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Biological Flora of the British Isles: *Crataegus monogyna*

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Abstract

1. This account presents information on all aspects of the biology of *Crataegus monogyna* Jacq. (Hawthorn) that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *Biological Flora of the British Isles*: 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. *Crataegus monogyna* is native to the British flora, occurring frequently in hedgerows, scrubs, thickets and woodland. It can be found throughout almost all of Europe, on all soils of medium conditions regarding pH value, nutrient and water supply.
3. *Crataegus monogyna* is a deciduous shrub or rarely a small tree of 2–8 m. Its twigs and branches bear sharp thorns about 1 cm long. *Crataegus monogyna* is of both ornamental and ecological value. During flowering in May and June, shrubs may appear white through a multitude of flowers, presenting pollen and nectar to a variety of different insects. Starting in August, almost the whole shrub can become dark red with the huge number of small red berries (pomes) produced during fruiting. The fruit are a preferred food for many birds.
4. Although hybridizing freely and frequently with the other native species, *Crataegus laevigata* (Poir.) DC., the two species are easily recognizable in natural stands in the British Isles. Elsewhere, and with the occurrence of horticultural naturalizations and many intermediate forms of hybrid origin with closely related *Crataegus* species (especially the similar looking one-styled species *Crataegus rhipidophylla* Gand. s.l. and *Crataegus* × *subsphaerica* Gand. s.l.) expert knowledge is required to avoid misidentifications and thus inaccurate understanding of frequency and distribution–not only on continental Europe but also increasingly in the British Isles.
5. Identification in the field is further complicated by inbreeding of horticultural stock, which suffers from a myriad of descriptions and given names at different hierarchical levels. Cultivars are commonly planted in hedges and along roadsides or for ornamental purposes. The origin of this stock is not always known, so genetic exchange with the natural populations may lead to introgression and thus genotypes that are more adapted than the local genotypes in a changed environment.

Nomenclature of vascular plants follows Stace (2019) and, for non-British species, *Flora Europaea*.

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KEYWORDS
communities, *Crataegus monogyna*, geographical and altitudinal distribution, germination, herbivory, hybridization, parasites and diseases, reproductive biology

Hawthorn (Common hawthorn, Maythorn or May). Rosaceae. *Crataegus monogyna* Jacq. (Homotypic synonyms: *Mespilus monogyna* (Jacq.) All., *Oxyacantha monogyna* (Jacq.) M. Roem., *Crataegus oxyacantha* subsp. *monogyna* (Jacq.) Syme, *Mespilus oxyacantha* subsp. *monogyna* (Jacq.) Čelak.) is a deciduous, much-branched, mostly thorny shrub to small tree with a rounded-ovoid, densely twiggy crown. Height 2–8(10) m, trunk to 30 cm in diameter. Bark greyish-brown, smooth when young, pinkish-brown and scaly when mature. Buds to 3 mm, terminal ones may be larger, ovoid; scales reddish-brownish, glabrous, up to 16. Leaves alternate, often ± coriaceous, glabrous except for hair-tufts in the axils of the lower veins beneath (acarodomatia), discolorous (±shiny, dark or bright green above, greyish-green or glaucous-green beneath, with ± dense waxy bloom), ovate or obovate in outline, attenuate or cuneate, rarely more or less rounded at the base; lamina of subterminal leaves 1.0–5.7 × 0.8–6.0 cm, simple, (3–)5(–7)-lobed to subpinnate, leaf lobes acute or obtuse, entirely or sparingly serrate near their apices, sinuses open and deep, cutting the lamina at least halfway to the midrib, lateral veins curving downward; petiole up to 3 cm; stipules (on flowering short shoots) up to 3–16 mm long, lanceolate-subulate, entire or denticulate with one to eight teeth and caducous; lamina of leaves on elongate shoots appear larger; stipules larger and more serrate.

