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**Abstract**

The olive is a medium-sized evergreen tree, which integrates a unique set of morphological and developmental characteristics suited to the relatively dry, rustic conditions of its Mediterranean origin. Also particular to the olive tree are its numerous small fruits, which are rich in oil that is highly appreciated for both flavor and health benefits. The *Olea europaea* species includes both wild and cultivated forms, and both a long period of domestication and the perseverance of wild varieties provide a range of morphological variation, as does the developmental plasticity of this species. This chapter reviews the general growth and taxonomy of the olive tree and describes its vegetative and reproductive morphology and anatomy. Basic structural features of the trunk and branches, leaves, roots, flowers, fruits, and seeds are described. Current research is indicated for the structures discussed, and information provided regarding adaptive significance, environmental influences, and genetically based variability among cultivars or between wild and cultivated genotypes.

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## 1 The Olive Tree

### 1.1 Description and Habit

The olive is a medium-sized evergreen tree, which grows natively in relatively dry, rustic conditions with a Mediterranean climate. Its numerous small fruits are rich in oil, which is highly appreciated for both flavor and health benefits. Numerous wild, cultivated, and feral genotypes exist, particularly in the Mediterranean Basin, where it is widely spread and emblematic of the diet and landscape. A long history of domestication, in which cultivars have been

selected at multiple times and locations, has produced a range of tree architecture and fruit morphology. Tree characteristics such as vigor, stature, and crown density are genotype related, as is fruit size and shape. In addition, the olive tree is highly plastic in its development, so environmental conditions and agricultural management practices, in particular pruning and irrigation, impact greatly on both tree and fruit forms.

A unique set of characteristics is integrated into olive tree morphology and development. The olive is a woody plant, which may grow as a tree with a large central trunk that becomes characteristically gnarled and twisted in old trees, or as a multi-trunk, shrubby bush-like structure. The tree trunk and limbs have a high capacity for forming new lateral branches from numerous meristematic zones or axillary buds formed at the time of leaf initiation, and suckers sprout frequently around the collar at the trunk base. The olive tree's high branching capacity and the longevity of the axillary buds have further implications for its growth habit and agricultural management. Sprouting provides healthy regrowth following pruning or grazing and has been useful for vegetative propagation as well as contributing to the long endurance, sometimes multiple centuries, of individual trees. Heavy branching and the accompanying formation of numerous leaves also tend to produce a dense canopy which, for optimum fruit production, requires thinning to allow light penetration and reduce disease.

The olive tree is recognized as well adapted to the dry Mediterranean environments where it is native. Trunk and branches, leaves, fruits, and roots all contain structural features considered xerophytic adaptations, which aid in reducing water loss (see future sections). As a woody plant, the olive is characterized by a long juvenile period, as much as 10–15 years under natural conditions, until the tree is capable of forming flowers, the structures responsible for sexual reproduction. In its reproductive behavior the olive tree tends to relatively pronounced alternate bearing, in which years of heavy flowering and fruiting alternate with those with highly reduced

crop levels. While these processes can be modified by environmental conditions and tree developmental physiology, there is a genetic component involved in the regulation of both the juvenile period length and the tendency to alternate bearing, with differences expressed among cultivars.

The fruit of the olive tree is unusual in the plant kingdom in that oil, in the form of fatty acids, is the major storage component. It is a drupe, in which the fleshy, oil-containing mesocarp or pulp surrounds a substantial, highly lignified endocarp or pit (see future sections). Olive fruits are consumed in the wild by birds and small mammals and under domestication by humans, principally as extracted oil but also as pickled or processed fruit.

## 1.2 Taxonomy

The olive, *Olea europaea* L., belongs to the Oleaceae, a medium-sized family comprising approximately 25 genera and 600 species distributed throughout temperate and tropical regions of the world (Besnard et al. 2009). The plants in this family are primarily evergreen trees and bushes along with a number of vines, many of which produce essential oils in their flowers or fruits. Other economically important genera of this family are *Fraxinus*, (ash), which is used for lumber, *Jasminum* (jasmine), *Ligustrum* (privet), *Phillyrea*, and *Syringa* (lilac), utilized for ornamental purposes, but only the olive is cultivated for its edible fruit.

Olive morphology is logically representative of the Oleaceae family, for which it is the type species. Oleaceae diagnostic characters are principally related to leaf and flower structure (Heywood 1985): Leaves are simple and generally occur opposite each other along the stem, or else pinnate, with opposite leaflets along the leaf axis. Flowers are frequently grouped in terminal or axillary inflorescences. The flowers are radially symmetrical and usually hermaphrodite, but sometimes unisexual. The calyx (sepal unit) and corolla (petal unit) are hypogenous, inserted below the ovary, with the sepals united in a

bell-like shape and the petals sometimes united. Generally, there are two stamens which are inserted on the petals. The ovary is superior, inserted above the petals and sepals, consistent with their hypogenous arrangement. Typically, the ovary originates from two carpels and is composed of one to two locules, each containing two ovules. Morphological distinction between the cultivated variety *O. europaea* subsp. *europaea* var. *europaea* and the wild *O. europaea* subsp. *europaea* var. *sylvestris* has been mainly based on the small fruit and pit size of the wild variety and is considered rather unprecise and a potential source of error (Ganino et al. 2006).

