additional rate (Meilleur and

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Hodgkin 2004) and eco-tourist icons (Moriondo et al., 2013). Recently, the research on ancient olives have demonstrated that grafting practices have been widely applied both by using seedlings and oleasters (Pannelli et al., 2010; Diez et al. 2011; Baranzani et al. 2014; Valeri et al., 2022) increasing the olive genetic patrimony. Furthermore, the preservation against the abandonment, indicated that the traditional agricultural practices made by small-holder farmers preserved the biodiversity and avoid the landscape simplification and homogenization. In fact, agro-silvopastoral activities, through the centuries, allowed the conservation of agricultural heritage systems and therefore the biodiversity (Piras et al., 2023). The restoration of abandoned olive orchards may have avoid soil erosion especially in sloping lands which the erosion increases after abandonment (Areal and Riesgo 2014) and the farmers must be supported encouraging them to cultivate these orchards in order to diminish serious society and landscape problems in the near future. Another important aspect that should be considered is the strong impact on flowering and therefore fruit-set of olive deriving from the fluctuations in pollen production due to the abandonment (low amount of pollen) and rehabilitation (high quantity of pollen) of olive orchards (Langgut et al., 2014). This aspect is fundamental to increase the fruit production both in the original olive orchards and in the neighbor olive plantations, which are influenced also by abandoned of the ancient olive trees after centuries of cultivation, which could consequently decrease the inter-compatibility (Mariotti et al., 2021). Traditional olive-based agrosystems call for extraordinary attention from European and national legislatures for their environmental benefits preventing land degradation especially after landslides and wildfires; moreover, the recovery of abandoned olive orchards could defend soil health by assuring the resilience of a high-quality landscape (Brunori et al., 2020).

In this scenario to give more opportunities to re-discovery of traditional and abandoned olive orchards a scientific approach was made by studying the genetic resources and predicting the age of the most ancient olive trees re-found from uncultivated areas of Capri Island. One of the main problems in studying ancient olive trees is related to estimating their age, in fact, olive have a peculiar wood growth showing a rapid decay of the original stem growing through numerous cords without maintaining a single trunk. Therefore, dendrochronology may not be applied, but only used as complementary information to trace the true age of the plant (Arnan et al., 2012; Cherubini et al., 2013). Age determination by radiocarbon (^{14}C) dating may be helpful in establishing the age of most ancient wood along main trunk, but ^{14}C analysis should be supported by a thorough evaluation of several parameters such as genotype vigor, days of seasonal growing, climatic and soil conditions. The application of algebraic formulas could provide an estimate of the true age of the plant especially when the innermost and therefore ancient part of the stem is missed. Different parameters have been considered such as stem radius, length of the missing wood's radius to the presumed pith and growth rate to better estimate the number of missing years (Pannelli et al.; Bernabei 2015). Literature regarding the radiocarbon dating individuated a maximum wood's age for an olive tree (still alive) of 635 ± 35 years in Israel at Garden of Gethsemane (Bernabei 2015). By using the same algebraic formulas, the most ancient olive tree was shared between this field and Umbria region (center of Italy) with an estimated age up to a thousand of years (Pannelli et al., 2010). Genotyping of unknown ecotypes and ancient trees could allow to recognize the genetic identity of some of them, which assumes clonal multiplication and therefore they probably represent remnants of ancient cultivations, since hundreds or thousands of years ago (Pannelli et al., 2010; Diez et al. 2011; Valeri et al., 2022). In Capri Island, the presence of olive trees and fruit trees of all kinds diffused in these steep landscapes is mentioned in various texts, such as the report by Fabio Giordano dated on 1570, (Douglas, 1995) following by the 1776 description of D.A. de Sade (de Sade, 2008) or the text by L. Giustiniani (1797). This latter author mentioned vineyards, olive groves, and the lack of water that made the villagers obliged to equip themselves with collection tanks highlighting the ability of species such as olive trees to adapt and resist conditions of scarce water reserves. Even F. Gregorovius in "Isola di Capri" (1853), describes Anacapri as a small citadel where small houses are scattered among gardens with luxuriant vegetation made up of vineyards and olive trees. E.L.V. de Laveleye in "Almanac of Capri" (1878–1879), describes the island as cultivated throughout its territory, with the construction of stone steps on the escarpments, where arable land was accumulated and on these superimposed terraces, olive groves and vineyards, under which wheat and lupine were grown.

During our inspections on the territory of the Island, some olive trees of considerable size with an estimated age of hundreds of years have been found especially after the hard work did by the association 'Oro di Capri', who has given light to this hidden treasure. This study aims to explore the genetic diversity of ancient olive trees in Capri Island to investigate to what extent the ancient olive trees are the result of grafting and will look for evidence for the selection of individual genotypes of both scions and rootstocks for olive tree cultivation. In addition, this study will give a scientific estimate of the trees' ages, to determine whether the trees are even-aged or were planted during different time-periods.

2. Materials and methods

2.1. Plant material and DNA extraction

After an intense work of cleaning from the infesting species, which by now had submerged the orchards (Supplementary Figure S1A and B), hundreds of olive trees have seen the light again and some of which showed a considerable trunk or stump size. We therefore concentrated on trees with larger dimensions by taking leaf samples from both the canopy and the basal part of the trunk (potentially rootstock) to highlight or not an eventual grafting scenario. 40 olive trees were collected from Capri Island (Table 1; Fig. 1): from 27 monumental olive trees both canopy (C) and rootstock (R) were collected for a total of 54 samples; while, from the other 13 trees, only the canopy has been sampled since they were often represented by bushes or by several small trunks resprouting from the original stump. The collected samples were in total 67. These trees were mostly located in the Municipality of Anacapri in the Capri Island from Campanian Archipelago and were often close to ancient olive mills, gardens, or old farmland. The basal part of the trunk ranging between 60 and 155 cm at 130 cm from soil. The reported names were codified to decrease the complexity of the original name applied by the locals (Table 1).

Total DNA was extracted by using a GeneElute Plant Genomic DNA Miniprep Kit (Sigma-Aldrich), following the manufacturer's instructions. These accessions were compared to 475 unique SSR profiles belong to olive cultivars covering the worldwide diversity and stored at CNR IBBR database (S. Mousavi et al., 2017b; Valeri et al., 2022; Karamatlou et al., 2023) to evaluate their relationships with the most cultivated olive trees (Supplementary Table S1).

2.2. Genetic diversity of the Capri samples by Simple Sequence Repeat (SSR) markers

All the Capri accessions were genotyped by using standard dinucleotide SSRs markers, widely applied for cultivar characterization in most olive germplasm collections (El Bakkali et al., 2019; Trujillo et al., 2014; S. Mousavi et al., 2017b). Ten highly polymorphic markers were applied, including DCA3–5–9–16–18, EMO90, GAPU71B-101–103A and UDO-043 (Sefc et al., 2000; Carriero et al., 2002; Cipriani et al., 2002), previously selected as the best performing loci (S. Mousavi et al., 2017a) and common to the other published works. Forward primers carried VIC, FAM, PET, or NED labels at their 5′-end.