Inflorescence borne on a leafy short shoot of the current year, 1.5–5.0 cm, 10- to 18-flowered, corymbose composed of three to five branches, lax. Flowers bisexual, regular, 10–15 mm in diameter; pedicels *c*. 4 cm, ±glabrous; sepals 5, ±triangular, acute to obtuse at apex; petals 5, 3–7 × 4–7 mm, subrotund, very short clawed, white, or rarely pink or red; stamens 20, seldom 19, filaments whitish, anthers pink, yellowish-brown after anthesis; pollen yellow; style 1, greenish, small and simple, stigma capitate. Ovary inferior, one-celled, each cell containing two ovules of which the upper does not develop; rarely with two ovaries in central flowers of the inflorescence. Nectary a lobed ring. Fruit 6–11 × 5–10 mm, broadly ovoid or broadly ellipsoid, crowned by the persistent, mostly deflexed sepals, glabrous, a bright to deep red drupaceous pome; flesh yellowish, mealy, containing one single-seeded nutlet. Nutlets 6.5–7.5 × 4–5 mm, broad ellipsoid, dorsally and ventro-laterally sulcate, somewhat laterally compressed, slightly erose, with two or three longitudinal shallow furrows on the dorsal side, surface lustreless, fine tuberculate, coloured dark brownish.

The genus *Crataegus* is largely confined to the temperate regions of the Northern hemisphere (Christensen, 1992a). It is well-defined and at the same time the species within are taxonomically challenging, as there are apomixis, hybridization and introgression with other closely related species, and descriptions are based on slight morphological differences. Depending on treatment there are 50 to 100 species native to Eurasia and 100 to 1,100 to North America (Christensen, 1992a; Krüssmann, 1976; Lippert, 1995; Sell & Murrell, 2014). *C. monogyna* belongs to Section *Crataegus*, which is limited to Europe, Northern Africa and West Asia (Christensen, 1992a).

Do Amaral Franco (1968) recognizes six subspecies *C. monogyna* subsp. *monogyna*, subsp. *nordica* Franco, subsp. *leiomonogyna* (Klovov) Franco, subsp. *brevispina* (Kunze) Franco, subsp. *azarella* (Greiseb.) Franco, and subsp. *aegeica* (Pojark.) Franco with partially overlapping areas of distribution. Except subsp. *aegeica*, all of these subspecies are mentioned by Sell and Murrell (2014) for Britain and Ireland despite their non-British distribution according to *Flora Europaea*. Furthermore, the authors subdivide them and give subsp. *monogyna* as two forms, subsp. *brevispina* and *nordica*, with two varieties each, the latter with five forms. Clapham et al. (1989) refer all native British material to subsp. *nordica*. So does Stace (2019), but additionally referring to subsp. *azarella* as being commonly planted. In contrast Kurtto et al. (2013) work with a broad species concept and reject any subspecies or varieties to overcome the myriad of different taxonomic descriptions and combinations. Thus, they provide a list of 193 synonyms. Krüssmann (1976) lists a number of cultivars and forms of horticultural interest; noteworthy is *C. monogyna* 'Biflora', the 'Glastonbury Thorn', with a second flowering period during winter. Other forms with pink to red coloured or double flowers, given in Sell and Murrell (2014), have to be allocated to cultivars of *Crataegus* × *media* Bechst. (Jablonski, 2020; Schmidt, 2017b). Several intra- and extrasectional hybrids are known (Section 8.2).

Crataegus monogyna is native to the British Isles, throughout Europe and adjacent regions, but has been widely planted across Europe (Hegi, 1923). It is best known as a shrub in hedges, as wind-break along roadsides, or as a living fence to enclose stock (Hegi, 1923). There it is an eye-catching landscape component during its flowering period in May and early June, giving rise to its common English name 'May'.

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Crataegus monogyna can be commonly found in scrub and thickets, hedgerows and at the edges of forests throughout the British Isles but is rare in northern-most Scotland, for example, in the Northwest Highlands and parts of the Grampian Mountains (Figure 1; Preston et al., 2002). In north-west Scotland, and many of the Hebridean islands, the native status of *C. monogyna* is uncertain (Pearman et al., 2008). It is introduced to the northern islands of Orkney and Shetland. Hill et al. (2004) list *C. monogyna* as being present in 2,496 hectads (10-km squares) in Great Britain and the Isle of Man (89%), 946 in Ireland (96%) and 13 in the Channel Islands (93%).