Following a thorough revision by Green (2002), the genus *Olea* is considered to include 33 species and nine subspecies. Six of these subspecies form the *Olea* subsection or complex: *O. europaea*, *O. cuspidata*, *O. laperrinei*, *O. maroccana*, *O. cerasiformis*, and *O. guanchica*. This complex extends through Macronesia (*O. cerasiformis*, and *O. guanchica*), Mediterranean (*O. europaea*), African (*O. maroccana*), and Asian (*O. cuspidata*) regions. Green's taxonomic scheme further recognizes the close relationship between the cultivated olive and its wild relative, often referred to *oleaster* or *silvestris*, as two varieties within the *Olea europaea* subspecies: *Olea europaea* subsp. *europaea* var. *europaea* and *O. europaea* subsp. *europaea* var. *silvestris*.

Historically there have been many and differing opinions as to nomenclature and hierarchies within both the olive genus and species, particularly because of the use of morphological characters which often vary in relation to environmental conditions or phenological stage. For example, certain taxonomic confusion within the species seems to have arisen because one of the morphological characters used for taxonomic identification is leaf size, and the juvenile foliage of germinated seedlings or resprouted vegetation of heavily grazed cultivars is easily misinterpreted as the small leaves characteristic of the wild type. Molecular techniques are proving highly useful in clarifying taxonomic relationships in *O. europaea* (Green 2002; Baldoni et al. 2006; Besnard et al. 2008, 2009).

The wild *O. europaea* subsp. *europaea* var. *silvestris* is considered to be the main wild progenitor of the cultivated olive, based on similar morphology and ecological requirements and ploidy level (Green 2002; Besnard and Rubio de Casas 2016). It is generally agreed that subsequent to domestication, introgressive hybridization between cultivated and wild populations in different locations has played an important role in the evolution of olive cultivars (see following chapters). There is debate, however, as to whether olive domestication was initially a single (Besnard and Rubio de Casas 2016) or multiple events (Díez et al. 2015).

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## 2 Vegetative Morphology and Anatomy

### 2.1 Trunk and Branches

Olive tree architecture, the structural pattern of trunk and lateral shoot growth, shows high phenotypic diversity as well as ontogenetic modification as the plant matures (Rallo et al. 2008; Hammami et al. 2012; Ben Sadok et al. 2013). Evaluation of cultivars and of progenies in breeding programs have demonstrated clear genetic influence and heritability in olive architectural traits, along with a highly plastic response to environmental and management conditions. Young olive plants show a prevalent tendency to form a single-axis trunk. Lateral shoots sprout along the trunk from one or both of the two lateral buds present at each node. Branched and unbranched nodes are distributed vertically along the trunk in a scattered or irregular manner, although long areas of no branching are infrequent. Within this diffuse pattern there appear to be relatively equal tendencies for different dominant zones of more numerous and more vigorous branching: basitony near the trunk base, mesotony in the central region, acrotomy in the upper or distal zone, or the absence of a dominant zone. Branch orientation is more frequently upright (orthotropic) than horizontal (plagiotropic), and while the majority of

branches are straight there are often substantial numbers, which bend upward or downward. Olive genotypes with a drooping or pendulous branching habit are considered to be of particular interest for hedgerow orchard systems (Rallo et al. 2008).

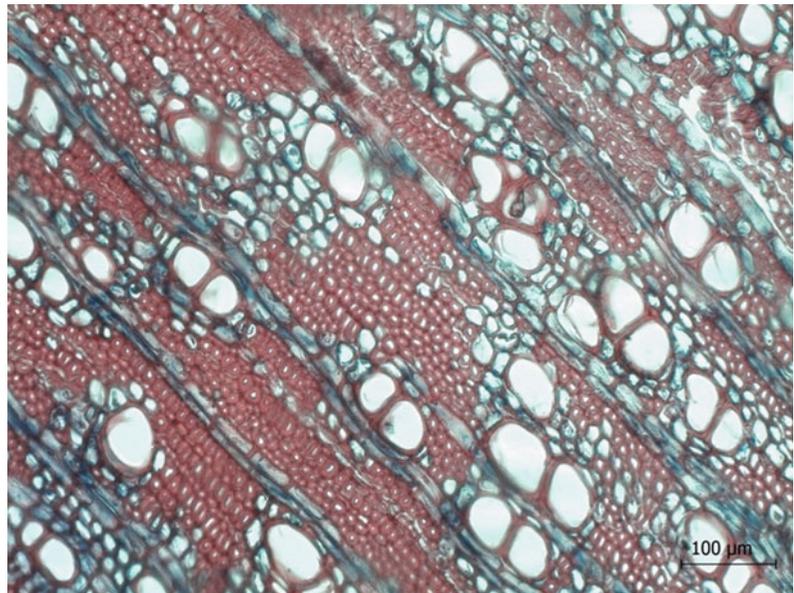
Over time, olive trees exhibit a continuous branching hierarchy, forming second order, third order, fourth order branches, and so on throughout the tree canopy. The branching system is monopodial, in which the main shoot and branch axes are maintained and their apices continue to be active, rather than being overtaken by lesser order lateral shoots. In older trees branching follows a proleptic pattern, in which new-shoot sprouting from dormant lateral buds occurs periodically, once a year. In contrast, young trees and regrowth following heavy pruning often present syllepsis, where multiple orders of branches develop in the same growth season due to reduced bud dormancy. Sylleptic branching in the olive has a significant genetic component and a strong role in early tree morphology (Ben Sadok et al. 2013).