2.3. Genetic differentiation and frequency analysis

Phylogenetic tree was constructed with MEGA7 (Kumar et al., 2016)

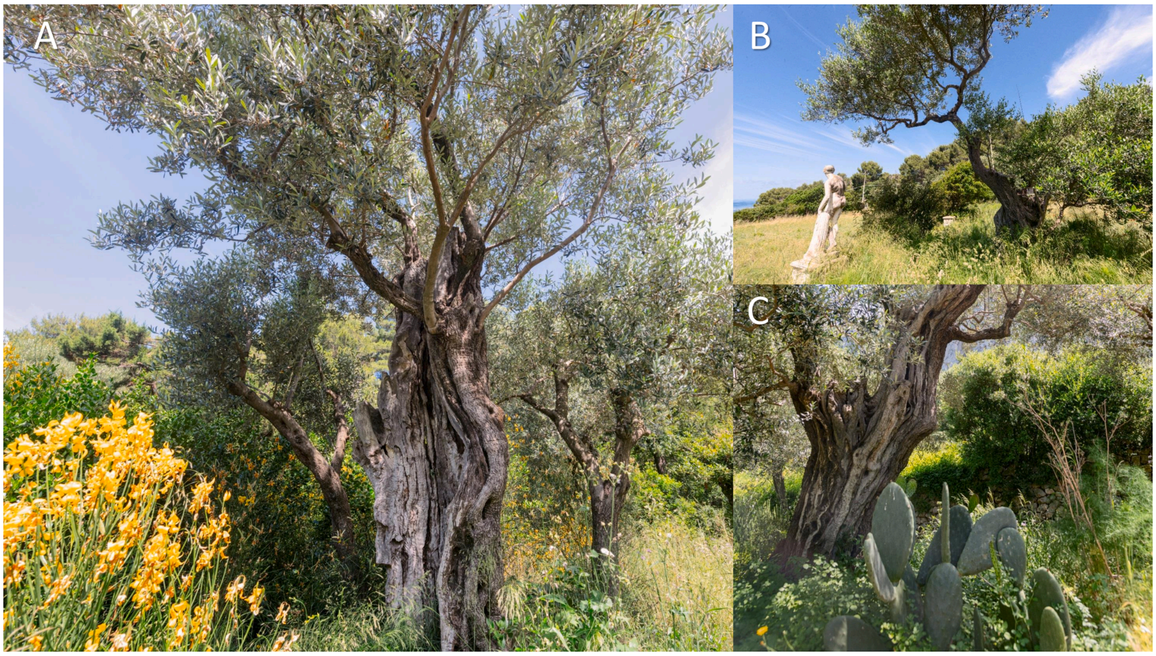

Fig. 1. Some of the studied ancient trees in the Capri Island. A) Oe CI 10, B) Oe CI 13 and C) Oe CI 39.

including 67 samples from Capri Island and 475 worldwide varieties previously published (El Bakkali et al., 2019; Trujillo et al., 2014; S. Mousavi et al., 2017a and b) for a total of 542 genotypes. The tree was drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Neighbor Joining (NJ) method. Intra- and inter-population genetic statistics were calculated using GenAlEx 6.5 (Peakall and Smouse, 2013), which including: number of alleles (Na), number of effective alleles (Ne), observed (Ho) and expected (He) heterozygosity and fixation index (F). Polymorphic information content (PIC), the Hardy-Weinberg equilibrium test (HW), and the presence of possible null alleles (Fnull) were calculated with CERVUS v.3.0 software (Marshall et al., 1998) within the Capri samples for each microsatellite locus and by excluding the olive cultivars used for the comparison. GenAlEx 6.5 was also used to estimate pairwise population matrices of Dest, Gst statistics and Fst pairwise distance with 999 permutations, to detect the differentiation between the Capri samples and 475 worldwide cultivars.

2.4. Radiocarbon dating of the monumental olive trees in Capri

Non-destructive dating analyses on trunks of ancient olive trees are very complex. Counting the circles is not feasible to keep the olive tree alive but also because this growth is not constant and the circles have non-uniform trends (Cherubini et al., 2014). Furthermore, the non-correspondence between the annual growth and the number of circles was also reported and it was assumed that this species is not fitting for dendrochronological dating (Friedrich et al., 2014; Cherubini et al., 2013). Therefore, the residual wood closest to the original centre of the plant must be collected and analysed. This procedure requires measurements of the stem and the plotting of intercepts to determine the assumed distance of residual wood to the estimated centre of the plant (Fig. 2). In fact, following the first years of growth, the central part will be decomposed by lignivorous fungi and, with the passing of decades, open trunks with a considerable cavity are commonly found and the oldest wood is missing.

Considering the twelve selected olive plants for radio dating analysis, sometimes, it was difficult to reconstruct the most likely width of the tree trunk, and to calculate the approximate position of its pith. Some of the studied monumental trees were subjected to drastic topping while the others have loose completely the internal part and the measurements were taken from the remained skeletal perimeter. From the innermost centres of all trees, small fragments of wood were collected from each plant for submission to radiocarbon analysis (Supplementary Figure S2). The samples indicated in Table 3 was subjected to dating with the radiocarbon method using the high-resolution mass spectrometry (AMS) technique, at the Centre for Dating and Diagnostics (CEDAD), Department of Engineering for Innovation, University of Salento, Lecce, Italy. The diagnostic laboratory has been identified the macro-contaminants present in the samples by optical microscope observation and have mechanically removed them. Subsequently, the chemical treatment to remove the contamination was carried out by subjecting the selected material to alternating acid-alkaline-acid chemical attacks. The extracted material was subsequently converted into carbon dioxide by combustion at 900 °C in an oxidizing environment, and then into graphite by reduction. H_2 was used as the reducing element and iron powder as the catalyst. The quantity of graphite extracted from each sample was sufficient for an accurate experimental determination of age. The radiocarbon concentration was determined by comparing measured values of ^{12}C and ^{13}C currents, and ^{14}C counts with values obtained from standard C_6 sucrose samples provided by the IAEA. Conventional radiocarbon dating was corrected for isotopic fractionation effects both by measuring the $^{\delta 13}C$ term directly with the accelerator and by measuring background. Samples of known concentration of oxalic acid provided by NIST (National Institute of Standard and Technology) were used as a quality control of the results. To determine the experimental error in the radiocarbon date, both the scattering of the data around the mean value and the statistical error deriving from the ^{14}C count, were considered. The radiocarbon dating (uncalibrated) for the samples with indication of the absolute error of the measurement was determined. The radiocarbon dating for the samples was then calibrated to calendar age using OxCal Ver. 3.10 software (Bronk Ramsey, 2001; Quarta et al., 2010) based on INTCAL20 (Bayliss et al., 2020) atmospheric data.

