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Biology and ecology of *Juniperus drupacea* Labill.

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Abstract: This literature review focuses on the biology and ecology of *Juniperus drupacea*. Within the context of the series ‘Our Forest Trees’ by the Institute of Dendrology PAS at Kórnik, the following key topics are discussed: taxonomy with paleo-records, morphology, anatomy, geographical distribution, ecology (including habitat, communities, response to biotic factors and the environment, and phenology), disease, and conservation. *Juniperus drupacea*, also known as the Syrian juniper, is a dioecious evergreen gymnosperm found primarily in two distribution centers: one in the southern Peloponnese in Europe and the other in the mountains along the Mediterranean Sea in Southwest Asia. The populations from Europe and Asia differ genetically, biochemically, and morphologically. *Juniperus drupacea* is a medium-sized tree occurring in mountains, predominantly at elevations of 800–1400 m, on basic to moderately alkaline soils and even on calcareous rock. It is a component of fir, pine, cedar, and sometimes also juniper forest, rarely entering maquis. As with other junipers, it is a light-demanding, moderately frost- and drought-resistant, sometimes acting as an invader of abandoned fields and pastures. It is rarely grazed by goats. Its low palatability is a result of the high content of volatile oils in the needles and cones. The volatile oils have been extensively used in folk medicine and have been investigated for new medicinal uses. The species is rare, endangered and protected in Greece, parts of Turkey and Lebanon. Its ecological niche could potentially be reduced by global climate change.

Key words: taxonomy, morphology, geographical and altitudinal distribution, plant communities, climate limitation, germination, grazing, use

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Taxonomy

Palaeo-records

Juniper species evolved in the arid environments (Willis & McElwain, 2002; Stockey et al., 2005) and their macrofossils are only partially preserved and are scarce. This concerns also the subfossil material and pollen. Additionally, the latter are very similar among species and determined as a rule to the genus level (Carrión, 2002; Carrión et al., 2001; Barrón et al., 2010). Also, fossil woods are recognized as cupressoid (*Cupressinoxylon* Göppert) (e.g. Román-Jordán et al., 2017; Güngör et al., 2019) or *Juniperoxylon* (Houlbert) Kräusel, (e.g. Klusek, 2014; Akkemik, 2021). The species identified in the petrified wood exhibit distinct micro-structures, each possessing striking similarities to modern taxa (Akkemik, 2021; Imandei et al., 2022). Nevertheless, only macroremains of the leaves and cones give the data determined to the species level.

The oldest, early Oligocene fossil leaves determined as *Juniperus* sp. aff. *J. drupacea* Labill. foss. were reported from the area of Bulgaria (Palamarev, 1967; Palamarev et al., 2005), and justified molecular dating of the species divergence. The shoot of juniper determined as *Juniperus* sp. originating from early Miocene (before 20–18 Ma) deposits at Güvem (central Anatolia), could represent *J. drupacea* due to very broad needles (Denk et al., 2017: 248, Plate 6. 1, 2) and occurrence with *Cedrus* Mill. and *Pinus* L. in the same assemblage (Koç et al., 2022), however, this is only a suggestion and should be verified.

The subfossil material, referred to as *J. drupacea-pliocenica* Rér., were reported mainly from the sediments of Miocene (20.3 to 5.33 MA) and Pliocene (5.33 to 2.58 MA), from the areas of present-day Spain, France, Poland, Ukraine, Bulgaria and Georgia (Czeczottowa, 1951; Palamarev, 1989; Palamarev et al., 2005). The geographic distribution of palaeo-remnants suggests the occurrence of a *J. drupacea* ancestor in the central and southern Europe and in western Asia during the Miocene, in the area close to the Parathetys (Popov et al., 2006; Ivanov et al., 2011). During Pliocene its occurrence was restricted to the areas closer to the Mediterranean Sea, however, the palaeo data are scarce and this information should be treated as provisional. The current area of distribution of extant *J. drupacea* has a relict character, formed during Pliocene climate cooling and Pleistocene climate oscillations. These climatic changes led to the disappearance of numerous woody genera from western Eurasia and a reduction in the occurrence of others (Magri et al., 2017).

Systematics

The genus *Juniperus* L. is a monophyletic group of ancient origin from the early Cenozoic, when it diverged from *Cupressaceae* during turn Palaeocene/Eocene (Mao et al., 2019). The diversification rate from the divergence to the Pleistocene was unstable, with the highest intensity during Miocene, Pliocene and Pleistocene (Mao et al., 2010), which could be interpreted as a reaction to the global climate changes (Zachos et al., 2001). *Juniperus drupacea* Labill. belongs to the oldest among juniper species, diverged from the ancient junipers during the turn Eocene/Oligocene, before about 35 MA (Mao et al., 2010).

With almost 100 taxa (species, subspecies, and/or varieties) (Farjon, 2005, 2010; Adams, 2014), the genus *Juniperus* ranks as the second most abundant conifer genus in the northern hemisphere, following *Pinus* (Farjon, 2005, 2010; Adams & Schwarzbach, 2013; Adams, 2014a). The earliest diverged three lineages (Mao et al., 2010) are currently recognized as sections within the genus (Adams & Schwarzbach, 2013; Adams, 2014a).

1. Section *Juniperus* (sect. *Oxycedrus* Spach): leaves acicular, seeds mainly three, free, mature cones black or brown, ca 1 cm in diameter, ca 18 taxa in northern hemisphere of Europe, Asia, Africa, and North America.
2. Section *Caryocedrus* Endlicher: leaves acicular, seeds three, fused into a false drupe, mature cone ca 2 cm in diameter; only one species, *J. drupacea* in Mediterranean South-East Europe and West Asia.
3. Section *Sabina* (Miller) Spach: leaves acicular only on seedlings, on the adult individual leaves squamiform, seeds one to eight (or more) not fused, mature cone to ca 1 cm in diameter, black or brown; ca 80 taxa in Europe, Asia, North America, and Africa.

Historically, the deep differences between *J. drupacea* and other representatives of the genus *Juniperus* have become the basis to create for the Syrian juniper its own genus *Arceuthos* Ant. & Kotschy (Antoine & Kotschy, 1854). Shortly latter, the three sections mentioned above were recognized as separate genera by Antoine (1857). We adopted the sections proposed last decades by Adams and Schwarzbach (2013) and Adams (2014a), despite this inter-generic taxonomy of *Juniperus* is not always followed, with the inclusion of section *Caryocedrus* into section *Juniperus* (e.g. Coode & Cullen, 1965; Farjon, 2005, 2010).

Juniperus drupacea Labill. was known in Europe as “genevrier majeur” (*Juniperus major*) thanks to the description by Pierre Bellon (1553) from the Taurus Mountains. The formally proper description was published by Jacques Julien Houton de Labillardière (1791), who has given the correct diagnosis,

according to the rules of the ‘International Code of Nomenclature for Algae, Fungi and Plants’ (Turland et al., 2018).

The European populations of *J. drupacea* differ from the Asiatic ones at nuclear microsatellite markers (nSSR), in cone, seed, and needle characteristics (Sobierajska et al., 2016) and in the essential oil content and composition (Adams et al., 2017), however, these differences have not been used to taxonomic subdivision of the species until now. Additional differentiation of the species was found using the same set of genetic, biochemical, and morphological characteristics between populations from the Taurus and Lebanon mountains (Sobierajska et al., 2016; Adams et al., 2017). Hybrids of *J. drupacea* with other species of the genus are unknown.

Structure

Morphology

Tree morphology

Juniperus drupacea is a medium-sized, monocomp tree, usually about 15–18 m high (Talhouk et al., 2014), although individuals reaching 20–23 m were



Fig. 1. Large, 16–17 m high tree of *Juniperus drupacea* with conical crown; Greece, Parnon Mountains, above Panagia Malevi Monastery near Agios Petros, 37.34° N, 22.58° E, elevation 950 m (Photo by A. Boratyński 2018)

found in Greece (Boratyński & Browicz, 1982) and even 40 m in Turkey (Karaca, 1994). The trunk circumference at a height of 130 cm above the ground predominantly does not exceed 180–200 cm, however, the thickest ones reached 350 cm in Turkey (Karaca, 1994). The trunk bark is not very thick, resinous, dark grey to reddish brown, longitudinally fissured, and peeling with long, narrow stripes. The root system is widely spread, not too deep. Branches grow out from the trunks at nearly right angles, but are erected further from the trunk, forming conical crowns, on the open areas frequently from the ground level (Fig. 1). Only very old specimens sometimes have irregular crowns. Twigs of *J. drupacea* are spreading in three dimensions (not flattened), terete, slender, smooth and somewhat shiny, between nodes triangular on the cross-section. Buds on the twig tops are ca 3 mm long, covered with green leaf-like, triangular scales.

Leaf morphology

Leaves of *J. drupacea* are broadly acicular, 10–15 mm long and 2–4 mm wide, keeled at the bottom and boat-shaped, widest slightly above the base, sharply pointed at the top, and prickly (Sobierajska et al., 2016); arranged in alternative whorls of three (Fig. 2). The needle keel contains one vascular bundle and resin duct directly below it (Güvenç et al., 2011). The needles have two bright bands of stomata on the upper (adaxial) side, 0.5–0.6 mm wide each. The stomatal number on the 1 mm long section of the needle central part varied between 120 and 165 (Sobierajska et al., 2016). The dispersed stomata are also present at the bottom (abaxial) side of the needle (Farjon, 2005; Güvenç et al., 2011). The needle surface is covered with epicuticular waxes, which can form specific structures, this however, have not been

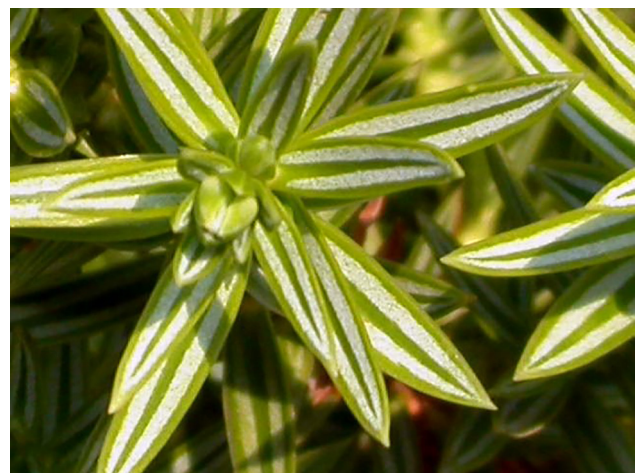


Fig. 2. Arrangement of needles on the shoot and apical bud *Juniperus drupacea*; Greece, Parnon Mountains, N of Kosmas, 37.13°N, 22.76°E, altitude 900 m (Photo by A. Boratyński 2005)



Fig. 3. Male (pollen) cones during and just after shedding pollen; Tahta, Kadirli, Osmaniye 37.58°N, 36.25°E, altitude about 700–800 m; photo in 2023, May 5th, by Tolga Ok

recognized in *J. drupacea*. The waxes on *J. communis* L. needle are composed of nonacosanol tubules (Ensik et al., 2006). In the case of *J. deltoides*, the waxes are n-alkanes, with higher participation of longer chain n-alkanes in the more arid regions (Rajčević et al., 2020).