Vigor is a morphological characteristic, which refers to overall plant growth rate and size. In cultivated olive varieties, vigor is considered to be an important agronomic component which is

relevant to juvenile period length and variety choice for planting density and has noted genotypic tendencies (de la Rosa et al. 2006; Rallo et al. 2008; Farinelli and Tombesi 2015). Olive tree vigor may be classified qualitatively as high, medium, or low, as in the official Olive Oil Council cultivar passport criteria (Barranco et al. 2000), or measured as canopy volume, canopy surface parallel to the ground, or trunk diameter at a specified distance from the soil surface (Rallo et al. 2005). Although trunk growth is clearly influenced by multiple factors, a molecular marker for olive trunk diameter has been recently identified at the seedling stage (Atienza et al. 2014).

Young olive shoots are slender, and their anatomy is characterized by small xylem vessels, a large central pith, and a notable sclerenchyma ring composed of fiber bundles and sclereids internal to the phloem. Secondary xylem in the olive stem and trunk is diffusely porous, in which the relatively small-diameter vessels are distributed uniformly within the annual growth ring. The xylem tissue (Fig. 1) is also rich in fibers and contains a relatively low proportion of parenchymatic cells (Salleo et al. 1985; Rossi et al. 2013). In a 1-year-old stem, vessel diameters are typically lower than 40  $\mu\text{m}$ , with 90 % in

**Fig. 1** Microphotograph of xylem tissue sampled within a yearly ring of an olive stem. Xylem vessels (*large and red*), numerous fibers (*small and red*), and both axial and ray parenchyma cells (*blue*) are visible (*photograph credit Luca Sebastiani*)



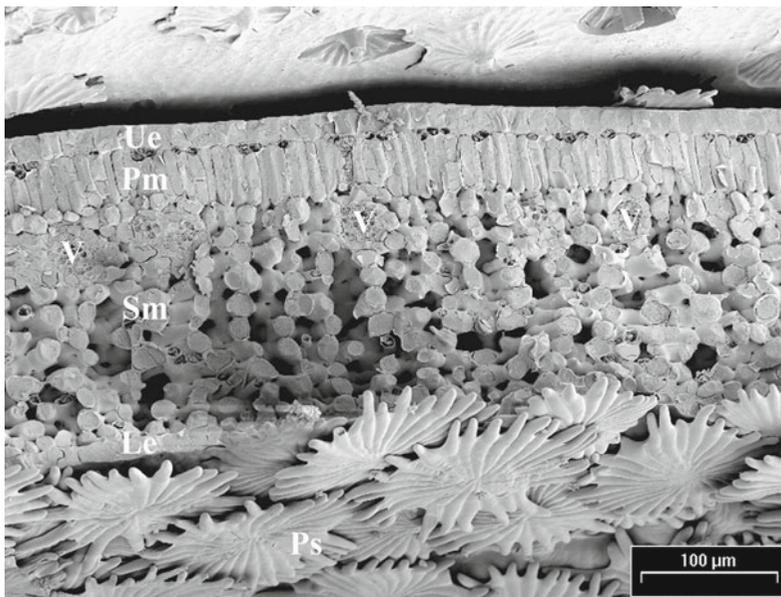
diameter classes around 20  $\mu\text{m}$  (Lo Gullo and Salleo 1990). In mature olive plants the vessel diameters can vary among different years and according to water availability, indicating a strong capacity to respond to the environment. Rossi and coworkers (2013) found that irrigated olive trees formed fewer small-diameter xylem vessels ( $<20 \mu\text{m}$ ) than rainfed trees, while vessels with diameters higher than 20  $\mu\text{m}$  were more abundant. These authors hypothesize that the narrow xylem vessels could contribute to olive tree tolerance of low water availability.