As mentioned above the central and therefore the oldest part of the trunk is often missed in centennial olive trees and for this reason it was tried to reconstruct the tree age by applying a formula already published and ascertained by different collecting trials (Clark and Hallgren, 2004; Arnan et al., 2012; Bernabei, 2015; Pannelli et al., 2010). The following

Table 1
List of analyzed samples collected in the Capri Island with original name and code gave specifically for this study. Canopy samples are indicated with letter C and rootstocks with letter R.

Original Sample Name	Code used in the present study	Genetic identity
ARTIMO H BELLAVISTA SELVATICO	Oe CI 1 C	Unique genotype
ARTIMO H BELLAVISTA	Oe CI 2 C	cv. Dritta
BELVEDERE SELVATICO	Oe CI 3 C	Unique genotype
CANNULA C	Oe CI 4 C	cv. Dritta
CANNULA P	Oe CI 4 R	
CAPRI 2 C	Oe CI 5 C	Unique genotype
CAPRI 2 P	Oe CI 5 R	
CAPRI 3 C	Oe CI 6 C	cv. Dritta
CAPRI 3 P	Oe CI 6 R	
CAPRI OSPIZIO C	Oe CI 7 C	Unique genotype
CAPRI OSPIZIO P	Oe CI 7 R	
CARRUBO CONFINE INFERIORE ASSURGENTE	Oe CI 8 C	Similar to cv. Throumbolia
CHIUSARANO M PISANZIO	Oe CI 9 C	cv. Dritta
FARO AMMIRAGLIO C	Oe CI 10 C	cv. Throumbolia
FARO AMMIRAGLIO P	Oe CI 10 R	
FARO INGRESSO 600 C	Oe CI 11 C	cv. Throumbolia
FARO INGRESSO 600 P	Oe CI 11 R	
FARO TDS C	Oe CI 12 C	cv. Dritta
FARO TDS P	Oe CI 12 R	
FARO VENERE C	Oe CI 13 C	cv. Dritta
FARO VENERE P	Oe CI 13 R	
GROTTA delle FELCI C	Oe CI 14 C	Unique genotype
GROTTA delle FELCI P	Oe CI 14 R	
GUARDIA M PISANZIO	Oe CI 15 C	cv. Dritta
INGRESSO CANCELLO PINO C	Oe CI 16 C	Similar to cv.
INGRESSO CANCELLO PINO P	Oe CI 16 R	Throumbolia
LA GUARDIA FRANTOIO C	Oe CI 17 C	cv. Frantoio
LA GUARDIA FRANTOIO P	Oe CI 17 R	
LA GUARDIA LECCINO C	Oe CI 18 C	cv. Leccino
LA GUARDIA LECCINO P	Oe CI 18 R	
MARESUTTO C	Oe CI 19 C	cv. Dritta
MARESUTTO P	Oe CI 19 R	
OLIVELLA GIARDINO	Oe CI 20 C	cv. Dritta
OLIVETO NUOVO C	Oe CI 21 C	cv. Dritta
OLIVETO NUOVO P	Oe CI 21 R	
ORRICO BOSCHETTO SOTTO PINO	Oe CI 22 C	Unique genotype
ORRICO C	Oe CI 23 C	cv. Dritta
ORRICO P	Oe CI 23 R	
ORRICO FALEGNAMERIA	Oe CI 24 C	Unique genotype
ORRICO OLIVETO BASSO PIANTA SPINOSA	Oe CI 25 C	Unique genotype
ORRICO VILLA CUCINA	Oe CI 26 C	cv. Dritta
PINO CASETTA ASSURGENTE C	Oe CI 27 C	Similar to cv. Throumbolia
PINO CASETTA ASSURGENTE P	Oe CI 27 R	cv. Throumbolia
PINO CURVA PIANTA DOPPIA C	Oe CI 28 C	cv. Dritta
PINO CURVA PIANTA DOPPIA P	Oe CI 28 R	Unique genotype
PINO DEI MONACI CASETTA RURALE C	Oe CI 29 C	cv. Dritta
PINO DEI MONACI CASETTA RURALE P	Oe CI 29 R	Unique genotype
PINO E APREA C	Oe CI 30 C	Unique genotype
PINO E APREA P	Oe CI 30 R	
PINO INGRESSO C	Oe CI 31 C	cv. Itrana
PINO INGRESSO P	Oe CI 31 R	cv. Dritta
PINO LIMONCELLO	Oe CI 32 C	cv. Dritta
PINO MOZZATA C	Oe CI 33 C	Unique genotype,
PINO MOZZATA P	Oe CI 33 R	identical to Oe CI 22 C
PINO SOTTO IL PINO C	Oe CI 34 C	cv. Dritta
PINO SOTTO IL PINO P	Oe CI 34 R	
PINO della FEMMINA C	Oe CI 35 C	cv. Dritta
PINO della FEMMINA P	Oe CI 35 R	
QUAGLINO C	Oe CI 36 C	cv. Dritta
QUAGLINO P	Oe CI 36 R	
RONDINELLA C	Oe CI 37 C	Unique genotype
RONDINELLA P	Oe CI 37 R	
STALLE C	Oe CI 38 C	Unique genotype
STALLE P	Oe CI 38 R	
VECCHIONE C	Oe CI 39 C	Unique genotype
VECCHIONE P	Oe CI 39 R	
VETERINO L FERRARO ASINI	Oe CI 40 C	cv. Dritta

formula was applied, considering that a growth rate based on linear functions would overestimate the tree's age:

$$R = L1 / A$$

$$D = (R \times L2) + A$$

R: growing rate on the last 'A' years; L1: radius of the existing part of the trunk, from the collected and dated wood to the external part of trunk; A: wood age from uncalibrated radiocarbon dating; D: estimated age of tree; L2: the length of the missing wood's radius to the presumed pith.

2.5. Organoleptic and phenols amount of monumental olive trees oil in Capri islands

To give an idea of the potential interest of these trees, in 2021 harvesting season, we performed a raw survey on few plants (four monumental olive trees) where fruit material with high quantity was available. The extracted extra virgin olive oils have been analysed for the total amount of polyphenols and organoleptic profile. The content of total polyphenols was measured at the Chemical Laboratory Division of the Chambers of Commerce of Naples (ACCREDIA LAB N 0394 L). Results, expressed in mg kg^{-1} of caffeic acid (CA), were obtained through a standardized calibration curve.

The same laboratory performed the organoleptic profile of the oil samples though the analytical method of Panel test (Reg. CEE 2568/1991; All XII Reg. UE1348/2013; Reg CEE 1604/2019). Olfactory and gustatory sensations were evaluated considering the median of fruity, defect, bitterness, and pungency for each oil in a scale between 0 (not determined) and 10 (maximum level).

3. Results

3.1. Genetic diversity of Capri genotypes

NJ tree based on the SSRs data of Capri Island genotypes together with 475 worldwide genotypes showed the presence of two main olive varieties cultivated in the Island (Fig. 3). In addition, 67 analysed accessions were belonged to 21 different genetic profiles. The grafting scenario has been identified only in two olive trees Oe CI 28 and Oe CI 29. In both trees the canopies were belong to cv. Dritta di Moscufo which grafted on the rootstock belongs to two unique genetic profiles (Table 1; Supplementary Table S2).