Reproductive structures

Juniperus drupacea is dioecious (Farjon, 2005; Adams, 2014a). Male cones (microstrobili) during the pollination are composed in spherical or ovoid formations about 4–5 mm in diameter, initially yellowish, orange and brownish after pollen release (Fig. 3); set on short shoots in the needle axils, usually 2–3 per whorl. The male cones form branched structures, not found in other species of the genus *Juniperus* (Lemoine Sébastien, 1967a; Dörken, 2019).

Female cones (macrostrobili) are hidden between scaly needles at the apices of short shoots, about

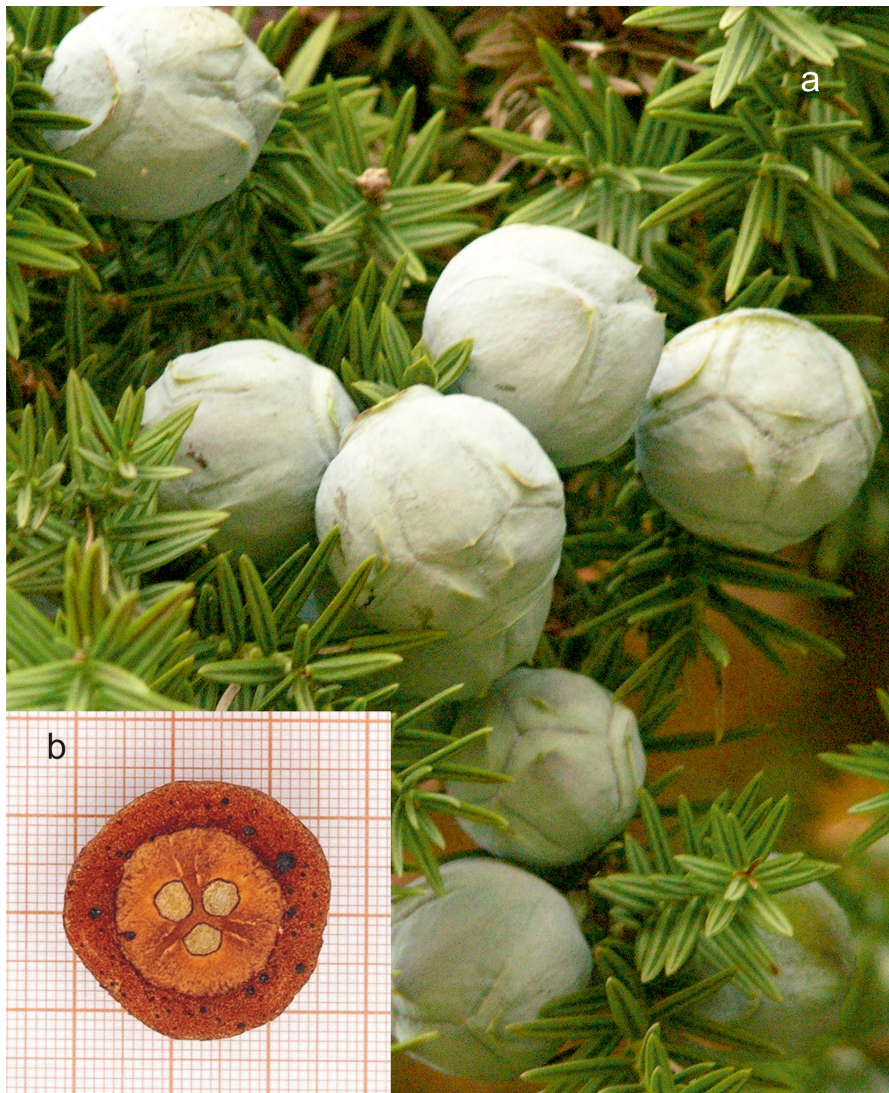


Fig. 4. Female cones of *Juniperus drupacea*: a – in the third vegetation season after pollination, Greece, Parnon Mountains, above Panagia Malevi Monastery, 37.32°N, 22.59°E, 1100 m (Photo A. Boratyński 2018); b – cross-section of mature cone with connate three seeds

2–3 mm in diameter during pollen perception, whitish to yellowish (Lemoine Sébastien, 1967b; Eliçin, 1974, 1977; Maerki & Frankis, 2015: Figs 10 and 35). Strobilus is composed of 3–4 alternate whorls of about 2 mm long scales; the scales of the uppermost whorl form one ovule each, extreme rarely could be find two ovules on one scale. Ripe seed cones are brown to dark brown, sometimes dark blue, pruinose, \pm globose, about (10-) 20–25 (-33) mm in diameter (Fig. 4a); are composed of two to four whorls of completely connate but well visible scales (Eliçin, 1974; Sobierajska et al., 2016; Yavuz & Yılmaz, 2017); cones composed of two scales in whorl can be found sporadically (Sobierajska, 2011; Sobierajska et al., 2016). Seeds connate, forming \pm globose, drupe-like structure (Fig. 4b), 12–22 mm long and 10–18 mm in diameter (Sobierajska et al., 2016; Yavuz & Yılmaz, 2017). The weight of a single cone is 4.66 g on average, the three seeds in woody seed-coat (a ‘drupe’) 2.13–2.49 g, and a single seed 0.045 g (Yavuz & Yılmaz, 2017). The seed coat usually contains three seeds, but quite common are cones with one or two well-developed seeds, or all seeds empty (Maerki & Frankis, 2015; Yavuz & Yılmaz, 2017), which could result from ovules abortion due to lack of fertilisation, as in *J. oxycedrus* L. (Arista et al., 2001). Seeds retrieved from the seed coat are 10.07 mm long and 3.30 mm wide (Yavuz & Yılmaz, 2017). The fleshy part of the cone developed from cone scales is about 50% of the total cone weight.

Seedlings

One-year-old seedlings of *J. drupacea* have two cotyledons (Farjon 2005) and juvenile, acicular, prickly leaves, which are half as narrow as adult ones (Fig.

5a). Seedlings in the Peloponnese are generally rare (Marki & Frankis, 2015), growing under the canopy of mother trees, in open areas and/or in maquis. In the region around the Parnon, seedlings and saplings in some places, as on the hills easterly of Achladocambos, tend to form a forest. Only single seedlings had been observed in the Parnon area in Greece (Marki & Frankis, 2015) and in the Lebanon mountains (Douaihy et al. 2017). Similarly, rare seedlings were observed in the Taurus mountains, in Kadirli-Osmaniye region in Turkey (Fig. 5b). The natural regeneration of the species has not been studied and data concerning seedling densities in particular regions and site conditions are lacking.

Anatomy

Developmental remarks

Anatomical studies on junipers have been limited and have not encompassed the complete plant structure and development. There is insufficient knowledge regarding the bud, primary and secondary growth, development of micro- and macro-strobili, as well as cone and seed development. This lack of understanding also applies to *J. drupacea* (Esau, 1977; Heynowicz, 2002; Evert & Eichhorn, 2006). To address this gap, we provide additional data on other European and Mediterranean junipers.

The apical meristem of *J. communis* is covered with primordial, single-layer tunic. Below them are primordial cells and ‘mantle’ stem cells (leaf parenchyma, primary stem bark, and conductive tissues of leaves and stem and the columnar parenchyma of the stem core, Cebrat, 2007: 360). The occurrence of the meristem in the leaf axil of *J. communis* appears due

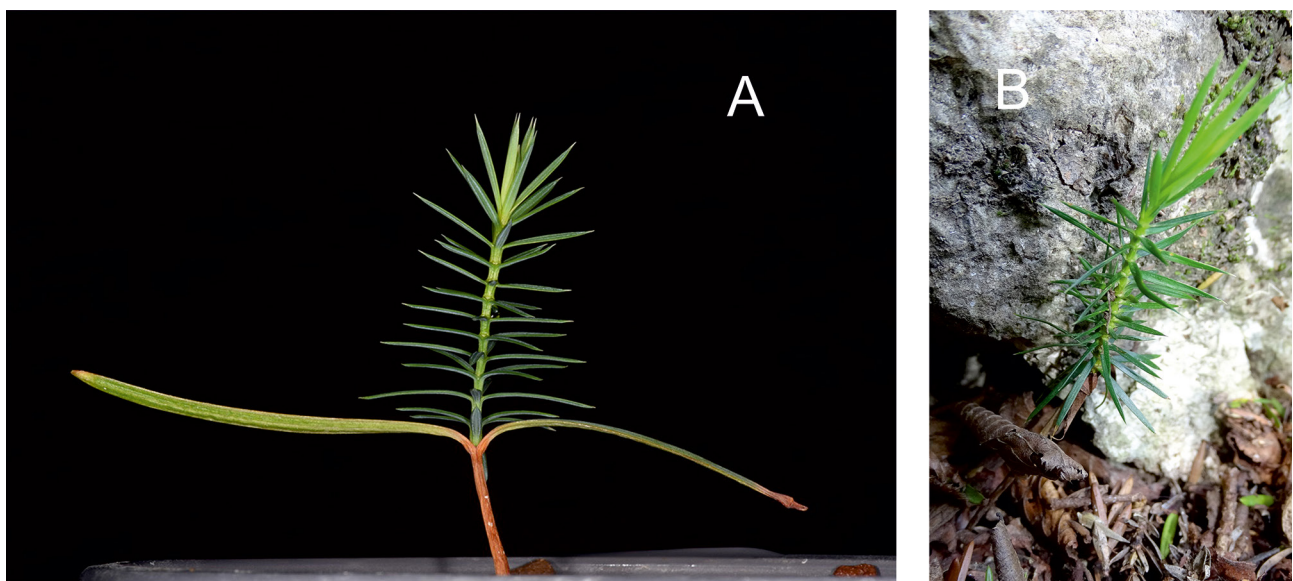


Fig. 5. Seedlings of *Juniperus drupacea*: a – one-year-old seedling germinated in controlled conditions (Photo by Ori Fragman-Sapir, <https://flora.org.il/en/plants/jundru/>), b – seedling in the third vegetation season after germination in the Taurus Mts, vicinity of Tahta village near Osmaniye (Photo by Tolga Ok)

to divisions of the first sub-epidermal layer of the cells, under the leaf axil epidermis, which forms a single-layer meristem tunic. The growth and division of sub-epidermal cells are most active in the distal part of the meristem (Cebrat, 2007: 361). The cell layers divide almost exclusively or predominantly by anticlinal walls (Evert & Eichhorn, 2006).

Leaf anatomy

The leaf anatomy of *J. drupacea* was described by Güvenç et al. (2011). They find the transverse section of leaves semi-circular. The epidermis is covered with a thick cuticle, which penetrates toward the border between the cells. The epidermal cells on the upper needle surface are usually square-shaped, with thick walls and a small lumen. The epidermis is uni-layered (Güvenç et al., 2011). The cuticle of *J. drupacea* is covered by cuticular waxes (authors' observations). The *J. drupacea* needles are amphistomatic. The stomata, deeply sunken within the epidermis, are composed of small cells with 4–6 angled, irregular form, with the subsidiary cells partly lignified (Güvenç et al., 2011). The hypodermis is single-layered except for the marginal parts of the needle, where there are two or even three layers of hypodermal cells. The cells of hypodermis are fibre-like with very small lumens. Hypodermis cells do not occur under the rows of stomata on the upper needle surface (Güvenç et al., 2011: Fig. 1).

