

BIOLOGICAL FLORA

International Biological Flora No. 4

International Biological Flora: *Ceratonia siliqua*Peter A. Thomas¹  | Xavier Garcia-Martí²  | Tarek A. Mukassabi³  | Joan Tous⁴¹School of Life Sciences, Keele University, Staffordshire, UK²Escola de Capatassos Agrícoles de Catarroja, Diputació de València, Spain³Faculty of Sciences, University of Benghazi, Benghazi, Libya⁴Empresas Innovadoras Garrofa, Tarragona, Spain

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Abstract

1. This account presents information on all aspects of the biology of *Ceratonia siliqua* L. (Carob) that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *International Biological Flora*: distribution, habitat, communities, responses to biotic factors, responses to environment, structure and physiology, phenology, floral and seed characters, herbivores and disease, history and conservation.
2. *Ceratonia siliqua* is a lowland evergreen shrub or tree, native around the Mediterranean basin and widely cultivated in areas with a warm temperate and subtropical climate, with more than 100 named cultivars. Carob grows on a wide range of soils including nutrient-poor and strongly calcareous, dry soils.
3. Carob is dioecious or rarely hermaphrodite although females dominate in cultivation due to their fruit. Pollination is primarily by insects and the relatively large seeds are spread mainly by ingestion of fruits by mammals. Seed dormancy is imposed by a hard seed coat and seeds germinate readily after natural or artificial scarification.
4. Drought tolerance is very high, acting as a drought avoiding water spender. Carob is also very tolerant of saline conditions and tolerant of fire and can act to restrict wildfire spread by generating fuel discontinuity. It shows high post-fire regrowth. Old individuals house a diversity of associated fauna and are comparatively unaffected by serious pests and diseases.
5. Carob has a long cultural history around the Mediterranean as a food source for humans and domesticated animals, in herbal and modern medicine and, more recently, for the carob bean gum used in a variety of domestic products and foods. Commercial production of fruits has declined over past decades but the low cultural care needed in growing orchards, potential new markets for fruit and seeds, and growing use of the tree to prevent soil erosion and sequester carbon gives carob a brighter future.

KEYWORDS

climatic limitation, conservation, ecophysiology, geographical and altitudinal distribution, pests and pathogens, plant communities, production, reproductive biology

Nomenclature of vascular plants follows Royal Botanic Gardens, Kew: Plants of the World Online.

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Carob. Fabaceae (Subfamily Caesalpinioideae). *Ceratonia siliqua* L. (*C. coriacea* Salisb., *C. inermis* Stokes) is a sclerophyllous evergreen shrub or tree to 10 (20) m high, broad hemispherical crown, thick trunk up to 2 m diameter, bark initially grey, smooth, later rough and dark brown. Branches sturdy. Naked buds. Leaves 10–20 × 3–15 cm long, alternate, paripinnate, rarely bipinnate, 4–8 (12) normally opposite pairs, with or without a terminal leaflet. Leaflets 2–8 × 1–4.5 cm, obovate or elliptic to suborbicular, coriaceous, entire, apex rounded, dark green and shining above, dull grey-green beneath, finely veined with margins slightly undulate, stipules minute, caducous, petiolule <0.5 cm. Petiole and rachis contiguous, 7–15 cm long, reddish, with longitudinal furrow along upper surface. Inflorescences cylindrical, rigid, 3.5–15 × 0.8–2.5 cm, bearing 20–60 densely packed flowers, spirally arranged in catkin-like racemes, axillary, borne on spurs mainly on old wood 2+ years old and even on the trunk (cauliflory). Flowers 6–12 mm, green, 5-merous, petals absent; calyx disc-shaped, sepals hairy, toothed, reddish green. Flowers initially hermaphrodite, but usually develop into functionally male or female. Inflorescences can be entirely male, female or hermaphrodite, generally dioecious, rarely with unisex or hermaphrodite flowers borne in the same inflorescence. Female flowers greenish, pistil 6.0–8.5 mm, peltate stigma 2.5 mm long, two-lobed, style 1.75 mm, superior unilocular ovary inserted in a central depression in the nectarial disc, rudimentary stamens. Male flowers red-yellow, four to seven stamens with oval anthers and long filaments around a nectarial disc, rudimentary pistil. Hermaphrodite flowers contain pistil and stamens. Male and hermaphrodite flowers with unpleasant odour, females less so. Fruit indehiscent legume, compressed, straight or curved, thickened at the sutures, 10–30 × 1.4–3.5 × 0.5–0.8 cm (Korkmaz et al., 2020) with blunt or subacute apex; green at first, shiny, dark brown when ripe, wrinkled leathery surface, pendent. Seeds transverse in fruit, separated by sugary mesocarp; very hard, numerous, compressed ovate-oblong, 8–10 × 7–8 mm, 3–5 mm thick; testa hard, smooth, glossy brown, hilum minute.

Ceratonia was originally thought to be monotypic but a second species, *C. oreothauma* Hillc., G.P. Lewis & Verdc., native to Oman and Somalia, was described by Hillcoat et al. (1980). Centuries of cultivation of *C. siliqua* has resulted in c. 100 named cultivars of limited geographical range, mostly of unrecorded origin. The most commercially important cultivars, for example, 'Matalafera', 'Rojal', 'Duraió' and 'Sayalonga' in Spain, and 'Mulata' and 'Galhosa' in Portugal, are described by Batlle and Tous (1997) and Tous and Franquet (2024). Carob cultivars show large variation in habit, vigour, size and quality of fruits, seed yield, productivity and pest and disease resistance (Batlle & Tous, 1997). However, there are comparatively small genetic differences between cultivars or between cultivars and feral or wild populations (Baumel et al., 2022; Tous et al., 1992)—Section 10.1.

Carob is native to the Mediterranean region (Section 1) but has been extensively cultivated and widely naturalised throughout the Mediterranean and in suitable climatic areas around the world. Grafted carob trees are common in traditional Mediterranean orchards, which have given rise to feral plants naturalised in surrounding areas. Carob orchards have been cultivated due to their ability to

produce fodder and food, particularly their fruits, in marginal lands, especially during unfavourable years (Baumel et al., 2022). Global production of the fruit is however declining, falling from 300–350,000 t/year in 1985–1990 to 235–250,000 t in 2020 (Tous & Franquet, 2024) due to labour-intensive harvesting, pressure of land use and changing markets. Nevertheless, new markets are emerging (Brassesso et al., 2021) and the decline shows signs of reversing.

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

The natural distribution of carob within the Mediterranean is obscure. It was originally thought to be native to the eastern Mediterranean, probably Turkey, Syria and possibly Yemen, but there is evidence (see Section 10) that, before this in the late interglacial, it was also native to the High Atlas of Morocco and migrated northwards and eastwards (Baumel et al., 2022). It is now widely cultivated and naturalised around the whole of the Mediterranean (Figure 1). It has been thought that naturalised plants are almost all feral derivatives of domesticated cultivars (Batlle & Tous, 1997), but recent microsatellite investigations support the native origins of many populations around the Mediterranean (Baumel et al., 2022; Viruel et al., 2020) overlain with movement of cultivated varieties over the last 8000 years. However, cultivation has had a small influence on the main patterns of genetic diversity across the Mediterranean. As such, carob is included in phytosociological studies as a natural component of Mediterranean communities—Section 3 (de Bolòs, 1970; Zohary & Orshan, 1959). Wild populations are most common at low altitudes along the Spanish Mediterranean coast, Southwest Spain, Southern Portugal, the Balearic Islands, Southeast France, the shores of Southern Italy including Sicily, the Adriatic coast of Croatia, the Aegean region in Greece and Turkey, along the Northern and Southern ranges of Cyprus, in the islands of Malta, in the maritime belt of the Levant north to Syria, the north and south of Morocco and the coastline in Tunisia and Libya (Batlle & Tous, 1997; Custódio, 2005; Jafri & El-Gadi, 1978; Zohary, 2002). Schweinfurth (1894) considered carob to also be native to the highlands of Yemen.

From the mid-19th century onwards, carob was introduced to other regions (Figure 1) including California, Arizona, Mexico, Chile and Argentina in the Americas, and to Australia, South Africa, India, The Philippines and Iran (Ali et al., 2019; Batlle & Tous, 1997; Condit, 1919; Tous & Esbenshade, 2016; Winer, 1980; Yatim et al., 2022). Introductions are within 30°–45° in northern latitudes and between 30° and 40° in southern latitudes (Batlle & Tous, 1997). In the 1950s, there was a 'carob crusade' in California promoting carob as a dryland crop requiring little irrigation which resulted in a number of orchards being planted in the south of the state (Batlle & Tous, 1997), and male trees being used as street trees in southern California and Arizona (Condit, 1919; Schroeder, 1952). In Australia, carob was introduced around 1850 by Mediterranean emigrants, but large plantings were not made until the 1980s, mainly in Western

vegetative growth or flower and fruit production. *Ceratonion oreo-thauma* is much more limited in range, apparently due to its greater sensitivity to cold (Batlle & Tous, 1997).

Carob can survive and produce fruits with as little as 250 and 550 mm of precipitation per year, respectively (Nasar-Abbas et al., 2016; Tous et al., 2013). New growth on branches of around 4 cm over 3 months has been observed at 300 mm (Correia & Martins-Loução, 2004), but fruit production is poor below 350 mm and for commercial crops 400 mm (northeast Spain) to 500–550 mm (Algarve) is needed (Tous & Batlle, 1990). In Portugal, <400 mm results in great variability in annual fruit production from 20 to 90 kg (fresh mass) per tree (Correia et al., 2020). In Cyprus, with annual precipitation of 300–500 mm in the lowlands, fruit production is closely tied to variation in the amount of winter and spring precipitation, with higher rainfall in one year usually resulting in higher fruit yield the following year (Orphanos, 1980). Using 30 years of fruit production data from an orchard in the Algarve, Correia et al. (2020) found no relationship between yield and air temperature but noted that lower precipitation in the flowering season (September to November) resulted in higher yields, which was presumed to be due to higher rainfall disrupting insect activity and pollination. Moreover, a field experiment by Correia and Martins-Loução (2004) found that the number of inflorescences in autumn was inversely related to total precipitation in April–June, suggesting a shift from reproductive to vegetative growth with low spring rainfall. Carob can produce good fruit crops with less water than any other common Mediterranean fruit tree (Condit, 1919) and so usually does not need irrigation but, like other propagated Mediterranean trees, rootstocks require some irrigation during the first 2–3 years to achieve good vegetative growth and reach suitable size for grafting (Correia et al., 2010).

Around the Mediterranean, most of the precipitation falls during the 3 months of September–November, the main growing season of evergreen sclerophyll shrubs, and only 6% of annual precipitation typically falls during the summer months of June–August (Rhizopoulou & Davies, 1991; Rhizopoulou & Mitrakos, 1990). The climate of the western Mediterranean is moderated by the Atlantic while the eastern Mediterranean is more continental with a lower rainfall and higher temperatures (Harding & Palutikof, 2009). Moreover, there is a large variation in precipitation between years (Correia et al., 2020). Within this climatic pattern, carob has evolved a number of drought-resistant mechanisms (Section 5.3) and is a useful crop where irrigation is impractical or rainfall unreliable.

2.2 | Substratum

Carob can grow on a wide range of soils including poor sandy soils and rocky hillsides with soils 20–30 cm deep, although growth and productivity may be low due to low storage of rainwater (Margues et al., 2001; Orphanos, 1980). The best growth occurs on sandy well-drained, moderately rich loams with low to medium organic matter content, pH 5.7–6.6, although calcareous soils with high lime content, up to at least pH 7.97 are also suitable

(Batlle & Tous, 1997; Condit, 1919; Correia et al., 2018; Margues et al., 2001; Orphanos, 1980; Pérez-Pastor et al., 2016). Indeed, carob can thrive on heavy textured soils in the Algarve with >10% calcium carbonate and pH >8.0, with little organic matter and low levels of N and P but high K (Correia et al., 2018, 2020; Correia & Martins-Loução, 2004). In Cyprus, carob grows mainly on calcareous soils which are either reddish in colour with around 20% calcium carbonate overlying highly calcareous subsoil or white in colour and highly calcareous containing up to 80% calcium carbonate (Orphanos, 1980). Both soil types overlay bedrock of limestone or marl.

The most important limitation imposed by soils is their shallowness, which results in poor storage of rainwater and limits root penetration, reducing the size of the tree. Orphanos (1980) stated that the depth of soil can be judged from the size of the trees. Carob is usually associated with poor quality soils, making it a useful plant to prevent soil erosion.

Carob is absent from waterlogged soils and certainly, in California, an important soil requirement is reported to be free-drainage (Condit, 1919). Carob tolerates soil salinity well, showing no effect of soil salt content of up to 3% sodium chloride (Winer, 1980)—see Section 5.3.

3 | COMMUNITIES

Carob is native in lowland dry and rocky hillsides in garrigue, coastal and sub-maritime maquis and in transitional zones between Mediterranean scrub and the Sahara (de Bolòs, 1970; Zohary & Orshan, 1959). Carob is most closely associated with *Pistacia lentiscus* and *Olea europaea* subsp. *europaea*, forming the Thermo-Mediterranean *Oleo-Ceratonion siliquae* alliance (EU Habitats Directive habitat type 9320; Natura 2000 sites habitat site 391) in the order Pistacio lentisci-Rhamnetalia alaterni (Batlle & Tous, 1997; European Environment Agency, 2023). Here, carob is associated with a number of species but most frequently with *Pinus halepensis*, *Quercus coccifera*, *Myrtus communis*, *Rhamnus alaternus*, *Asparagus acutifolius*, *A. albus*, *Clematis cirrhosa*, *Phillyrea angustifolia*, *Prasium majus*, *Lonicera implexa*, *Juniperus phoenicea*, *Rubia peregrina* subsp. *longifolia*, *Arum pictum*, *Smilax aspera*, *Euphorbia dendroides*, *Ulex parviflorus* and *Chamaerops humilis* (Baumel et al., 2018; Gianguzzi & Bazan, 2019; Lahssini et al., 2015; Rey et al., 2009).

Within this vegetation type, Baumel et al. (2018) identified five distinct alliances around the Mediterranean. Indicative species are given in Table 1. *Oleo sylvestris-Ceratonion siliquae* is typical of humid and sub-humid areas, including western Spain, the Balearic Islands, France, coastal Italy, Croatia, Sicily, Tunisia, Algeria. This is characterised by abundant *Pistacia lentiscus*, *P. terebinthus*, *Rhamnus lycioides* subsp. *graeca* and *R. alaternus*, depending upon location (Blasi et al., 2000; Ighbareyeh et al., 2021). *Asparago albi-Rhamnion oleoides* is found in more arid and sub-humid areas adjacent to the Gibraltar strait (north Morocco, southern Portugal and southern Spain) where *Asparagus acutifolius* is a constant (Boudik et al., 2024; Jahns, 2003).

TABLE 1 Indicative plant taxa associated with alliances containing *Ceratonio siliqua* in the Mediterranean region, listed in decreasing order of their indicative value.

Oleo sylvestris- Ceratonion siliquae	Asparago albi- Rhamnion oleoidis	Ceratonio siliquae- Rhamnion oleoidis	Senecio anteuphorbii- Arganion spinosae	Sarcopoterion spinosi
<i>Asparagus acutifolius</i>	<i>Phlomis purpurea</i>	<i>Rubia tenuifolia</i>	<i>Lavandula dentata</i>	<i>Thymbra capitata</i>
<i>Rubia peregrina</i>	<i>Aristolochia baetica</i>	<i>Rhamnus punctata</i>	<i>Genista tricuspidata</i>	<i>Drimys maritima</i>
<i>Pinus halepensis</i>	<i>Rhamnus lycioides</i>	<i>Sarcopoterion spinosum</i>	<i>Tetraclinis articulata</i>	<i>Lamyropsis cynaroides</i>
<i>Rhamnus alaternus</i>	<i>Daphne gnidium</i>	<i>Calicotome villosa</i>	<i>Thymus satureioides</i>	<i>Crucianella latifolia</i>
<i>Brachypodium retusum</i>	<i>Arisarum simorhinum</i>	<i>Pistacia palaestina</i> (= <i>P. terebinthus</i> L.)	<i>Genista ferox</i>	<i>Leontodon tuberosus</i>
<i>Euphorbia dendroides</i>	<i>Chamaerops humilis</i>	<i>Hypericum thymifolium</i> (= <i>H. humboldtianum</i> Steud.)	<i>Argania spinosa</i> (= <i>Sideroxylon spinosum</i> L.)	<i>Phlomis fruticosa</i>
<i>Calicotome spinosa</i>	<i>Cistus albidus</i>	<i>Cyclamen persicum</i>	<i>Globularia alypum</i>	<i>Genista acanthoclada</i>
<i>Thymus vulgaris</i>	<i>Arbutus unedo</i>	<i>Pinus brutia</i>	<i>Carlina involucreata</i>	<i>Hypericum empetrifolium</i>
<i>Rosmarinus officinalis</i> (= <i>Salvia rosmarinus</i> Spenn.)	<i>Crataegus monogyna</i>	<i>Stachys distans</i>	<i>Eryngium tricuspidatum</i>	<i>Scaligeria napiformis</i>
<i>Ononis minutissima</i>	<i>Quercus ilex</i> subsp. <i>ballota</i> (= <i>Q. rotundifolia</i> Lam.)	<i>Origanum syriacum</i>	<i>Phagnalon saxatile</i>	<i>Urospermum picroides</i>

Source: Baumel et al. (2018).