Thirty out of 67 accessions were genetically identical to the Abruzzian cv. Dritta di Moscufo. This olive variety is also called cv. Minucciola in the Campania region, where Capri Island is placed, and has another known synonym in Umbria under the name of San Felice. The other group of clones included five genotypes that was identical to cv. Throumbolia, which is mostly diffused in Greece and prevalently in Crete Island. Genetically near to this cluster, other two branches (each with two genotypes) showed a slight difference with cv. Throumbolia (Oe CI 16 C, Oe CI 16 R, Oe CI 8 and Oe CI 27 C), by the mutation of one or both alleles of the DCA9 SSR affected the fragment length. It was interesting to notice that the sample Oe CI 27 R was identical to the cv. Throumbolia while its canopy showed the previous mentioned slight mutation. In the cluster of cvs. Canino, Olivastra Seggianese (both from Italy), Dokkar (Tunisia), and other few cultivars the canopy and rootstocks of Oe CI 39 and Oe CI 14 samples together with Oe CI 1 were placed. The accession Oe CI 37, which its canopy and rootstock showed

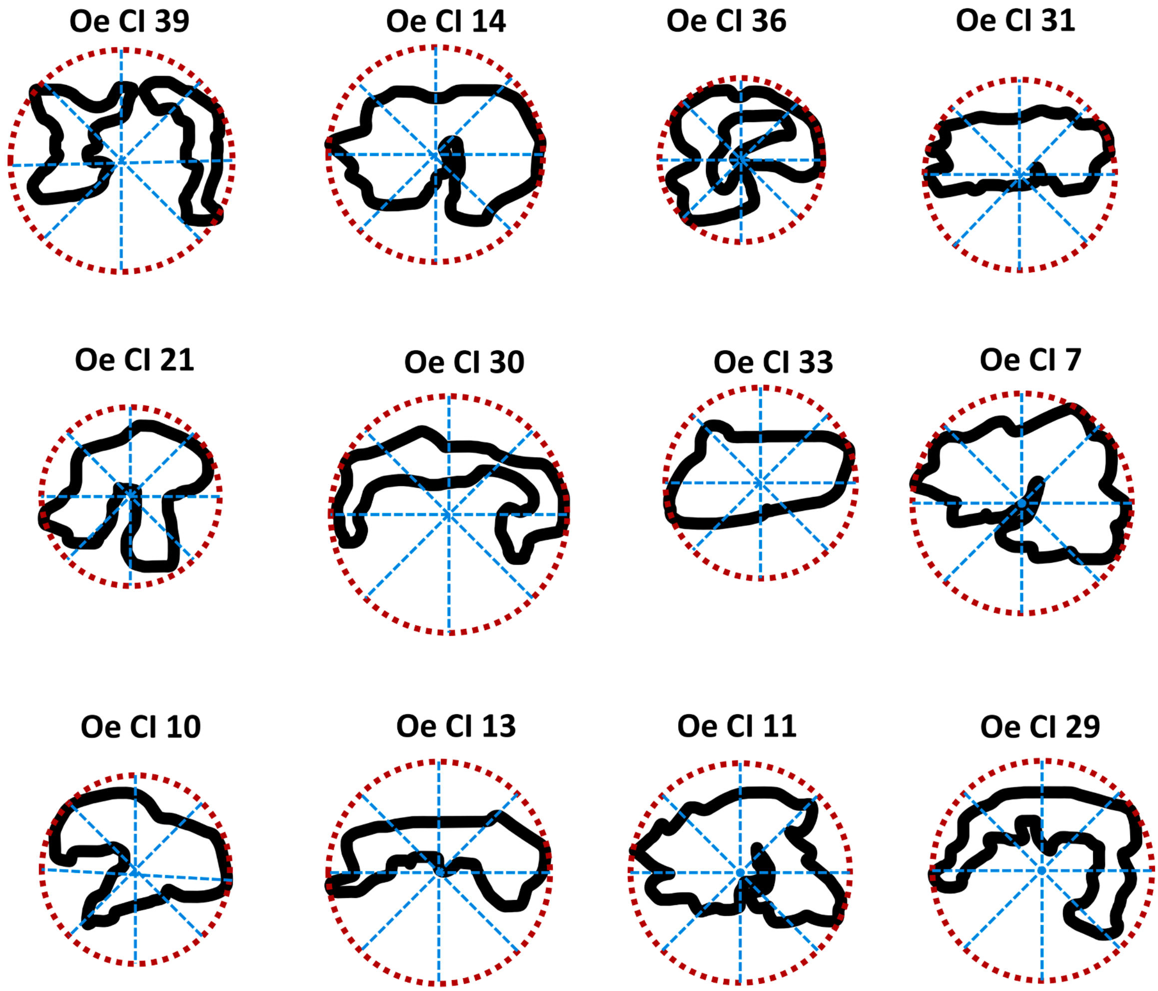

Fig. 2. Taking samples for radiocarbon dating from 12 ancient trees in the Capri Island. Cross-section at ground level determining the stem's shape. The dot in the centre indicates the presumed position of the pith.

the same molecular profile, were close to the Turkish cv. Ayvalik. Oe CI 7, Oe CI 24, and Oe CI 30 were in the same branch of the Italian cvs. Capolga and Sant'Agatese, this latter showed only few alleles different to cv. Throumbolia and presumably derived from this one. Two of the analysed Capri monumental trees, which were not corresponding to any of the 475 known olive varieties here studied, were genetically identical among them, Oe CI 22, and Oe CI 33. The canopy of Oe CI 31 resulted a clone of cv. Itrana, also known under the synonym name of Oliva di Gaeta cultivar, mainly diffused in the border between Campania and Latium regions. The two trees named Oe CI 17 and Oe CI 18 corresponded to the known cvs. Frantoio and Leccino as already reported in their original names (Table 1) and they were not grafted but derived directly from rooted cuttings. The sample Oe CI 25 did not correspond to any of the analysed genotypes both from Capri Island and the reference cultivars, its clusterization allowed to hypothesize a genetic relationship to the cv. Ravece originated in Campania, the same Italian region of Capri Island.

3.2. Genetic frequency of analysed olive trees

A considerable genetic diversity was observed in the Capri Island (Table 2). The total number of allele (Na) was 10.2, ranged from the 15 of DCA9 to the six of GAPU71B. The Polymorphism Information Content (PIC) was 0.693 highlighted ones again the ability of the selected SSR markers to well discriminate the olive cultivars worldwide. The highest PIC value was for DCA16 with 0.811 while the lowest 0.575 for GAPU71B. For what concern the analysed Hardy-Weinberg Equilibrium (HW) all the SSRs resulted to be in statistically significant while DCA16, GAPU103A and UDO-043 were not. The average value of observed heterozygosity (Ho) was considerable higher compared to the expected one (He), 0.878 and 0.734, respectively. The locus DCA9 showed the maximum detectable level of heterozygosity (Ho= 1) while DCA3 the lowest 0.448. This genetic differentiation observed in the Capri olive samples was confirmed by the Fixation index (F), which in average was negative and equal to −0.201, only the locus DCA3 had the F value positive (0.277). In the same locus was observed the unique positive possibility to have the presence of null allele (Frequency of null allele= 0.207) within Capri samples.