The two types of mesophyll can be distinguished in the cross-section of *J. drupacea* needle. The palisade mesophyll consists of one or two layers of thin-walled and \pm compactly arranged cylindrical parenchymatic cells. The layer of the palisade contacting with the hypodermis is composed of longer cells than the inner layer. The palisade parenchyma does not occur under the rows of stomata on the upper side of the needle. The cells of the palisade parenchyma contain starch granules. The spongy parenchyma is located between the layer of palisade parenchyma and the vascular bundle, only under the rows of stomata on the upper side of the needle occur just close to the epidermis. The spongy parenchyma is composed of orbicular or ellipsoidal cells with large intercellular spaces (Güvenç et al., 2011).

The vascular bundle is the collateral type, with the xylem at the upper and the phloem at a lower side. It is located in the leaf centre, elliptical on the needle cross-section, surrounded by thick-wall cells forming coat. The transfusion cells are thin-wall cells and are close to the vascular tissue in the direction of the marginal sides of the needle. The single, large secretory canal is just below the vascular bundle. Secretory thin-walled cells form one layer and are surrounded by a fibrous sheath composed of cells with lignified walls, also forming one layer (Güvenç et al., 2011). The close to the vascular bundle position of

the secretory canal is specific for *J. drupacea* among other juniper species with acicular leaves.

Wood structure

Most of the infrastructural studies on the juniper were devoted to their wood properties and, in Europe concerned predominantly *J. communis* (e.g. Surmiński, 2004; Kozakiewicz & Życzkowski, 2015) and *J. excelsa* M.Bieb. (Adamopoulos & Koch, 2011). Independently on the species, juniper wood does not contain the resin canals (Esau, 1977; Heynowicz, 2002). Frequently the juniper wood in the cross-section has light sapwood and brown to reddish-brown heartwood zones (e.g. Eliçin, 1977; Adamopoulos & Koch, 2011). The annual rings are well visible but narrow and frequently undulating. The tracheids of the early wood are \pm quadrangular on the cross-section, while those of the late wood are rectangular, with significantly shorter side along the trunk radius (Kozakiewicz & Życzkowski, 2015). The secondary phloem of junipers can contain the fibres (Heynowicz, 2002; Schweingruber et al., 2006). The wood of *J. communis* contains the fibre cells (Evert & Eichhorn, 2006).

In *J. drupacea*, the sapwood is light yellow or grey-yellow, with well-visible yearly increments, mainly due to the small cell light of the late xylem. The heartwood is only slightly reddish (Eliçin, 1974). The cross-section of wood contains 2695 tracheids per 1 mm² on average. The tracheids of early wood are 15.9–33.9 μ m, and of late wood 8.5–9.1 μ m long (Eliçin, 1974). The wood rays are uniserial and are composed of 1–6 (-16) homogeneous parenchymatic cells, except for marginal, which are triangular on cross-section (Eliçin, 1974). The ray height oscillates between 31 and 317 μ m, and an average length of cells in the ray oscillates between 10.5 and 26.0 μ m. The pits in the crossing fields between wood tracheids and ray parenchymatic cells are of the cupressoid type (Eliçin, 1974).

Biochemical data

To our knowledge, there is limited information available regarding the elemental composition of leaves, wood, and cones in *J. drupacea*. Junipers, including *J. drupacea*, have been subjects of biochemical research primarily due to their essential oils, which are utilized in medicine and cosmetics. In some cases, these investigations also contribute to taxonomic studies (e.g. Hörster, 1974; Adams, 1997; Sezik et al., 2009; Fandi et al., 20114; Adams et al., 2017; Baydoun et al., 2017; Ari et al., 2018; Çizgen et al., 2018). The content and biochemical composition of essential oils depend on the part of the tree and are different in the leaves, cones, and wood. These biochemical characteristic can also differ between

populations originated from various regions (Adams, 1997; Sezik et al., 2009; Adams et al., 2017). The cones of several juniper species are used as spice of dishes and even as main components of specific meals or drinks, and their chemical compositions are studied to determine content of sugars, fats and other nutritional measures (Miceli et al., 2011; El-Juhany, 2021 and literature cited herein).

The essential oils obtained from fresh leaves of *J. drupacea* collected from Gözne Plateau (Mersin, Turkey) contain 14.29% α -pinene, 0.54% α -fensen, 0.72% β -pinene, 3.53% myrcene, 13.16% δ -3-carene, 55.58% limonene, 0.32% γ -terpinene, 0.75% terpinolene, 0.25% α -kubeben, 0.13% α -copaene, 0.62% β -caryophyllene, 0.34% α -humulene, 0.42% δ -kadinene, 1.91% unknown sesquiterpene (MA 204), 0.17% γ -kadinene, 4.27% 1.8-cineole, 0.17% linalool and 0.2% terpinen-4-ol12 (Kocakulak, 2007; Sezik et al., 2009).

The essential oils distilled from cones of *J. drupacea* allow identifying of 73 volatile oils, among them 23.7–44.2% α -pinenes, 17.3–22.3% of thymol, methyl, ether, and 10.1–19.7% of camphor (El-Ghorab et al., 2008). The essential oils distilled from leaves, unripe and ripe cones of *J. drupacea* consisted of monoterpenes, mostly cyclic and only occasionally aliphatic and to a lesser percent of diterpenes (Evergetis et al., 2016).

The mineral composition of dry cones from Anti-Taurus in Turkey indicated high levels of such minerals as potassium (K, 15.9 g/kg), calcium (Ca, 842.6 mg/kg), sodium (Na, 67.6 mg/kg), magnesium (Mg, 491.4 mg/kg), iron (Fe, 49.8 mg/kg), copper (Cu, 4.95 mg/kg), zinc (Zn, 17.3 mg/kg) and manganese (Mn, 13.9 mg/kg) (Odabaş-Serin & Bakir, 2019). At the same time, dry cones from the Anti-Taurus contained 2.9% of protein, 4.67% of lipids, 15.15% of holocellulose, 17.96% of lignins, and attained pH=5.59 (Odabaş-Serin & Bakir, 2019).

The dry mass of *J. drupacea* sapwood contains even 8.2, while the heartwood only 0.62 mg.g⁻¹ of sugar and sugar alcohols. In contrast, the content of phenolic diterpenoids in the sapwood is 0.022 while in the heartwood is 7.2 mg.g⁻¹ (Willför et al. 2007: Table 2). Among diterpenoids, the ferruginol content was of 2.6–3% in the knots of *J. drupacea*, the highest among other compared species (Willför et al., 2007).

Genetics

Junipers stands out among conifers and represents a distinct genus within gymnosperms, alongside *Cupressus L.* and *Ephedra L.* where polyploidy is common (Farhat et al., 2019, 2020).

Junipers are characterized by possessing large genomes (mean genome size for diploid

taxa = 25 pg/2C), with extensive variation between species (ranging 3.2-fold from 21.81 to 71.32 pg/2C). This large variation perfectly corresponds to known ploidy levels (2–6 \times). As a stand alone species in the section *Caryocedrus*, *J. drupacea* have 23.48 pg/2C and 2n=2 \times =22 chromosomes (Bou Dagher et al., 2013; Farhat et al., 2019, 2020).

To our knowledge, *J. drupacea* has not been tested in common-garden plantations, so-called provenance experiments, where growth traits, phenology, resistance to various factors of the species different populations are compared. The molecular and biochemical characteristics of the species were used in taxonomic comparisons of several species of junipers (Mao et al., 2010, 2019; Adams & Schwarzbach, 2013; Güvendiren, 2015; Uckele et al., 2021). The study on the differentiation of *J. drupacea* between natural populations from Greece and Turkey and specimens planted in Crimea indicated differences between them in content and composition of essential oils (Adams, 1997). These studies extended latter, indicated differentiation among populations from different regions (Sezik et al., 2009; Fandi et al., 2014).

The phylogenetic relation of seven juniper species native to Turkey based on cpDNA sequences, confirmed the distinction of the three sections and indicated some differentiation of particular species populations (Güvendiren, 2015). The populations covering nearly entire geographical range of *J. drupacea* were compared by Sobierajska et al. (2016), using nuclear microsatellite markers (nSSR). They detected higher level of genetic diversity within Asian than the European populations of the species, and moderate but significant (FST = 0.101, P < 0.001) differentiation among 12 compared populations. The main differences were between European and Asiatic populations, and further difference were detected between populations from the Taurus mountains and Lebanon mountains (Sobierajska, 2011; Sobierajska et al. 2016). Similar pattern of differentiation was also detected in the multi-character differentiation of phenotypic traits of cones and needles (Sobierajska, 2011; Sobierajska et al. 2016). The high level of differences between European and Asiatic populations and further differences between populations from the Taurus and Lebanese mountains was then confirmed using 16 major terpenoids, found in the cones of *J. drupacea* (Adams et al., 2017).

The genetic relations among subpopulations of *J. drupacea* around the Parnon mountains were tested lately using amplified fragment length polymorphism (AFLP) and epigenetic using methylation-sensitive amplification polymorphism (MSAP). The level of genetic diversity was higher than epigenetic one, but no differentiation of subpopulation was detected (Avramidou et al. 2023).

Geographical and altitudinal distribution

Palaeobotanical data indicate that *J. drupacea* had broad distribution during Neogene. Subfossil *J. drupacea-pliocenica* Rér. was reported from the area of modern Spain, France, Poland, Ukraine, and Georgia (Palamarev, 1989). The species broadly distributed in Tertiary survived Pleistocene glaciations in the refugia in southwest Asia and southeast Europe. The current geographic range of *J. drupacea* (Fig. 6) covers restricted area in the mountains Parnon and Taygetos in southern Peloponnese in Europe and the Taurus, Amanos, Syrian and Lebanon mountains in southwest Asia (Browicz & Zieliński, 1982; Boratyński et al., 1992), the regions recognized as refugial areas of the Tertiary floras (Médail & Diadema, 2009).