This alliance forms a very open, mixed woodland especially at higher elevations, with *Quercus faginea*, *Quercus rotundifolia* and *Abies pinsapo* with a diverse understorey layer dominated by *Juniperus oxycedrus*, *Phillyrea latifolia*, *Pistacia atlantica*, *Ulex parviflorus*, *Cistus creticus* subsp. *creticus*, *C. salviifolius*, *Lavandula lanata*, *L. dentata* and *L. stoechas* (Arista et al., 1999; El Ghalabzouri et al., 2015; Lahcen et al., 2012). In Morocco, carob is typical of the *Ceratonio siliquae-Tetraclinietum articulatae* and *Clematidi cirrhosae-Ceratonietum siliquae* associations (Fennane, 2003). The alliance *Ceratonio siliquae-Rhamnion oleoidis* is located in Turkey, Lebanon, Syria, Cyprus and Libya and forms a shrubby maquis mainly on limestone and near the coastline dominated by *Olea europaea* subsp. *europaea* var. *sylvestris* with *Pinus brutia* in Turkey and *Juniperus phoenicea* in Cyprus (Abbo et al., 2015; Gianguzzi & Bazan, 2019). The shrubby alliance *Senecio anteuphorbii-Arganion spinosae* is restricted to semi-arid areas of south-west Morocco, and the final shrubby alliance, *Sarcopoterion spinosi*, is located in arid areas of western and southern Greece and lowland Crete, including *Euphorbia dendroides* in southern Greece and spiny shrubs such as *Genista acanthoclada* and *Euphorbia acanthothamnus* in Crete (Jahns, 2003; Tsiourlis et al., 2007). In general, western alliances are more species rich, due to a higher number of rare species, while eastern alliances have a higher diversity of abundant species (Baumel et al., 2018). In southwest Morocco, on the slopes of the High Atlas Mountains, where *Quercus ilex*, forms 80%–90% cover, carob is a very occasional component of the woodland on deep but sloping soils of the alliance *Acacion gummiferae* in the class *Quercetea ilicis* (Médail et al., 2001).

In the Levant bordering the Mediterranean, carob is common in the *Ceratonieto-Pistacietum lentisci* alliance (Zohary & Orshan, 1959) which occurs to the west and east of the main western mountain range on stony, semi-arid soils. It is characterised by single or small groups of carob trees growing among evergreen shrubs dominated by *Pistacia lentiscus* and *Capparis spinosa* var. *aegyptia* (Ighbareyeh et al., 2014; Zohary, 1973). The commonest association within this alliance is *Ceratonieto-Pistacietum typicum* in the western foothills, characterised by *Olea europaea* subsp. *europaea*, *Salvia fruticosa* and *Ephedra foeminea* with a high species diversity. On the mountain slopes, carob is found within the *Ceratonieto-Pistacietum orientale* association, characterised by *Pistacia lentiscus* being replaced by *Rhamnus alaternus*, *Pistacia atlantica*, *Prunus amygdalus*, *Ziziphus lotus* and *Capparis spinosa* var. *canescens* (Zohary & Orshan, 1959). Carob is also found in western sand dunes and derived sandstones on the Sharon plain in the well-developed *Ceratonieto-Pistacietum arenarium* association characterised by *Lycium barbarum*, *Ephedra ciliata*, *Ballota philistaea* and *Asparagus horridus* (Liphschitz, 1987; Zohary & Orshan, 1959). Individuals of carob and *Pistacia lentiscus* are also found at higher elevations, within the *Quercus calliprinos-Pistacia palaestina* or *Ceratonio siliquae-Quercetum calliprini* association (Ighbareyeh et al., 2021).

Cultivation of carob around the Mediterranean basin has led to many feral carob trees escaping outside of plantations, taking advantage of habitats opened by human activities and degradation of the original wild vegetation (Liphschitz, 1987; Ramón-Laca &

Mabberley, 2004). Cultivated carob trees have traditionally been interplanted with olives, grapes, almonds and barley in the most productive areas (Batlle & Tous, 1997) and as a consequence carob, olives and grapes are frequently found together in abandoned fields (Orphanos, 1980). As a result of cultivation, the escape of feral trees and, in some cases, rootstocks outgrowing and replacing grafted cultivars in old orchards, communities in which carob is a major or significant element may not reflect the original status of this species (Abbo et al., 2015; Baumel et al., 2022; Zohary, 1973).

4 | RESPONSE TO BIOTIC FACTORS

Ecological investigations of carob have concentrated on planted crops where planting density is low (Section 5.1) and surrounding shrubs and herbaceous plants are managed to reduce competition by cutting or ploughing. Manor et al. (2008) record that this is done every 5 years in the western Levant. As a consequence, little is known about the competitive ability of carob. Competition is likely controlled by root extension and competition for water, producing a random to overdispersed distribution (Section 5.1). In Cyprus, Orphanos (1980) recorded that wheat or barley was sown between trees but in most years competition for water meant that both crops suffered from water shortage, particularly the carob. But when irrigated, crops are freely grown between trees.

Carob seedlings can survive in deep shade but develop only a weak root system (Section 8.5). Consequently, shade given by woody plants acting as nurse trees may aid long-term survival of seedlings allowing carob to establish in more arid areas. This is true for many woody plant species. In arid areas of southeast Spain, 27 woody species were found established under carob trees. Moreover, woody plant density was higher under carob trees than in open areas (3.26 ± 1.6 vs. 1.93 ± 1.3 individuals/m², respectively; assumed to be SD, $n=20$) (Pausas et al., 2006). It appears that the carob trees facilitate seedling establishment by ameliorating conditions, particularly water stress, but also by acting as perches for defecating birds since the density of woody plants with fleshy fruits was c. 25 times higher under the carob trees (Pausas et al., 2006). Carob trees act as perches even when dead (Bonet, 2004). Facilitation of establishment particularly benefits the bird-dispersed shrubs *Rhamnus lycioides*, and *Pistacia lentiscus* in Eastern Spain (Bonet, 2004; Verdú & García-Fayos, 1996). However, there is no evidence of carob establishing under its own shade.

Although carob grows naturally on poor soil, and most plantations are not fertilised (Correia et al., 2020), fertiliser inputs have been shown to improve growth. For example, the addition to carob trees in Morocco of mixtures of tomato plant residues, phosphate sludge, sheep manure and olive pomace (the residue left after oil extraction from olive fruits) with total phosphorus content of 9.8%–10.5% resulted in increased height growth of seedlings of more than 65% and more than 90% increase in diameter growth over unfertilized controls (Baiz et al., 2021). Annual growth of shoots on poor soils of southern Portugal was also increased by N+K fertiliser

(0.8 kg N + 1 kg K₂O per tree) from c. 6–10 cm (between May and September) in control plants to c. 9–14 cm in fertilised trees (Correia & Martins-Loução, 2004).

Leaves grown in atmospheric pollution in urban Greece were thicker than leaves from suburban trees (e.g. $951.00 \pm 9.26 \mu\text{m}$ (SD) urban; $838.00 \pm 4.36 \mu\text{m}$ suburban), had a thicker palisade mesophyll (e.g. $438.41 \pm 5.87 \mu\text{m}$ urban; $289.36 \pm 7.25 \mu\text{m}$ suburban) and higher total chlorophyll (Papadopoulou et al., 2023). Given the long lifespan of carob leaves (Section 7), these traits may help survival under polluted conditions. In a restoration project of mining spoil in southwest Spain, Domínguez et al. (2010) found that the survival of 4- to 5-year-old planted carob trees decreased as trace element concentration increased and internal concentrations of As and Zn increased to 0.048 and 27.6 mg/kg, respectively, and soil aridity increased over the summer. Survival was similar to *Quercus ilex* but less than a number of other trees including *Olea europaea* var. *sylvestris*.

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

In commercial plantations, carob trees are usually equidistant apart and thus overdispersed, although wild trees can be more random and irregularly spaced (Orphanos, 1980). In dry Mediterranean orchards, 100–175 trees/ha is the norm—a spacing of 9×9 to 7×8 m—but can be as low as 45 trees/ha (Batlle & Tous, 1997; Condit, 1919; Correia et al., 2017; Pérez-Pastor et al., 2016). On fertile soils in southern Spain, density can rise to 330 trees/ha in plantations 26 years old but will require thinning at a later stage (Batlle & Tous, 1997; Palacios-Rodríguez et al., 2022). In naturalised populations, mixed with other Mediterranean trees, tree density may be lower but tends to still be overdispersed presumably due to competition for water. The decline and abandonment of domestic cultivation, as well as fires, has resulted in many old trees left as isolated individuals in semi-natural, agroforestry and agricultural habitats (Figure 2).

5.2 | Performance in various habitats

Annual growth in branch length is very variable between years. In Spain and Portugal, it can reach c. 20 cm per season (May to September), or even c. 28 cm with N fertilisation (Section 4) but in very dry years is negligible (Correia & Martins-Loução, 2004; Pérez-Pastor et al., 2016). Similarly, leaf area index can be as high as c. 3.5 m²/m² in April (similar to other Mediterranean woody plants) but in dry years can be as low as c. 1.5 m²/m² due to summer leaf abscission (Correia & Martins-Loução, 2004) which can reach 25% of all leaves (Correia & Martins-Loução, 1997). Carob in southern Spain, 44–50 years old, 2.2–3.4 m tall, grown at 110–156 trees/ha, added 23 cm² to the trunk cross section in a year (c. 4%) and twigs grew 19–23 cm in length (Pérez-Pastor et al., 2016).



FIGURE 2 An old carob tree at Foia Brel, L'Alfàs del Pi, Alicante, Spain, >3.2 m average diameter and c. 8 m tall, with local and international importance. Photograph by Xavier García Martí.

Seedling survival on dry sites may be improved with tree shelters, but not always (Padilla et al., 2011). On degraded areas in the Algarve, container grown carob trees 7.5 months old were planted in 60 cm tall solid plastic tree shelters on a 2 × 2 m grid. Survival after the first summer was 62%–84% in shelters and 12%–34% in control plants with no tube; at the end of the second summer, it was 34% and 2%, respectively (Margues et al., 2001). This compared to second summer survival of *Quercus suber* of 23% and 9%, respectively. There were no significant difference in height or stem diameter growth between treatments after two growing seasons, but specific leaf mass was lower inside the shelters (16.9 ± 4.37 [SD] mg/cm² shelters; 21.4 ± 2.85 mg/cm² controls) and leaf area ratio was higher (17.39 ± 5.68 cm²/g shelters; 8.43 ± 4.74 cm²/g controls), perhaps due to reduced light levels inside the shelters. Predawn leaf water potential was not significantly different (Margues et al., 2001).

Sakcali and Ozturk (2004) investigated carob on two sites in southern Turkey, one with natural vegetation and the other a degraded site largely cleared of vegetation. On the degraded site, they found that carob was not capable of compensating for water loss, and, even with almost complete closure of stomata (conductance reducing to 0.1 s/cm), leaf water potential dropped to −3.1 MPa (further details in Section 6.5). In addition to variation in growth between sites, there is also variation between different cultivars throughout the Mediterranean and in comparison with wild types; these are reviewed by Tous et al. (2013).

Fruit yield per tree is heavily affected by climatic factors since yield is very irregular between years in both wild and orchard trees. This variation is more pronounced on fertile soils; fruit production over a 30-year period in orchards in the Algarve ranged from 3.7 to 93.0 kg/tree while on non-fertile soils, it was between 0.6 and 16.6 kg (Correia & Pestana, 2018). Correia et al. (2017) reported that carob trees grown on their own in orchards (45 trees/ha, c. 10 years old) were less productive (7.7 kg/tree) compared to carobs in mixed orchards (33 trees/ha) with *Olea europaea*, *Ficus carica* and *Prunus*

amygdalus (28.5 kg/tree). In California, Condit (1919) recorded that trees 25–30 years old yielded around 200–250 kg of fruit annually while cultivars, 15 or 18 years after grafting, yielded 400–500 kg in good years, averaging 200 kg across years. Condit also reported that annual yields in southern Europe varied from 1 to 1300 kg per tree. Horticultural management techniques to maximise crop production are reviewed by Tous et al. (2013).

Since fruit yield is irregular, it is suggested that carbon sequestration might form a new income stream for farmers ensuring that other ecosystem services of carob trees are maintained (Correia et al., 2017). Estimates of carbon sequestration have been made. Orchards of carob in southern Spain with tree densities of 110–300 trees/ha, 3.4–4.3 m tall and >25 years old, growing in >500 mm annual precipitation, have been found to store between 4 and 5.4 t C equivalent/ha/year (Palacios-Rodríguez et al., 2022; Pérez-Pastor et al., 2016). This gave a mean total C in biomass of 34 kg/tree and a root biomass of 6.96 kg/tree, with a total of 40.96 kg C/tree, about 4 t C equivalent/ha, for a density of 100 trees/ha (Palacios-Rodríguez et al., 2022). In the Algarve, a lower density of trees (45/ha) where each tree was bigger, averaging 6.4 m tall and up to 12.9 m, yielded much higher carbon storage per tree at 445 kg C/tree with 20.0 t C/ha just in the above-ground biomass (Correia et al., 2017). The methodology of Correia et al. (2017) is different to the others and is the reason for different results of carbon sequestration in this crop. Carbon assimilation activity is similar to, or even higher than, other woody crops and suggests that it can be considerably enhanced through the optimization of cultural techniques and irrigation regimes.

5.3 | Effect of frost, drought, fire, etc.

Given the Mediterranean climate favoured by carob, trees can withstand high summer temperatures up to 40°C but can tolerate only light winter frosts. Leaves and leaf buds are damaged by temperatures of −6 and −7°C, respectively, and are more sensitive than *Olea europaea* (−12°C for leaves and leaf buds), *Pistacia lentiscus* (−13°C) and *Quercus coccifera* (−14°C) (Christodoulakis, 1992; Tous et al., 2013). The smaller resistance to freezing of carob is attributed to the buds lacking protective scales. Young carob trees and their flowers are even more sensitive to low temperatures since they flower and fruit in late summer/winter, and can be damaged when temperatures fall below −4°C (Tous et al., 2013; Tous & Batlle, 1990). Condit (1919) recorded that many carob trees in the northern half of California succumbed to frost in 1888, and it was found that young trees were 'no hardier than orange trees' though, once established, carob was more frost-resistant than oranges (presumably *Citrus × aurantium* f. *aurantium*). Condit (1919) also reported that carob was uninjured at −8°C at Santa Barbara and several varieties survived −6 to −8°C at Chico, both mid-California. Severe frosts have also been reported to kill entire trees in Europe, notably in 1956 and 1985, and generally carob trees have not been planted above 500 m a.s.l. or in areas known to be at risk of frost (Batlle & Tous, 1997). Acclimation

to low temperatures requires a number of days or weeks of reducing temperatures for maximum tolerance to develop. Photoperiod seems to be involved in the process in carob, as in many other evergreen species (Batlle & Tous, 1997).

Frost sensitivity varies between cultivars; the Portuguese cultivar 'Galhosa' appears to be more cold tolerant than 'Mulata', and in Andalusia, ungrafted trees of the cultivar 'Bravia' appear more tolerant than grafted cultivars (Batlle & Tous, 1997). Such is the problem that cultivators in southeast Spain have traditionally protected against damage from occasional frosts by covering the main trunk with jute cloth or by surrounding carob trees with stone walls.

Older trees with large branches are inevitably susceptible to loss of limbs by high winds. Wind can also prematurely remove unripe fruit, reducing income. In southeast Spain, it is common for large, horizontal branches to be supported with stone walls (X. Garcia-Martí, personal communication).

Carob is unable to withstand waterlogging but is resistant to drought, acting as a drought avoiding water spender (Ezzine et al., 2023; Nunes et al., 1989) resistant to drought-induced cavitation—see Section 6.5. As such, it is often better able to survive in semi-arid Mediterranean areas where water is periodically available compared to *Olea europaea* subspecies and *Laurus nobilis* (Lo Gullo et al., 2003; Salleo et al., 2001). However, since carob requires sufficient water in the soil to fund its water spending habit, carob is less likely to grow in very low rainfall areas where *O. europaea* can still survive (Lo Gullo & Salleo, 1988) but is still often more drought tolerant than *Quercus ilex*.

High leaf water content can be maintained despite stomata remaining open even under low soil water availability (Nunes et al., 1989) but leaf water potential can reduce rapidly in response to small water losses (Catarino et al., 1981; Lo Gullo & Salleo, 1988). Water loss is reduced by leaf wax (Section 6.1), reducing cuticular permeability and thus water loss (Baker & Procopiou, 1980), and wax synthesis has been shown to increase in dry conditions to 53 ± 1.4 (SE) $\mu\text{g}/\text{cm}^2$ compared to $32 \pm 4.9 \mu\text{g}/\text{cm}^2$ in an irrigated habitat, which is higher than the normal wax content of $10\text{--}30 \mu\text{g}/\text{cm}^2$ of temperate plants (Baker & Procopiou, 1980). Increases in wax content with dryness were much smaller in *Olea europaea* (Baker & Procopiou, 1980). Carob also has an extensive root system that penetrates deep into the soil—similar to *Pistacia lentiscus*—with the ability to develop new, deep roots at times of low water moisture content (Christodoulakis, 1992), thus funding the water loss caused by open stomata. Lateral roots formed c. 50% of root biomass of 2.3-year-old seedlings, similar to that in *Quercus coccifera* and *Pinus halepensis* (Azar et al., 2023). The roots of experimentally unwatered plants were found to be shorter than those of well-watered plants, but root dry mass of unwatered plants in the upper soil horizons was similar to that of well-watered plants. This may be due to increased suberization and/or lignification in dry soils which could prevent water movement from the root into very dry soil (Rhizopoulou & Davies, 1991). The primary roots also have large stomata that are permanently open which may increase gas exchange or increase water and nutrient uptake (Christodoulakis et al., 2002). The

importance of the roots in water supply in carob was demonstrated by Azar et al. (2023) who showed that carob shoots were more highly stressed by experimental root loss of up to 75% of their depth than either *Pinus halepensis* or *Quercus coccifera*.

Differences in drought resistance have been noted between plants of different geographical origin (Zagoub et al., 2023) and between cultivars. Correia et al. (2001) noted that 'Galhosa' in southern Portugal was the only cultivar in which leaf water potential did not fall below the turgor loss point and leaf relative water content remained above 90%. This cultivar was found to have the widest xylem conduits of any tested, which may partly explain why midday leaf water potential in 'Galhosa' remained higher than -2.0 MPa even at the end of a summer drought. Osório et al. (2011) exposed 1-year-old seedlings to two temperature regimes of $25/18^\circ\text{C}$ and $32/21^\circ\text{C}$ day/night (12h each) with some plants not watered for 15 days to create water stress. Photosynthetic rate was decreased by 33% compared to controls at the lower temperature range but adding water stress had little effect on photosynthesis. At the higher temperature range, photosynthetic rate was reduced by 84% and drought significantly reduced the yield of PSII photochemistry and favoured the overproduction of reactive oxygen species. Despite this, carob showed a high capability for photosynthetic recovery 36h after rewatering, which suggests that carob can cope with predicted climate change (Osório et al., 2011)—see Section 11.