The pairwise population matrix of Fst, Gst and Dest values between Capri samples and the 475 International cultivars showed a slight differentiation with 0.047, 0.045 and 0.331, respectively, with a probability (P), based on 999 permutations, $\geq$ 0.001. Only three alleles, expressed in length of base pairs, were detected as private of Capri population, '168′ for DCA9, '216′ DCA16 and '161′ DCA18, the samples having these lengths are Oe CI 29 R (168-DCA9) and Oe CI 30 (both, 216-DCA16 and 161-DCA18).

3.3. Radiocarbon dating of twelve monumental olives of Capri Island

Twelve ancient olives were selected based on the trunk dimension, integrity of principal stem, and ability to collect the wood from the most ancient part of original trunk (Fig. 4; Table 3). The sampling part varied

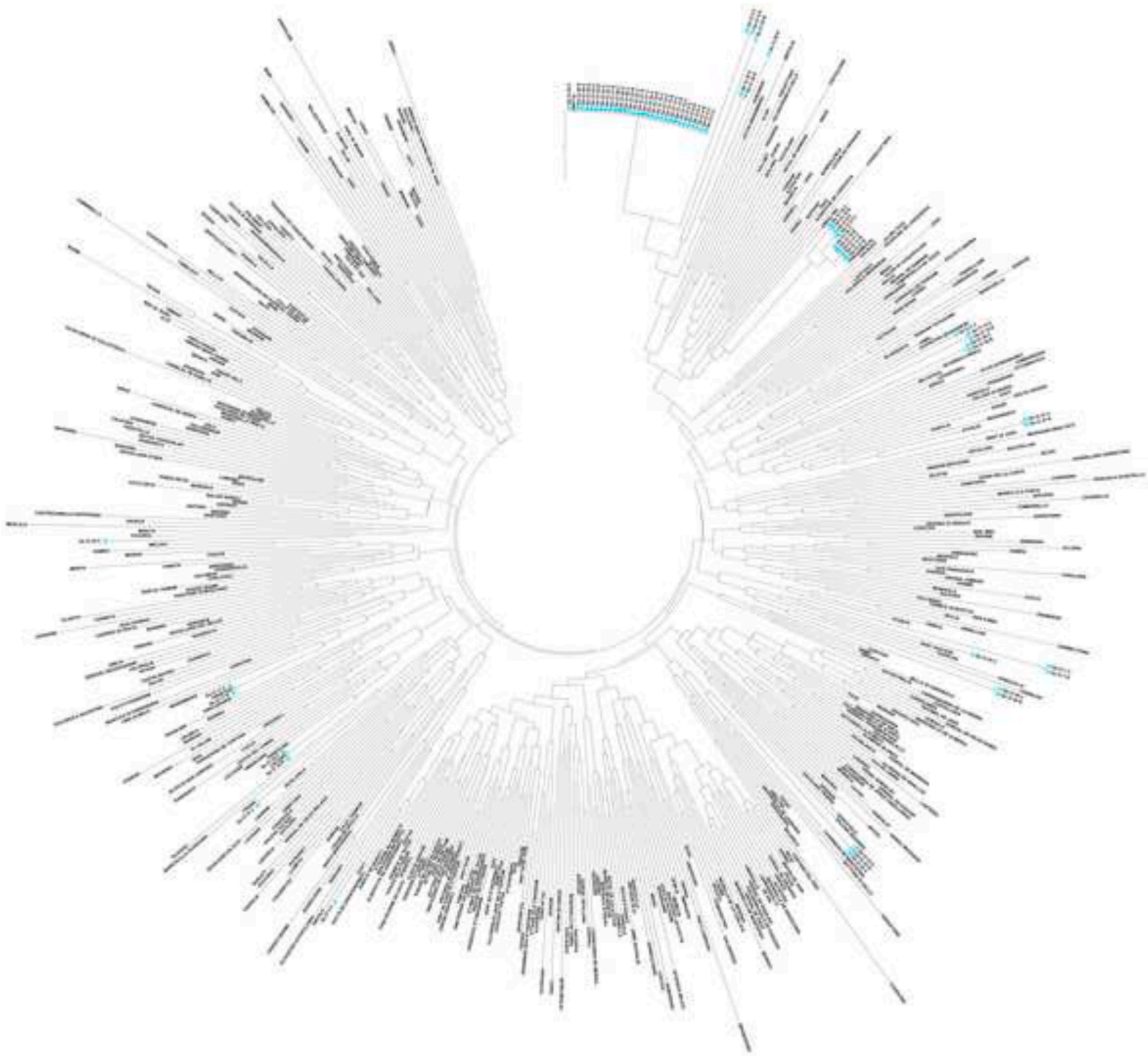

Fig. 3. Genetic dendrogram of the evolutionary history of Capri genotypes inferred by using the Neighbor-Joining method. The sky-blue triangles indicate the analysed accessions in the Capri Island.

Table 2
Frequency analysis, heterozygosity, and polymorphism by population for codominant data for the Capri Island samples.

Locus	N	Na	Ne	I	Ho	He	uHe	F	PIC	HW	F(Null)
DCA3	67	9.000	2.627	1.418	0.448	0.619	0.624	0.277	0.596	***	0.2072
DCA5	67	9.000	3.619	1.505	0.970	0.724	0.729	−0.341	0.677	***	−0.1563
DCA9	67	15.000	4.489	1.958	1.000	0.777	0.783	−0.287	0.754	***	−0.1506
DCA16	67	13.000	5.868	2.067	0.925	0.830	0.836	−0.115	0.811	NS	−0.0673
DCA18	67	11.000	3.733	1.577	0.896	0.732	0.738	−0.223	0.689	***	−0.1162
EMO90	67	10.000	4.035	1.637	0.970	0.752	0.758	−0.290	0.715	***	−0.1431
GAPU71B	67	6.000	2.679	1.222	0.851	0.627	0.631	−0.357	0.575	***	−0.1861
GAPU101	67	11.000	3.746	1.652	0.955	0.733	0.739	−0.303	0.694	***	−0.1466
GAPU103A	67	10.000	4.083	1.698	0.896	0.755	0.761	−0.186	0.721	NS	−0.1015
UDO-043	67	8.000	3.750	1.577	0.866	0.733	0.739	−0.180	0.696	NS	−0.0916

Sample Size (N), Number of Alleles (Na), Number of Effective Alleles (Ne), Information Index (I), Observed Heterozygosity (Ho), Expected (He) and Unbiased Expected Heterozygosity (uHe), Fixation Index (F), Polymorphism Information Content (PIC), Hardy-Weinberg Equilibrium (HW), Frequency of Null Allele (F(Null).

from the ground level up to 1.70 meter (m) above the soil. The stems diameter in average were between 0.75 m and 1.575 m. The distance from the collected material for radiocarbon analyses and the external part of stem ranging from 0.22 m to 0.80 m, while the gaps between the harvested woods and the hypothetical centre of the original trunk varying from 0.10 m to 0.80 m (Table 3).