Most of the current *J. drupacea* localities are located in southern Turkey, in the Taurus (Antalya, Konya, Mersin provinces) and Amanos Mountains (Adana, Osmaniye, Hatay provinces) (Eliçin, 1974; Browicz & Zieliński, 1982; Kandemir & Gezmiş, 2018; Walas et al., 2019). In Syria, it occurs in the mountains along the Mediterranean coast, and in Lebanon in the Lebanon mountains, up to Mount Hermon in the south. In Europe, it has been known since the mid-19th century from the Parnon mountains (Boratyński & Browicz, 1982). During the last decades, its sites were also found in the Taygetos Mountains

(Tan et al., 1999; Gletsos, 2017) and in many places scattered around the Parnon massif (Maerki & Frankis, 2015; Walas et al., 2019). The northernmost positions were described from Europe, from about 37°30'N between Achladokambos and Myloi (Boratyński & Browicz, 1982; Boratyński et al., 1992; Maerki & Frankis, 2015), the southernmost from Asia, from Mount Hermon at about 33°20'N, the westernmost ones from the Taygetos at 22°17'E while the easternmost from the East Taurus at about 37°02'E (Walas et al., 2019). The newly found localities of *J. drupacea* in the Taygetos and dispersed on the hills around the Parnon could be interpreted either as remnants of once widespread frequent occurrence of the species, or as its modern expansion. The first hypothesis is confirmed by some genetic and morphological differences between populations from the Parnon and Taygetos (Sobierajska et al., 2016: Figs 1 and 4).

In Asia, *J. drupacea* has the most stands in Turkey, where its composition is noticeable in forests in areas located in the Taurus (Toros Dağları) and in Amanos (Nur Dağları). Larger concentrations of *J. drupacea* trees are found locally in the calcareous mountains near Akseki, Anamur, Mersin, Adana, Osmaniye, and Kahramanmaraş (Eliçin, 1974; Browicz & Zieliński, 1982; Kocakulak, 2007; Yavuz & Yılmaz, 2017). In Lebanon, Syria, and Israel, *J. drupacea* is an endangered species with limited occurrence (Talhouk et al., 2001; Douaihy et al., 2017; Bou Dagher Kharrat

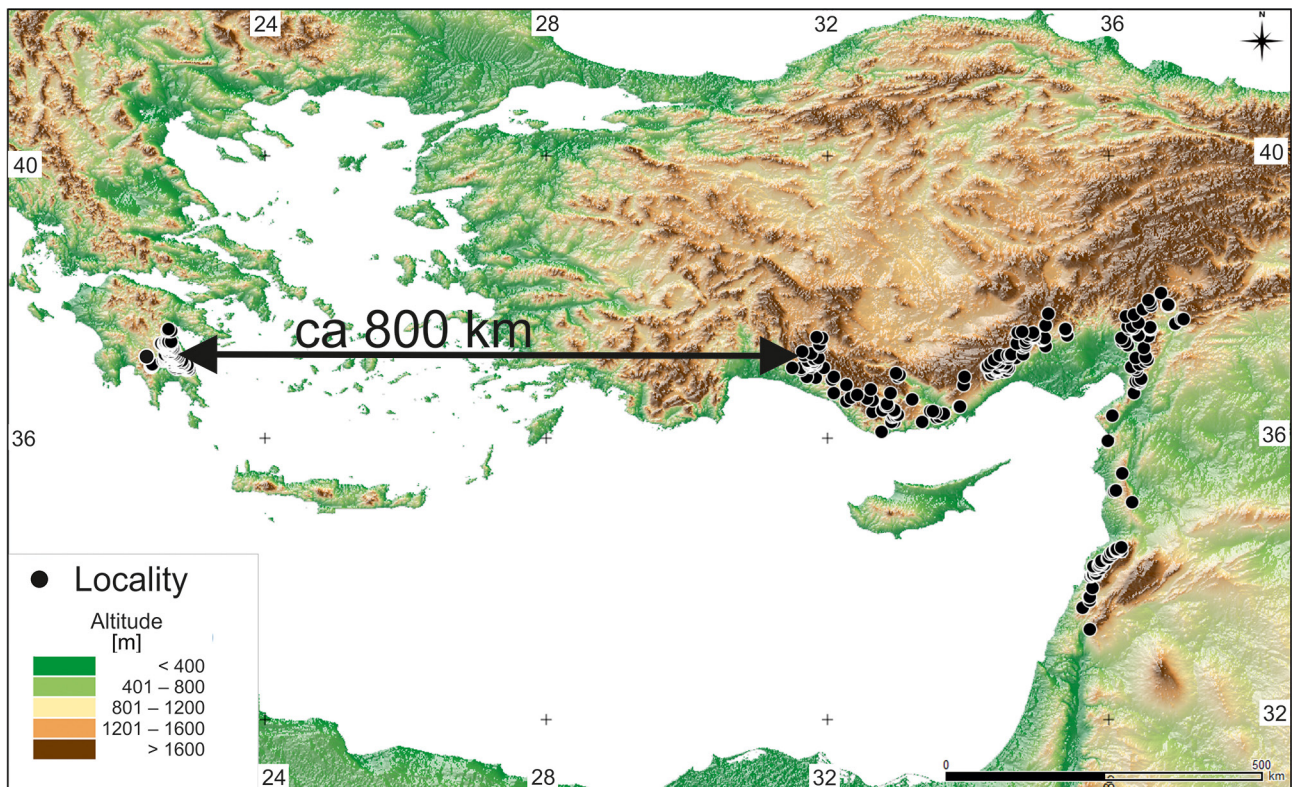


Fig. 6. Geographical distribution of *Juniperus drupacea* localities (after Walas et al., 2019, changed and supplemented)

et al., 2018). Interestingly, the Lebanese populations differ genetically and morphologically from the Turkish populations, as found in *Abies cilicica* (Antoine & Kotschy) Carrière populations (Boratyńska et al., 2015; Sękiewicz et al., 2015), *Cedrus libani* A. Rich. (Bou Dagher et al., 2007) and other species (Bou Dagher Kharrat et al., 2018).

The disjunction between European and Asiatic parts of the geographic range of *J. drupacea*, at a distance of about 800 km (Fig. 6), could result from geological and climate change processes, which took place during Pliocene and Pleistocene. At first, it could result from the reduction of the European geographic range of *J. drupacea* ancestor to the Peloponnese and Asiatic ancestor to the Anatolia during Miocene and Pliocene climate cooling, connected with reduction of Parathetys (Hewitt 2004; Popov et al., 2006; Jalut et al. 2009; Ivanov et al., 2011). The other possible explanation is the ancestor of the species might have evolved in Anatolia in the turn of Eocene/Oligocene (Mao et al., 2010) and afterward moved

with the continental plateau of the Balkans, when it splits from Anatolia and joined Europe (Goes et al. 2004; Popov et al., 2006; Ivanov et al., 2011).

The Pliocene cooling and Pleistocene oscillations of the climate finally reduced the geographic range of *J. drupacea* to the mountainous regions close to the Mediterranean Sea (Sobierajska et al., 2016; Walas et al., 2019). The extensive reduction of fir forests in the Peloponnese, and fir and cedar forests in the mountains of Anatolia, Syria, and Lebanon due to exploitation by humans during recent millennia could be a reason for some extension of the occurrence of *J. drupacea* (Talhok, 2001; Douaihy et al., 2011, 2012; Awad et al., 2014).

Juniperus drupacea is a Mediterranean mountain (oro-Mediterranean) species. In the mountains of Europe, in Taygetos and Parnon mountains in Greece, is most often found at the altitudes between 900 and 1200 m above sea level (Fig. 7). The lowest localities of *J. drupacea* in Greece were found on the hills between Myloi and Achladokambos, at an altitude of about 360–400 m, and below the Eloni Monastery (Moni Elonis) even at about 300 m above sea level. The highest place of occurrence was recorded on the slopes of Parnon below the shelter, at 1790 m (Maerki & Frankis, 2015). In Asia, *J. drupacea* occurs higher by about 100–200 m than in Europe, most often at altitudes of 1000–1600 m above sea level, and in the mountains of Lebanon slightly higher than in Taurus. The highest positions were given from 2000 m and even 2050 m above sea level from the Anti-Taurus massif (Aladağlar) (Schiechl et al., 1965).

Outline of ecology

Topographic conditions

In the Parnon mountains, *J. drupacea* grows from nearly flat terrains to steep slopes (Boratyński & Browicz, 1982; Bergmeier, 2002) and in the crevices of the limestone precipices. At the lowest elevations, it more frequently occurs on the northern expositions, while at the centre of their occurrence at elevations above 900 m it grows independently on slope exposition. However, the pure forests of *J. drupacea* or with only a few other trees are observed mostly on north-facing slopes. In the Taygetos, *J. drupacea* were found in similar conditions (Tan et al., 1999; Gletsos, 2017). In the Taurus and Amanos mountains, *J. drupacea* occurs on the slopes of the mountains and frequently in the karstic areas (Yaltrık, 1993; Koç, 2016; Özalp, 2016; Akkurt Gümüş, 2020; Vermez et al., 2018; Yücedağ et al., 2021a). Under the latter conditions, it grows on the deep soils in depression areas and on the slopes among rocks. The depressions are usually pasture lands (Akkurt Gümüş, 2020), with

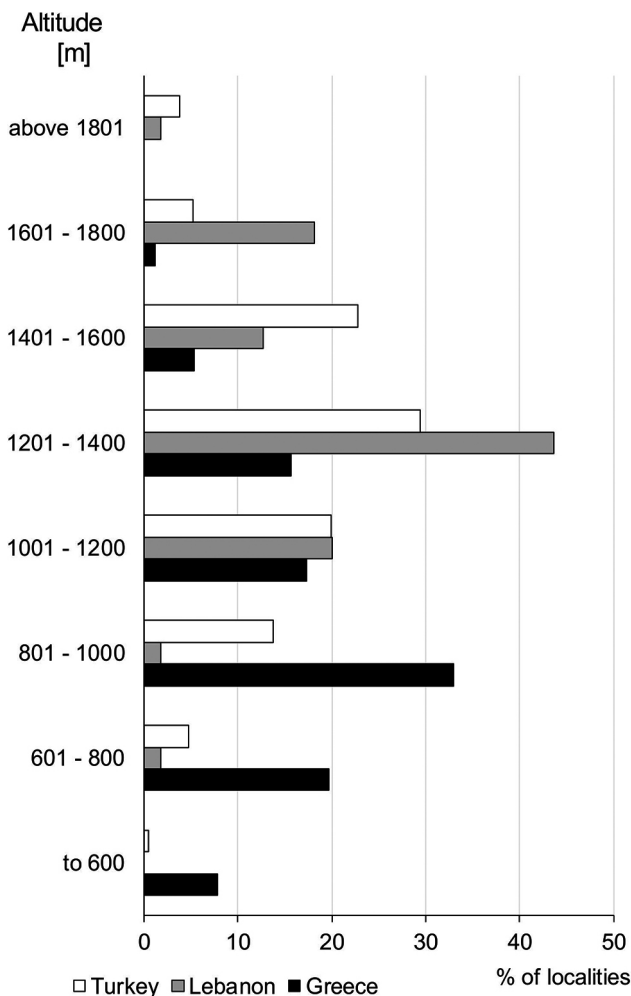


Fig. 7. Vertical distribution of *Juniperus drupacea* localities in the mountains of Turkey (Turkey), Lebanon together with Syria (Lebanon) and Greece (Greece) (after Walas et al., 2019, supplemented)

only single trees. In Lebanon occurrence of *J. drupacea* is confined mostly to the higher elevations and rather north- and/or west-facing, more humid slopes (Talhok et al., 2001, 2014). The southern exposition, as offering more extreme and dry conditions, are avoided.