## 2.2 Leaves

The olive tree is evergreen and its leaves usually live for two to four seasons, although older leaves may remain on the tree longer. The small leaves are simple, with an elongated blade (3–9 cm long) and a very short petiole (approximately 0.5 cm). Blade shape varies from the slightly wider and more symmetrical elliptical form to lanceolate, where the width is greatest at

the base and blade length is greater than six times its width. A thick, highly visible central vein divides the leaf in half along its length and protrudes along the lower surface. The leaves are positioned on the branches with decussate phyllotaxy: There are two opposite leaves ( $180^\circ$  apart) at each node, alternating at right angles with those of the nodes above and below. Shoot growth producing new nodes and leaves may occur at any time of the year, depending on water supply, temperature, and solar radiation, but usually is only active or most active in spring and autumn (Connor and Fereres 2005).

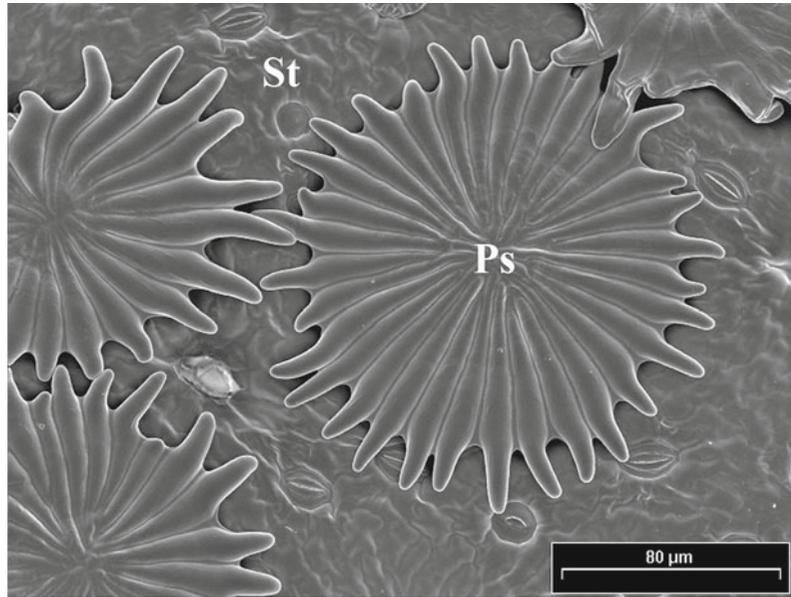
Olive leaf anatomy and surface characteristics (Fig. 2) are typical of drought-resistant sclerophyllous vegetation, including small size, thick cuticle, high stomatal density, high pubescence, and compact mesophyll cells (Bacelar et al. 2004). The upper surface of the leaf is dark green and glossy, covered with a thick cuticle. The lower surface appears gray or pale in color due to the presence of numerous multicellular trichomes in the form of umbrella-shaped peltate scales, forming a dense protective layer. The stomata



**Fig. 2** Cryo-SEM image of frozen-hydrated young leaf (cv. Leccino), freeze fractured transversally showing cell types. At the figure, top, the upper epidermis (Ue) and palisade mesophyll (Pm); in the center, the spongy

mesophyll (Sm) traversed by veins (V); and below, the lower epidermis (Le). The lower surface is covered by numerous overlapping trichomes (Ps, peltate scales) (*photograph credit* Antonio Minnocci)

**Fig. 3** Cryo-SEM image of frozen-hydrated young leaf (cv. Leccino), lower surface. The trichomes (Ps, peltate scales) and the stomata (St) they will eventually cover are in early stages of development (photo credit Antonio Minnocci)



form only on the underside of the leaf, where they are shielded by the peltate trichomes or scales (Fig. 3). Internally, the upper zone of the leaf mesophyll is composed of palisade parenchyma consisting of several layers, usually two to three, of compact, relatively elongated cells. The spongy mesophyll, composing the lower portion of mesophyll, is characteristically replete with large intercellular spaces. Directly below the lower leaf epidermis, between that tissue and the spongy mesophyll, is frequently a second palisade or pseudo-palisade parenchyma, consisting of a continuous single layer of elongated cells, although shorter and less densely packed than the principal palisade tissue (Chartzoulakis et al. 1999; Bacelar et al. 2004; Moreno-Alías et al. 2009). Within the leaf, where the palisade parenchyma and spongy mesophyll meet, is a dense reticulate network of secondary veins, and throughout both mesophyll layers are numerous long, slender branched sclereids (Arzee 1953). These latter structures contribute to the characteristic toughness of the olive leaf, also considered a typical structural feature of leaves adapted to dry environments.

Olive leaf size and structure vary in relation to genotype and development, and in response to growth conditions. Leaves of juvenile plants tend

to be smaller and to have a lower length-to-width ratio, less peltate trichomes, and no second palisade parenchyma layer (Moreno-Alías et al. 2009). Leaves from wild genotypes are also frequently small and more elliptical in form. Under water stress, cell density increases for all leaf tissues, and the cuticle is substantially thicker (Chartzoulakis et al. 1999).