C. monogyna occurs 'almost throughout Europe except the northern and eastern margins' (Figure 2; Do Amaral Franco, 1968). It extends northwards to latitudes of about 63°N in Norway along the

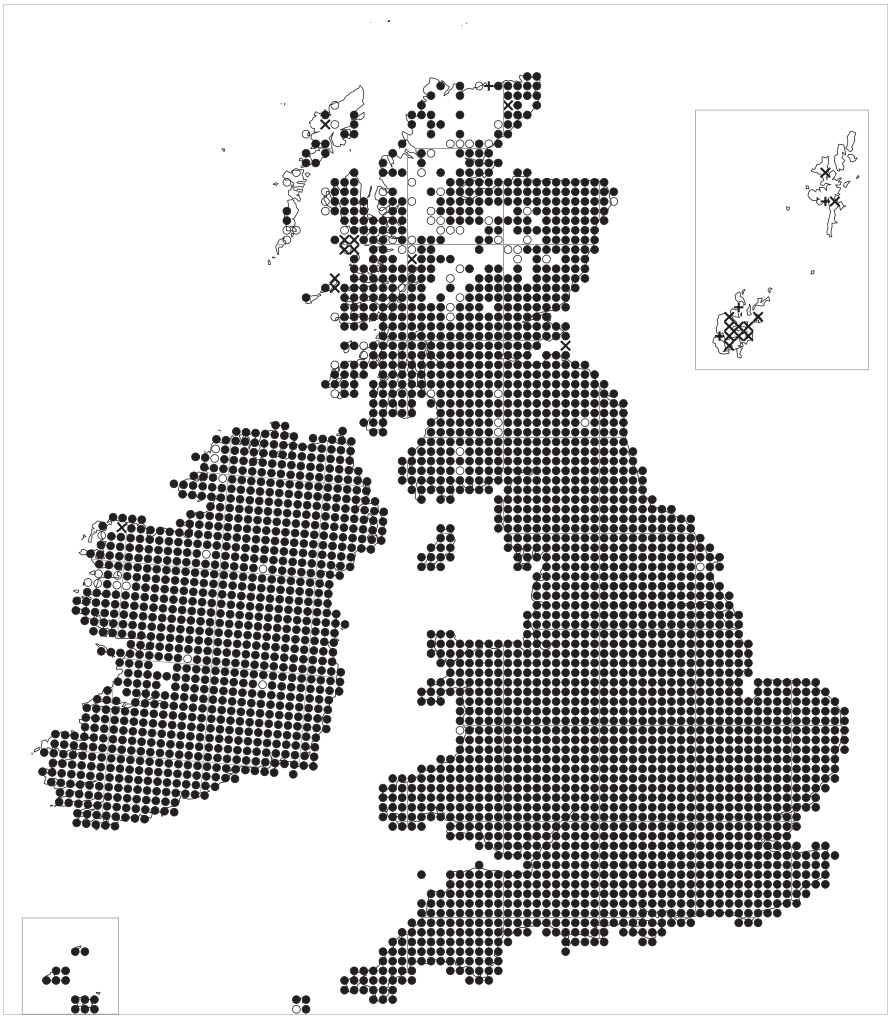

FIGURE 1 Distribution of *Crataegus monogyna* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (●) native 1970 onwards; (○) native pre-1970; (×) non-native 1970 onwards; (+) non-native pre-1970. Mapped by Colin Harrower, Biological Records Centre, Centre for Ecology and Hydrology, mainly from records collected by members of the Botanical Society of Britain and Ireland, using Dr A. Morton's DMAP software