The results from radiocarbon dating, reported as 'uncalibrated', scored from a minimum of 86 years (y) (Oe CI 7) to a maximum of 410 y (Oe CI 29). The calibrated dating obtained through OxCal Ver. 3.10 software is fully reported as supplementary tables for each of the twelve analysed olive trees (Supplementary Table S3; Supplementary Figure S3).

To estimate the age of the entire stem the algebraic formula was applied considering the distance from the place of wood, collected for radiocarbon dating, the reconstructed centre of stem and the radius of the existing part of the trunk, from the collected and dated wood to the

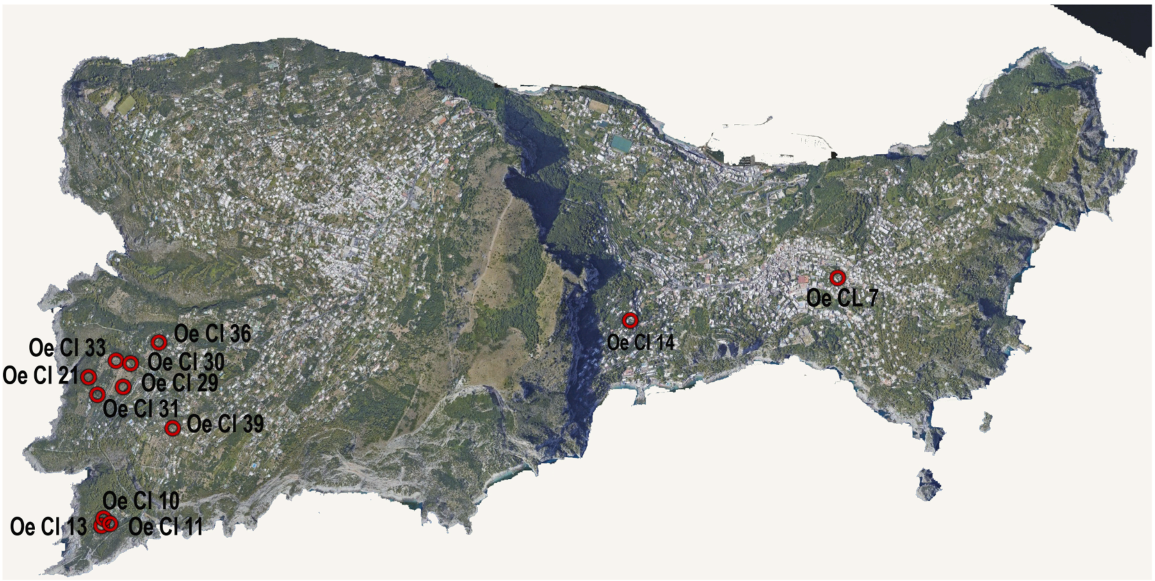

Fig. 4. Capri Island map from satellite view, red rings indicate the position of each monumental tree estimated by radiocarbon analysis with the relative code.

external part of trunk. The estimated age of each monumental olive trees from Capri Island ranged from a hundred years to 932 years (Table 3). Furthermore, the same formula was applied to predict the error range from the estimated age; the results indicated that this delta was between ±51 and ±168.

Oe CI 29 sample resulted the most ancient tree analysed in Capri with 932 ± 102 years (Fig. 5). As reported above this tree was grated with the cv. Dritta di Moscufo as canopy while the rootstock did not correspond to any of the analysed national and international olive varieties and only a close relationship with cv. Throumbolia was detected. Its stem was not as big as expected from an olive tree with this age, in fact, the average diameter was 0.95 m and therefore its circumference is near to 3 m, but presumably, the state of abandonment strongly affected its growth. Other two monumental olive trees resulted to have five centuries old. The first is Oe CI 39 constituted by four main branches raising up from the same trunk in which the distance between the collected wood and the reconstructed centre of stem was 0.80 m. This sample showed a unique genetic profile when compared to all the studied cultivars both from Capri and worldwide. The other multi-secular olive from Capri Island was Oe CI 13, 464 years old ±105, and it was found genetically identical to cv. Dritta di Moscufo. The 'youngest' analysed by radiocarbon tree was Oe CI 7 with and age close to 100 y ± 53, this olive has a circumference close to 4 m and is nine meter taller, but since it was found in a garden of a Monastery (Capri municipality), it could probably have grown well privileged, with continuous availability of water and fertilization deriving from the surrounding vegetables and small poultry.

3.4. *Total polyphenol and organoleptic perceptions of four olive oils from monumental trees*

Four monumental olive trees from Capri Island were selected to extract olive oils and to verify their potentiality for nutraceutical and organoleptic point of views. The polyphenol total amount was considerable high among the analysed samples. The lowest level was 514 ± 41 mg kg^{-1} detected in Oe CI 33. This tree has 175 ± 57 years old and the genetic uniqueness was reported in the paragraph above as well as its genetic identity to Oe CI 22 highlighting the possibility of clonal propagation of this genotype in the Island at least two hundred years ago. The most ancient olive tree estimated in the present study, Oe CI 29, showed a very high amount of total polyphenol 764 ± 41 mg kg^{-1}, demonstrating that the cv. Dritta di Moscufo, called cv. Minucciola by locals, could be considered in Capri Island a health bearer. Considering the number of clones of this olive variety, which are remnant of ancient cultivation, confirming the importance of this cultivar for olive oil production. The oils of the other two analysed monumental trees, were also exceed 700 mg kg^{-1} of total polyphenols, with 720 ± 41 mg kg^{-1} for Oe CI 30 and the highest value observed 787 ± 41 mg kg^{-1} for Oe CI 11 tree which is genetically identical to cv. Throumbolia.

The organoleptic profile of the oils from the selected trees was analysed by an official panel test searching for four main parameters in a range between 0 and 10: Fruity, Defects, Pungency and Bitterness. Considering the total amount of polyphenols individuated it was expected to have medium bitterness perception, in fact, for three out of four oils the median values started from 4.2 to 5, this latter detected in Oe CI 30 sample. No defects have been remarked, while both pungency and fruity were observed with an average level higher than 3 (Fig. 6). Therefore, not only at nutraceutical point of view but also for the organoleptic balancing between spicy and bitterness perceptions these monumental olive trees from Capri Island are real candidates for restarting the olive cultivation.