Carob is one of the most salt-tolerant trees grown in Mediterranean orchards. One-year-old carob rootstocks growing in soil were able to tolerate 2 months of exposure to salinity at $6.8 \text{ mS}/\text{cm}$ or more than $40 \text{ mmol NaCl}/\text{L}$ (Batlle & Tous, 1997; Correia et al., 2010), similar to that of *Olea europaea*, *Ficus carica* and *Cocos nucifera* (Ebert, 2000). Only *Phoenix dactylifera* was more tolerant of higher salinity up to $10 \text{ mS}/\text{cm}$ (Ebert, 2000). Correia et al. (2010) also found that leaves were shed in plants receiving $>80 \text{ mmol NaCl}/\text{L}$ for 40 days and no new leaves were produced at $>40 \text{ mmol NaCl}/\text{L}$. Leaf dry mass per unit plant dry mass decreased to 0.21 after 60 days at $240 \text{ NaCl}/\text{L}$, compared to 0.36–0.37 in a non-saline control (Correia et al., 2010). Carob seeds were found to be tolerant of different chloride salts (KCl , NaCl , CaCl_2 , MgCl_2) up to 120 mM , the highest concentration tested, showing c. 50% of the germination of the control, and with similar hypocotyl and radicle length to the control (Dadach et al., 2023). Resultant seedlings used the biosynthesis of sugars and proline to cope with salt stress. El-Dengawy et al. (2011) irrigated 1-month-old carob seedlings with seawater solutions with an assumed concentration of 8, 16 and 24% seawater. Seedling survival decreased from 100% in a non-saline control to 70% in the strongest seawater. Increasing concentration also decreased growth of shoots and roots in all parameters measured. For example, shoot length was significantly reduced by 8% and root length by 51.4% at the highest seawater concentration compared to the control. Total chlorophyll was $12.91 \mu\text{g}/\text{cm}^2$ in the control, reducing to $7.72 \mu\text{g}/\text{cm}^2$ in 24% seawater, while other factors significantly increased with increasing salinity, including concentrations of proline (an osmolyte; 0.38 and $5.36 \text{ mg}/\text{g DW}$ in the control and 24% seawater, respectively), Na (0.33% and 1.01%), Cl (0.66% and 1.16%) leaf diffusion resistance to

water vapour (4.39 and 32.22 s/cm) and percent of leaves showing damage (0% and 46.3%). Seedlings inoculated with the bacterium *Azospirillum lipoferum* through the growing medium showed significantly increased root growth in the strongest seawater, and this may help commercially grown plants cope with salt stress due to sea water intrusion in deep wells, particularly during dry years, when irrigation water will become increasingly saline (Correia et al., 2010).

Carob is remarkably tolerant of fire because its leaves have low flammability compared to other Mediterranean woody plants and because it accumulates less dead plant material on the ground than other trees (Srećec et al., 2017). Due to these factors, groups or lines of carob trees can be used for firebreaks in low- and medium-altitude forest areas by creating fuel discontinuities, and will be one of the main strategies used for preventing and reducing the severity of forest fires in coastal and sub-coastal areas of the eastern Iberian Peninsula. Old carob trees are likely to survive higher fire frequency and fire intensity resulting from climate change and so will become even more important on the landscape for biodiversity conservation (Section 11). However, carobs are susceptible to subsurface fires in the stem and roots (which happens to a lesser extent in *Olea europaea*) which impairs the ability to regrow if the root system is severely damaged (Juli G. Pausas, personal communication). Carob is unlikely to be dependent on fire for seed germination (Section 8.4).

Carob is tolerant of air pollution (Section 4) but is highly sensitive to radioactive elements and certain heavy metals such as chromium, cobalt, vanadium and lead (Salazar Hernández et al., 2002).

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Due to the large compound leaves, compared to most Mediterranean trees, carob trees have comparatively few, thick branches arising from a thick trunk. Growth is initially monopodial but soon forms an open hemispherical crown. In large trees, especially those previously pruned and then abandoned, the crown can open up due to progressive breaking of the branches and decay of the trunk(s). The initial bark phellogen is maintained for around 40 years resulting in smooth bark, helped by shedding thin layers of bark in a similar manner to birches. Thereafter, deeper phellogens are initiated leading to a rougher bark (Arzee et al., 1977).

The leaves of carob are usually large (<10–100 cm² depending upon cultivar) and thick (556 µm) for a Mediterranean tree (Christodoulakis, 1992; Lo Gullo et al., 1986). Leaf area index of carob leaves grown in full sun (0.62 g/cm³) is intermediate between other species tested (Christodoulakis, 1992) but carob has a leaf mass per unit area of 22.9 mg/cm², similar to *Olea europaea* (22.1 mg/cm²) and lower than *Pistacia lentiscus* at 33.7 mg/cm² (Clemente et al., 2004). Although carob normally grows in full sunlight (Section 6.5), Catarino et al. (1981) found that leaves of carob seedlings grown in 10% full sunlight were half the thickness of those in full sun. The leaf epidermis on the adaxial surface (41 ± 7 µm thick) is multilayered

(Nikolopoulos et al., 2024) and twice as thick as other species tested (*Olea europaea*, *Pistacia lentiscus*, *Quercus coccifera*) and is impregnated with condensed phenolics; the abaxial epidermis (21 ± 7 µm) is similar to the other species (Christodoulakis, 1992). Part of this epidermal thickness is due to a thick cuticle on both sides, 5 and 3 µm on the adaxial and abaxial sides, respectively (Lo Gullo et al., 1986), with wax rods on the adaxial side and an intricate network of randomly arranged nanometre-thick and micrometre-long wax plates on the abaxial surface (Pereira et al., 2022). Both surfaces are highly hydrophobic, but the abaxial especially so with a water contact angle of 162° (Kolyva et al., 2012; Pereira et al., 2022). The abaxial surface also has a higher light reflectance than that of the adaxial surface (Pereira et al., 2022). Rodríguez et al. (2021) suggest that these work as a sophisticated light and water management system, reflecting light to maintain a lower surface temperature, and a superhydrophobic character to keep the surface dry to aid gas exchange.

Stomata are present only on the abaxial surface and arranged in clusters (Christodoulakis, 1992; Nunes & Linsens, 1980) with wax platelets surrounding the stomatal pores (Kolyva et al., 2012). Stomatal density varies from c. 180/mm² in open conditions to c. 230/mm² in 80% light, reducing to c. 130/mm² and c. 100/mm² in 50% and 10% sunlight, respectively (Catarino et al., 1981; Christodoulakis, 1992). Stomata have also been found on the primary roots of carob seedlings, even into the root hair zone, which remain permanently open (Christodoulakis et al., 2002). Stomatal development is slow and in the youngest leaves of a tree, the young guard cells are not separated by a stomatal aperture and only 3% may be functional (Lo Gullo et al., 1986). About 77% of the stomata were mature in the fourth oldest leaf back from the apex and all stomata were fully functional in the seventh leaf.

The leaves of carob are not shed in the autumn but rather in July of the second year. Leaf duration thus varies between 16.8 and 26.7 months, with leaves at the end of a branch living longer than those nearer the start of the year's growth. This is similar to *Olea europaea* (19.4–26.7 months) and *Myrtus communis* (17.9–25.9 months) but twice as long as *Pistacia lentiscus* (7.9–15.7 months) and *Quercus coccifera* (10.9–18.3 months) (Batlle & Tous, 1997; Diamantoglou & Mitrakas, 1981).

The inflorescence is generally a raceme but can be cymose with secondary branching (Custódio, 2005). The inflorescence is generally longer in male trees than in females (means of 5.71 and 4.45 cm, respectively), with more flowers (means of 42 vs. 30 flowers, respectively) (Gharnit et al., 2004). Four inflorescence types are recognised: male, female, polygamous and hermaphrodite (Section 8.1). Hermaphrodite flowers were measured by Custódio et al. (2005) to weigh 100 ± 10 mg (SE, *n* = 3 of 30 flowers each) while male and female flowers were significantly lighter (30 mg). Male flowers can vary in the number of parts contained. Gharnit et al. (2004) noted in Morocco that 71.6% of flowers had five sepals and five stamens, 11.3% had an extra stamen and 15.8% had an extra sepal and stamen. Similarly, in female flowers, they found a varying number of sepals and a pistil that was either curved (35% of flowers), slightly curved (34.8%) or straight (30.2%). Hermaphrodite flowers could have an

extra stamen and the stamens persist after pollination until the fruits are mature (Gharnit et al., 2004). Microsporogenesis of male flowers is described by Custódio et al. (2005). Pollen grains are ellipsoidal/spheroidal and tetracolpate, $(23\text{--}29\text{--}38) \times (23\text{--}28\text{--}34) \mu\text{m}$ (El Kholly et al., 2023; Ferguson, 1980; Linskens & Scholten, 1980).

Wild trees tend to have smaller curved fruits lacking fleshiness compared to cultivated trees, smaller seeds (Section 8.3), less fruit pulp and a lower sugar content, but there is a degree of overlap. Fourier transform infrared (FTIR) spectroscopy shows promise as a method for separating wild trees and cultivars (Christou et al., 2018). Many papers give extensive details of sizes of leaves, fruits and seeds from different cultivars (Ali et al., 2019; Barceló-Anguiano et al., 2024; Gharnit, 2003; Gharnit et al., 2005; Papadopoulou et al., 2023).

Seedlings rapidly develop a tap root (Section 8.5). Older plants have an extensive root system with a well-developed taproot which penetrates deeply into the soil (Custódio, 2005; Tous et al., 2013) although no quantitative data on depth or spread are available. The breadth and depth of the roots allow water to be taken up during extended dry periods (Custódio, 2005)—Section 5.3.

6.2 | Mycorrhiza

Carob roots are known to support arbuscular mycorrhizal (AM) fungi; no ectomycorrhizal association has been found (Batlle & Tous, 1997). Spores of AM fungi were extracted from beneath carob trees in Morocco and identified as *Rhizophagus irregularis* (Błaszk., Wubet, Renker & Buscot) C. Walker & A. Schüßler (= *Glomus intraradices*), *G. aggregatum* N.C.Schenck & G.S.Sm., *G. constrictum* Trappe (Glomeromycota, Glomerales) plus two further unidentified *Glomus* species and two species of *Gigaspora* (Glomeromycota, Diversisporales). A mean total spore number of 2100 spores/100g dry soil (range 600–4000 spores/100g of dry soil) was found, significantly higher than previously recorded under other Mediterranean species (Lahcen et al., 2012).

While a study that added a mix of AM and ectomycorrhizal fungi to young seedlings planted in a reclamation project in a limestone quarry in southwest Portugal, found that the inoculum made no difference to any growth parameters or survival (Clemente et al., 2004), the majority of studies have found that carob shows better growth and reproduction in severe environmental conditions when mycorrhizal associations are formed (Boutasknit et al., 2020, 2021, 2022; Essahibi et al., 2018). Lahcen et al. (2012) used spores collected from soil samples as an inoculum for carob seedlings in otherwise sterile soil in a glasshouse. Six months after adding inoculum, mycorrhizal plants were significantly larger ($p < 0.05$) in all growth parameters measured, being taller (22 ± 1 cm control vs. 29 ± 3 cm inoculated; assumed SD) with more leaves (35.75 ± 1 vs. 55.25 ± 1.5), higher root dry mass (2.45 ± 0.25 g vs. 3.24 ± 0.6 g) and higher total biomass (8.13 ± 1 g vs. 10.90 ± 1.4 g). Inoculated plants also had higher total P above and below ground (32.07 ± 2.6 mg/plant control vs. 61.32 ± 3.4 mg/plant inoculated) and total N (126.96 ± 13 mg/plant

control vs. 355.94 ± 4.1 mg/plant inoculated). Similarly, seedlings grown in soil with AM inoculants composed of a mix of AM fungal species resulted in improved seedling performance over 8 months with an increase in plant height of between 33% and 70% compared to an uninoculated control. Above-ground dry mass also increased between 62% and 124% and root dry mass increased between 24% and 86% compared to the uninoculated control (Outamamat et al., 2022).

Colonisation of AM fungi is associated with soil nutrient availability. Cruz et al. (2004) watered seedlings with either Hoagland's solution (supplying N, P and K) or low nutrient water every 3 days and either inoculated or not with *Rhizophagus irregularis*. On low nutrient soil, biomass growth after 3 months was c. 30% higher (DW) when inoculated and 30%–36% of roots were colonised by AM fungi compared to 11%–12% in high nutrient soil. Moreover, inoculated plants on low nutrient soil had significantly higher nitrate and ammonium uptake (c. $28 \mu\text{mol plant}^{-1} \text{h}^{-1}$) than uninoculated plants ($17 \mu\text{mol plant}^{-1} \text{h}^{-1}$). No significant difference in nutrient uptake was found between inoculated and uninoculated plants on high nutrient soil (Cruz et al., 2004). Indeed, phosphate fertilisation can negatively influence the establishment and functioning of mycorrhizal fungi (Essahibi et al., 2019). They inoculated rooted cuttings of carob with AM fungi - either *Funneliformis mosseae* (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler, *Rhizophagus irregularis* or *R. fasciculatus* (Thaxt.) C. Walker & A. Schüßler (Glomeromycota, Glomerales). Cuttings supplied with less than 25 mg P/kg soil grew better when inoculated, particularly with *F. mosseae*. With this low phosphorus input, inoculated plants showed higher mineral uptake (P, K, Na and Ca), photosynthetic activity, stomatal conductance, total chlorophyll content and soluble sugar accumulation, plus had strongly increased acid phosphatase activity in roots and rhizospheric soil and maintained high membrane integrity (over 80%) and low hydrogen peroxide and malondialdehyde content compared to uninoculated plants (Essahibi et al., 2019). However, with high phosphorus input at 100 mg P/kg soil, inoculation made no significant difference to growth and negatively affected root colonisation by AM fungi (Essahibi et al., 2019). Inoculation with AM fungi also helps cuttings withstand drought stress (See Section 6.5).

6.3 | Perennation: Reproduction

As a phanerophyte, carob trees can readily resprout from the base after cutting, burning or shoot death due to drought (Domínguez et al., 2010), but they do not naturally reproduce vegetatively from root suckers or by layering. Female plants considered superior in form, growth or fruit production have traditionally been clonally propagated by grafting (Zohary, 2002) with wild carob trees often being used as rootstocks (Baumel et al., 2022; Zohary, 1973). Thus, while sex ratios are approximately 50:50 male:female in wild populations (Section 8.1), cultivated areas are dominated by female plants since they produce the commercially used fruit. In carob strongholds, such as the Spanish east coast, it was common practice to

graft onto a male rootstock ('borde macho' in Spanish) and allow a few branches of it to grow to facilitate pollination and increase the quantity and quality of fruits. Similarly, a few male seedling trees may be kept. Hermaphrodite trees are also used in commercial orchards which have the advantage of some fruit production but since this is not as high as in female trees they are not normally in high numbers. The generally recommended ratio in commercial orchards is for one in eight trees (12%) to be male or hermaphrodite pollinators, spread evenly through the orchard (Tous & Batlle, 1990). In Cyprus, Orphanos (1980) recorded that very few carob trees are planted but are grafted onto wild trees in situ. There is thus an intergrade between wild trees, feral trees (wild rootstock taking over from the grafted cultivar) and those cultivated. Wild trees generally have several trunks and small curved fruits while grafted cultivated trees in orchards have larger, straighter fruits.

Vegetative propagation of carob from cuttings is traditionally considered difficult (Fadl et al., 1979; Lee et al., 1977). However, adventitious rooting is possible with subterminal hardwood cuttings, 2 or 3 years old, treated with sulphuric acid and the addition of sugars to the growth medium, or 7500–10,000 ppm of Indole-3-butyric acid (IBA) (Batlle & Tous, 1997). Well-drained soil with bottom heat (24°C) and misting once every 2 min during daylight is also needed (Alorda et al., 1987; Custódio, Martins-Loução, & Romano, 2004). Cuttings are best taken in March–April; Fadl et al. (1979) in Egypt found zero rooting in January and February compared to 57% of cuttings rooting in April if buds were left in place (almost as high in March and May) and 39% in July for disbudded cuttings. In contrast, Lee et al. (1977) used IBA (unstated concentration) and sulphuric acid and achieved 100% rooting in January and 75% in June. It appears that cultivars differ in their rooting ability and is most successful in 'De la Mel' (syn. 'Negriño') (85%) and 'Galhosa' (44%) compared to 'Mulata' (27%) (Batlle & Tous, 1997). Exposure to mycorrhizal fungi can also help cuttings to root and to better survive transplantation (Essahibi et al., 2017). Carob can also be successfully air-layered (Gubbuk et al., 2011).

Carob can be micropropagated using both juvenile and adult tissues (Gonçalves et al., 2005; Hsina & El-Mtili, 2009; Lozzi et al., 2019; Naghmouchi et al., 2008, 2012; Romano et al., 2002; Sayed et al., 2020; Sebastian & McComb, 1986; Shahzad et al., 2017; Vinterhalter et al., 1992). This is possible by axillary budding from nodal explants of young stems and by apex culture (Costa-Pérez et al., 2023; Gonçalves et al., 2005), and somatic embryogenesis from immature cotyledons (Canhoto et al., 2006; El Bouzdoudi et al., 2017), mature cotyledons (Lozzi et al., 2015), zygotic embryos (Custódio & Romano, 2006) or immature seeds (Ksia et al., 2008). Micropropagated plants can match the field performance of plants from seed (Osório et al., 2012).

Carob readily reproduces by seed and feral seedling 'escapes' are common around orchards (Batlle & Tous, 1997). Feral trees are likely to have a different genotype to the mainly female orchard trees depending upon the origin of the pollen (Introductory paragraph; Sections 6.1 and 8.1). Carob tends to flower and fruit well every second year. It is suggested that an abundance of fruits has an inhibitory

effect on the current season's flower differentiation, mainly during the period of most intensive fruit and seed growth from April to June (Batlle & Tous, 1997).