Substratum

The soils on the localities of *J. drupacea* are of terra rossa type, in higher locations of terra rossa with signs of browning or brown soils. These substrata are moderately alkaline, with a pH of about 8, a relatively high content of calcium, about 10–11%, a significant content of organic matter and are usually heavily skeletal (Mayer & Aksoy, 1986; Bergmeier, 2002; Koç, 2016; Özalp, 2016; Vermez et al., 2018; Akkurt Gümüş, 2020).

In the Taurus mountains in the Mediterranean region of Turkey, there are frequently developed karstic ecosystems (Dindaroğlu, 2021; Utlu & Öztürk, 2023). These kind of specific site conditions are among others, settled by *J. drupacea*. In the Sarımsak Mountain near Andırın (Turkey), *J. drupacea* grows in the karstic area among limestone outcrops, on the soils 75–100 cm deep in karst depressions and <50 cm in slope areas. The rocks cover about 70–75% of the karstic area on average, are composed of calcite minerals of fossiliferous or of brecciated texture (Vermez et al., 2018). The soil is moderately alkaline, with a pH up to 8.1, and with very high content of the organic matter (4.33%), high capacity of the cation exchange (32.6 cmol kg⁻¹) and high calcium content, 10.77% on average (Vermez et al., 2018). Similar karstic sites settled by *J. drupacea* can be observed from the vicinities of Akseki on the West to the Kahramanmaraş and Osmaniye in the East of Anatolia.

The soils developed from the calcareous bed-rock dominate also in the localities of *J. drupacea* on the Peloponnese (Greece) (Boratyński & Browicz, 1982; Tan et al., 1999; Bergmeier, 2002; Gletsos, 2017) and in the mountains of Lebanon (Talhok et al., 2001; Douaihy et al., 2017). In the Peloponnese there are soils developed from marbles, Tripolitza limestones and dolomites (Bergmeier, 2002). In Lebanon, *J. drupacea* is considered as growing on the clay and sands, but neutral or alkaline (Talhok et al., 2014).

Climate limitations

Light

Juniperus drupacea is light-demanding species (Zohary, 1973; Yaltırık, 1993; Talhok et al., 2014; Douaihy et al., 2017). This statement results from the field observations, not supported by specific data resulting from measurements. *Juniperus drupacea* trees occur in not compact, light-full forests

or more frequently at the forest edges. In the forest, it grows under the canopy of *Pinus nigra* or between *Abies cephalonica* Loudon or *A. cilicica* and *Cedrus libani* A.Rich. trees, in slightly restricted or at least not full sun-light access. The specimens in dense forests are rare, present a poor appearance and do not form cones (authors' field observations). The reaction of *J. drupacea* to particular photon flux densities has not been verified.

Temperature

Occurrence of *J. drupacea* is connected with the supramediterranean and oromediterranean climate termotype, subhumid to humid ombrotype, where it grows in the areas under the maritime (oceanic) influence (Rivas-Martínez et al., 2004; 2011). The Asiatic part of *J. drupacea* geographic range is connected with the subhumid Mediterranean climate (Atalay et al., 2014: Fig. 3; Fandi et al., 2014; Talhok et al., 2014; Douaihy et al., 2017).

The geographic range of *J. drupacea* lies in the Mediterranean climate, with high summer temperatures and rather mild winter. The thermal-connected bioclimatic variables rather did not influence the occurrence of *J. drupacea* within its range. Among them, only temperature seasonality seemed to influence the species distribution in the Peloponnese and, to a smaller degree, also in the Taurus mountains (Walas et al., 2019: Table 1). In the Parnon mountains in the Peloponnese, the average yearly temperature is about 15–18 °C at the lower localities (Bergmeier, 2002), while the minimal temperatures in the highest localities of the species can be at about –10––5 °C (Zeferos et al., 2011; Walas et al., 2019). The species is considered as frost- and drought-tolerant but rather heat-resistant in Lebanon (Talhok et al., 2014).

In the part of the geographic range of *J. drupacea* covering the Taurus and Amanos mountains, the average yearly temperatures are at a similar level, as in the mountains of Peloponnese, reaching about 12–18 °C (Atalay et al., 2014). The summer average temperatures oscillate around 20–21 °C, with absolute maxima of about 28–30 °C (Walter & Lieth, 1964; Quézel & Médail, 2003; Orcan et al., 2004; Finné et al., 2011; Linello, 2012; Lionello et al., 2012; Atalay et al. 2014: 795; Koç, 2016; Akkurt Gümüş, 2020). During winter, however, temperatures could drop down to –5 °C, occasionally even –10 °C (Orcan et al., 2004: 310; Bakker et al., 2013: 63; Akkurt Gümüş, 2020). The upper limit of *J. drupacea* occurrence may be determined there by low temperatures combined with the relatively low precipitation above the cloud level. Inversely, the high summer temperatures together with drought could determine the low limit of *J. drupacea* occurrence (Atalay et al., 2014; Walas et al., 2019). The yearly average temperature in the Lebanon mountains is 9.0–11.5 °C, with a mean

daily maximum of 22.8–23.5 °C in August and a minimum of –3.4––0.6 °C in January (Ramadan-Jaradi, 2004a, b).

Water relations

Juniper species evolved in arid environments (Willis & McElwain, 2002; Stockey et al., 2005), are tolerant to water deficit (Farjon, 2005; Talhouk et al., 2014), and even drought. The needle-leaved *J. communis* is much more drought tolerant than *Pinus sylvestris* L. and *Quercus pubescens* Willd. (Thomas et al., 2007; Zweifel et al., 2009). The juniper species with scaly leaves are also tolerant to drought (e.g. Álvarez-Rogel et al., 2007; Allen et al., 2010; Lloret & Granzow-de la Cerda, 2013; Lloret & García, 2016). The leaf midday water potential of *J. drupacea* (Ymd, water potential under maximum daily water demand) did not correlate with genetic diversity, but negatively correlate with epigenetic diversity (Avramidou et al., 2023). However, *J. drupacea* physiological demands and reaction to the water stress have not been studied in details and we can only conclude this based on the field observations.

Juniperus drupacea occurs in oceanic pluviaseasonal bioclimate and humid to subhumid ombrotype (Rivas-Martínez et al., 2004; 2011). It is relatively more moisture demanding than other juniper species and grows predominantly in the places with yearly precipitation attaining at least 600 mm (Douaihy et al., 2017). In the forest communities with frequent or even dominant participation of *J. drupacea* in the Parnon mountains on Peloponnese (Grece), this species is less water demanding than *Abies cephalonica* and *Pinus nigra* J.F.Arnold (*Juniperus* < *Abies* < *Pinus*) (Bergmeier, 2002), while in Lebanon it is less drought-tolerant than other junipers (Douaihy, et al. 2017).

Regarding the plant water balance, except for direct precipitation, the great influence has also absorbance from dew (Tullus et al., 2014). However, the dew absorbance by junipers' leaves is restricted, as a result of its' xeromorphic structure, which is generally a small number of stomata and a thick layer of epicuticular waxes (Xu et al., 2022). This aspect of water relation in *J. drupacea* should be confirmed in the special study.

The average precipitation in the Parnon mountains in Peloponnese attains about 800 mm year⁻¹ at an altitude of 900–1000 m and 1200 mm year⁻¹ at an altitude above 1400–1500 m (Bergmeier, 2002; Zeferos et al., 2011), and is even higher in the Taygetos Mountains, which are higher than Parnon, and more exposed to western winds carrying the humid air (Bergmeier, 2002). The precipitation during the coldest months, December – February, attains even 400–500–(600) mm year⁻¹ (Walas et al., 2019, Fig. 5). The precipitation during that time in the higher position in the mountains is normally associated

with snow. The snow cover in terrains elevated above 800–1000 m in the mountains of Peloponnese could be deep and may last for few weeks (Bergmeier, 2002; Lionello et al., 2012). The high positive influence on the potential geographic niche of *J. drupacea* in the Peloponnese has also precipitation during driest months, connected with the storms (Walas et al., 2019), however, such events in the Parnon mountains are rare, but appear somewhat more frequently in the Taygetos (Zeferos et al., 2011).

In the Taurus and Amanos mountains within the geographic range of *J. drupacea*, the average precipitation attains ca 800 mm year⁻¹ (Türkeş, 2003; Atalay et al., 2014), but depending on the altitude and in some degree exposition of the slope, may attain 1200 mm year⁻¹ (Atalay et al., 2014). There is observed high precipitation seasonality typical for the Mediterranean climate, with the concentration of precipitation during winter and low precipitation during summer months. During cold period, the winter months of December, January, and February, the average precipitation is about 500–600 mm (Atalay et al., 2014). This bioclimatic factor was found as influencing to the potential current ecological niche of *J. drupacea* in the Taurus at the highest degree (Walas et al., 2019: Table 1). In the mountains, the winter precipitation is in form of snow, which at the altitudes 1000–1200 m above sea level could be up to about 30 cm deep and lasting for few weeks (Türkeş, 2003; Lionello, 2012; Atalay et al., 2014).

The precipitation of the warmest and driest months influenced to the current distribution of the species in the Taurides at a lower degree than in the cold period. This could result from the mist concentration at an altitude of 1000–1200 m above sea level during summer, which reduces the water deficit (Atalay et al., 2014). Nevertheless, the precipitation during the driest months has also a positive influence on the geographic range of *J. drupacea* in Turkey. There was high inter-annual variability in precipitation during the summer months (Thompson, 2005, 2020; Lionello, 2012; Atalay et al., 2014; Touchan et al., 2014), and while was on average 100–150 mm annually, there was more than 200 mm in some years (Atalay et al., 2014). *Juniperus drupacea* does not occur in the regions with a more continental type of climate in Turkey, where precipitation seasonality and Emberger's pluviometric quotients have low values (Touchan et al., 2014; Walas et al., 2019: compare Figs 1 and 5).

For the occurrence of *J. drupacea* in the Lebanon mountain, the most important was precipitation during winter (Walas et al., 2019: Table 1). The average precipitation in the mountains where *J. drupacea* grows is about 1000–1200 mm year⁻¹ or even more, with concentration during winter months. There are about 50–95 days with snowfall, and snow cover may

attain even more than 1–2 meters in depth (Ramadan-Jaradi, 2004a, b). The water access on the west-erly exposed slopes is magnified by frequent mist accumulation during all seasons of the year at elevations above 1000 m, the region of *J. drupacea* occurrence (Ramadan-Jaradi, 2004a, b).

Juniperus drupacea occurs in areas prone to drought. The Parnon is the mountain range most exposed to the drought and aridity in the entire Peloponnese (Nastos et al., 2013; Paparrizos et al., 2016). The Taurus and Amanos, similarly to the Lebanon parts of the species geographic range, are less arid (Türkeş, 2003; Ünal et al., 2003). The high aridity in the Parnon influence on *J. drupacea* causes dye-back of single specimens (Maerki & Frankis, 2015; Walas et al., 2019). The low temperatures at the most elevated localities of *J. drupacea*, combined with the lower precipitation above the cloud level in the Taurus, Anti-Taurus, Amanos and Lebanon mountains are recognized as a restricting factor for the species occurrence (Walas et al., 2019).