4. Discussion

The ancient trees still conserved in situ surely enrich the genetic patrimony of olive, including several major and minor olive cultivars. The extraordinary longevity of the species and its high adaptation to different environmental constraints have allowed the survival of these monumental olives, which hold naturalistic, landscape and historical importance and could carry characters of genetic and agronomic interest. Several monumental olive trees are still present in Italy, Greece, Spain, Portugal, Near and Middle East countries, but their number is decreasing every year due to numerous environmental and human threats (Pannelli et al., 2010; Diez et al. 2011; Barazani et al., 2014; Valeri et al., 2022; Mariotti et al., 2023). In fact, as happened for other crops, olive is undergoing a decrease in genetic variability because of the past and recent grafting of autochthonous olive germplasm with some cultivars, and because of the replacement of ancient orchards with intensive and super intensive growing systems including only few varieties (Valeri et al., 2022; Mariotti et al., 2023). Nowadays, human's contribution has been devastating to the drastic decrease in olive variability at all levels from subspecies to cultivars. In fact, during the last century, many uncontaminated environments have been subject to anthropization, and native olive trees have been explanted. It is mandatory to retrieve the remnants of ancient genotypes starting from

Table 3
The twelve analyzed samples collected in the Capri Island were fully reported with their precise geolocalization, position above the soil where the most ancient wood was collected with other measurements which were used to reconstruct the tree age. Furthermore, it was reported the genetic identity found after genetic analysis and the dating from the radiocarbon analysis and calculated by the algebraic formula.

NAME	GPS	HEIGHT OF COLLECTION (m)	AVERAGE DIAMETER (m)	EXTERNAL DISTANCE (m)	HYPOTHETICAL CENTRE DISTANCE (m)	GENETIC ID	C^{14} DATING (year)	C^{14} ERROR (±year)	ANNUAL GROWTH (cm)	CALCULATED PLANT AGE (year)	CALCULATED AGE ERROR (±year)
Oe CI 39 C and R	40.54306° N 14.20528° E	0.35	1.275	0.25	0.80	UNKNOWN	120	40	0.208333	504.00	168.00
Oe CI 14 C and R	40.54833° N 14.23417° E	0.40	1.325	0.30	0.20	UNKNOWN	190	40	0.157895	316.67	66.67
Oe CI 36 C and R	40.54722° N 14.20444° E	0.20	0.750	0.23	0.12	DRITTA	129	40	0.178295	196.30	60.87
Oe CI 31	40.54472° N 14.20056° E	0	1.550	0.40	0.40	C ITRANA, R DRITTA	108	40	0.37037	216.00	80.00
Oe CI 21 C and R	40.54556° N 14.20000° E	0.30	0.925	0.55	0.30	DRITTA	113	40	0.486726	174.64	61.82
Oe CI 30 C and R	40.546211° N 14.202658° E	0.60	1.575	0.80	0.10	UNKNOWN	328	45	0.243902	369.00	50.63
Oe CI 33 C and R	40.546347° N 14.201734° E	0.50	0.975	0.46	0.12	UNKNOWN	139	45	0.330935	175.26	56.74
Oe CI 7 C and R	40.550291° N 14.247275° E	1.50	1.25	0.55	0.10	UNKNOWN	86	45	0.639535	101.64	53.18
Oe CI 10 C and R	40.538783° N 14.200950° E	1.70	0.95	0.27	0.26	THROUMBOLIA	179	40	0.150838	351.37	78.52
Oe CI 13 C and R	40.538433° N 14.200825° E	0.90	0.75	0.32	0.43	DRITTA	198	45	0.161616	464.06	105.47
Oe CI 11 C and R	40.538527° N 14.201368° E	1.70	0.95	0.30	0.10	THROUMBOLIA	269	45	0.111524	358.67	60.00
Oe CI 29	40.545095° N 14.202187° E	0.40	0.95	0.22	0.28	C DRITTA, R UNKNOWN	410	45	0.053659	931.82	102.27

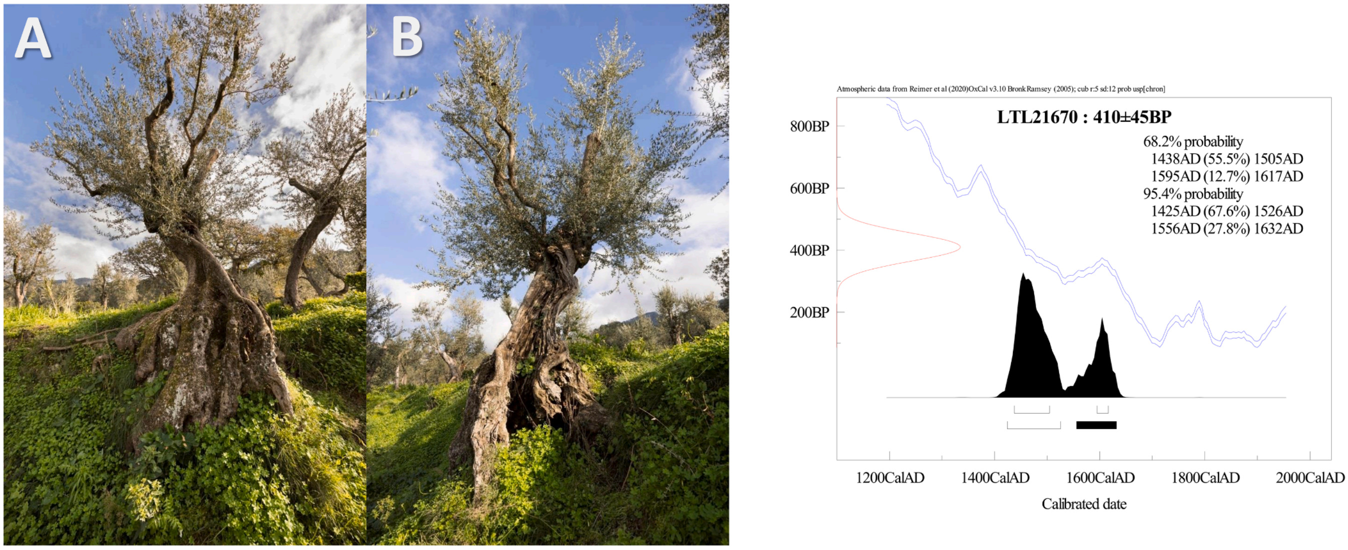

Fig. 5. Two different views, A) and B), of the most aged olive tree, Oe CI 29, of Capri Island. C) The wiggle matching calibration of the radiocarbon dates with the estimation of age together with its dating period expressed in percentage of probability.

Fig. 6. Spider graph and quantity of polyphenols representation of four monovarietal extra virgin olive oils obtained from the respective monumental trees of Capri Island.

the study of monumental olive trees and their rootstocks and the preservation, constituting protected natural areas, of the 'real' autochthonous olive germplasm. These genotypes could represent an amazing reservoir of genetic diversity which can also be used in further breeding programs, by diversifying the quality of the products and the possibility of responding to climate change and biotic stresses.