Flowers are first produced on trees grown from seed when around 7–8 years old. Commercial trees traditionally involve grafting female buds onto 2- to 4-year-old seedling rootstocks (Batlle & Tous, 1997) which can produce flowers 4–5 years after grafting but taking up to 8 years in poor soils or under inhospitable conditions such as intense competition or low rainfall (Batlle & Tous, 1997). There is also variation in age of first flowering between cultivars with some flowering as early as 4–5 years after grafting, such as *Ceratonía* 'Rojal', 'Ramillete', 'Mulata' and 'AIDA', while others are renowned for starting later, such as *C.* 'Banya de Cabra', 'Cacha' and 'Sandalawi' (Batlle & Tous, 1997). Hermaphrodite individuals normally start flowering before female cultivars, as, for example, in the clones e-13P, e-14P and 'Turis' (Tous & Franquet, 2024). Fruit production begins at around 10–15 years of age, increasing over the next 10–15 years as the canopy grows larger, and reaching a maximum at around 20–30 years of age, remaining stable until the tree declines with age (Custódio, 2005).

Individual trees live for at least 70 years (Correia et al., 2020), but the maximum age possible is open to speculation. The Monumental Trees Database (2023) records a tree of c. 10.10 m girth (at 1.3 m above ground) in Valencia, eastern Spain as being c. 133 years old, but this is likely to be an underestimate, and larger and undoubtedly much older trees exist (Figure 2). Indeed, the Monumental Tree Database (2013) includes exceptional carob trees from 6 to almost 13 m in girth located in Italy (Sicily), Croatia, Greece, Malta and Portugal. Large carob trees are often hollow, but can be found solid to the centre (more so than in *Olea europaea*), so carbon dating is a possibility.

6.4 | Chromosomes

The diploid chromosome number for *Ceratonía* is $2n=24$ whereas many members of the same Cassieae tribal complex have $2n=48$ (Goldblatt, 1981). Triploid and tetraploid carob trees have been recorded in Israel by Bureš et al. (2004), but there appear to be no other records. The mean nuclear genome size of carob was measured in Tunisian trees at $2C=1.20$ – 1.30 pg (El Ferchichi Ouarda et al., 2008), and is made up of between 492 and 570 Mbp (Bibi et al., 2023; Bureš et al., 2004). This contains an estimated 43,965 genes, comparable to other plant species, with c. 17% of species-specific genes, a relatively large proportion compared to other plants (Bibi et al., 2023). Chlyah et al. (2024) have published the complete genome sequence of *Ceratonía siliqua*.

6.5 | Physiological data

Ceratonía siliqua is adapted to grow in full sun. Total chlorophyll content in the field was measured at 0.343 ± 0.030 (SE, $n=5$) g/m²

with chlorophyll a c. 0.4 g/m^2 , chlorophyll b c. $0.1\text{--}0.2\text{ g/m}^2$, giving a ratio of 3.1–3.5, which is typical of sun plants (Osório et al., 2012). According to Clemente et al. (2004), carob chlorophyll content lies between that of *Olea europaea* (mean of 0.148 g/m^2) and *Pistacia lentiscus* (0.105 g/m^2). However, in full sun, the mean values for the maximum photochemical efficiency of PSII (Fv/Fm) remained close to the maximum at 0.75–0.85 in full sun (Osório et al., 2012) with maximum rates of photosynthesis ranging from $0.011\text{ mmol m}^{-2}\text{ s}^{-1}$ in newly established trees to $2.9\text{--}4.3\text{ mmol m}^{-2}\text{ s}^{-1}$ in established trees >44 years old (Osório et al., 2012; Pérez-Pastor et al., 2016). Catarino et al. (1981) germinated seeds of carob in a glasshouse at various light intensities and found total chlorophyll content increasing from 10.96 mg/g fresh mass at 100% light to 11.48, 14.76, 19.52 mg/g at 80, 50 and 10% light, respectively. Cuticular resistance also increased from $163\text{--}245\text{ s/cm}$ at 100% to 401 s/cm at 10% light, giving the highest resistance in leaves with the thinnest cuticle. Specific leaf area decreased with shade from c. 0.9 g/cm^2 to c. 0.3 g/cm^2 in 10% light. Biomass of seedlings was strongly reduced in 50 and 10% light, and at 10% light was not adequate for prolonged growth (total dry mass of 8-month-old seedlings: 11.01 g , 100% light; 11.30 g , 80%; 9.56 g , 50%; 1.83 g , 10%). Root:shoot ratio generally increased with shade (1.82, 100%; 1.46, 80%; 2.01, 50%; 2.98, 10%). The poor shade tolerance of seedlings matched that of *Quercus* spp. (Catarino et al., 1981). Sack et al. (2003) measured leaves from open and shaded stands in southern Spain and found that, while the leaf lamina area of carob was not significantly different between sun leaves (10.5 ± 1.85 [SE, $n=10$] cm^2) and shade leaves ($11.5 \pm 0.560\text{ cm}^2$), specific leaf area was significantly lower in sun than shade leaves (64.0 ± 3.16 , $100 \pm 11.0\text{ cm}^2/\text{g}$, respectively). They concluded that differences between sun and shade leaves were marginal.

Highest photosynthesis rates are measured in the spring and autumn, reaching $25\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ under optimal temperature (23°C) and soil water at field capacity. Rates are lower in winter, due to lower night temperatures ($4\text{--}6^\circ\text{C}$) and in June when soil water may drop to <5% field capacity but are frequently still around $15\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ which is still 75% of spring levels. Only after prolonged summer drought over several weeks when available soil water was depleted down to 50cm would photosynthesis approach zero (Nunes et al., 1992). Sakcali and Ozturk (2004) found that on the most open, degraded sites in Turkey, carob leaves were no longer capable of compensating for water loss and the leaf water potential would fall to -3.3 MPa , compared to -2.2 MPa on a more vegetated, moister site. Normally, rapid falls in leaf water potential help ensure adequate supply of water to the leaves, such that the difference in water potential between full turgor and incipient plasmolysis was measured at just 17% in September and loss of turgor never occurred in the field (Lo Gullo & Salleo, 1988). This is matched by stomatal conductance which in well-watered carob trees can be $>200\text{ mmol m}^{-2}\text{ s}^{-1}$ and stays high, between 60 and $100\text{ mmol m}^{-2}\text{ s}^{-1}$, even when soil water is reduced to 25% field capacity, and will only drop to around $20\text{ mmol m}^{-2}\text{ s}^{-1}$ under extended summer drought (Essahibi et al., 2019; Ezzine et al., 2023; Lo Gullo et al., 2003; Nunes

et al., 1992; Osório et al., 2012; Pérez-Pastor et al., 2016). As a consequence, carob was much more water efficient at $165\text{--}190\text{ }\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ compared to $63\text{--}74\text{ }\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ in apricot *Prunus armeniaca* (Pérez-Pastor et al., 2016).

Even in summer, healthy and apparently turgid leaves are the norm on trees even in apparently dry soil, since carob is a 'water spender' (cf Basu et al., 2016) with high rates of water transport (Nunes et al., 1992). The high relative water content decreased from 99% to 97% over daytime, and only reached turgor loss point under severe summer drought (Lo Gullo et al., 1986, 2003). Carob leaves stressed to a water potential of -2.0 MPa , can maintain stomatal conductance equal or higher than that reported for competing species such as *Olea europaea* (Lo Gullo et al., 2003) which close their stomata for part of the day (Lo Gullo et al., 1986). The youngest leaves within a year's growth are potentially more vulnerable to water loss, even though only 3% of their stomata may be functional, greatly reducing stomatal transpiration. However, the osmotic potential at full turgor decreases with the leaf age from 0 to 7 MPa in the youngest leaf to -1 to 65 MPa in the oldest (and -1 to 8 MPa in last year's leaves) plus the cells of younger leaves lack rigidity which, in older leaves, helps resist the loss of turgor (Ezzine et al., 2023; Lo Gullo et al., 1986). This potential problem is overcome by >90% of leaves being produced between January and May (Section 7) when water is more readily available and so the youngest leaves are drought escaping (Lo Gullo et al., 1986).

Relatively wide xylem vessels in the twigs (35% of them up to $50\text{ }\mu\text{m}$ in diameter) and veins of leaflets (up to $15\text{ }\mu\text{m}$ diameter) can provide leaves with sufficient water to maintain turgor (Kikuta et al., 1997; Lo Gullo & Salleo, 1988; Salleo et al., 2001). Some cavitation in stems and leaves is therefore inevitable but tolerated to allow high gas exchange and productivity. Salleo and Lo Gullo (1989) measured the percentage of air-filled xylem vessels in cross sections of seedlings and found 2% air-filled in watered controls, rising to 5.2%, 13.8% and 40.4% in seedlings unwatered for 9, 16 and 23 days, respectively. At the junction between the stem and petiole, 18.5% of cross-sectional areas was air-filled only in the plants unwatered for 23 days, presumed to be due to the high number of narrow vessels, preventing cavitation in leaves travelling back into the stem. Fortunately, carob is also very good at recovering from cavitation-induced xylem embolism, making it a successful drought strategy (Lo Gullo et al., 2003). Salleo and Lo Gullo (1989) found that 2 days after rewatering their stressed seedlings, 100% of the vessel blockages had cleared in plants unwatered for 9 days and c. 33% had cleared in plants unwatered for 16 days.

Although the carob tree is a legume, it is considered not to produce root nodules in nature (Martins-Loução & Rodríguez-Barrueco, 1982). Nitrogenase activity inside carob roots was detected by El Idrissi et al. (1996) along with Gram-negative bacteria. It is not clear, however, whether these bacteria contributed any significant amounts of N to the carob plant. Rhizobacteria experimentally inoculated into the rhizosphere of carob seedlings have been found to increase the mass of all parts of the plant which was attributed to nitrogen fixation by the bacteria (El Kakhahi et al., 2019) suggesting that internal fixation of N is normally minimal.

Cruz et al. (1991) found 70% of nitrate reductase activity in carob seedlings was in secondary roots (which made up 43% of fresh plant mass), reaching $4.22 \mu\text{mol nitrite h}^{-1} \text{g}^{-1}$ fresh mass, whereas leaves (making up 44% of fresh plant mass) contained 20% of nitrate reductase activity at $1.20 \mu\text{mol nitrite h}^{-1} \text{g}^{-1}$. The low nitrate reductase activity in leaves was attributed to a limited supply of nitrate from the roots due to limited loading of nitrate into the xylem. As a consequence, nitrate concentration was very low in the leaves: fully expanded leaves of 2-month-old plants contained $0\text{--}1 \mu\text{mol nitrate/g}$ fresh mass, a concentration 100 times lower than that in the main roots, 200 times lower than in secondary roots and approximately 650 times lower than in root tips (Cruz et al., 1991).

Nitrogen levels within leaves vary little through the year suggesting that the N in flowers was taken from stores in the trunk and roots rather than being translocated from the leaves (Custódio et al., 2007). Flowers had higher concentrations of N, P and K but lower levels of Mn than leaves. Female flowers tended to contain lower concentrations of nutrients than males or hermaphrodites; for example, females contained 18.5g/kgN compared to 20.7 and 22.1g/kg in male and hermaphrodite flowers (significant at $p < 0.05$), respectively (Custódio et al., 2007). The high levels of N in flowers have been taken to indicate the importance of N supply in maintaining commercial fruit yield (Correia & Martins-Loução, 1993, 1997, 2005). Indeed, the number of inflorescences on a tree is known to be affected by the time and the level of N fertiliser application (Correia & Martins-Loução, 1997; Custódio, 2005).

Carob seedlings were found to have 33%–37% more P in the roots and shoots compared to control plants when given an experimental application of Saharan desert dust at 100g/m^2 , which is within the range of annual dust deposition in the southern Negev desert (Starr et al., 2023), where the P was absorbed directly through the leaf surface. This was, however, accompanied by a 17%–30% reduction in photosynthesis due to shading by the dust. A negative relationship has been found between amount of fruit produced and leaf P concentration (Correia et al., 2002) suggesting that P is translocated from leaves to flowers and fruit (Custódio, 2005). Fertilising carob with K has no appreciable effect on branch growth or fruit yield but adding K with N increased the number of inflorescences more than N by itself (Correia et al., 2008; Correia & Martins-Loução, 2004). Slow-release NPK fertiliser (10:10:10) added to 2-year-old seedlings planted on limestone in southwest Portugal, significantly increased shoot growth from c. 20 cm in controls to 45 cm in the first year, and increased basal diameter growth from c. 10 to c. 16 mm (Clemente et al., 2004). Fertilisation appears to be effective even without irrigation (Correia & Martins-Loução, 1995).

Although carob is frequent on calcareous soils (Section 2.2), Fe uptake rarely appears to be low enough to cause chlorosis. Pestana et al. (2012) found that 15 cm tall seedlings grown in nutrient solutions maintained a steady growth rate of 2 mm per day irrespective of Fe^{3+} levels given. High ferric-chelate reductase activity of c. $1.5 \text{nM Fe}^{2+} \text{min}^{-1} \text{g}^{-1}$ fresh mass was found even when Fe was present in

the nutrient solution, rising sharply to c. $2.1 \text{nM Fe}^{2+} \text{min}^{-1} \text{g}^{-1}$ in the absence of Fe. Carob appears to maintain a large capacity for reductase activity to prevent iron deficiency.

6.6 | Biochemical data

As shown in Table 2, biochemical components of carob can vary greatly, depending on origin of the plant, whether it is a wild plant or cultivar (and which cultivar) and time of year (Calixto & Cañellas, 1982; Stavrou et al., 2018; Vardar et al., 1972). For example, sucrose increased from c. 2.5% in late March to c. 35% when the fruit ripens in mid-August in Cyprus (Davies et al., 1971) and polyphenols, flavonoids, condensed tannins, antioxidant capacity and mineral composition are highest per unit of dry mass in unripe fruit as they protect the developing seeds (Albanell et al., 1996; Correia et al., 2018; Kyriacou et al., 2021; Othmen et al., 2019). Higher concentrations of phenols and antioxidants are recorded in plants growing in more arid areas in Tunisia (Richane et al., 2022) where it is harder to replace parts lost to herbivory. This fits with research in Italy that showed that of the seven different species tested, leaves from carob, *Myrtus communis* and *Salvia rosmarinus* had the highest phenolic content (16.43 ± 0.24 ; 16.01 ± 1.32 ; $16.47 \pm 0.05 \text{mg/g}$, respectively) and much higher than in *Arbutus unedo* and *Eucalyptus camaldulensis* (5.97 ± 0.75 and $5.88 \pm 0.31 \text{mg/g}$, respectively) (de Falco et al., 2021). Antioxidant activity showed a similar pattern. Ripe carob fruits contain a large amount of condensed tannins, 16%–20% of dry mass (Würsch et al., 1984). A detailed review of polyphenols of various parts of the carob plant is given by Stavrou et al. (2018). Similarly, reviews of the nutritional value of many carob products are given by Papaefstathiou et al. (2018) and Rasheed et al. (2019).

Powdered carob fruits have been found to contain a number of phenolic compound, particularly pyrogallol (4970 ppm), catechol (165 ppm), chlorogenic acid (101 ppm), protocatechuic (79 ppm) and caffeine (48 ppm), and to a lesser extent catechin (28 ppm), vanillic (14 ppm), ferulic (10 ppm), gallic acid (10 ppm), cinnamic (8 ppm) and coumarin (4 ppm) (Youssef et al., 2013). Chlorogenic acid and caffeic acid are known antioxidants while others have anti-cancer properties (Section 10.2).

In Turkey, seeds from cultivars and wild plants contained 1.73% and 1.82% of oils (Matthaus & Özcan, 2011). The four most common fatty acids in carob are recorded in Table 2 but up to 17 fatty acids have been identified in carob seeds (Youssef et al., 2013), characterised by >69% unsaturated fatty acids with high levels of linoleic acid (omega-6) and low contents of omega-3 (Ben Ayache et al., 2021; Fidan et al., 2020; Yatim et al., 2022). Carob powder is also a valuable source of vitamins E, D, C, Niacin, B6 and folic acid with smaller amounts of vitamins A, B2 and B12 (Youssef et al., 2013). The vitamin E tocopherols are γ -tocopherol (53.1%), α -tocopherol, δ -tocopherol and β -tocopherol (Ben Ayache et al., 2021; Fidan et al., 2020; Matthaus & Özcan, 2011), offering protection against diabetes (Di Vincenzo et al., 2019). The lipid fraction also contains a number of sterols, notably β -sitosterol (>70%) campesterol (5%), stigmasterol

	Fruit pulp	Seeds	Leaves	Sources
Polyphenols mg/g	7.4–19.0	0.7–4.1	91–680	1, 2, 3, 4, 5, 19
Flavonoids mg/g	0.2–0.3	0.3–3.3		4, 19
Total lipids %	0.4–1.5	1.5–2.9		4, 5, 6, 7, 8, 9, 10, 18
Linoleic acid % of total	23	32–62		2, 7, 11, 12, 13
Palmitic acid % of total	11	10–20		
Oleic acid % of total	41	8–45		
Stearic acid % of total	3	1–5		
Cerotic acid % of total		0.5–5		
Total sugar %	37–56	6.6–9.3		4, 5, 10, 14
Sucrose % of total	31–45			3, 8
Fructose % of total	5–11			
Glucose % of total	2–6			
Total protein %	2.7–6.8	17–65		3, 4, 9, 15
Ash %	1.6–3.8	3.9–4.6		3, 4, 10, 16, 17
Fibre %	4.9–9.6	11.5		3, 9, 10
Minerals mg/100g				3, 4, 9, 16
P	70–146		125	
N	5.3–6.2	36–40		
K	970–1120		590–860	
Ca	171–493		670–2275	
Mg	40–96		125–270	
Na	13		0.5–2.4	
Cu	0.2–0.9		0.3–0.4	
Fe	1.3–2.6		3.0–4.7	
Mn	0.4–1.3		2.3–3.8	
Zn	0.5–0.8		0.5–1.7	
Ni	0.02–0.05		0.04–0.06	
Cr	0.002–0.005		0.02–0.03	
Al	0.3–1.5		1.7–4.5	

TABLE 2 Biochemical composition of plant parts of *Ceratonia siliqua*.