### 2.3 Roots

Olive tree root morphology varies with growth conditions, including soil characteristics, nutrition, and water, and with the origin of the plant as a seedling or cutting; however little information is available with respect to cultivar differences or genetic control. Seedlings produce a single long, primary taproot, whereas in rooted cuttings the multiple roots tend to branch more profusely and closer to their junction with the stem.

Anatomically, the olive tree root presents attributes related to withstanding water stress and like the shoot shows the capacity to rapidly modify its structure in relation to water availability (Rapoport 2010; Tataranni et al. 2015). Root hairs, the elongated lateral outgrowths of

the epidermal cells which are responsible for absorption, are relatively short but numerous. The endodermis is the cell layer located within the root between the cortex and vascular cylinder and contains a prominent Casparian strip on its radially oriented cell walls. The substantial suberin composition of the Casparian strip is impermeable to water and forces the water movement through the endodermal cell protoplasts, providing the metabolically controlled hydraulic gates for the entry of water into the plant vascular system. The endodermis of olive roots is well differentiated and furthermore has demonstrated the capacity to undergo additional suberization in response to exposure to water (Lo Gullo et al. 1998) and salinity stress (Rossi et al. 2015).

The external cell layers of the cortex, those that lie directly below the epidermis, also exhibit structural modifications to create a hypodermis or exodermis. The hypodermal cells undergo specialized secondary wall differentiation, which includes thickening and deposition of suberin, acting as an additional barrier to water movement and protecting the root from water loss. In fact, under water-limiting conditions olive roots produce added hypodermal cell layers and increased suberization hypodermal as well as endodermal cell walls (Tataranni et al. 2015).

### 3 Reproductive Structures and Development

#### 3.1 Inflorescence and Flower

In the year prior to bloom, the inflorescences originate as buds in the leaf axils of new shoots. The buds (Fig. 4) are small, highly reduced shoots composed of 4–5 nodes, and each with two oppositely positioned leaf primordia (Fabbri and Alerci 1999; de la Rosa et al. 2000). All of the buds are structurally identical and basically vegetative; that is, they do not present any morphological differences which distinguish between vegetative and reproductive buds (Pinney and Polito 1990; Andreini et al. 2008). Subsequent bud fate, depending on a complex combination of endogenous and exogenous factors, will follow one of four pathways: (1) development of an inflorescence (reproductive bud), (2) growth of a shoot branch, (3) continue dormant, and (4) death and abscission. The lack of microscopically visible differences between buds with reproductive and vegetative fates has long been an obstacle for the investigation on olive tree flowering controls. Molecular tools offer great potential for identifying vegetative and reproductive buds and providing a means of advancing in this area (Amasino 2010).



**Fig. 4** Olive axillary bud (*left*) and early reproductive and vegetative sprouting (*center* and *right*). The axillary bud is a relatively undifferentiated structure composed of opposite pairs of leaf primordia. In reproductive sprouting (*center*), the peduncle axis elongates, the leaf primordia

form small bracts, and inflorescence development occurs within the bracts. Vegetative sprouting (*right*) begins with elongation of the branch axis and the external leaf primordia, which will develop into the first pair of leaves (*photograph credit* Franco Castillo-Llanque)

Reproductive differentiation proceeds the following spring under adequate environmental conditions in buds, which have received the necessary induction and initiation stimuli. Olive flowers are borne on 1.5–4.0 cm long inflorescences that develop from the lateral buds or directly at the shoot apex. The paniculate inflorescence has a central axis or rachis, on which individual flowers or secondary flower-bearing axes (rachillas) arise at a series of bilaterally symmetrical branching points. One inflorescence may contain from 10 to 35 flowers, of which only one or a few will set fruit. The number of flowers in an inflorescence is influenced by the cultivar and growing conditions, including the position of the inflorescence on the tree and the fruiting shoot.

The olive flowers are small and have actinomorphic (regular) symmetry and hypogenous arrangement, in which the masculine and accessory flower organs are attached in successive whorls below the ovary base. The sepals are fused to form a small green conical calyx at the flower base. Within the calyx are four white symmetrically arranged petals, joined at their base, composing the corolla. The androecium, the male reproductive system, consists of two stamens, each with a relatively large, plump bright yellow anther, which are attached to the petal bases by a short filament. In the flower center is the gynoecium, the female reproductive system, a single pistil composed of a long, two-lobed stigma, a short white style and a small round green ovary (Fig. 5).