Phenology

The shoots of *J. drupacea* start to grow in spring, depending on the geographic position, it takes place in May or later in the more elevated localities in the mountains of Peloponnese, earlier in the lowest localities in the Asiatic part of the species geographic range. The longitudinal increment of the branches terminates during June. The leaves are growing together with sprouts and are fully developed in June, at the most elevated localities in the mountains at the end of June (based on the herbaria review and authors field observations). *Juniperus drupacea* is an evergreen tree with leaves persisting on the trees for five years, sometimes even eight. The summer high temperatures and drought do not reduce the one-two-years-old leaf persistence, but can be a reason for the dying of single of the oldest ones, which than persist on the twigs for some time as a brown and dry.

The buds are formed when twig growth ends, during July–August. The infertile, apical buds are visible until August and grow during the end of summer. The male cones develop at the end of summer in the year preceding pollination. The male cone is visible in the needle angles on very short shoots as a small, whitish spherical structure during winter preceding pollination. Pollen release takes place during the spring of the next year, at the end of April and in May (Fig. 3), depending on the position of the tree (Maerki & Frankis, 2015), and in the same place can last about 1–2 weeks, depending on tree and weather. After pollen shedding, the whole structure persists on the tree for a few months (Maerki & Frankis, 2015).

Female cones are formed at the end of the summer in a year preceding pollination, in the needle axels.

The pollinated female cones are small, surrounded with green, leafy scales, and preserved in such a state to the spring of the next year, when they start to grow. In spring a year after pollination, the cones are green, not fully grown, with thickened, fused together, fleshy scales forming berry-like, globose structures (Maerki & Frankis, 2015: Figs 10 and 35). At the end of the second vegetation period after pollination, the cones are green, large but smaller, than ripe ones. The cones grow and reach final dimensions during summer in the third year after pollination (Maerki & Frankis, 2015). The ripe, coloured seed cones dry up and fall during winter and in the spring of the fourth year after pollination. The cones with empty seeds or seeds injured by pests drop down earlier, in the summer-autumn of the second and/or third year after pollination.

Nutrition

Junipers are trees growing on different substrates, generally poor with nutritional substances and independently on the soil pH (e.g. Coode & Cullen, 1965; Mayer & Aksoy, 1986; Christensen, 1997; Talhouk et al., 2001; Quézel & Médail, 2003; Caravaca et al., 2006; Adams, 2014a; Stephan et al., 2020). However, *J. drupacea* is the species connected with calcium-containing soils, predominantly with calcareous rocks of various origins or with the soils developed from the limestone base rock. Such substrates are neutral or moderately alkaline (pH: 6.8–8.1) soils (Bergmeier, 2002; Vermez et al., 2018). The reaction of *J. drupacea* to deficit or overabundance of macro- and micro-elements in the soil and its tolerance to the soils and air pollution have not been verified experimentally.

Mycorrhiza

The mycorrhiza in European and Mediterranean juniper species remains poorly recognized. The ecto- and endomycorrhizal fungi species were reported for *J. communis* from Central Europe (Dominik, 1951; Błaszowski et al., 1998; Balazs et al., 2015), *J. oxycedrus* from the Iberian Peninsula (Caravaca et al., 2006; Alguacil et al., 2006), *J. osteosperma* (Torr.) Little from the North America (Reinsvold & Reeves, 1986), *J. phoenicea* L. from the Mediterranean region (Sanguin et al., 2016; Fakhech et al., 2020) and *J. procea* Host from Africa (Alghamdi & Jais, 2013; Birhane et al., 2020). Unfortunately, *J. drupacea* mycorrhiza has not been investigated.

Plant communities

Juniperus drupacea is a component of *Abies cephalonica* and sometimes *Pinus nigra* forests in the Parnon mountains of Peloponnese in Europe, where it

also enters maquis and colonises abandoned fields. In Taurus and in the Lebanon mountains in Asia, *J. drupacea* enters *Abies cilicica*, *Pinus nigra*, and *Cedrus libani* forests. In Lebanon it grows in the fragments of *Cedrus libani* and *Abies cilicica* forests, but is found also in the open forest composed of *Quercus coccifera* L., *Q. infectoria* Oliv., and *Q. cerris* L. (Abi-Saleh & Safi, 1988; Abi-Saleh et al., 1996). *Juniperus drupacea* forms sometimes the specific juniper forests, in the Asiatic part of their geographic range together with other juniper species (Zohary, 1973; Browicz & Zieliński, 1982; Mayer and Aksoy, 1986; Bergmeier, 2002).

In the Parnon mountains in Peloponnese, *J. drupacea* is a component of communities included in relict supramediterranean fir and black pine montane forests from alliance *Abietion cephalonicae* Horvat et al. 1974 (Mucina et al., 2016). It was reported from the Parnon fir forests (Barbero & Quézel, 1976), and then described in detail by Bergmeier (2002). The latter author indicated occurrence of *J. drupacea* in the fir forests from associations *Helictotricho convoluti-Abietetum cephalonicae*, *Junipero drupaceae-Abietetum cephalonicae* and in the pine forest association *Pyrolo chloranthae-Pinetum nigrae*.

The forest community *Helictotricho convoluti-Abietetum cephalonicae* was found as multiform in floristic composition. *Juniperus drupacea* enters as a frequent forest component of the sub-associations of *Helictotricho convoluti-Abietetum cephalonicae* with *Ononis pusilla* L. and *Pteridium aquilinum* (L.) Kuhn (Bergmeier, 2002). The stands of the first sub-association are open, with coverage of 40–45% and about 15 m height on average. The forest is composed of *A. cephalonica*, *P. nigra* or both species. It is developed in the marginal part of Mt. Parnon at elevations between 900 and 1270 m, on the slopes facing mostly to the west, west-north or north (Bergmeier, 2002). *Juniperus drupacea* forms there a low tree or shrub layer. Other tree taxa which can be seen are *Juniperus oxycedrus* (we assumed after Adams (2004, 2014b) that all specimens of *Juniperus oxycedrus* from the eastern Mediterranean region should be treated as a separate species *J. deltooides* R.P.Adams), *Quercus pubescens*, sometimes also *Q. coccifera*, and *Acer sempervirens* L. The trees of *Abies cephalonica* are frequently parasited by *Viscum album* subsp. *abietis* (Wiesb.) Abrom. (Bergmeier, 2002).

Helictotricho convoluti-Abietetum cephalonicae with *Pteridium aquilinum* developed at relatively low elevations of the Parnon mountains, at about 1100–1480 m, on the steep, North- to West-facing slopes, on the poorly developed soils with frequent outcrops of the marble rocks. The stand is about 15 m high, with coverage of 40–50%, mostly with the predominance of *A. cephalonica* or sometimes mixed fir-pine. As in the previous association, *J. drupacea* is there a

frequent component of the second tree layer (Bergmeier, 2002).

Juniperus drupacea is a main component of the forest community *Junipero drupaceae-Abietetum cephalonicae*, in the Parnon mountains. Depending on the local condition, the association *Junipero drupaceae-Abietetum cephalonicae* develops in three variants. Variant with *Phillyrea latifolia* L. covers the central and northernmost part of the mountains, the submontane slopes north- to east-facing at elevations of 890–1110 m. The stands, about 14 m high, with coverage of 45–50%, are composed of *Abies cephalonica* with *J. drupacea*, sometimes with the prevalence of one of these species. The typical variant of *Junipero drupaceae-Abietetum cephalonicae* occurs mainly in the southern and central parts of the Parnon mountains, on the montane slopes at elevations between 1180 and 1520 m. The stands with a coverage of 54%, are composed of *Abies cephalonica* trees 13 m in height. *Juniperus drupacea* occurs there mainly in the second tree layer, with a single high trees. The *Junipero drupaceae-Abietetum cephalonicae*, *Pteridium* Gled. ex Scop. subcommunity occurs in the northern and central Parnon mountains, mainly on steep slopes and in ravines, at altitudes between 940 and 1280 m. The stand is formed by *Abies cephalonica* with a coverture of about 55% and average height of 16 m. *Juniperus drupacea* occurs in the second tree layer and in the shrub layer (Bergmeier, 2002). *Juniperus drupacea* in the Parnon mountains grows also, but rarely in the second tree layer or as a shrub in the pine forests from association *Pyrolo chloranthae-Pinetum nigrae*, which was developed mainly on flysch (Bergmeier, 2002).

Juniperus drupacea shows the ability to colonize abandoned agricultural areas and persist in agricultural-forest landscapes, like many other juniper species (García et al., 2014). It grows on uncultivated slopes and escarpments, but also inhabits abandoned fields and pastures in the lower parts of the Parnon mountains. Significant areas formerly cultivated in the hills between Moni Malevis and Agios Ioannis were colonized by *J. drupacea* as a result of the outflow of the rural population to cities (Wagstaff, 1968). In addition to *J. drupacea*, there are usually single specimens of *Pyrus elaeagrifolia* Pall., thickets of *Quercus coccifera*, *Calicotome villosa* (Poir.) Link and *Acer sempervirens*, *Quercus pubescens*, *Crataegus monogyna* Jacq., *C. heldreichii* Boiss., *Prunus cocomilia* Ten., *Rosa canina* L., *Lonicera etrusca* Santi and *Spartium junceum* L. (Boratyński & Browicz, 1982).

In Asia, *J. drupacea* is a component of the forest communities from order *Quercus pseudocerridis-Cedretalia libani* Barbéro, Loisel & Quézel 1974, that is a relict supramediterranean cedar woods of Southern Anatolia, Syria and Lebanon (Mucina et al., 2016). Occurrence of *J. drupacea* in the *Cedrus libani*, also *Abies cilicica* and sometimes *Pinus nigra* forests

were reported from several parts of the Taurus and Amanos in Turkey, the Ansariye mountains in Syria, and Lebanon mountains of Lebanon (Zohary, 1973). Some more details can be found in the review of the Turkish forest by Mayer and Aksoy (1986) and Ketenoğlu (2010). Mayer and Aksoy mention *J. drupacea* (under the name *Arceuthos drupacea*) from *Thlaspi cataonicum-Cedrus libani* (= *Thlaspi cataonici-Cedretum libani* Akman, Barbéro & Quézel 1979) forest, endemic to East Taurus. This forest type occurs on the soils developed from the limestone rock, at the West-, North- and East-facing slopes at elevations of 1600–1900 m. The stand is composed with *Cedrus libani* with a rare admixture of *Abies cilicica* and *Pinus nigra*, sometimes with understore of *Quercus libani* G.Olivier, *Q. cerris* and *Q. petraea* (Matt.) Liebl. (Mayer & Aksoy, 1986; Ketenoğlu, 2010). The presence of *Juniperus excelsa* and *J. drupacea* is higher in degraded forms of this forest type on the limestone rocks. *Juniperus drupacea* is specific for the meso-xerophilic form of *Abies cilicica* forest formed at an elevation of 1450–1700 m on South-facing calcareous slopes (Quézel & Pamukçuoğlu, 1973).