Sources: 1. Stavrou et al. (2018), 2. Fidan et al. (2020), 3. Khlifa et al. (2013), 4. Fadel et al. (2020), 5. Avallone et al. (1997), 6. de Falco et al. (2021), 7. Matthaus and Özcan (2011), 8. Tous et al. (2013), 9. El-Shatnawi and Ereifej (2001), 10. Binder et al. (1959), 11. Yatim et al. (2022), 12. Ben Ayache et al. (2021), 13. Abbassy et al. (2020), 14. Nasar-Abbas et al. (2016), 15. Dakia et al. (2007), 16. Müller et al. (2020), 17. Darwish et al. (2021), 18. Vardar et al. (1972), 19. Amrani et al. (2023).

(0.6%–11.4%), avenasterol (3.0%–3.5%) and chlerosterol (1.3%–1.0%) (Ben Ayache et al., 2021; Fidan et al., 2020; Matthaus & Özcan, 2011) involved in inhibition of oxidative reactions and in the inhibition of carcinogenesis (Yatim et al., 2022). The detailed composition of oils extracted from fruits is given by Abbassy et al. (2020).

Cultivars generally have higher concentrations of proteins, sugars and fatty acids, but lower levels of polyphenols than wild trees, and seeds from cultivars contain lower levels of the main fatty acids, tocopherols, sterols, total nitrogen and ash content (Biner et al., 2007; Matthaus & Özcan, 2011; Oziyici et al., 2014; Tetik et al., 2011; Vekiari et al., 2012).

Total protein in the leaves is lower than in seeds (Table 2); soluble protein in the leaves has been measured at c. 2.7 g/m² by Osório et al. (2012). Eighteen amino acids were found in the fruit, more than in apple (13), banana (14) and kiwifruit (14) (Avallone et al., 1997). Aspartic acid (18.25 mg/g dry mass) was the predominant amino acid in the fruit (Ayaz et al., 2007) but also include alanine, glycine, leucine, proline and valine (Batlle & Tous, 1997).

Seed endosperm contains a galactomannan, a polysaccharide composed of mannose and galactose (ratio 4:1), and used commercially as carob bean or locust bean gum—Section 10.2 (Batlle & Tous, 1997).

The heartwood of carob is high in phenols (50.43 mg/g dry mass; methanol extraction) in comparison to other Mediterranean trees, dominated by gallic acid (14.83 mg/g) and proanthocyanidins (10.27 mg/g) (Balaban, 2004). Sapwood has lower levels of phenolics (4.28–23.8 mg/g dry mass) dominated by gentisic acid, involved in the degradation of the plant signal salicylic acid (Balaban, 2004; Custódio et al., 2013). Other chemical components of sapwood and heartwood are given by Balaban (2004).

The distinctive aroma of carob flowers and fruits is dominated by propanoic acid, isobutyric acid and, in flowers, ethanol (Krokou et al., 2019). The most notable volatile organic compounds (VOCs) emitted from carob fruit were acids (82%) followed by esters (14%) and aldehydes/ketones (3.7%), whereas carob flower VOCs were dominated by terpenoids (Krokou et al., 2019)—see Section 8.1 for details.

7 | PHENOLOGY

As in other Mediterranean evergreen shrubs, vegetative growth in carob normally ceases in the summer and declines in winter when temperatures fall below 10°C, but in wet, warm years, carob can continue growing year round (Batlle & Tous, 1997; Liphshitz & Lev-Yadun, 1986). Similarly, vascular and bark cambial growth can be active throughout the year (so xylem growth rings are not necessarily annual) but generally ceases over winter and is active from February to the end of September (Arzee et al., 1977; Fahn, 1953). In most years, axillary and apical vegetative buds emerge from January to June (Martins-Loução & Britu de Carvalho, 1989) and vegetative growth continues uniformly until as late as September. Leaves expand over a 3- to 4-month period, reaching maturity by July, with a weaker second flush possible, but sometimes missing, in the autumn (Correia et al., 2001; Custódio, 2005; Diamantoglou & Meletiou-Christou, 1980; Diamantoglou & Mitrakos, 1981; Fadl et al., 1979; Rhizopoulou & Davies, 1991; Tous et al., 2013). The lifespan of leaves is normally 20 months (but see Section 6.1), being shed in the summer, usually July (Diamantoglou & Mitrakos, 1981; Lo Gullo et al., 1986).

Around the Mediterranean, carob flower buds and the first flowers appear in June with the main flowering season from late August to September until the end of November–December, peaking in October (Leshem & Ophir, 1977; Tous et al., 2013). However, the timing and duration of flowering depends on local climatic conditions. Moreover, female and hermaphrodite trees may flower for 2–4 months while male trees last about 1 month (Retana et al., 1994; Tous et al., 2013). Female cultivars flower before the male which may reduce pollination (Retana et al., 1994). It is said that carob is the only Mediterranean tree with the main flowering season in autumn rather than spring but others also flower in winter including *Arbutus unedo* and *Erica multiflora*. Fertilisation occurs soon after pollination (Bosch et al., 1996; Custódio, 2005; Ilahi & Vardar, 1976), the pollen tube taking 1–5 days to reach successive ovules (von Haselberg et al., 2004). Most fruit set is

between the end of September and the end of December with a peak in October, and some occurring through to February (Arista et al., 1999; Bosch et al., 1996). Shedding of flowers and young fruits occurs from October to December, slowing during January–February and is rare from June onwards although some ripening fruits can fall off throughout the next year (Bosch et al., 1996; Ortiz et al., 1995; Tous et al., 2013). Bosch et al. (1996) observed 59%–90% of fruits being shed. With the advent of cold weather, fruit growth stops and then resumes from April, fruits reaching full size and sugar content in June at the beginning of the summer dry period and ripening and becoming dry (from c. 70% to c. 12%–18% moisture) in July, and changing from green to brown in early August, around 10 months after flowering (Bosch et al., 1996; Davies et al., 1971; Tous et al., 2013). Between 5000 and 6000 h above 10°C is required for fruits to ripen (Tous et al., 2013). Thus, flowering occurs when fruits are mature, making commercial fruit harvesting more difficult since the trees are in full flower. Carob normally has a 2-year cycle of alternating 'good' and 'bad' years or fruit production since a large fruit load reduces flower bud initiation on the trees for the next year (Gur, 1985).

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

All flowers start as hermaphrodites but most become functionally male or female (Figure 3); even cultivars that were hermaphrodite early in the season tend to become progressively male through the flowering season (Batlle & Tous, 1997). Meikle (1977) identified five main inflorescence types: (1) male with long filaments and abortive pistils, (2) male with short filaments and abortive pistils, (3) hermaphrodite with fully developed stamens and pistils, (4) female with abortive staminodes and fully developed pistils and (5) polygamous inflorescences with a mix of male, female and hermaphrodite flowers.

As a mainly dioecious tree, carob is largely an obligate outcrosser. Wild carob populations are usually 1:1 male and female with around 1% hermaphrodite (Condit, 1919). However, hermaphrodite frequency varies and is higher in the Balearic Islands than the Iberian Peninsula and Morocco (Tous et al., 2001). In grafted orchards, female trees are more common, and in Cyprus, the ratio ranges from 1:3 to 1:6 (Orphanos, 1980). Like many other dioecious trees, carob trees can change sex (Batlle & Tous, 1997; Tous et al., 2013; Zohary, 2002).

Female inflorescences have a mean of from 9 to approaching 50 flowers, ranging up to almost 100 (Arista et al., 1999; Batlle & Tous, 1997; Bosch et al., 1996; Ortiz et al., 1999). Flowers open first at the inflorescence base, moving towards the apex, although each flower is open long enough for the whole raceme to be in flower for a short time (Bosch et al., 1996).

The nectar of carob flowers was found in Israel to contain 355.6 ± 219.1 (SD) $\mu\text{g}/\mu\text{L}$ of sugar averaged across time of day,



FIGURE 3 *Ceratonia siliqua*, (a) fruit, (b) male inflorescence, (c) hermaphrodite inflorescence, (d) female inflorescence, (e) seeds, (f) leaf. Photograph by Joan Tous.

composed of 59.7% fructose, 39.1% glucose and 1.2% sucrose with traces of maltose (Levy, 2006). Seventeen amino acids were also found with a mean concentration of $1444 \pm 1178 \text{ ng}/\mu\text{L}$, dominated (90.5%) by proline, alanine and, to a lesser extent, serine and tyrosine. No consistent significant differences were found in sugar or amino acid concentration between male and female flowers, but in most cases, male nectar was more concentrated than female nectar in sugar and amino acid content (Levy, 2006). Nectar appears to be secreted continuously through the day and night (Levy, 2006). Female flowers, however, produce more nectar per flower ($2.02 \pm 0.25 \mu\text{L}$, SE) than male ($0.78 \pm 0.13 \mu\text{L}$) and so female flowers contain more sugar ($0.17 \pm 0.02 \text{ mg}$) than males ($0.07 \pm 0.01 \text{ mg}$) (Ortiz et al., 1996). However, male trees have a higher number of flowers per inflorescence (Retana et al., 1994) so the total amount of sugar on offer may be similar between female and male trees.

A musky scent is present with the nectar although female flowers are less scented than male (Custódio, Nogueira, & Romano, 2004). Thirty-five compounds were detected in the scent by Levy (2006), dominated by >40% monoterpenoids (pinene, β -myrcene, β -linalool, d-limonene) and benzenoids with additional fatty acid derivatives and sesquiterpenoids (Custódio, 2005; Custódio et al., 2005; Custódio, Nogueira, & Romano, 2004; Levy, 2006). Male flowers had higher levels (70%) of monoterpenes than hermaphrodite (52%) and female (43%) flowers, but lower levels of sesquiterpenoids (Custódio, 2005). Female flowers had a higher diversity of volatiles than male and hermaphrodite, particularly during the day, while male flowers produced a more diverse scent at night (Custódio, 2005; Levy, 2006).

Pollination is primarily by insects. Since carob flowers appear in the autumn when bees are scarcer, flies (particularly hoverflies) and night-flying moths are also important pollinators (Table 3) which may explain why carob flowers for a more extended period (Section 7)

than many other fruit trees (Ortiz et al., 1996; Retana et al., 1990, 1994; Salazar Hernández et al., 2002). An extended flowering season also helps compensate for unstable weather and ensures that at least some flowers will be pollinated in a spell of good weather and insect activity (Battle & Tous, 1997). In southern Spain, Hymenoptera and Diptera made up 55.7% and 44.3% of total insects visits, respectively (Arista et al., 1999), and in northern Israel, Hymenoptera and Diptera made up 78.6% and 21.4% of total visits, respectively (Levy, 2006). Mean time spent on an inflorescence in Spain was recorded by Retana et al. (1990) as hoverflies $55.4 \pm 66.1 \text{ s}$ (SD), large flies (>7 mm in length) $139.2 \pm 173.0 \text{ s}$, small flies $118.3 \pm 138.5 \text{ s}$, although the hoverflies touched more stigmas (3.91 ± 2.55) than the small flies (2.70 ± 2.23). Levy (2006) noted that both Hymenoptera and Diptera foraged for pollen from 05:30 to 09:30, both pollen and nectar between 09:30 and 10:30, and then mostly nectar from female trees between 10:30–11:30 and 15:30–16:30.

Male flowers are generally more attractive to insects than females; the mean length of time spent per flower was significantly higher for the male flowers than for the females even when pollen foraging is excluded and considering only nectar foraging (Levy, 2006; Ortiz et al., 1996). This may possibly be due to male flowers being more scented (Custódio, Nogueira, & Romano, 2004). Linskens and Scholten (1980) recorded that, in Portugal, bees were especially frequent on male flowers while flies seem to prefer females. Retana et al. (1990) in Spain recorded 127 honey bees and 41 flies on male flowers, and 7 bees and 53 flies on females. In Israel, Levy (2006) observed *Apis mellifera* L. (Hymenoptera, Apidae) made 71.5% of total visits to males and 68% of visits to females while *Eristalinus taenipos* (Wiedemann) (Diptera, Syrphidae) made 12% of visits to males and 18% of visits to females.

In southwest Spain, Arista et al. (1999) noted that fruit set was highest at the tip of the inflorescence (Section 8.3) whereas the

TABLE 3 Insects (including records for families) observed on *Ceratonla siliqua* flowers.

Species classification	Source
Hymenoptera	
Apidae	
<i>Apis mellifera</i> L.	1, 2
<i>Amegilla</i> Friese sp.	1
Vespidae	
<i>Polistes</i> Latreille spp.	3
<i>Vespa orientalis</i> L.	1, 4
Halictidae	
<i>Halictus</i> Lat. sp.	1
Diptera	
Anthomyiidae (1 sp.)	2
Calliphoridae	4
Lauxaniidae (1 sp.)	2
Scatophagidae (1 sp.)	2
Syrphidae	4
<i>Episyrphus balteatus</i> (De Geer)	3
<i>Eristalis tenax</i> (L.)	3
<i>Eristalinus taenipos</i> (Wiedemann)	1
<i>Eumerus</i> Meigen spp.	3
Muscidae	4
<i>Musca domestica</i> L.	1, 2
Calliphoridae	
<i>Calliophora</i> Robineau-Desvoidy sp.	2
<i>Lucilia sericata</i> (Meigen)	1, 2
Lepidoptera	5, 6
Eponomeutidae (1 sp.)	1
Geometridae	
<i>Xanthorhoe</i> Hübner sp.	1
Noctuidae	
<i>Agrotis bigramma</i> (Esper)	1
<i>A. ipsilon</i> (Hufnagel)	1
<i>A. puta</i> (Hübner)	1
<i>A. trux</i> (Hübner)	1
<i>Aporophyla australis</i> (Boisduval)	1
<i>A. canescens</i> (Duponchel)	1
<i>Caradrina amseli</i> (Boursin)	1
<i>C. atriluna</i> (Guenée)	1
<i>Dryobotodes eremita</i> (Fabricius)	1
<i>Helicoverpa armigera</i> (Hübner)	1
<i>Leucania loreyi</i> (Duponchel)	1
<i>L. punctosa</i> (Treitschke)	1
<i>Noctua comes</i> Hübner	1
<i>N. pronuba</i> (L.)	1
<i>Olivenebula subsericata</i> (Herrich-Schäffer)	1
<i>Polymixis trisignata</i> (Ménétriés)	1

(Continues)

TABLE 3 (Continued)

Species classification	Source
<i>Spodoptera littoralis</i> (Boisduval)	1
<i>Xestia xanthographa</i> (Denis & Schiffermüller)	1
Pyralidae (2 spp.)	1

Sources: 1. Levy (2006), 2. Linskens and Scholten (1980), 3. Xavier Garcia-Martí (personal communication), 4. Arista et al. (1999), 5. Retana et al. (1990), 6. Ortiz et al. (1996).

norm in Fabaceae is for more fruit at the base. They concluded that since the ovaries bend towards the base of the raceme, this partially hid the basal flowers and made access to their nectaries harder, and so pollinators visit the apical flowers most often, particularly Diptera. Arista et al. (1999) found at different sites that the probability that an apical flower is first visited by an insect (43%–55%) was higher than for basal flowers (12%–18%). When insects (particularly wasps) arrived first at the base it was by walking along the branches. This affected pollen deposition since the stigmas of apical flowers received a mean of 41.2 pollen grains while for basal flowers, it was 10.9 grains, lower than the 10–20 ovules per flower. When a third or two-thirds of the flowers were removed from the outer end of the inflorescence, fruit set improved in the remaining flowers (Al-Ghazawi et al., 2014a). The high number of seeds in mature fruit (Section 8.3) suggests flowers that receive a small pollen load are selectively aborted which may be enhanced by low pollen receptivity of the stigma (Salazar Hernández et al., 2002).

Pollination can be significantly reduced by high temperatures (leading to death of pollinators) and by autumnal rain (Sfakiotakis, 1978). In such situations, supplementary hand pollination has been found to increase fruit production from 4.5% of flowers setting fruits up to 18.68% with hand pollination, increasing the number of seeds per fruit from 7.5 to 10.0 (Al-Ghazawi et al., 2014b). Pollen germination can be as low as 4%–5% but is usually 40%–90% (Ciampolini et al., 1986; Linskens & Scholten, 1980; Sfakiotakis, 1978). This variability is likely to depend upon extreme weather (Tous et al., 2013), but Ferguson (1980) found a high level of pollen abnormality in carob, up to 36% with aberrations. Pollen can be cryopreserved for up to 5 months at –80°C with pretreatment using 0.5 M sucrose (Custódio, 2005).

Ants may play a limited role in pollination (Linskens & Scholten, 1980). Wind is unlikely to be very effective in carob pollination, since isolated females unlikely to be reached by insects carrying carob pollen were observed to carry few fruits (Batlle & Tous, 1997) and Retana et al. (1990) found that excluding insects with bags resulted in no fruit. Self-pollination is possible although Al-Ghazawi et al. (2014a) found significantly fewer seeds per fruit in inflorescences bagged to prevent cross-pollination (9.03 seeds) compared to open-pollinated fruits (10.9 seeds) and the seeds had lower germination (57% self-pollinated, 82% cross-pollinated).

Pollination in orchards of mainly female trees has traditionally been ensured by either keeping a branch from a male rootstock in the centre of the tree or grafting a male or hermaphrodite branch

onto the tree if the rootstock is female. Male or hermaphrodite trees can also be planted around the orchard, normally forming 4%–20% of the trees (Batlle & Tous, 1997). To help identify male trees before flowering, Kaya and Dalkılıç (2021) have identified an RAPD marker with 80% reliability in identifying male plants.

8.2 | Hybrids

Wild and feral carob trees reproduce by seed, but interspecific hybrids of *Ceratonia siliqua* are not known. Carob's late flowering season from September to November (Section 8.1) does not overlap with that of *C. oreoethauma* which flowers from March to April (Hillcoat et al., 1980). The natural distribution of *C. oreoethauma* in Oman to Somalia may overlap that of *C. siliqua* (Section 1) but *C. oreoethauma* grows naturally at higher altitudes (1500–1800 m a.s.l.) than *C. siliqua* (Batlle & Tous, 1997) imposing a spatial as well as a temporal separation, making hybridization even less feasible.