coast of the North Sea (as far as Nordmöre) and up to 60°N in the south of Sweden (Gestrikland and Wermland) across Åland to Åbo (Mossberg & Stenberg, 2010). Following 53°N to Kazan, the distribution reaches the Volga River in the east, the western and southern Caspian Sea, Ciscaucasia and Transcaucasia (Pojarkova, 1939) with the exception of some Inner Anatolian areas. Further east to Syria and Northern Iraq, there are only scarce occurrences (Browicz, 1972). *C. monogyna* can be found in the coastal Middle East, on Cyprus, the Aegean Islands, and Crete, Corsica, Sardinia and Sicily reaching Africa only in the Maghreb (Hegi, 1923), where Maire and Quézel (1980) list it for the different subranges of the Atlas Mountains. It is widespread throughout the whole Iberian Peninsula (Muñoz Garmendia et al., 1998) but missing as a native from the islands and archipelagos of the Atlantic Ocean, for example, the Canary Islands (Acebes Ginovés et al., 2009), Madeira (where it was introduced, Muñoz Garmendia et al., 1998), the Azores, the Faroe Islands, Iceland and Svalbard. It is the most widespread hawthorn in the Old World.

Outside Europe *C. monogyna* has been introduced to N. America (Phipps, 1998; with occurrences in Ontario, Quebec, the Great Lakes area, New York State and New England in the east and British Columbia, Washington and Oregon in the west; USDA & NRCS, 2019). In the southern hemisphere the species has been introduced to Argentina (Ezcurra, 2005) and South Africa (Reichard et al., 2001; South African National Biodiversity Institute, 2019). Settlers brought *C. monogyna* to Australia before 1850 (Bass, 1990a; Bass et al., 2006) where it is now naturalized in New South Wales, Victoria, Tasmania, South Australia and Queensland (Australian Plant Census website, 2019), and to New Zealand in 1899, where it occurs on both islands (Webb et al., 1988).

The altitudinal distribution of *C. monogyna* depends on regional climatic and edaphic conditions. While the highest occurrences of *C. monogyna* in Great Britain have been recorded at 610 m a.s.l. at Melmerby High Scar, Cumberland, England (Pearman & Corner, 2017), the species reaches higher elevations in lower latitudes. In Central European low mountain ranges, it grows at a local maximum of 1,100 m a.s.l. in the Black Forest (Sebald et al., 1992). In the Alps, it reaches 1,270 m a.s.l. in the Bavarian Alps and in climatically favoured areas like South Tyrol and the Valais, it reaches up to 1,450 and 1,525 m a.s.l. respectively (Meusel et al., 1965). Maximum elevations are 1,800(–2,000) m a.s.l. in Turkey (Browicz, 1972) and 2,200 m a.s.l. on the Iberian Peninsula (Muñoz Garmendia et al., 1998) as well as in the Atlas Ranges (Maire & Quézel, 1980).