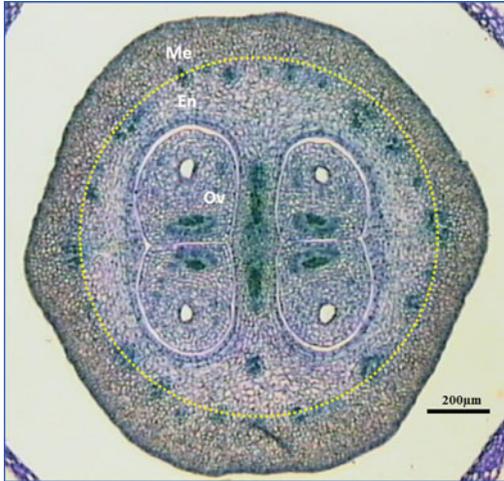
The elongated, two-lobed stigma surface is composed of multicellular papillae and is classified as wet type because of the secretion it produces, a heterogeneous substance including carbohydrates, lipids, and proteins (Serrano et al. 2008). Below the papillae lies a funnel-shaped receptive tissue, which is continuous with and similar in structure to the columnar transmitting tissue in the center of the solid style (Suarez et al. 2012). The ovary (Fig. 6) has two locules or cavities, derived from its two-carpel origin. Each locule contains two ovules, each joined to the upper part of the placental separation between the locules. Olive ovules are anatropous and during development undergo a turning movement, which orients the micropyle, the embryo sac's entranceway for the pollen tube, upward toward the style (King 1938). Fertilization of one of the four ovules is required for fruit development.

Within the olive ovule, macrogametophyte differentiation follows a bisporic pattern in which two of the four megaspore nuclei produced during meiosis abort and two survive, generating an 8-celled embryo sac (Extremera et al. 1988). The olive ovule is tenuinucellate and unitegmic, signifying that the nucellus, the ovule tissue where the embryo sac forms, is thin at ovule maturity and is surrounded by only a single integument. Full development of the ovule occurs in the three weeks prior to flowering, at which time the embryo sac is mature and capable of fertilization. Differentiation is sometimes incomplete and no embryo sac forms within the ovule, only a



**Fig. 5** Microphotograph of a longitudinal section of olive gynoecium, composed of a single stigma, style, and ovary. The upper stigma surface has received pollen grains. The funnel-shaped receptive tissue of the upper style is continuous with the stigma papillae. Indicated

between *circles*, the mesocarp or future pulp forms the outer part of the ovary. Within the ovary endocarp, one ovule is visible in each of the two locules (*photograph credit* Hava Rapoport)



**Fig. 6** Microphotograph of a central transverse section of olive ovary. A ring of vascular bundles, indicated by the dotted line, lies between the ovary mesocarp (Me) and endocarp (En). Each of the two locules contains two ovules (Ov); in this ovary, all four ovules are fully developed, evidenced by the round clear areas (*photograph credit* Ester García-Cuevas)

residual atrophied nucellus at the base of a long micropylar canal. Such incomplete ovule development was first identified in the non-fruiting ornamental cultivar Swan Hill, but also occurs in fruiting cultivars to varying degrees, clearly associated with genotype (Rallo et al. 1981; Moreno-Álias et al. 2012). Fertilization of the undeveloped ovules is not possible, but, usually other, fully differentiated and competent ovules are also present in the ovary, allowing fertilization to proceed. That factor, along with the olive tree's tendency to produce numerous flowers, means that in normal, good flowering years the presence of undeveloped ovules will not likely cause a drop in fruit production (Rapoport and Rallo 1991).

The olive tree sexual system is andromonoecious, with two sexually different kinds of flowers present together within the same inflorescence: (1) hermaphroditic or bisexual flowers, with both male and female reproductive organs, and (2) staminate, with only male reproductive parts. The hermaphroditic flowers are also referred to as perfect flowers, and the staminate flowers, imperfect. Staminate flower development involves varying degrees of pistil

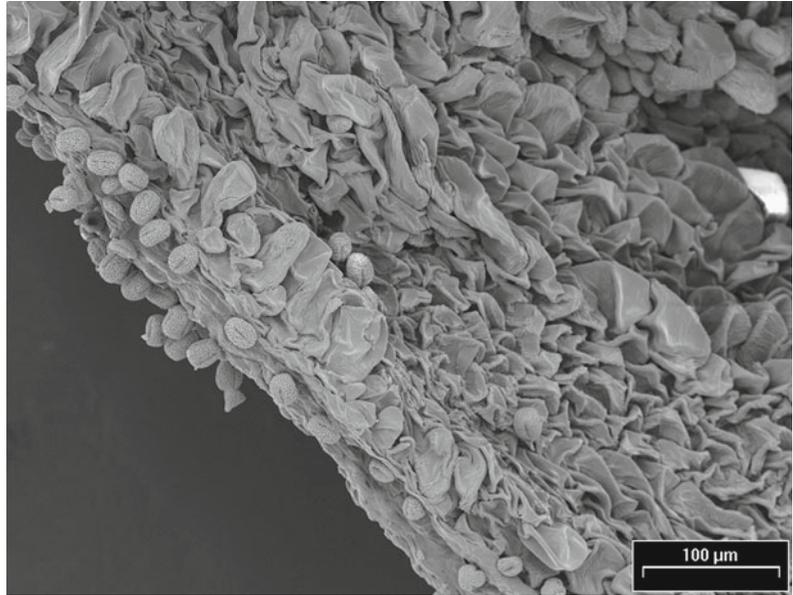
abortion, and a residual atrophied pistil is often visible within the center, but stamen development and pollen production are similar in both flower types (Cuevas and Polito 2004). The proportion of imperfect flowers varies according to cultivar and is also influenced by environmental conditions, such as temperature, mineral nutrition, and water availability, and substrate competition among flowers when flower number is high. The critical role of substrate supply in the differentiation of the two flower types is evidenced by the much higher starch accumulation in perfect than staminate flowers (Reale et al. 2009). Within the inflorescence, there appear to be preferred positions for perfect flower formation, likely related to positional priorities for substrate supply (Cuevas and Polito 2004; Seifi et al. 2008).