8.3 | Seed production and dispersal

Fruit set is normally 3%–5% of flowers but can range from almost zero to 38% (Batlle & Tous, 1997; Bosch et al., 1996). Once the relatively few fruits are set, subsequent fruit shedding is high, typically 60%–90%, leading to 1.65–4.6 fruits per raceme per tree in female and hermaphrodite trees (Arista et al., 1999; Bosch et al., 1996; Ortiz et al., 1999). The number of fruits produced within an inflorescence varies by cultivar but in most cultivars up to 75% of inflorescences carry one or two fruits, and <10% carry >4 (Bosch et al., 1996; Retana et al., 1994). The number of fruits per raceme was increased significantly by hand pollination (Arista et al., 1999) but was still low: 69.7% of racemes produced at least one fruit in hand pollinated plants compared to 40.5% in open pollinated plants. Al-Ghzawi et al. (2014a) found production of mature fruit varied along an inflorescence in Jordan: 2.58% of flowers in the inner third of the raceme, 5.21% in the middle third and 17.95% in the apical third. More fruits are produced on fertile soils; Correia and Pestana (2018) noted that on fertile soils, fruit production per tree (over 30 years old) was 40.3 ± 20.0 (SD) kg (range 3.7–93.0 kg) and on non-fertile soils was 7.4 ± 5.0 kg (range 0.6–16.6 kg).

Mean fruit mass varies from 4 to 29 g across its range, with a mean mass of 11–18 g in the Algarve (Barracosa et al., 2008; Batlle & Tous, 1997; Korkmaz et al., 2020) rising as high as a mean of 38 g in Sicily (La Malfa et al., 2012). Mean fruit mass has a similar range for both wild and cultivated trees. In Morocco, smaller fruits are associated drier conditions (Kassout et al., 2023). Despite the variation in fruit size, seed number per fruit is less variable (range 5–14 in the Algarve; Barracosa et al., 2008), with a mean of between 8 and 17 (Ali et al., 2019; Bosch et al., 1996; Boublenza et al., 2019; Gharnit et al., 2006; La Malfa et al., 2012; Naghmouchi et al., 2009; Ortiz et al., 1999; Sidina et al., 2009). By weight, carob fruits are 73%–95% pulp and 8%–16% seeds, varying between cultivars (Batlle & Tous, 1997; Marakis et al., 1988).

Mean seed mass has been recorded as varying from 0.14 to 2.44 g (Al-Ghzawi et al., 2014a; Ali et al., 2019; Barracosa et al., 2008; Boublenza et al., 2019; Sidina et al., 2009). This variation partly depends upon climate (largest seeds in semi-arid land, smallest seeds in subhumid and arid regions: Boublenza et al., 2019; Kassout et al., 2022, 2023), and seed size increases with altitude and latitude (Kassout et al., 2022). There is also some evidence that seeds from wild plants are smaller than those from cultivars (Bolarić et al., 2021; Gharnit & Ennabili, 2016; Korkmaz et al., 2020; Naghmouchi et al., 2009; Russo & Polignano, 1996); however, seed size can vary widely in cultivated carob trees, for example, from 0.17 to 0.42 g in Morocco (Gharnit & Ennabili, 2016) muddying the comparison. Seed mass also appears to increase with age of the tree. Gharnit et al. (2006) measured seed mass of 1.66 ± 0.89 g (SD assumed) in trees <25 years old, 2.04 ± 0.68 g at 25–50 years old and 2.12 ± 1.08 g in trees >50 years old. Fruits also become bigger and hold more seeds with age (7.87 ± 3.88 seeds in trees <25 years old, 9.39 ± 2.48 in 25–50 years old, 10.1 ± 2.38 in trees >50). There is also some evidence from Mallorca that mean seed mass from female trees (0.201 ± 0.002 g, SD assumed) is heavier than from hermaphrodites (0.176 ± 0.007 g) (Turnbull et al., 2006). Endosperm makes up 41%–60% of dry seed mass, embryo plus cotyledons 18%–21% and tegument 18%–21% (Gharnit et al., 2006).

The traditional view is that carob seeds varied little in mass and so could be used as the *carat*, the unit of weight for gemstones and gold. The *siliqua* was also a subdivision of the Roman pound weight. The carat has historically varied from 187 to 216 mg and was standardised in 1907 at 200 mg (Zhengzhang, 1991). Turnbull et al. (2006) acknowledges the natural variation in seed mass and states that observers could discriminate differences in carob seed weight of around 5% by eye, and so could choose standard sized seeds.

Seeds are dispersed by fruits being eaten by animals, attracted by the sweet pulp. Animals such as cows, foxes, sheep and goats, and coyotes in North America, drop the seeds in faeces (El-Shatnawi & Erefej, 2001; Ortiz et al., 1995; Sanders & Friedman, 1996) and these are still viable (Section 8.4). In Israel, the Egyptian fruit bat *Rousettus aegyptiacus* (Geoffroy) has been recorded as eating carob fruits; the seeds, still viable, are spat out in pellets away from the parent tree (Izhaki et al., 1995). Larger birds are also likely to be seed dispersers.

8.4 | Viability of seeds: Germination

Fruits mature in early August (Section 7) and some germination may occur in November through to March–April (Batlle & Tous, 1997; Condit, 1919) but the majority of seeds take one or more years to germinate, forming a persistent soil seed bank. Carob seeds are orthodox and have a physical dormancy due to their hard seed coat preventing water uptake, and can be stored for 5 years at 5°C in sealed containers (Batlle & Tous, 1997; Shepperd, 2008). Dormancy varies between trees (Pérez-García, 2009) part of which may be

associated with seed colour which varies between cultivars and populations of wild trees. Zemouri et al. (2020) in Algeria showed that yellowish-brown seeds had a high dormancy (2% germination in untreated seeds) whereas chocolate brown seeds were largely non-dormant (80%–88% germination).

Germination occurs in the wild when the seed coat is broken by fungal or climatic conditions but not by fire, and indeed, fire appears to reduce germination. Exposure of unscarified seed to 100°C for 5 min resulted in 50% germination, 10 min in 28.5% germination and 15 min in no germination; at 150°C, germination was 100% after 1 min but zero after 5 min. A control of scarified seed gave 99%–100% germination (Ortiz et al., 1995).

Carob seeds can be found in animal faeces (Section 8.3). Ortiz et al. (1995) recorded 11 carob seeds in a fox scat although fewer than four was the norm; carob seeds were also found in 11% of cow pats though some could contain 'several hundred'. Scarifying these seeds with sandpaper resulted in 94% and 100% germination of seeds from fox and cow faeces, respectively. However, unscarified seeds showed just 13%–14% germination, so passing through foxes and cows does not reduce viability but does not increase germination without further treatment. By contrast, El-Shatnawi and Ereifej (2001) found that untreated seeds recovered from sheep and goat faeces germinated well, reaching a maximum of 74% after 24 h in the digestive system of sheep and 80% after 48 h inside goats.

Untreated seeds typically show a germination of <10% (Ali et al., 2021; Cavallaro et al., 2016; El-Shatnawi & Ereifej, 2001; Ortiz et al., 1995). Dormancy can be broken by a number of treatments, some of which can occur naturally under field conditions while others are used to artificially break dormancy:

- Mechanical scarification—sandpaper, using sand in a pestle and mortar for 20 min or cutting with a scalpel; germination can exceed 85% (Al-Ghazawi et al., 2014a; Batlle & Tous, 1997; El-Shatnawi & Ereifej, 2001; Kruger et al., 2018; Ortiz et al., 1995);
- Soaking in water at room temperature for 1–15 days—generally ineffective: 23%–27% germination compared to 99% by scarification (Pérez-García, 2009);
- Soaking in boiling water at 90–100°C for 5 min then immersion in cold water for 24 h; germination 72% to >90%; immersion for 30 min reduced germination to 24% (Cavallaro et al., 2021; Kruger et al., 2018; Martins-Loução et al., 1996);
- Soaking in 50%–100% sulphuric acid for 5–60 min then rinsing with water for up to 2 days giving 80%–100% germination (Ali et al., 2021; Bostan & Kiliç, 2014; Cavallaro et al., 2021; Kruger et al., 2018; Martins-Loução et al., 1996; Nia et al., 2021; Pérez-García, 2009);
- Soaking in 500–1500 mg/L gibberellic acid for 24 h: ≤29% germination; 250 mg/L did not increase germination (Pérez-García, 2009; Bostan & Kiliç, 2014; Ali et al., 2021);
- Dry heat at 100°C for 0.5–30 min (Ortiz et al., 1995; Pérez-García, 2009) although, as described above, this can reduce seed viability;

- Immersion in ethanol (90% for 20 min) or potassium nitrate (0.02 M for 290 min) (Martins-Loução et al., 1996);
- Electrical shock at 3 Amps for 3–6 min, increasing germination from 30.5% in control to 40.7% with treatment (Ali et al., 2021).

Once treated, surface sterilisation with mercuric chloride (1 g/L for 10 min) or sodium hypochlorite (2.6% for 20 min) may further improve germination (Nia et al., 2021). Photoperiod does not affect germination (Kruger et al., 2018), nor does chilling. Germination is generally quick, starting 4 days after treatment and reaching 95%–100% germination within 6–20 days (Batlle & Tous, 1997; Ortiz et al., 1995). Optimum temperature for germination is 25–27.5°C (Mitrakos, 1981), but germination is generally high between 20 and 35°C. Batlle and Tous (1997) recorded that 50% germination of seed samples took 11.0 days at 15°C and 11.5 days at 35°C compared to c. 5.5–6.7 days between these temperatures. Within carob's native range, optimum temperatures occur in June–September when water is largely unavailable. Spyropoulos and Lambiris (1980) found that even very mild water stress (imposed using different concentrations of polyethylene glycol) will greatly reduce carob germination. Germination is thus primarily restricted to winter and spring (Batlle & Tous, 1997).

8.5 | Seedling morphology

Martins-Loução et al. (1996) describe germination in detail. The radicle emerges and grows geotropically, quickly producing short-lived root hairs perhaps due to the inability of carob to form nodules (Figure 4). A hypocotyl hook forms for epigeal germination and draws the cotyledons from soil c. 6 days after germination at which point half the endosperm mass has been used, the embryo has doubled in mass and hypocotyl dry mass decreased by 20%. Cotyledons maintain their mass as they become dark green and photosynthesise, and maintain a high degree of succulence (50–70 mg/cm²) and so appear important in water storage. The epicotyl starts growing after opening of the cotyledons and significant root growth occurs. The expansion and elevation of the cotyledons suggests their importance in early carbon fixation in seedlings.

The tap root of young seedlings is three or four times as long as the shoot (Condit, 1919). Sack et al. (2003) noted that the rooting depth of juvenile carob plants was as deep as in deciduous *Quercus* species which are noted for deep roots. Juvenile plants of unknown age collected from the field in southern Spain rooted to 8.9 ± 2.5 cm (SE, *n* = 10), similar to other species tested, but the proportion of mass underground was 0.19–0.20 (95% CI) for carob, which was less than in *Viburnum tinus* (0.29–0.33) and *Phillyrea latifolia* (0.34–0.39) which, like carob, cope with summer drought but grow in higher shade. Catarino et al. (1981) found that seedlings growing in 10% of full sunlight, simulating growing under a dense canopy, could initially survive, but the root system was very weak with a much higher root:shoot ratio in shaded plants (2.98) than those in full sun (1.82), but see Section 4.

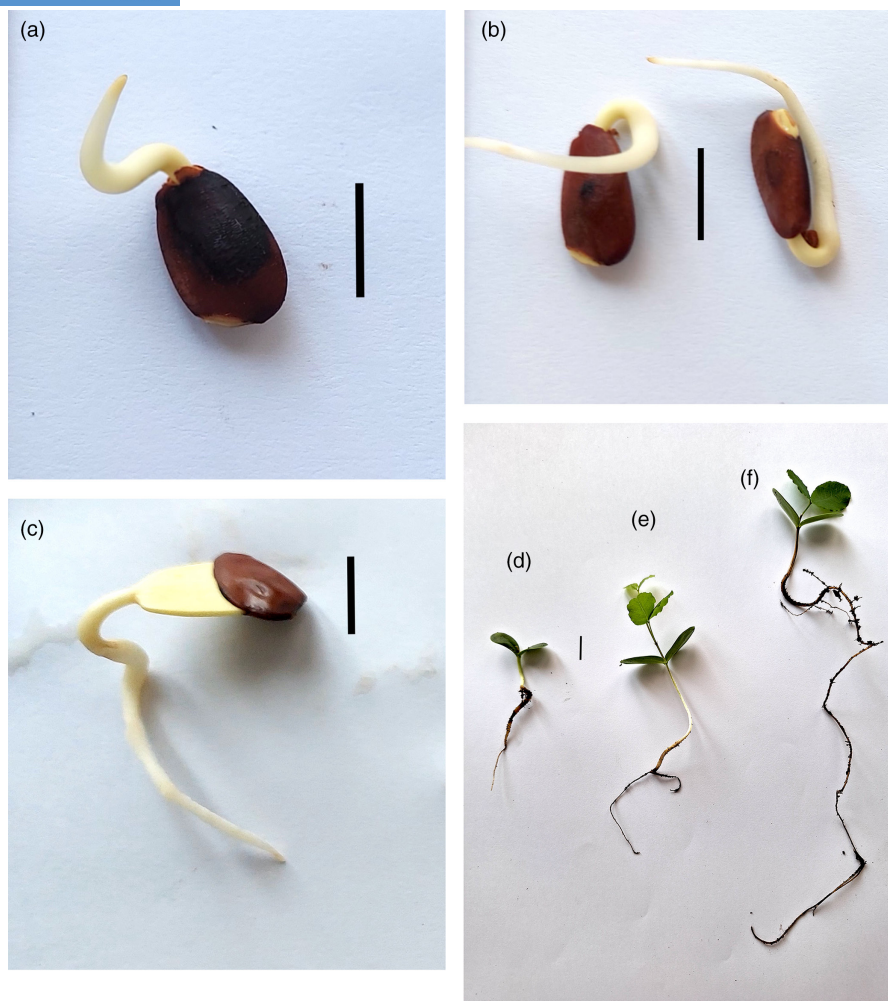


FIGURE 4 Seedling morphology of *Ceratonia siliqua*, (a) 2 days, (b) 3 days, (c) 7 days, (d) 11 days, (d) 16 days, (f) 21 days (bar = 1 cm). Photographs by Tarek Mukassabi.

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

Most of the insects recorded on carob are globally widespread species that live on a wide range of plants (Table 4). The majority of these, including the mealybug larvae, scale insects and mites, occur sporadically on carob and so cause little damage. The most widespread insect that is damaging and economically problematic is the carob moth *Ectomyelois ceratoniae* (Zeller) (Lepidoptera, Pyralidae) that infests carob fruits both in the field and during storage (Gugliuzzo et al., 2019). In Spain, the most damaging insect is the polyphagous larva of the leopard moth *Zeuzera pyrina* L. (Lepidoptera, Cossidae) that attacks wood and branches, causing severe damage to young trees. Nevertheless, carob is relatively free of problem insects and traditionally is a crop that is not sprayed with insecticides (Agroforestry Database, 2023; Tous et al., 2013). However, Italy and Spain are currently threatened by the invasive black twig borer *Xylosandrus compactus* Eichhoff (Coleoptera, Curculionidae), among the most damaging of the

Ambrosia beetles. The economic impact of this pest has increased over recent years mainly due to increased global plant trade and a higher frequency of extreme climatic events (Gugliuzzo et al., 2019).

A common custom in the municipality of Chiva (Valencia, Spain) is to plant *Agave americana* L. near each carob tree to repel adult leopard moths, although there is no quantitative data that it works. European earwigs *Forficula auricularia* L. are common on carob trees (Salazar Hernández et al., 2002) but cause no damage.

Rodents can occasionally cause severe damage to carob orchards, including *Apodemus sylvaticus* (L.) and rats, primarily *Rattus rattus* (L.). Rats eat the bark, even on older shoots, thus ring-barking trunks and shoots, and also eat the fruits (Orphanos, 1980). In California, a number of small rodents including voles (*Pitymys* spp.), rats and especially gophers (*Geomys* spp.) can severely damage the root system of young trees (Condit, 1919).

The fruits of carob contain 1%–2% digestible protein and provide a similar nutritional value as most cereal grains (National Research Council, 1979). Total protein is higher (Section 6.6) but the 16%–20% dry mass of condensed tannins reduces its digestibility (Loo, 1969;

TABLE 4 Insects and mites occurring on *Ceratonia siliqua* in the field.