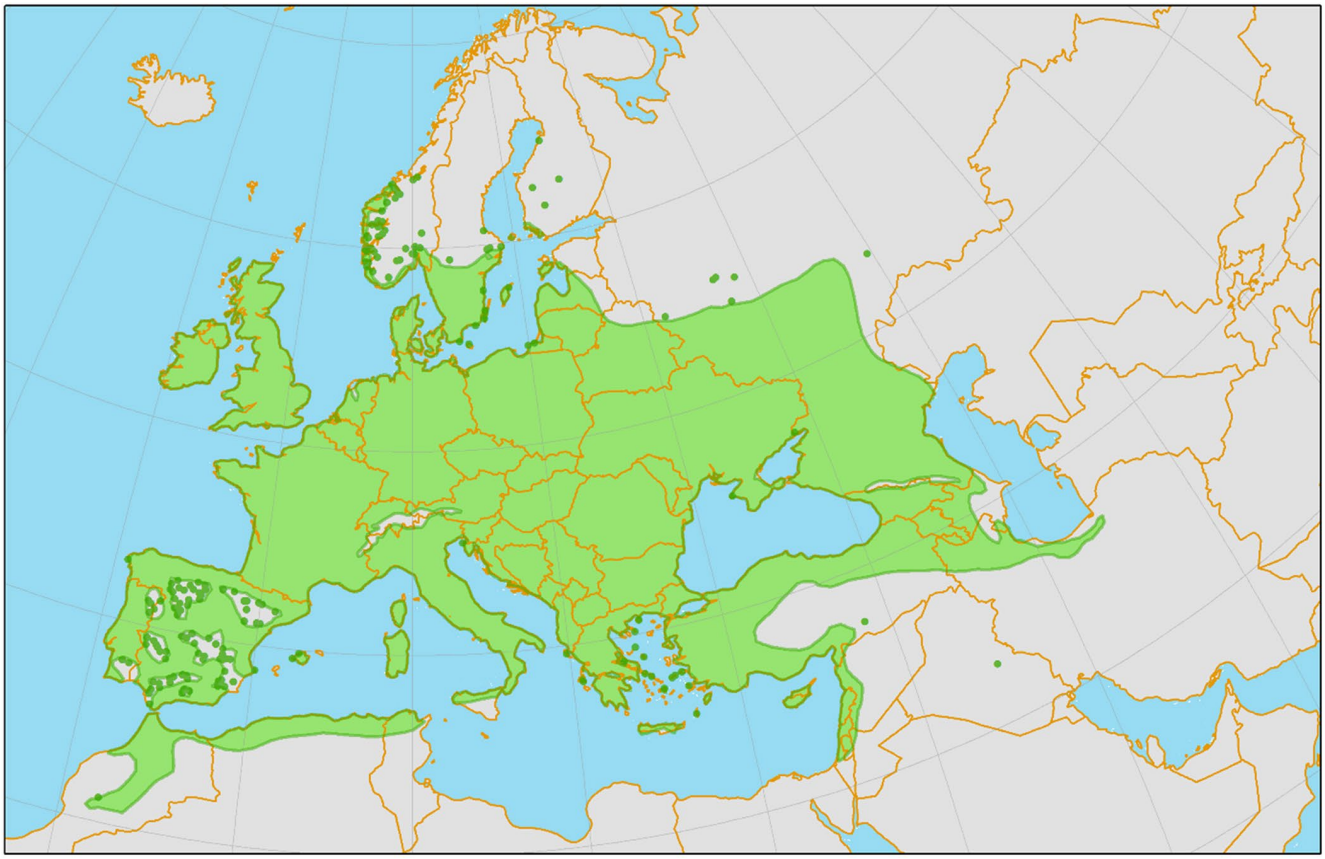

FIGURE 2 Distribution of *Crataegus monogyna* in Europe and adjacent regions, after Meusel et al. (1965) redrawn by Dr. Erik Welk. The standard European distribution map from *Atlas Florae Europaeae*, with somewhat narrower range, is provided for comparison in Figure S1

2 | HABITAT

2.1 | Climatic and topographical limitations

In its natural and naturalized ranges, *C. monogyna* grows in humid and subhumid temperate regions (Parsons & Cuthbertson, 1992) tolerating climates that range from cool temperate (Northern Europe) to Mediterranean (southern Europe, northern Africa, Minor Asia and the Middle East) and subcontinental (eastern Europe). For its British distribution Hill et al. (2004) provide calculated mean temperatures of 3.6°C in January and 14.7°C in July respectively. The Ellenberg value for temperature (*T*) is 5, representing a mean annual temperature *c.* 6°C (5–7°C) for Central Europe (Ellenberg et al., 2001). This reflects occurrences from foothills to montane zones throughout Europe and additionally in subalpine zones of mountain ranges in Southern Europe as *C. monogyna* is missing in those of Northern Europe. Conolly and Dahl (1970), cited in Rodwell (1991) list *C. monogyna* as a part of communities with a mean annual maximum temperature of at least 26°C. Kean (2009) calculated an optimum temperature ranging from 18 to 26°C from its natural distribution by using a fitted CLIMEX model and 6 and 30°C as the lower and upper thresholds of viability. These thresholds reflect the northern and southern edge of its European distribution. Parsons and Cuthbertson (1992) consider annual rainfall of 600 mm as a minimum, while Pasiecznik (2008) gives seven consecutive months of rainfall less than 40 mm as maximum dry duration, and 400 and 1,400 mm as lower and upper limit of mean annual rainfall. The mean of the annual precipitation in its British distribution is 1,073 mm (Hill et al., 2004). The *Fraxinus excelsior–Acer campestre–Mercurialis perennis* woodland (Section 3) in which hawthorn grows in Britain is confined to sites with an annual rainfall of <1,000 mm and <160 wet days per year (Chandler & Gregory, 1976; Climatological Atlas of the British Isles, 1952; Ratcliffe, 1968; all cited in Rodwell, 1991). *C. monogyna* tolerates exposure to cold or salt-laden air (McIndoe, 2019), but especially in coastal locations, growth is heavily affected by wind. With its strong stem and flexible twigs *C. monogyna* is sculpted by the wind, leaning away from it (M.B. Usher, pers. comm.), providing shelter for other herbs (Stoutjesdijk & Barkman, 2014).