The olive anthers produce large quantities of pollen (Fig. 7) which as well as being critical for fertilization of the flowers is also a source of allergic reactions. Pollination is anemophilous, by wind, and the pollen may travel over very large distances, a process recently confirmed by molecular paternity testing. Olive cultivars express varying degrees of self- and inter-incompatibility.

### 3.2 Fruit

The olive fruit is a drupe, an indehiscent fleshy fruit composed of three principal tissues, the endocarp, mesocarp, and epi- or exocarp, each of which follows a very distinct form of growth and differentiation during fruit development. Together they form the pericarp, initiated as the ovary wall. At bloom, the ovary contains a ring of vascular bundles which lies between the mesocarp and endocarp (Fig. 6), at this time composed of small parenchymatic cells (King 1938; Rallo and Rapoport 2001; Rosati et al. 2012). Observations of the olive ovary cells and tissues have shown that ovary size and cell number at bloom are highly correlated with cultivar fruit size (Rosati et al. 2009, 2012) and that ovary size differences among cultivars are mainly due to cell number in both the endocarp and mesocarp (Rosati et al. 2011).

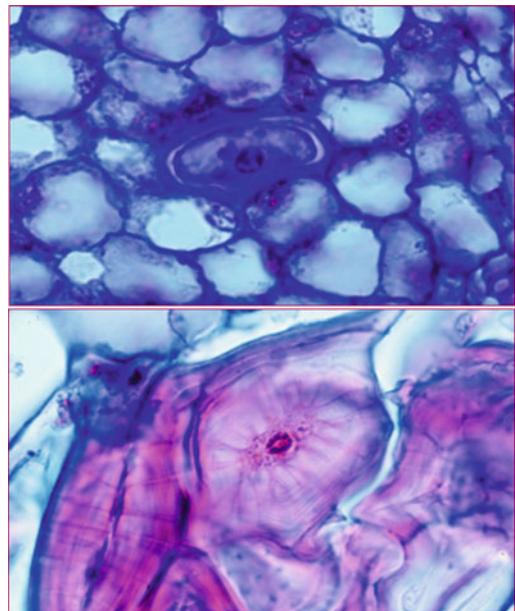
**Fig. 7** Cryo-SEM image of an olive anther with numerous pollen grains (photograph credit Antonio Minnocci)



The endocarp is the fruit pit, a hard, woody structure, which surrounds the seed in the fruit center. During fruit growth the endocarp cells undergo the differentiation process of sclerification, in which a thick secondary wall rich in lignin is deposited, eventually filling the entire cell and obliterating its living contents (Fig. 8). As the endocarp grows, sclerification is initiated in successively increasing numbers of its cells (Hammami et al. 2013), while the cells which previously started sclerification continue to undergo lignin deposition and cell wall thickening. Physical hardening intensifies after maximum endocarp size is reached, the time when the majority of endocarp cells have initiated sclerification and can no longer expand nor undergo division. Afterwards hardening continues, as do cell sclerification and the associated endocarp dry weight increase (Hammami et al. 2013; Rapoport et al. 2013).

Exterior to the endocarp is the mesocarp (Fig. 9), or fruit pulp, the major and edible part of the olive fruit, and the site for oil metabolism and storage. Oil deposition, for many years mistakenly thought to occur in the large, aqueous vacuole of the mesocarp cells, takes place in the cytoplasm, a process consisting of the formation and coalescence of small oil bodies to become increasingly larger oil droplets (Rangel et al.