Species classification	Ecological notes	Source
Hemiptera		
Coccidae		
<i>Ceroplastes floridensis</i> Comstock	Scale insect; polyphagous, global	1
<i>Coccus hesperidum</i> (L.)	Scale insect of mainly citrus, widespread	1
<i>C. longulus</i> (Douglas)	Scale insect; polyphagous, widespread	1
<i>Saissetia oleae</i> (Olivier)	Black scale of <i>Olea europaea</i>	1
Diaspididae		
<i>Aonidiella aurantii</i> (Maskell)	Scale insect, global	1
<i>A. orientalis</i> (Newstead)	Oriental red scale, leaves, polyphagous	1
<i>Aspidiotus nerii</i> Bouché	Oleander scale, polyphagous, widespread	1, 13
<i>Chrysomphalus aonidum</i> (L.)	Scale insect, polyphagous, widespread	1
<i>C. dictyospermi</i> (Morgan)	Scale insect, polyphagous, particularly <i>Citrus</i> spp., widespread	1
<i>C. pinnulifer</i> (Maskell)	Scale insect, polyphagous, widespread	1
<i>Diaspidiotus lenticularis</i> Lind.	Polyphagous on trees, Europe	1
<i>D. pyri</i> (Licht.)	Polyphagous on trees, Europe	1
<i>D. zonatus</i> (Frauenfeld)	Polyphagous on trees, Europe, Asia	1
<i>Dynaspidotus britannicus</i> (Newstead)	Wide range of woody plants, widespread	1
<i>D. ericarum</i> (Goux)	Limited range of woody plants; France, Iran, Turkey	1
<i>Hemiberlesia cyanophylli</i> (Signoret)	Scale insect, polyphagous, widespread	1
<i>H. lataniae</i> (Signoret)	Scale insect, polyphagous, global	1
<i>H. rapax</i> (Comstock)	Scale insect, polyphagous, widespread	1
<i>Lepidosaphes conchiformis</i> (Gmelin)	Scale insect, polyphagous, widespread	1
<i>L. pistaciae</i> Archangelskaya	Limited range of woody plants, widespread	1
<i>L. tapleyi</i> Williams	Woody plants, widespread	1
<i>L. ulmi</i> (L.)	Wide range of woody plants, widespread	1, 13
<i>Parlatoria oleae</i> (Colvée)	Scale insect, polyphagous, global	1
<i>P. pergandii</i> Comstock	Scale insect, polyphagous, global	1
<i>Saharaspis ceardi</i> (Balach.)	Limited range of woody plants, Europe	1
<i>Voraspis ceratoniae</i> (Marchal)	Carob, <i>Olea europaea</i> and <i>Argania spinosa</i> , southern Mediterranean	1
Monophlebidae		
<i>Gueriniella serratae</i> (Fabricius)	Bark, polyphagous, Mediterranean	1
Pseudococcidae		
<i>Maconellicoccus hirsutus</i> (Green)	Widespread, polyphagous mealybug	1
<i>Planococcus citri</i> (Risso)	Widespread, polyphagous mealybug	1, 13
<i>P. ficus</i> (Signoret)	Mealybug, predominately on grape vines	1
<i>Pseudococcus viburni</i> (Signoret)	Mealybug, predominately on grape vines	1
Coleoptera		
Anthribidae		
<i>Araecerus fasciculatus</i> (De Geer)	Boring weevil in seeds, woody hosts, widespread	1
Buprestidae		
<i>Ptosima undecimmaculata</i> (Herbst)	Boring larvae, dead wood, polyphagous, widespread	1, 13
<i>Agrilus roscidus</i> Kiesenw.	Larvae, borer of woody plants, Europe and Balkans	1

(Continues)

TABLE 4 (Continued)

Species classification	Ecological notes	Source
<i>Anthaxia millefolii</i> subsp. <i>smaragdifrons</i> Marseul	Boring larvae, Tunisia	1
Bostrichidae		
<i>Apate monachus</i> Fabricius	Boring larvae and adults, dead or decaying wood, range of woody plants	1, 6
Bostrichidae		
<i>Bostrichus capucinus</i> (L.)	Boring larvae, woody plants, widespread	1
<i>Scobicia chevrieri</i> (Villa & Villa)	Boring, dead wood, widespread	1
<i>Sinoxylon sexdentatum</i> Olivier	Boring larvae, dead wood, various Mediterranean trees	1, 13
<i>S. ceratoniae</i> (L.)	Europe to Asia	1
<i>Trogoxylon impressum</i> (Comolli)	Boring larvae, polyphagous, widespread	1
<i>Xyloperthella picea</i> (Olivier)	Wood boring, Europe, Africa	1
Cerambycidae		
<i>Axinopalpis gracilis</i> (Krynicky)	Polyphagous in deciduous trees	12
<i>Cerambyx cerdo</i> L.	Boring larvae, deciduous trees, Africa to Asia	1, 12, 13
<i>C. welensii</i> (Küster)	Boring larvae of mainly <i>Quercus</i> , widespread	1, 12
<i>Chlorophorus damascenus</i> (Chevrolat)	Polyphagous in deciduous trees	12
<i>Gracilia minuta</i> (Fabricius)	Polyphagous	12
<i>Hesperophanes sericeus</i> (Fabricius)	Polyphagous in deciduous trees	12
<i>Nathrius brevipennis</i> (Mulsant)	Polyphagous in deciduous trees	12
<i>Niphona picticornis</i> Mulsant	Broadly polyphagous	12
<i>Phenichroa fasciata</i> (Stephens)	Boring larvae of dead or thin branches/trunk, widespread	1, 12
<i>Prinobius myardi</i> Mulsant	Polyphagous in deciduous trees	12
<i>Purpuricenus desfontainii</i> (Fabricius)	Polyphagous in deciduous trees	12
<i>Stromatium auratum</i> (Böber)	Polyphagous, dead, dry wood	12
<i>Trichoferus fasciculatus</i> (Fald.)	Boring larvae, dead wood, trunks, Europe	1, 12
<i>T. griseus</i> (Fabricius)	Polyphagous but particularly <i>Ficus carica</i>	12
<i>T. kotschy</i> Ganglb.	Polyphagous in deciduous trees	12
<i>T. spartii</i> (Müller)	Uncommon; mainly on <i>Spartium</i> , <i>Rhus</i> , <i>Paliurus</i> , <i>Coronilla</i>	12
<i>Xylotrechus stebbingi</i> Gahan	Polyphagous in deciduous trees	12
Curculionidae		
<i>Otiorhynchus ceratoniae</i> Davidian, Gültekin & Korotyaev	Monophagous weevil on carob, leaves, Turkey	1, 2
<i>Echinodera ibleiensis</i> Stüben	<i>Castanea</i> , <i>Quercus</i> , carob, Sicily	1, 3
<i>E. incognita</i> (Hoffmann)	Spain	1
<i>Kyklioacalles maroccensis</i> (Stüben)	High Atlas, Morocco	1, 4
<i>Torneuma maltense</i> Magnano & Mifsud	Various trees, Malta, Madeira, Spain	1, 5
<i>Xylosandrus compactus</i> (Eichhoff)	Bark beetle, polyphagous on woody plants, widespread; causing a large amount of damage to carob in Italy and Spain	1, 7
<i>X. crassiusculus</i> (Motsch.)	Bark beetle, polyphagous, widespread	1
Diptera		
Cecidomyiidae		
<i>Asphondylia gennadii</i> Marchal	Carob midge but polyphagous, widespread, galls on carob fruits causing stunting and deformation to <20% crop	1, 8, 9

TABLE 4 (Continued)

Species classification	Ecological notes	Source
Culicidae		
<i>Aedes albopictus</i> (Skuse)	Males and females feed on carob nectar in Israel; highly attracted to damaged fruits of carob releasing sugary sap	10
<i>Culex perexiguus</i> Theobald	Feed on sugary exudate of fruits damaged by <i>Ectomyelois ceratoniae</i>	11
<i>C. pipiens</i> L.	Feed on sugary exudate of fruits damaged by <i>Ectomyelois ceratoniae</i>	11
Lepidoptera		
Cossidae		
<i>Cossus cossus</i> (L.)	Burrowing larvae, polyphagous	13
<i>Zeuzera pyrina</i> (L.)	Larvae feed on branches of many fruit trees, widespread, important pest in Spain	1, 13
Pyralidae		
<i>Cadra calidella</i> (Guenée)	Larvae feed on dried fruits, Mediterranean, Asia	1, 13
<i>C. cautella</i> (Walker)	Larvae feed on fruits and grain, polyphagous, widespread	1
<i>C. figulilella</i> (Gregon)	Larvae feed on dried fruits, widespread	1
<i>Ectomyelois ceratoniae</i> (Zeller) (= <i>Myelois ceratoniae</i> Zeller)	Carob moth, larvae feed on fruits of a number of tree species, widespread	1, 8, 13
<i>Euzopherodes vapidella</i> (J. J. Mann)	Adults fruit feeders, mainly citrus, Mediterranean, Africa	1, 13
<i>Plodia interpunctella</i> (Hübner)	Larvae feed on fruits and grain, polyphagous, widespread	1
Acari		
Eriophyidae		
<i>Calepitrimerus ceratoniae</i> Malandraki & Emmanouel	First eriophyid mite known to occur on carob, Greece	12
Tetranychidae		
<i>Bryobia siliquae</i> Hatzinikolis & Emmanouel	Monophagous on carob leaves, Greece	1
<i>Tetranychus urticae</i> C. L. Koch	Red spider mite, polyphagous, leaves, widespread	1

Sources: 1. Gugliuzzo et al. (2019), 2. Davidian et al. (2017), 3. Germann and Schütte (2021), 4. Stüben and Astrin (2010), 5. Magnano and Mifsud (2000), 6. Bonsignore (2012), 7. Riba-Flinch et al. (2022), 8. Orphanos (1980), 9. Skuhravá et al. (2002), 10. Müller et al. (2011), 11. Müller et al. (2010), 12. Malandraki and Emmanouel (2001), 12. Özdikmen (2023), 13. Salazar Hernández et al. (2002).

Würsch et al., 1984) and may act to reduce the growth of animals fed on a high carob diet (Kamarinou et al., 1979). However, the reduced growth may be due to the low energy content of carob, which can be compensated for by increased consumption of food by the animals (Louca & Papas, 1973). Chickens fed 20% of their diet as carob grew as well as chickens fed no carob (Vohra & Kratzer, 1964).

9.2 | Plant parasites and epiphytes

The yeast *Cryptococcus gattii* (Vanbreus. & Takash.) Kwon-Chung & Boekh. (Basidiomycota, Tremellales), which can cause respiratory disease in humans and other animals, is known to live saprophytically on the outside of leaves and bark of carob and other Mediterranean trees (Colom et al., 2012). The most frequent saprophytic fungal species (all Ascomycota, Eurotiales) isolated by Charpentie and

Marakis (1980) on mouldy fruits were *Aspergillus flavus* Link and *Penicillium expansum* Link, and on both fruits and soil *Aspergillus niger* Tiegh., *Penicillium glabrum* (Wehmer) Westling (= *P. frequentans* Westling) and *Paecilomyces variotii* Bainier, although *Penicillium glabrum* can also be pathogenic. Khassali et al. (2020) list bacterial and fungal species in soil below carob trees in Morocco.

A common fungal parasite of carob is *Pseudocercospora ceratoniae* (Pat. & Trab.) Deighton (= *Cercospora ceratoniae* Pat. & Trab.) (Ascomycota, Dothideales) which causes small (2–3 mm wide) circular or angular brown necrotic spots, surrounded by a pale halo later in the summer, and visible on both sides of the leaf (Perrotta et al., 1998; Stevenson, 1926; Varo et al., 2010). The spots are usually most numerous along the midrib but in humid conditions, the spots can be extensively scattered over the leaf blade and coalesce into larger areas. Severely affected leaflets are shed, leaving the petiole attached to the tree but effectively defoliating the tree, leading

to reduced fruit production (Perrotta et al., 1998; Varo et al., 2010). A second common fungal parasite is carob mildew caused by *Pseudoidium ceratoniae* (Comes) Braun & Cook (Ascomycota, Helotiales) which affects fruits, leaves and twigs mainly in spring and autumn. Severe damage occurs only in some cultivars (Tous et al., 2013). For example, ‘Rojal’, ‘Matalafera’, ‘Duraíó’, ‘Amele di Bari’ and ‘Racemosa’ are fairly tolerant to this disease, while ‘Negra’, ‘Melera’, ‘Costella’ and ‘Santa Fe’ are susceptible. Other fungal parasites are given in Table 5.

Given the arid habitats of carob, few epiphytes have been recorded but *Ramalina lacera* (With.) J.R. Laund. (Ascomycota, Lecanorales) has been recorded on carob twigs in northeast Israel (Garty et al., 2003).

9.3 | Plant diseases

The most widespread diseases periodically occurring on carob orchards are caused by fungal parasites (Section 9.2), notably powdery mildew caused by *Pseudoidium ceratoniae* and cercospora leaf spot caused by *Pseudocercospora ceratoniae*. Similar symptoms of so-called fungal ‘black leaf spot’ diseases (caused by, e.g. *Pestalotiopsis*, *Phyllosticta*, *Alternaria* and *Septoria* spp.) are reported in carob orchards with variable frequency.

Ceratonia blight disease is caused by *Alternaria alternata* (Fr.) Keissl. (Ascomycota, Pleosporales) and incidence has been

recorded on 10%–100% of leaves on both wild and domesticated carob trees from Turkey to Libya (Basim et al., 2018; El-Gali, 2015). *Diplodia olivarum* A.J.L. Phillips, Frisullo & Lazzizera (Ascomycota, Botryosphaeraiales) was found in 2009 to be causing canker, branch dieback and foliage reddening on carob trees in several wild carob populations in Italy. Between 5% and 80% of trees were affected across different sites, and for most areas, it was nearly 15%. Affected trees have dark necrotic areas of the bark that penetrate the cambium and sapwood of the trunk and branches. Resulting cankers frequently girdle the stem or branch, causing wilting and death of distal parts (Granata et al., 2011). Fruits and seeds once dispersed or collected are prone to a number of Ascomycete pathogens under high humidity including species of *Alternaria* (Pleosporales), *Aspergillus*, *Penicillium* (both Eurotiales), *Colletotrichum* (Glomerellales) and *Fusarium* (Hypocreales) (Trapero et al., 2022).

Carob trees growing both in glasshouses and in the field have proven resistant to honey fungus (Basidiomycota, Agaricales) in Europe and North America, including *Armillaria mellea* (Vahl) P. Kumm., *A. obscura* (Schaeff.) Herink and *A. ostoyae* (Romagn.) Herink (Batlle & Tous, 1997; Loreto et al., 1993) although these may affect young plants (Salazar Hernández et al., 2002). *Laetiporus sulphureus* (Bull.) Murrill (= *Polyporus sulphureus* (Bull.) Fr.) (Basidiomycota, Polyporales) is a common saprophyte of woody plants causing brown rot, but it can also be a weak parasite in carob (Batlle & Tous, 1997; Sillo et al., 2018). On the Spanish east coast in particular,

TABLE 5 Fungal parasites recorded from *Ceratonia siliqua*.

Species classification	Ecological notes	Source
Ascomycota		
Botryosphaeraiales		
<i>Phyllosticta calaritana</i> Briosi. & Cay.	Irregular marginal brown blotches on leaves	Stevenson (1926)
<i>P. ceratoniae</i> Berk.	Irregular marginal black spots on leaves	Stevenson (1926)
Capnodiales		
<i>Cylindroseptoria ceratoniae</i> Quaedvlieg, Verkley & Crous (= <i>Septoria ceratoniae</i> Pass.)	Spots on leaves in Italy and France, Spain	Stevenson (1926); Quaedvlieg et al. (2013)
<i>Septoria carrubi</i> Pass.	Dark-brown, irregular spots on leaves and fruits. Said to menace the existence of the trees in France and Malta	Stevenson (1926)
Dothideales		
<i>Pseudocercospora ceratoniae</i> (Pat. & Trab.)	Necrotic spots on leaves	Stevenson (1926); Perrotta et al. (1998); Varo et al. (2010)
Helotiales		
<i>Pseudoidium ceratoniae</i> (Comes) Braun & Cook (= <i>Oidium ceratoniae</i> Comes)	Mildew of fruits, leaves and twigs, particularly in periods of high humidity	Batlle and Tous (1997); Braun and Cook (2012); Tous et al. (2013)
Mycosphaerellales		
<i>Ramularia australis</i> Saco.	Leaf spots	Stevenson (1926)
Xylariales		
<i>Pestalotiopsis maculans</i> (Corda) Nag Raj	Necrotic spots on leaves of carob and <i>Arbutus unedo</i>	Trapero et al. (2007)
<i>P. uvicola</i> (Speg.) Bissett.	Necrotic black lesions on leaves	Carrieri et al. (2013)
<i>Rosellinia necatrix</i> Berl. ex Prill.	Rot of secondary roots	Salazar Hernández et al. (2002)

it is a recurrent secondary pathogen in very old trees, weakening the wood which has a characteristic bright red colour, and in many cases causing breakage of the main trunk and subsequent death of the tree. In Valencia, Spain, the fruiting bodies of *L. sulphureus* are collected for eating only from carob, locally called 'bolo' or 'pan de lobo' (wolf bread).

Carob is proving resistant to *Xylella fastidiosa* Wells et al. (Pseudomonadota, Xanthomonadales) and so is an alternative crop to almond, olive and grapes (IVIA, 2018).

10 | HISTORY

10.1 | Origin and domestication

Ceratonia is likely to have originated from the xerotropical Indo-Malesian flora (Barracosa et al., 2007) and is considered to be an isolated remnant of a part of the family now largely extinct (Hillcoat et al., 1980; Zohary, 1973). *Ceratonia* pollen has been found in deposits dating since the Oligocene and its ancestors were widely distributed around the Tethys Ocean (Palamarev, 1989; Ramón-Laca & Mabberley, 2004). *Ceratonia oreothauma* Hillcoat, Lewis & Verdc., described in 1980, has smaller pollen grains than *C. siliqua* and they are evolutionarily more primitive, being tricolporate rather than tetracolporate as in *C. siliqua* (Ferguson, 1980). Thus, *C. oreothauma* is suggested to be an ancestor of the cultivated *C. siliqua* (Hillcoat et al., 1980), or more likely a sister species, both arising from a common ancestor, separating 6.4 Ma in the Late Miocene (Viruel et al., 2020). Before 3.5 Ma, *Ceratonia* pollen occurs primarily along the northern margin of the developing Mediterranean Sea with many other tropical and subtropical trees including *Pistacia*, *Nerium* and *Bombax* (Bessedik et al., 1984). *Ceratonia* is rarely found in the pollen fossil record from the Pleistocene, sometimes as only single grains (Jahns & van den Bogaard, 1998) as Pleistocene climate cooling greatly reduced the range of the genus (Ramón-Laca & Mabberley, 2004; Suc et al., 2018).