2.2 | Substratum

Throughout its distribution area *C. monogyna* is found in nearly all geological settings, whether of siliceous, mixed or calcareous constitution, for examples, granite, gneiss, silicate slate; siliceous lime, limestone shale, flysch, sandstone; lime, dolomite (Aeschimann et al., 2004). It grows on a wide range of soil textures, preferring humic and moist to dry clays and fine-grained to heavy loams (Hess

et al., 1977). Suitable soil types are the natural profiles of different degrees of maturity (e.g. rankers, brown podzolic soils and podzols, base-poor brown earths, mulls, rendzinas and brown calcareous earths; Rodwell, 1991), as well as man-made raw soils on rock waste, and on restored ground. The Ellenberg values for pH ($R = 7$; Hill et al., 1999) suggest soil reactions from relatively base-poor (pH 6, e.g. in brown earths) to very base-rich (pH 7 and higher, e.g. in rendzinas). *C. monogyna* is found on soils of any conditions from poor in nutrients to highly eutrophic, as expressed by a mean Ellenberg value for fertility (*N*) equal to 6 (Hill et al., 1999). Drainage conditions ranging from slightly impeded to fully drained can be tolerated, resulting in its occurrence in moist, mesic and dry conditions (Hellwig, 2006). This is again expressed by the mean Ellenberg value for moisture (*F*) of 5 (Hill et al., 1999). However, these values taken as single numbers reflect a general direction and not a range. *C. monogyna* rarely occurs on wet peat or poor acidic sands (Clapham et al., 1989). Sebald et al. (1992) mention occurrence also in rocky habitats. The preferred form of soil humus is mull.

3 | COMMUNITIES

Sell and Murrell (2014) describe *Crataegus monogyna* as 'frequent in [British] woods, copses and hillsides, [and] the main constituent of most of [British] hedgerows'. Hedges are defined as linear man-made habitats in contrast to the natural appearance of spontaneous scrub (Tüxen, 1952; Wirth, 1993). Scrub also appears as a natural community on forest borders. Moreover, communities can be stages in secondary successions on neglected arable land, meadows and pastures as well as replacement communities after forest degradation. Rodwell (1991) described two main British plant communities containing *C. monogyna*. Relevés of these, the *Crataegus monogyna–Hedera helix* scrub (W21) and the *Fraxinus excelsior–Acer campestre–Mercurialis perennis* woodland (W8), contain hawthorn at least to 60% and 40% respectively.

In the W21 community, besides *Rubus fruticosus* agg. and *Hedera helix*, *C. monogyna* is one of the constant species, which can dominate the more or less abundant *Prunus spinosa* as an additional spiny species of this community. Ivy commonly forms a ground carpet and in general leads to a species-poor field layer. W21 is divided into four subcommunities reflecting edaphic and climatic factors, as well as the developmental history of the vegetation. Concerning the latter factor, *Crataegus–Hedera* scrub is often found on abandoned arable land, whereas only the *Mercurialis perennis* subcommunity (W21b) derives from degenerate Carpinion or Fagion woodland on ill-draining clays and shales with stagnogleys and pelosols. Besides species of the respective woodland field layer, *Mercurialis perennis* as well as the nitrophilic *Sambucus nigra*, *Urtica dioica* and *Galium aparine* are frequent. Like the former, the *Hedera helix–Urtica dioica* subcommunity (W21a) has moister and more nutrient-rich situations. In addition, there are numerous Arrhenatherion species (e.g. *Arrhenatherum elatius*, *Holcus lanatus*, *Heracleum sphondylium* and *Silene dioica*). These species are members of a preceding herbaceous vegetation that have survived after grazing and mowing were abandoned. By contrast, the *Viburnum lantana* subcommunity (W21d) is found in warmer places, on oligotrophic rendzinas with a higher base saturation, and has calcicolous and relict Mesobromion species (e.g. *Bromus erectus*, *Brachypodium pinnatum* s.l., *Sanguisorba minor*, *Origanum vulgare* and *Teucrium scorodonia*) in combination with frequent woody species like *Ligustrum vulgare*, *Viburnum lantana*, *Cornus sanguinea*, *Clematis vitalba* and *Tamus communis*. The *Brachypodium sylvaticum* subcommunity (W21c) is a kind of intermediate as its species composition is similar to the *Hedera helix–Urtica dioica* subcommunity but on oligotrophic rendzinas. Nitrophilic *Sambucus nigra*, *Urtica dioica* and *Galium aparine* are less frequent, but *Brachypodium sylvaticum* often occurs as a more shade-tolerant survivor of abandoned ploughland. *Fragaria vesca* and *Viola riviniana* occur only in this subcommunity.