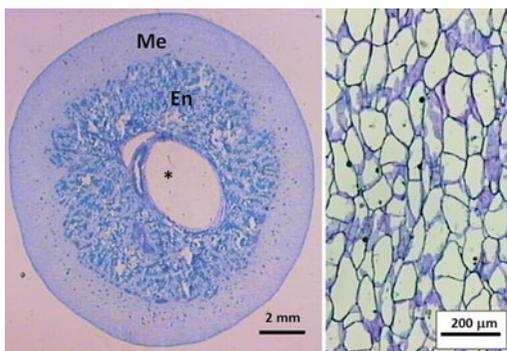
1997). The mesocarp is a fleshy tissue composed of parenchyma cells, whose capacity for cell division and expansion drives the long-term growth of this tissue. The highest rate and



**Fig. 8** Sclerification of olive endocarp cells which produces pit hardening: a thick secondary wall rich in lignin is formed (upper photo) which progressively thickens, eventually obliterating the cell contents (lower photo) (photo credit Hava Rapoport)

amount of olive fruit mesocarp cell division occur in the period immediately following bloom, although some cell division continues at a reduced rate throughout fruit development (Hammami et al. 2011). Cultivar differences in fruit size depend principally on cell number, not cell size, but the seasonal pattern of cell division intensity is consistent for olive cultivars with a wide range of fruit size (Hammami et al. 2011).

The epicarp or exocarp, the fruit skin, constitutes the external fruit tissue. The exocarp is principally composed by the epidermis, the external layer of cells with its thick protective cuticle. In an attempt to clarify different views as to whether any or how many subepidermal cell layers also constitute part of the exocarp, recent studies of cell dimensions (Hammami and Rapoport 2012) indicate that approximately five layers of subepidermal cells, although continuous with and similar in structure to mesocarp cells, show structural and developmental patterns more unified with the epidermis. Scattered across the exocarp are lenticels, derived from ovary stomata which become atrophied early in fruit growth and are subsequently covered with the cuticle. The lenticels are most visible during mature green stages of fruit growth as light-colored specs, and their size and frequency are characters used in cultivar identification (Barranco et al. 2000).



**Fig. 9** Microphotograph of a central transverse section of olive fruit (cv. Manzanilla de Sevilla) 8 weeks after bloom (*left*) and detail of parenchymatous mesocarp at fruit maturity (*right*). At 8 weeks the mesocarp (Me) is expanding and the endocarp undergoing sclerification; within the endocarp the locule containing the growing seed has expanded (\*). (*photo credit* Ester García-Cuevas)

The fruits of cultivated olive varieties are 1–4 cm long, 0.5–2 cm in diameter, and can weigh as much as 10 g fresh weight, 2.5 g dry weight. Fruit form ranges from spherical to ellipsoidal or elongated, with varying degrees of asymmetry and a rounded or pointed apex. While there is a tendency for the cultivars with smaller fruits to be destined for oil production and those with larger fruits for table use, many are of double aptitude and size is not a strict determinant of use. Fruits of wild genotypes are commonly much smaller (length 0.5–1.5 cm, width less than 1 cm, and weight less than 2 g) and have a much higher proportion of endocarp as compared to cultivated varieties.

### 3.3 Seed and Embryo

Within the endocarp, the olive fruit contains one, sometimes two, or very rarely three elongated seeds, a characteristic which seems to be associated with the cultivar. The seed coat, derived from the single ovule integument, is thin, tough, and permeated by numerous vascular strands. The embryo is straight, with long, flat, spatula-shaped cotyledons, and fills most of the seed volume. Between the embryo and seed coat is a small amount of endosperm, rich in starch, proteins, and oil (Alché et al. 2006).

Immediately following fertilization the multicellular endosperm is formed and commences rapid growth, accompanied by notable expansion of the ovule and differentiation of ovule vascular tissues. In contrast, embryo development is delayed, and after approximately 3–4 weeks a single-celled proembryo, connected to a long filamentous suspensor, appears at the tip of the now endosperm-filled embryo sac. Embryogenesis follows the classical sequence from multicellular embryo proper to globular and then heart-shaped embryo, and 2 months after bloom the two cotyledons are clearly formed. At 4–5 months, the mature olive embryo contains a well-differentiated root apex at the tip of a short embryo axis, and appreciable provascular strands and storage substances in the axis and cotyledons. Between the cotyledons, however, the

shoot apex is flat, or sometimes slightly domed, with a subtending zone of intense metabolic activity but no other visible differentiation or plumule formation (Germanà et al. 2014).

As the fruit matures, physiological dormancy is imposed on the seed, with factors apparently located in the endosperm as well as the embryo itself (Germanà et al. 2014). Thus olive seed germination procedures require removing the mechanical barrier of the hardened pit, and cold stratification to remove physiological dormancy. Among tested genotypes, optimum germination was consistent with stratification at 14 °C for 30 days, although germination rate was highly related to genotype (Morales-Sillero et al. 2012).

At maturity, numerous olive fruits contain empty pits with no seed present. It appears that embryo and subsequently seed abortion are responsible for this phenomenon, evidenced by the consistent observation of growing fertilized ovules in young fruits, the occurrence of aborted embryos at two months, and by the enlargement of one of the ovary locules in the same manner as when a seed is present; that is, the locule expands to accommodate the growing fertilized ovule (Rapoport 2010). Early embryo abortion could possibly be related to post-zygotic incompatibility factors.

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