Island represents a limited micro-habitat in which genetic niches of significant interest could have been develop over time. Capri is an island in the Gulf of Naples, belonging to the Campanian Archipelago and part of the metropolitan city of Naples, located in front of the Sorrento peninsula. The Capri Island has been inhabited since early times and evidence of human settlement was discovered during the Roman era (Benario, 1982). Modern excavations have shown that human presence on the island can be dated to the Neolithic and the Bronze Age (Skeates and Skeates, 1993; Russo Krauss, 2019). The Greeks lived there for many centuries founding both Capri and Anacapri (the Greek suffice 'ana' means above) municipalities connected by the so-called 'Phoenician Staircase', still present today. The first and most probable reference to a residential settlement in Anacapri can be found in the Greek historian Strabone who lived at the turn of the first century BC, the first implicit reference to the existence of a small citadel in the upper part of the Island (Federico and Miranda, 1988).

The olive cultivation in this Island has been reported 500 years ago by Fabio Giordano (Douglas, 1995), and the study of olive genetic diversity and radiocarbon dating in Capri demonstrated the presence of monumental olives, which were probably related to that period uncovering the cultural and historical richness patrimony even for olive culture. Among 67 analysed ancient olive accessions, 21 unique genetic profiles have been identified. The focus of cultivation was mainly on two olive cultivars one the Italian cv. Dritta, which is mainly diffused in central regions of Italy and the second, cv. Throumbolia, diffused in the Greek country and, under the synonymous of cv. Safrawi, in the Middle East (Belaj et al., 2022). This olive variety was recently detected as one of the main founder varieties as direct parent of tens worldwide olive cultivars (Mariotti et al., 2023). The large number of identical genotypes detected among the centennial olive trees underlines that these represent primeval clonally propagated varieties, which were intensively exploited for olive culture (Anestiadou et al., 2017). The presence of two main genotypes highlights the imprint of Italian and Greek populations in the olive culture history in the Island. The Greek influence was observed also for the Oe CI 28 genetically close to cv. Koroneiki. At the same time, our research allows to detect new genotypes such as Oe CI 37, which is genetically like cv. Ayvalik, with Turkish origin, or even through another group of genotypes, Oe CI 1, Oe CI 14 and Oe CI 39, highly related to cvs. Olivastra Seggianese and Canino, which has probably a wild origin as recently described in Mariotti et al. (2023). The few evidence of grafting in Capri's ancient olives could highlight the practice of other clonal propagation such as cutting; since there are many ancient trees identical to cv. Dritta in which canopy and rootstock were belongs to this cultivar. In addition, in the only two trees propagated by grafting the canopy was identified as cv. Dritta, evidencing its important performance in this pedoclimatic condition and electing this variety as the best adapated in the municipality of Anacapri. The genetic position of the rootstocks, Oe CI 28 R and Oe Ci 29 R, between cv. Dritta and cv. Koroneiki in the NJ dendrogram, can highlight the use of seeds from these cultivars which were selected as rootstocks in historical times (Anestiadou et al., 2017; Brazani et al., 2014). The unicity of Capri ancient olive genotypes comparing them with 475 worldwide genotypes, show the strategic position of Island and its almost untouched diversity. The longevity of this species and the low breeding pressure has contributed to the conservation of its variability and that the reduced extent of genetic erosion within its germplasm has allowed the persistence of olive diversity (Aksehirli-Pakyurek et al., 2017). Our study highlights the importance to study the genetic diversity of ancient olive trees in other islands such as Sicily, Sardinia (Mariotti et al., 2023) and Malta (Valeri et al., 2022), where monumental trees, wild types, and cultivated forms are still present close each other. The mentioned approach could help to clarify the role of autochthonous versus allochthonous olive genotypes in different introgression events, uncovering possible ancient selection from wild types or crosses between eastern and western Mediterranean germplasm (Mariotti et al., 2023).

Estimating the age of these olive trees represents a very challenging task as the identification and interpretation of the annual tree rings is complicated, the inner part of the trunk is frequently absent due to wood decay (Arnan et al., 2012; Cherubini et al., 2013; Pannelli et al., 2010). Furthermore, there is still lack of information on factors directly affecting plant growth and loss of wood, such as physiological and developmental aspects (Díez et al., 2011; Michelakis 2002). These factors may result in different growth speeds and distort interpretations of tree age. However, the available studies (Pannelli et al., 2010; Arnan et al., 2012; Bernabei et al., 2015; Ehlrich et al., 2017) on olive age have evidenced the utility of the algorithms, which are based on trunk size to estimate age of ancient olive trees. Consequently, based on these calculations, it is conceivable that the age of the most ancient tree found in the Capri Island ranges from 410 to 931 years. The calculation of plant age through radiocarbon dating showed the olive plantation, which are still alive, in Capri Island has happen in different time-periods from the youngest one 100 years old to the ancient tree 931 years old. This evidenced the olive cultivation was much older than what we could found in the historical documents. The canopy of the most ancient olive tree was genetically identical to cv. Dritta (Oe CI 29 C), while the tree with 504 years old (Oe CI 39) had unknown genetic profile comparing with more than 450 worldwide genotypes as observed for the rootstock of the most ancient olive trees (Oe CI 29 C). This evidence highlights the interest of local farmers to increase the diversity not focusing only on the well-known cultivars from both Italy and foreign countries. Considering the scarcity of water in Capri Island based on what documented in L. Giustiniani of 1797, as the wood density is abruptly altered due to fluctuations in water availability, and their growth is halted and subsequently restarted (De Micco et al., 2016), the trunk diameter could not be only factor to estimate the age of these trees. Water availability was shown to have a positive effect on girth (Terral and Durand, 2006; López-Bernal et al., 2010) and vessel size in olive wood, with earlywood and latewood detected in rainfed trees but not in irrigated ones (Rossi et al., 2012).

The olive oil analysis of re-discovered monumental trees highlights the importance of these ancient genotypes for nutraceutical and sensorial character of their oils, even if it was just a glance on their potentiality for agronomical traits and a deep survey specially on the unknown genotypes should has been done. The survival of ancient olives throughout the Mediterranean area and beyond has been reported in several studies (Díez et al., 2011; S. Mousavi et al., 2017; Ninot et al., 2018), and their molecular identification has confirmed unknown genetic profile (Díez et al., 2011) in some of them. They are recurrently with stable production and high quality and quantity of the oil (Cicatelli et al., 2013). Considering the long lifetime of olive species together with the importance for the traditions of local communities, to preserve the beauty and defence of landscape, to decrease the depopulation of rural towns and assuming the significant tolerance to biotic and abiotic stresses the safeguarding and valorisation of biodiversity included in the abandoned olive orchards must be mandatory.

CRediT authorship contribution statement

Soraya Mousavi: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Saverio Pandolfi:** Writing – review & editing, Validation, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Angelo Lo Conte:** Writing – review & editing, Resources, Methodology, Data curation. **Carlo Alessandro Lelj Garolla:** Writing – review & editing, Visualization, Resources, Methodology, Data curation. **Roberto Mariotti:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Carlo Alessandro Lelj Garolla reports a relationship with Associazione L'Oro di Capri that includes: board membership and consulting or advisory. Angelo Lo Conte reports a relationship with Associazione L'Oro di Capri that includes: consulting or advisory and travel reimbursement. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Supplementary materials

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