Depending on the biotic and abiotic conditions *Crataegus–Hedera* scrub can develop to *Quercus–Pteridium–Rubus* woodland (W10) or *Fagus–Rubus* woodland (W14) on base-poor soils (Watt, 1924, 1934 as cited in Rodwell, 1991) and on base-rich but moist soils to *Fagus–Mercurialis* woodland (W12), locally to *Taxus* woodland (W13) or to W8 in areas beyond the natural dominance of beech (Brenchley & Adam, 1915; Rackham, 1975; Tansley, 1939; all cited in Rodwell, 1991).

Whereas *C. monogyna* plays only a minor role in most of these communities, it is at least a typical understorey component of all subcommunities of W8, *Fraxinus excelsior–Acer campestre–Mercurialis perennis* woodland. More or less closed canopies lead to *C. monogyna* being predominantly found in younger stands, plantation replacements and on scrubby margins. These canopies are formed by the constant trees *Fraxinus excelsior* and *Acer campestre*, with preferential suite-constants of either *Quercus robur* on soils of various levels of gleying or *Acer pseudoplatanus*, *Ulmus glabra* and *Quercus petraea*. Co-occurrences with sessile oak associated with more acidic soils seem to be equivocal (M.B. Usher, pers. comm.). Its sister taxon, *Crataegus laevigata* (cf. Thomas et al., 2021), is scarce in the suite with *Quercus robur* and is restricted to long-established stands. Another shrubby constant in W8 is *Corylus avellana*, which is rivalled by *C. monogyna* only in the *Hedera helix* and the *Geranium robertianum* subcommunities.

The group of the herbaceous constants (*Mercurialis perennis* and *Rubus fruticosus* agg.) and common preferentials like *Hedera helix*, *Urtica dioica* and *Galium aparine* show a certain similarity in species composition between these scrub subcommunities and their respective woodland subcommunity equivalents. Especially at intact woodland margins, with no sharp boundaries, there is a smooth transition to the *Crataegus–Hedera* scrub.

Apart from its main woodland habitat, *Fraxinus–Acer–Mercurialis* woodland (W8), hawthorn is found in other types of woodland. On moister and less base-rich brown earths *C. monogyna*, together with *Corylus avellana*, can build the understorey in two subcommunities within the *Alnus glutinosa–Fraxinus excelsior–Lysimachia nemorum* woodland (W7). Either because of climatic or edaphic conditions, it occurs only occasionally or scarcely in *Fraxinus excelsior–Sorbus aucuparia–Mercurialis perennis* woodland (W9), *Quercus robur–Pteridium*

aquilinum–Rubus fruticosus woodland (W10), *Quercus petraea–Betula pubescens–Oxalis acetosella* woodland (W11), *Fagus sylvatica–Mercurialis perennis* woodland (W12), *Taxus baccata* woodland (W13), *Fagus sylvatica–Rubus fruticosus* woodland (W14), *Quercus* spp.–*Betula* spp.–*Deschampsia flexuosa* woodland (W16) and *Quercus petraea–Betula pubescens–Dicranum majus* woodland (W17).