Ceratonia siliqua was long thought to have originated and survived the Pleistocene in the eastern Mediterranean region, possibly Turkey and Syria or down through the coastal Levant and the Arabian peninsula (De Candolle, 1883; Jahns, 2003; Liphschitz, 1987; Zohary, 1973, 2002) based on pollen and macro-fossil remains mostly in the eastern Mediterranean and Egypt from the early Neolithic onwards (Galili et al., 1997; Galili & Schick, 1990). However, a number of studies have shown the presence of carob in the western Mediterranean during the Pleistocene (Brenac, 1984; Servera-Vives et al., 2018; Zapata et al., 2013), centred around the foothills of the High Atlas Mountains in Morocco and south Spain. More recent investigations of the clustering of microsatellite polymorphisms suggest a set of distinct western populations with high genetic diversity that survived the last interglacial period (130–115 ka) and a smaller group in the east that suffered from an increasingly continental climate which was more pronounced in the east during the last interglacial (Di Guardo et al., 2019; Viruel et al., 2020). Viruel

et al. (2020) estimated that the divergence between the west and east part of the carob range could have happened 1815 generations ago (400–4640 generations, 95% confidence interval), suggesting a west-to-east expansion before the last glacial maximum but recent enough to explain the low genetic diversity of carob. However, Baumel et al. (2022) used nuclear microsatellite polymorphisms to identify seven genetic groups of carob across the Mediterranean, and found that rather than an east and a west origin, that carob arose primarily from a refugium in southwest Morocco leading to four discrete ancestral populations in Morocco and south Spain and two more ancestral populations in the east that gave rise to central-eastern populations. Indeed, modelling of species distribution by Baumel et al. (2022) suggests that parts of the western area could have been continuously suitable for carob for the last 130,000 years.

The pattern is complicated by subsequent development of domesticated cultivated varieties that were derived from wild varieties, with selection for larger and sweeter fruits, dating from around 8000–6000 years ago, and more extensively with the development of grafting methods c. 3000 years ago. Subsequent movement of cultivars was based on the use of local varieties with occasional long-distance movement from the east to the west associated with major migration events by Greeks, Romans and Arabs, and recent isolation of populations over the last two centuries due to anthropogenic pressure (Abbo et al., 2015; Barracosa et al., 2007; Batlle & Tous, 1997; Baumel et al., 2022; Mahdad & Gaouar, 2023; Makrem et al., 2006; Ramón-Laca & Mabberley, 2004). This has had a mixed impact on genetic diversity, undoubtedly due to multiple local origins of domestication but has been insufficient to hide the phylogenetic signal identified by Baumel et al. (2022) as has happened in other domesticated trees such as olive. Seventeen scattered populations of carob in Tunisia were shown to have high allozyme diversity within populations, with an average of 1.98 alleles per polymorphic locus and 83.4% of loci being polymorphic, and a mean observed heterozygosity of 0.247 and expected heterozygosity of 0.316 (Makrem et al., 2006). High genetic differentiation and low gene flow were detected among populations ($F_{ST}=0.200$) attributed to a high level of inbreeding within populations ($F_{IS}=0.231$).

10.2 | Uses

The scientific name of carob derives from the Greek *keras* (horn), and Latin *siliqua*, referring to the hardness and shape of the mature fruit. The common name originates from the Hebrew *kharuv*, from which comes the 12th century Arabic *kharrub* or *kharroub* meaning pod (Bellakhdar, 1997; Gharnit & Ennabili, 2016; Talhouk et al., 2005; Tous et al., 2013). Carob is also known as St. John's bread or locust bean in reference to the presumed use as food by John the Baptist (Coit, 1951; Tous et al., 2013) although his food of 'locusts' was likely the insect not carob (Evans, 2018).

Carob fruit have traditionally been used to feed humans and domesticated animals around the Mediterranean for thousands of years (Figure 5: Asma et al., 2023; Basharat et al., 2023; Jin et al., 2024;



FIGURE 5 Carob fruits on sale in Benghazi, Libya. Photograph by Tarek Mukassabi.

Meyer, 1980; Nasrallah et al., 2023). In some North African Bedouin tribes, it has long been a staple food (Salazar Hernández et al., 2002). The fruits are generally low in fat, protein and fibre content but rich in sugars, calcium and potassium (Albanell et al., 1991; El Hajaji et al., 2013). The fruits have long been used as fodder for ruminants (making up to 30% of their diet; Louca & Papas, 1973) and for non-ruminants such as geese and domestic pets (Sahle et al., 1992). In Norway, ground fruits were once fed to animals to protect livestock 'from evil and disease' (Alm, 2002). More recently, carob pulp powder has been used as animal food, for example, in chickens (Mahmoudi et al., 2022). Fruits are eaten by children as snacks and are still commonly used in cakes in Egypt, for jams and liquors in Turkey, Malta, Portugal, Spain and Sicily, and in Libya a syrup extracted from carob is used to make *asida*, a traditional dessert (Brassesco et al., 2021). In former times, fruits were ground into flour in times of famine (Issaoui et al., 2021; Tous et al., 2013), and the molasses obtained from carob pulp was important in alleviating the famine of many people after the Spanish Civil War in the regions of Valencia, Catalonia and the Balearic

islands. In rural areas of Spain, it is known as donkey chocolate (Xavier Garcia-Martí, personal communication). In Spain, carob honey is also in increasing demand (Salazar Hernández et al., 2002) for its light colour and its high carob pollen content (up to 45%), and in Libya, carob is the most common source of honey, followed by *Ziziphus spina-christi* and *Arbutus pavarii*. Portuguese carob honey has a high concentration of minerals, organic acids and protein, is darker than many other honeys, has a low pH (3.7–4.6) and a high proline content (1.2–1.8 mg/g) (Machado et al., 2022). Carob leaves have been used as a tanning agent for olives in brine, with the stipulation that the leaves should be from non-grafted trees (Laguna et al., 2017). Tous et al. (2013) give a good summary of historical uses and Laguna et al. (2017) have compiled the historical uses of the carob tree in Valencia, Spain.

The pulp from the fruits is high in sugar content (48%–56%) with c. 18% cellulose and hemicellulose and high in many minerals. It is now used to produce syrups and powder (Bengoechea et al., 2008; Brassesco et al., 2021; El Batal et al., 2011; Papaefstathiou et al., 2018). Perhaps the biggest use is as a low-calorie, caffeine-free cocoa substitute (Batlle & Tous, 1997; Laguna et al., 2017; Yousif & Alghzawi, 2000). Carob powder contains low levels of caffeine (0–0.067 mg/g) and theobromine (0–0.504 mg/g) compared to chocolate (0.138 mg/g and 1.95 mg/g, respectively) (Craig & Nguyen, 1984; Khelifa et al., 2013; Papaefstathiou et al., 2018). Carob powder from wild trees has less sugar but is still acceptable by consumers as a substitute for chocolate (Caliskan et al., 2023). Carob powder has also been used to produce ethanol and other products by fermentation (Yatmaz & Turhan, 2018) and as a substrate in microbial digestion to produce succinic acid, widely used in pharmaceuticals and technology (Carvalho et al., 2014). The powder has also been used to remove lead from contaminated water (Çiftçi & Coşkun, 2020) and defend plants against cobalt toxicity (Macar et al., 2020).

However, increasingly the seeds are of commercial interest. The seeds, accounting for 10%–20% of the mass of fruits, are high in antioxidant activity, rich in calcium, magnesium, protein and lipids (Section 6.6), making them a nutritional if underused food source (Fidan et al., 2020). More recently, the seeds have proved valuable due to the polysaccharide carob bean or locust bean gum (a galactomannan; E410) extracted from the endosperm, and widely used in pharmaceuticals and cosmetics, and as a thickener, gelling agent, stabiliser, emulsifier and foaming agent in a wide variety of foods and other products (Ayaz et al., 2007; Boublenza et al., 2019; Salazar Hernández et al., 2002; Sidina et al., 2009; Stavrou et al., 2018). One of the most important worldwide uses of the gum currently is as a thickener in ice cream (Joan Tous, personal communication). The gum has other uses; it is reputed to have been used as an adhesive in mummy binding in Egypt (Nasar-Abbas et al., 2016) and it is now used as a root covering to hold the spores of *Trichoderma* spp. which reduces galling by the root-knot nematode *Meloidogyne incognita* (d'Errico et al., 2021). Mediterranean cultivars of carob have larger fruit and low seed yield while wild and feral trees are now of greater interest since their seeds have a higher galactomannan content than traditional cultivars (Marakis et al., 1988; Winer, 1980).

The tree itself is also useful. Carob is widely planted as an ornamental or shade street tree in California, Australia and elsewhere since it is tolerant of drought and air pollution, and low maintenance although it can become tall and spreading with invasive roots (National Research Council, 1979). Carob has also been used as a windbreak around orchards and for intercropping between other fruit trees. Since carob tolerates poor, dry soils and is long-lived, it has been used to reforest degraded land (Winer, 1980). Large forest fires burnt through the Algarve in 2003–2004 and carob acted as a fuelbreak (Section 5.3) and was used in post-fire planting (Barracosa et al., 2008). Similarly, in eastern Spain, carob is recommended for planting at the urban–forest interface and in ‘pyrogardening’, planting to reduce fire risk (Pipió et al., 2020). The timber is hard and close-grained and has been used to make utensils and has also been much used for firewood and in producing a slow-burning charcoal (Batlle & Tous, 1997).

Carob has long been used in herbal and contemporary medicine (Asma et al., 2023; Ikram et al., 2023; Laguna et al., 2017; Martins et al., 2018). The high antioxidant capacity of carob fruits (Brassesco et al., 2021; Makris & Kefalas, 2004) has been used to treat male infertility (Aghajani et al., 2021), anxiety (Lakkab et al., 2019), reduce cholesterol levels (Nasar-Abbas et al., 2016), help toothache (Akbulut & Bayramoglu, 2013), help with gastrointestinal problems including constipation, diarrhoea, ulcers and cancers, likely due to the high condensed tannin levels in fruits (Brassesco et al., 2021; López-Sánchez et al., 2018; Senouci et al., 2023) treat anaemia, asthma, pharyngitis, bronchitis, colds and influenza and breast cancer (Alm, 2002; Elbouzidi et al., 2023; Sargin & Büyükcengiz, 2019), and improve the cryopreservation of human sperm (Farazmand et al., 2023). It may also have important antimalarial value (Custódio et al., 2008) and antimicrobial activity (Abbassy et al., 2020; Karmous et al., 2022) although evidence for the latter is contradictory (Azab, 2017).

Carob has also proved useful in animal husbandry since it acts as a diuretic (El-Haskoury et al., 2015), gives protection against diabetes and liver damage in rats and is used in treating osteoporosis, inducing puberty in rats (Khader et al., 2023; Neri et al., 2023; Rtibi et al., 2017; Uğurlu et al., 2023) and protecting the liver in mice from paracetamol-induced injury (Martić et al., 2022). Carob syrup can also boost the immune system of the Nile tilapia fish *Oreochromis niloticus* (L.) and improve their resistance to ammonia (Yilmaz, 2020). In mammals, carob extracts have been used against intestinal nematodes in lambs (Arroyo-Lopez et al., 2014). Laguna et al. (2017) noted that carob seeds have been boiled and then fried with the frying oil being used to treat wounds of horses' hooves. A review of the wide range of herbal medicinal uses is given by Azab (2017) and Brassesco et al. (2021), and wider uses by Hadi et al. (2017) and Rasheed et al. (2019).

11 | CONSERVATION AND MANAGEMENT

As a commercial crop (Figure 6), carob was in decline at the end of the last century (Section 12) as labour costs rose and the fruit crop became less profitable, and carob was replaced by more economic



FIGURE 6 Carob orchard in Tarragona, Spain. Photograph by Joan Tous.

crops (Gharnit et al., 2001; Makhzoumi, 1997). Semi-natural populations were also under threat due to expansion of agriculture and urban development in coastal areas (Talhok et al., 2005), and decline in traditional uses (Section 10.2). Extremes of weather and consequent devastating disasters, such as that caused on the coast of Libya by Storm Daniel in September 2023, have also removed large areas of carob. Due to this decline, carob has been included in national lists of priority forest genetic resources for conservation and management in a number of countries, including Lebanon and Tunisia (Bouzouita et al., 2007; Talhok et al., 2005). However, in this century, the value of carob in tourism and wildlife conservation, and the maintenance of cultural landscapes is more appreciated, as is the potential of payments for the carbon sequestered in carob (Correia et al., 2017; Tzatzani & Ouzounidou, 2023). Moreover, the price of carob fruits has increased 10-fold over the past 15 years due to the growing market in carob bean gum obtained from the seeds (Section 10.2), making their future more secure (Tous, 2021; Tzatzani & Ouzounidou, 2023). Semi-natural populations will continue to exist on soils with poor agricultural capability, in areas that are less accessible or are unsuitable for urban expansion. The International Union for Conservation of Nature (IUCN) conservation status of Least Concern (Rivers et al., 2019) is therefore justified. However, old and monumental carob trees have been included in conservation listings at different local and regional scales in Spain (Diari Oficial de la Generalitat Valenciana, 2006). A municipal catalogue of monumental carob trees in Chiva, Valencia, Spain includes 243 individuals with a girth >4 m (at 1.3 m above ground) and 61 individuals >6 m girth. This gives them in legal protection by legislative order against their destruction or translocation, thus making a former trade in moving old carob trees largely illegal.

In Mediterranean agroforestry systems, where in many cases, there are no other species of large trees, old feral and wild carob trees constitute important conservation units in themselves. The microhabitats in these old carob trees, such as cavities, broken and

dead branches, create numerous niches for many species of mammal, such as Common Genet *Viverra genetta* L., foxes, dormice and voles, and many species of birds, including day-flying and nocturnal raptors, and bats. Further research is needed into the role of large isolated carobs as a keystone species.

In situ conservation should concentrate on populations with a high level of genetic diversity and rare alleles. Ex situ preservation using field collections and seed storage banks are also important in maintaining this genetic diversity and should include both western and eastern populations, and also semi-natural populations and cultivars (Baumel et al., 2022; Makrem et al., 2006; Tous et al., 2013). Rivers et al. (2019) recognised 137 ex situ collections of carob in botanic gardens and Tous and Franquet (2024) list the current main carob cultivar trials and collections in the Mediterranean countries.

Research on the effects of climate change on carob is limited. Osório et al. (2011) investigated the effect of increased temperature and drought on carob (Section 5.3) and concluded that carob will cope with predicted climate change. Indeed, Cruz et al. (2003) found that biomass gain of plants grown in 800 ppm of CO₂ was 13%–100% higher than plants grown in ambient CO₂. However, more detailed modelling by Cartereau et al. (2023) suggests that carob will be comparatively sensitive to increases in aridity, ranking its risk of decline from aridification at 0.686 (0, no risk to 1, highest risk), putting it 78th most at risk out of 632 global dryland species. Moreover, Kassout et al. (2024) predicted that the area with suitable climatic conditions for carob in Morocco (currently 78,233 km²) will shrink by c. 10% by 2070, predominantly driven by reduction in precipitation in the coldest quarter of the year.

12 | GLOBAL HETEROGENEITY

It was originally thought that *Ceratonia siliqua* arose in the eastern Mediterranean, but it is clear that there is a strong west-east genetic structuring based on origins in the western Mediterranean (Section 10.1). Similarly, it was thought that domestication and breeding of cultivars from seed and by grafting arose in the east and spread west, but it is now appreciated that there were multiple centres of domestication across the Mediterranean (Baumel et al., 2022; Kassout et al., 2022) with around 100 named cultivars (Tous & Batlle, 1990; Zohary, 1983), predominantly in Spain, Portugal and Italy (Daris, 1964; Tous et al., 2013). Moreover, since there have been few international breeding programmes, each country still possesses its own carob varieties which are reproduced vegetatively with limited geographical movement (Baumel et al., 2022; Caruso et al., 2008; La Malfa et al., 2014), leading to large variations in fruit, seed size and morphology across the range of carob (Di Guardo et al., 2019; Viruel et al., 2018, 2020). More recent breeding programmes have aimed to increase seed production due to the increased market for the contained gum (Section 10.2) and other biotechnology uses (Makris & Kefalas, 2004; Naghmouchi et al., 2009). These new cultivars interbreed to a limited extent with

carob in semi-natural vegetation to increase genetic variation (Batlle & Tous, 1997) but how much interbreeding occurs depends upon the cultivars. For example, carob breeding in Andalusia and Morocco has been less intensive than elsewhere (Di Guardo et al., 2019) and carob fruits from cultivars are similar to those of surrounding semi-natural carob plants. In contrast, cultivars in the eastern and central Mediterranean regions, particularly Sicily, Crete, Cyprus and Spain (Tarragona, Majorca and Valencia), have been, and are being, artificially selected and show greater differences to wild carob trees (Baumel et al., 2018, 2022).

World carob production declined from 650,000 tonnes in 1945 to an average of 250,000 tonnes per year from 2000 to 2020, representing a loss of 62% over 70 years (Tous & Franquet, 2024). The main carob producing countries between 2000 and 2020 were Spain (60,000t), Morocco (55,000t) Portugal (40,000t), Italy (31,051t) and Turkey (14,110t) followed by Greece (13,750t), Algeria (10,000t), Cyprus (7082t) and Lebanon (3589t) (Tous & Franquet, 2024). The yield of carob fruits is variable and depends on cultivar, region, environmental conditions and cultural practices (Barracosa et al., 2007; Tous et al., 2013). In the major carob-producing countries of Spain and Italy, the average fruit yields in traditional orchards are c. 1300 and 2300 kg/ha, respectively, with 50 trees/ha, giving an average yield of 50–70 kg per tree (Tous & Batlle, 1990). Some modern orchards, 10–20 years old, in Spain and Portugal give higher average high yields of c. 6000–7000 kg/ha in dry conditions (c. 500 mm of rainfall) and 8000–10,000 kg/ha with deficit-regulated irrigation and densities of 150 trees/ha (Tous et al., 2013).

AUTHOR CONTRIBUTIONS

Tarek A. Mukassabi conceived the idea for this account; Peter A. Thomas, Tarek A. Mukassabi, Xavier Garcia-Martí and Joan Tous contributed written material; Peter A. Thomas compiled the first complete draft. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

Peter Thomas is grateful to Harvard Forest, Harvard University, United States, for access to their libraries. Xavier Garcia-Martí is grateful to Vicente Serena and Dr. Juli G^a Pausas who contributed information to this manuscript.

CONFLICT OF INTEREST STATEMENT

Peter Thomas is an Associate Editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper. No other author has a conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14325>.

DATA AVAILABILITY STATEMENT

This study does not include data.

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How to cite this article: Thomas, P. A., Garcia-Martí, X., Mukassabi, T. A., & Tous, J. (2024). International Biological Flora: *Ceratonía siliqua*. *Journal of Ecology*, 00, 1–38. <https://doi.org/10.1111/1365-2745.14325>