Juniperus drupacea is also present in the mountain juniper forests from the alliance *Berberido creticae-Juniperion foetidissimae*, which are degradation forms of *Abies cilicica* and/or *Cedrus libani* forests (Güngöroğlu, 2018), mainly on the soils originating from the limestone bedrock, especially on the karst areas (Varol, 2003, Varol et al., 2006). These communities are composed mostly of *Juniperus excelsa* and *J. foetidissima* Willd. (Mayer & Aksoy, 1986; Güngöroğlu, 2018), in some places with *Abies cilicica*, *Acer monspessulanum* L., also *A. sempervirens* and *Quercus trojana*. *Juniperus drupacea* grows singly among mentioned above trees, more frequently on the calcareous rocks (Varol et al., 2006; Doğan et al., 2011; Kocakaya et al., 2014; Koç, 2016; Özalp, 2016; Akkurt Gümüç, 2020). The forest habitats developed on karstic areas are settled by rare and protected species, as *Ostrya carpinifolia* Scop., *Sorbus torminalis* (L.) Crantz var. *pinnatifida* Boiss. (= *Torminalis glaberrima* (Gand.) Sennikov & Kurtto), *Fraxinus ornus* L. subsp. *cilicica* (Lingelsh.) Yalt., *Eriolobus trilobatus* (Labill. ex Poir.) M.Roem., *Taxus baccata* L. There are occurring also *Flueggea anatolica* Gemici and *Salvia marashica* İlçim, Celep & Dogan, the species listed in IUCN due to the risk of extinction.

In the Taurus mountains of Kahramanmaraş region, *J. drupacea* co-occure woody species such as *Abies cilicica* subsp. *cilicica*, *Juniperus excelsa*, *J. foetidissima*, *J. deltoidea*, *Pinus nigra* subsp. *pallasiana* (Lamb.) Holmboe, *Quercus libani*, *Q. cerris*, *Q. coccifera*, *Carpinus orientalis* Mill., *Ostrya carpinifolia*, *Acer monspessulanum* subsp. *oksalianum* Yalt., *Acer hyrcanum* Fisch. & C.A.Mey. subsp. *tauricola* (Boiss. & Balansa) Yalt., *Fraxinus ornus* subsp. *cilicica* (Lingelsh.) Yalt., *Cornus mas* L., *Cornus sanguinea* subsp. *cilicica* (Wangerin)

D.F.Chamb., *Sorbus umbellata* (Desf.) Fritsch, [= *Aria umbellata* (Desf.) Sennikov & Kurtto], *Hippocrepis emerus* (L.) Lassen subsp. *emeroides* (Boiss. & Spruner) Greuter & Burdet ex Lassen, *Pistacia terebinthus* L., *Fontanesia phillyraeoides* Labill., *Flueggea anatolica*, *Lonicera etrusca*, *Hedera helix* L., *Ampelopsis orientalis* (Lam.) Planch. and *Danae racemosa* (L.) Moench. The mentioned species grows among or on the calcareous rocks.

In the Taurus and Amanos mountains, *J. drupacea* occurs also in the forest included into sub-Mediterranean oak community, classified as *Quercetea cerridis* (Zohary, 1973), especially on the soils developed from the calcareous bedrock. This formation develops at elevations between 700 and 1600 m, in some places contacting with *Abies cilicica* forest. *Juniperus drupacea* occurs singly in exposed places, in degraded forms of the forest or on the rocks.

In the mountains of Lebanon and Syria, *J. drupacea* occurs in *Cedrus libani* and *Abies cilicica* forests, as well as in oak, mainly *Quercus coccifera* (= *Q. calliprinos* Webb) forests, on forest edges, in maquis communities, and singly on limestone rocks (Zohary, 1973; Abi-Saleh & Safi, 1988; Abi-Saleh et al., 1996; Talhouk et al., 2001; Douaihy et al., 2017). It is also an indicator of past over-exploitation of cedar and fir forests and their degradation (Talhouk et al., 2001; Douaihy et al., 2017).

Reproduction

Generative reproduction

Seed production and dispersal

The trees of *J. drupacea* become adult at the age of about 20–30 years, but massive cone production starts at ca. 50 years or later (Gültekin et al., 2004a, b, 2005). The seed cone production is uneven and vacillates from year to year, which can be inferred from the year-to-year differences in harvest for pekmez production (Çizgen et al., 2018).

In the wild, the seedlings were observed as rare, mostly under the crowns of mother trees (Maerki & Frankis, 2015). However, dispersal to more distant places surely plays an important role. Well known is hydrochory, i.e., a down-slope transportation of cones by streams, even summer-dry ones (Maerki & Frankis, 2015), but up-slope and distant transportation would be by animals. The cones of other juniper species are frequently eaten and transported by birds, mostly from the Turdidae family (Jordano, 1993; Jordano et al., 2007; Tellería et al., 2014; Wojtatowicz & Pietrzykowska, 2018). The cones of *J. drupacea* are too large for this group of birds, however, it cannot be ruled out that they are eaten by larger birds, such as ravens, which eat cones of other species of

junipers (Rumeu et al., 2011), or by jays or pigeons, which carry oak acorns (Bossema, 1979; Webb, 1986; Olszewski & Brzezicki, 2019), however, these hypotheses require confirmation from special studies.

The relatively high content of sugars in the arils of *J. drupacea* cones makes them an attractive food for mammals, which, however, may limit the distance of seed dispersion (Bou Dagher Kharrat et al., 2018). The juniper cones are eaten by foxes and martens (Matías et al., 2010; López-Bao & González-Varo, 2011), but this in the case of *J. drupacea* requires confirmation. Nevertheless, the cones of *J. drupacea* are eaten by wild and domestic goats and boars, after falling to the ground (observations by Prof. Gürlevik, cited in Maerki & Frankis, 2015). Additionally, the mature cones are eaten by sheep, wild boars, and bears according to observation by the local people of Manavgat, Antalya. These animals do not digest the woody seed coat, but contribute to the dispersal of seeds over short distances. It is believed, that the seeds, after passing through the digestive tracts of mammals germinate more easily, which, however, has not been confirmed experimentally. The arils of *J. drupacea* cones, after falling to the ground, are gnawed by goats and rodents, which may also facilitate germination near the mother trees.

Possible limited dispersion of *J. drupacea* seeds resulting from transport over short distances by mammals may be the reason for its rather significant genetic and morphological diversity, as well as the lack of localities on the Mediterranean islands between the Peloponnese and Anatolia (Bou Dagher Kharrat et al., 2018), despite favourable climatic conditions (Walas et al., 2019).

Viability of seeds and germination

The seeds of *J. drupacea* have morpho-physiological dormancy and need special treatments to germinate (Gürlevik & Gültekin, 2008; Douaihy et al., 2017). Although the period when starts the seed viability during their development on the mother tree has not been determined experimentally (Maerki & Frankis, 2015), the cone to reproduction are collected during late autumn of the third year after pollination. The seed with the drupe shall be removed from the fleshy part of the cone, otherwise their germination would be delayed at least by one year (Gültekin et al., 2004a, b, 2005), but even to five years (Christensen, 1997; Ioannidis et al., 2023).

In Lebanon, seed cones are collected during November and December. In this country, seeds to germinate are passed by boiling water (5–6 seconds), and afterward three months of cold, two months of warm and another three months of cold stratification (Colomer et al., 2014).

In Turkey, the cones of *J. drupacea* are collected during a similar period as in Lebanon. There are

15.1 ha of gene conservation forest area of *J. drupacea* (Yücedağ et al., 2021a). The species is of great interest due to local medicine. The seeds of three provenances from different elevations, Mersin, Adana, and Kahramanmaraş, germinated at 65.3% on average when germination temperature was 12 °C and pre-treatment included four weeks of warm stratification and nine weeks pre-chilling (Yavuz & Yılmaz, 2017). To obtain uniform germination and a higher percent of the seedlings emergence in the nursery, the populations from higher elevations (1400 m) combined with bottle-shaking with crushed glass, long cold and warm stratifications (220 and 65 days, respectively), plus applying bio-stimulators (PS-A6 + PS-K for 25 days) is recommended to be used. Moreover, the seeds from higher altitudes in the mountains have higher germination potential (Yücedağ et al., 2021b).

Perennation and vegetative propagation

Juniperus drupacea seems to propagate only by seeds. Vegetative perennation in the wild is unknown. The species is sometimes propagated in gardens by cuttings. A trial of micro-propagation gave positive result, however, a very small number of rooted explants was obtained (Ioannidis et al., 2023). This first step, however, is a good incentive for further research.

Herbivory and disease

Animal feeders or parasites

Mammals

Biochemical compounds make the leaves and young shoots of *J. drupacea* unpalatable to goats. The very prickly needles deter browsing, nevertheless, single trees intensively browsed have been noted in pastures (Maerki & Frankis, 2015), as well as exposed saplings. The conspicuous white stomatal stripes along the needles may function as a mechanism of Müllerian mimicry (Lev-Yadun, 2016), additionally preventing browsing.

The cones, due to a high content of nutritional compounds, are attractive to goats, wild boars, and even bears, also squirrels, and other rodents. The animals eat the arils or the entire cones when they drop to the ground at maturity (Maerki & Frankis, 2015). The cones of *J. turbinata* Guss. and *J. macrocarpa* Sm. are eaten by red foxes (*Vulpes vulpes* L.) and pine martens (*Martes martes* L.) (Matías et al., 2010, López-Bao et al., 2011, Farris et al., 2017). However, very few observations have been made on carnivore relationships with *J. drupacea*. In the Taurus mountains, the cones of *J. drupacea* were damaged by rodents,



Fig. 8. Cones of *Juniperus drupacea* damaged by Persian squirrel (*Sciurus anomalus*) on the ground under mother tree; Turkey, Taurus Mts. (Photo by Tolga Ok, 2023)

according to local population observations by squirrels (probably *Sciurus anomalus* Gldenstdt, 1785) (Abi-Said et al., 2014). The cones damaged by squirrels can be found on the ground under the crowns of female specimens of *J. drupacea* in the vicinities of Osmaniye and Kadirli (Fig. 8).

Birds

There is no literature on birds feeding on *J. drupacea*. However, several species of birds, mainly of the family Paridae, used to nest on juniper trees in the mountains of the Peloponnese. The juniper cones are frequently eaten by the birds from family Turdidae; however, cones of *J. drupacea* are too large to be consumed by them.

Insects

There is no data on the insects connected with *J. drupacea*. The relatively high content of biochemical compounds in all plant parts makes them unattractive or even toxic to the larvae and adult stages of insects. Leaves and young twigs are rarely affected by insect damage. Scale insects such as *Carulaspis minima* (Signoret 1869) alışkan Kee & Ulusoy, 2017) sometimes occur on the needles and cones but do no significant damage. Some other species of Diaspididae may be found on *J. drupacea*.

The cones of *J. drupacea* with frass expelled by larvae of cone tortricid moths *Pammene mariana* (Zerny 1920) (Tortricidae) were observed in the Parnon mountains (Roques et al., 2017).

Fungi

There is quite a complete lack of data on fungi occurrence on *J. drupacea*. We found only information on *Gymnosporangium clavariiforme* (Wulfen) de Candolle 1805 telia on the twigs of *J. drupacea* from Turkey (Bahcecioglu & Kabaktepe, 2012).

Plant parasites

Arceuthobium oxycedri (DC.) M.Bieb. (Fig. 9) is a frequent semi-parasite of different species of junipers, and sometimes, in combination with drought, leads to decline of their growth and dieback of the most attacked specimens (Tamudo et al., 2021). This dwarf mistletoe is a frequent semi-parasite of *J. drupacea* in the Anti-Taurus massif, in Turkey (Browicz & Zieliński, 1990). It occurs even on 7.78% of *J. drupacea* trees and in nearly fifteen individuals on one host tree in the vicinities of Kahramanmaraş, causing gradual dying of the apical parts of the twigs above the place of infection (Üstüner, 2018). In Lebanon, *A. oxycedri* is even more frequent and often causes

the death of *J. drupacea* individuals (Douaihy et al., 2017). Occurrence of *Arceuthobium oxycedri* was not observed on trees of *J. drupacea* in Greece.

Conservation

Juniperus drupacea is endangered due to climate changes. The area of potential ecological niche of the species can be reduced in 2070 to about 20% of the present, when the rate of climate warming would be at the level of 8.5 W/m², that is the average yearly temperature would increase by about 2 °C (Walas et al., 2019). The simultaneous reduction of precipitation and increased evapo-transpiration would be a great threat for species, especially for their south-easternmost populations (Walas et al., 2019; Stephan et al., 2020). Despite these threats, the conservation status of *J. drupacea* at global scale was considered as of Least Concern, according to International Union for the Conservation of Nature (IUCN) criteria, with a stable population trends (Gardner, 2013). However, its populations in Greece and generally in Europe are



Fig. 9. *Arceuthobium oxycedri* on *Juniperus drupacea*; Turkey, Taurus Mountains, near Akseki, 37.12°N, 31.77°E, 1230 m (Photo A. Boratyński 2005)

threatened under the IUCN criteria B1ab(iii) + 2ab(ii) (Gardner, 2017; Rivers et al., 2019). Additionally, it is strongly endangered in Lebanon (Douaihy et al., 2017) and in Israel (<https://flora.org.il/en/plants/jundru/>), due to restricted number of populations.

In Turkey, forests of *J. drupacea* cover 958.423 ha (OGM, 2015). The maintenance of the species is under forest legislation, which includes it as a protected component of the juniper forests endemic in Turkey, conserved as a part of 'Natura 2000'. *Juniperus drupacea* occurs in eleven national parks on the Mediterranean region of Turkey (Walas et al. 2019). The regions of its occurrence are also conserved in form of 'Small protected areas' (Kocyigit & Demirci, 2018).

In Greece, *J. drupacea* is vulnerable due to very slow regeneration and exposure to increasing aridity (Maerki & Frankis, 2015), especially in the eastern slopes of the Parnon mountains (Walas et al., 2019). The forests of this species in Greece are "Natural Monument under Preservation" since 1980. Near Moni Malevo in the Parnon mountains the dense forest of *J. drupacea* is protected in the form of nature reserve, and the great part of the Parnon mountain range is conserved in the form of Special Protected Areas (Constantinidis & Kalpoutzakis, 2015; Boglis, 2018; Ioannidis et al., 2023; Avramidou et al., 2023).

In Lebanon, *J. drupacea* is treated as 'endangered of special concern' due to lack of natural regeneration (Douaihy et al., 2017). In this country, the cutting of *J. drupacea* is forbidden by law. The species is present in areas of nature reserves for conservation of *Cedrus libani*, the cedar biosphere reserves at Jabal Moussa and Shouf, as well as in other areas under protection (Talhouk et al., 2002, 2014; Douaihy et al., 2017). *Juniperus drupacea* has an extensive distribution in the Mediterranean part of Turkey, and in the absence of specific threats such as local extinction, it remains unprotected. However, there is a program of gene conservation of *J. drupacea*, with 15.1 ha of gene conservation forest excluded from exploitation and preserved as a seed source (Yücedağ et al., 2021a).

Utilization

Similar to other juniper species, *Juniperus drupacea* is utilized locally in regions where it is commonly found.

Wood

Juniper wood, reddish, fragrant, durable and resistant to insect attack, was valued as a material for building, tool manufacture and even as a weapon in antiquity and in medieval times. The oldest known record of juniper wood usage is probably from Saqqara (Giza, Egypt). It is a ritual harpoon from the time

of King Djoser (ca. 2667–2648 BC) (<http://saqqara.uw.edu.pl/pl/obiekty/cor1/>). Local juniper species have also been used in the construction of Buddhist temples more than a thousand years ago (Gupta et al. 2020). In Europe the wood of *J. thurifera* was used for house building up to the recent times.

In the Parnon massif in Greece, *J. drupacea* wood, due to decay-resistant properties, was used as a material for simple construction in rural areas, and for carpentry. In the rural areas it was also a fuel, but currently its cutting is forbidden (Ioannidis et al., 2023). In Turkey, the wood was used mainly for burning, rarely as a building material. Its suitability for paper production proved to be limited (Kırcı, 2006). In Lebanon, the wood was also an important source of fuel (Baydoun et al., 2017).

Tar, obtained from the wood of *J. drupacea* (*Pix Juniperi drupacea*) by dry distillation of stems was used topically for alopecia, eczema and wounds from animals, and taken internally for coughs, common cold, urinary inflammations and diarrhoea (Miceli et al., 2011).

Leaves

Young branches and cones of *J. drupacea* were used as animal fodder in the absence of or inadequacy of animal feed during harsh winters in the Antalya region (Semiz et al., 2007). A decoction of fresh shoots with leaves is used in Turkey for urinary inflammation, gout and treatment of abdominal pain (Akkol et al., 2009). The extracts from the leaves and branches have antidiabetic and antioxidant properties (Deliorman Orhan et al., 2019).

Cones

The juniper cones have been known as a medicine for several human and animal illness from antiquity (Mohamed et al., 2021). The cones of junipers were used in ancient Egypt from 1500–1550 BC, for treating a tapeworm infection and for mummification, the volatile juniper seed oil as a laxative, and were reported from the tomb of Tutankhamen (1341–1323 BC) (El-Juhany, 2021 and literature cited herein). In present days, cones of *J. drupacea* are used in Eastern Mediterranean region, even outside the species' geographic range (El-Ghorab et al., 2008; Palabas Uzun & Koca, 2020; El-Juhany 2021).

The cones of *J. drupacea* contain a lot of sugar (Akinci et al., 2004). In dry mass, cones contain about 2.0–3.75% of protein, 4.0–5.5 g/100g of lipids, 14.5–17.3 g/kg of potassium, 790–890 mg/kg of calcium, 67.0–68.0 mg/kg of sodium, 440–540 mg/kg of magnesium, 34–65 mg/kg of iron, 4.4–5.5 mg/kg of copper, 16.5–18.1 mg/kg of zinc, and 4.7–5.1 mg/kg of manganese (Odabaş-Serin & Bakir, 2019). In

Turkey, the boiled decoction of crushed *J. drupacea* cones is used internally as an anthelmintic, to treat stomach-ache and against haemorrhoids (Miceli et al., 2011). The mature cones of *J. drupacea* are harvested from the trees in September and October. Afterwards, the seeds are removed from cones by squashing, and the fleshy tissue of the cones is used to yield a kind of syrup, called in Antalya 'enek pekmezi' (Semiz et al., 2007). Similar processes are used to obtain 'andız pekmezi' from the cones of *Cupressus sempervirens* L. in the Mediterranean region in Turkey. The *J. drupacea* pekmez is used in Turkey by the local population (Demirci & Özhatay, 2012; Ayas et al., 2017), mainly as a medicine for asthma, ulcers, eczema, itchy skin, bronchitis and jaundice. It also soothes coughs, prevents hair loss, improves blood circulation and body function, and is used even as an aphrodisiac (Çizgen et al., 2018). Most frequently pekmez is used as a cough and upper respiratory tract medicine, remedy for the circulatory system and stomach ailments (Özkan et al., 2021), also as a medicine for animals (Ari et al., 2018). The essential oils extracted from cones have antioxidant properties (El-Ghorab et al., 2008; Taviano et al., 2011; Ayas et al., 2017; Ari et al., 2018; Deliorman Orhan et al., 2019; Özkan et al., 2021). Pekmez contains more phenolic and flavonoid components than cones and its antioxidant activity is strong (Özkan et al., 2021).

In Turkey, several tons of *J. drupacea* cones are harvested annually from which pekmez is produced (Çizgen et al., 2018). In several regions of Turkey, the *J. drupacea* trees, which frequently and abundantly produce cones, are left in close proximity to farm buildings. Similarly, in Greece, in the Parnon mountains, *Juniperus drupacea* trees near farm buildings, houses and small churches are retained to provide shade for people and animals.

The extract from cones of *J. drupacea* has antidiabetic and antioxidant activities and can be used in diabetes treatment (Deliorman Orhan et al., 2019). This extract is also an effective mosquito repellent, especially against the tiger mosquito responsible for spreading numerous viruses and parasites (Evergetis et al., 2016). The use of extracts for medicinal and cosmetic purposes has also been reported in Lebanon (Baydoun et al., 2017).

In Turkey, the connate seeds of *J. drupacea* are used for making rosaries.

Ornamental purposes

The ornamental value of *J. drupacea* remains uninvestigated and underestimated, even in the countries of origin (Gültekin et al., 2004b). The rare use of *J. drupacea* as an ornamental was noted in Lebanon (Baydoun et al., 2017) and Turkey. It is seldom planted outside the countries of origin and mainly

in Mediterranean botanical gardens. Despite its hardness estimated as 8–9 (Krüssman, 1985; Welch, 1991; Auders & Spicer, 2012), it does not flourish or grow well in Central European countries.

Conclusions and perspectives

Chorological knowledge on *J. drupacea* has improved significantly since the 1980s, mainly thanks to the several papers published by Turkish, Lebanese and Greek botanists. Despite this, it is still necessary to intensify the field surveys to complete the distribution maps, especially in the Taurus mountains in Turkey and on Syrian territory. Thanks to the biochemical, genetic and morphometric studies, the diversity and differentiation of the species has been relatively well recognised. Also, the cone nutritious and pharmaceutical properties of the cones and benefits and ways to overcome seed dormancy are relatively well known. However, our study has uncovered substantial knowledge gaps regarding the environmental conditions of *J. drupacea* occurrence, its interactions with other organisms, and its potential use as an ornamental tree. Therefore, concerted efforts should be made to:

- complete the chorology and data on environmental conditions,
- recognize population dynamics and conservation needs,
- experimentally recognize the relation to environmental conditions (light, temperature, water),
- recognize the interactions with animals, fungi and plants,

Supplementing the knowledge in these areas will allow for better protection of the *J. drupacea* species itself, as well as the ecosystems in which it occurs.

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