Furthermore, *C. monogyna* is part of many successional sequences (Figure 3). The species is an important early invader in different grassland types characterized 'by a decline in grazing by stock or wild herbivores (rabbits) or by neglect of mowing in field corners or more inaccessible parts of the meadow' (Rodwell, 1991). When seedlings begin to survive due to abandonment of arable usage, saplings may establish scrub, which then may be taken over by colonizing trees to form different secondary woodland types (Tansley, 1939 as cited in Rodwell, 1991), sometimes via *Rubus–Holcus* underscrub (W24). The reverse process is also possible: As a result of cutting and/or burning the *Crataegus–Hedera* scrub (W21) may develop into W24 and, with a re-imposition of grazing or mowing, mainly to Arrhenatherion communities, although this is hard to manage.

In general, the range of the distribution of the *C. monogyna* is correlated with other species of the Southern European dry forest like *Prunus spinosa*, *Rosa* sect. *Caninae* or *Sorbus torminalis* (Meusel et al., 1965). Although *C. monogyna* occurs also in Quercetalia pubescentis or thermophilous Fagetalia (or even the Alno–Ulmion), and in Erico–Pinion communities, it is a constant species of the Prunetalia (Lippert, 2001). W21 relates on the one hand to the thermophilous scrubs of Berberidion, the calcicolous alliance of sub-Mediterranean-mid-European scrub, and on the other to mesophilic scrub of Carpino–Prunion, the alliance of suboceanic–mid-European scrub. Additionally, it belongs to southeast–European and (sub)continental scrubs of Prunion fruticosae alliance (Ellenberg et al., 2010). A noteworthy community is the endangered Hippophao–Berberidetum on sandy-gravelly and dry shores of middle courses of alpine rivers (Wirth, 1993). A list of species frequently accompanying *C. monogyna* in these different communities is provided in Table 1 (Oberdorfer, 1978, 1992a, 1992b; Rodwell, 1991, 1992; Schubert et al., 2001; Weber, 2003; Wirth, 1993).

4 | RESPONSE TO BIOTIC FACTORS

By applying different levels of shade to hawthorn Grubb et al. (1996) found total mortality of saplings in 0.3% daylight. In 1.6% daylight the death rate was 10%, except in saplings growing on nutrient-rich soil, as sufficient nutrient supply may appear toxic in shade (Hutchinson, 1967). Williams and Buxton (1989) concluded a mechanism of avoiding shade by strong monopodial growth by observing a significantly faster shoot growth rate and only a little increase in shoot number of saplings in 66% daylight than in 16% daylight. Besides that, the number of leaves and correspondingly the total leaf area increased significantly with higher irradiance (Grubb et al., 1996). Leaf thickness increased with irradiance too, so that leaf mass per area tended asymptotically to 10.12 mg/cm^2 (Aranda et al., 2004), leading towards significant gain in total dry weight (Grubb et al., 1996; Williams & Buxton, 1989). Among examined species (*Fagus sylvatica*, *Juniperus communis*, *Cornus sanguinea*, *Ligustrum vulgare*, *Prunus spinosa*, *Rosa canina*, *Euonymus europaeus*, *Rhamnus cathartica*, *Viburnum lantana* and *V. opulus*) Grubb et al. (1996) allocated *C. monogyna* together with *Cornus sanguinea*, *Juniperus communis*, *Ligustrum vulgare* and *Rosa canina* to a group of less shade-tolerant species. Aranda et al. (2004) found hawthorn to be the most shade-intolerant among *Ilex aquifolium*, *F. sylvatica*, *Quercus petraea*, *Q. pyrenaica*, *Prunus avium*, *Sorbus aria* and *S. aucuparia*. Bradshaw (1948) noted a more tree-like habit in shaded localities compared to *C. laevigata* (see also Thomas et al., 2021). The Ellenberg value for light (*L*) is 6 (Hill et al., 1999) indicating the growth of *C. monogyna* in partially shaded (rarely <20% daylight) to lit places. Its thorns may directly confer the ability to compete with more palatable plants (Section 9.1).

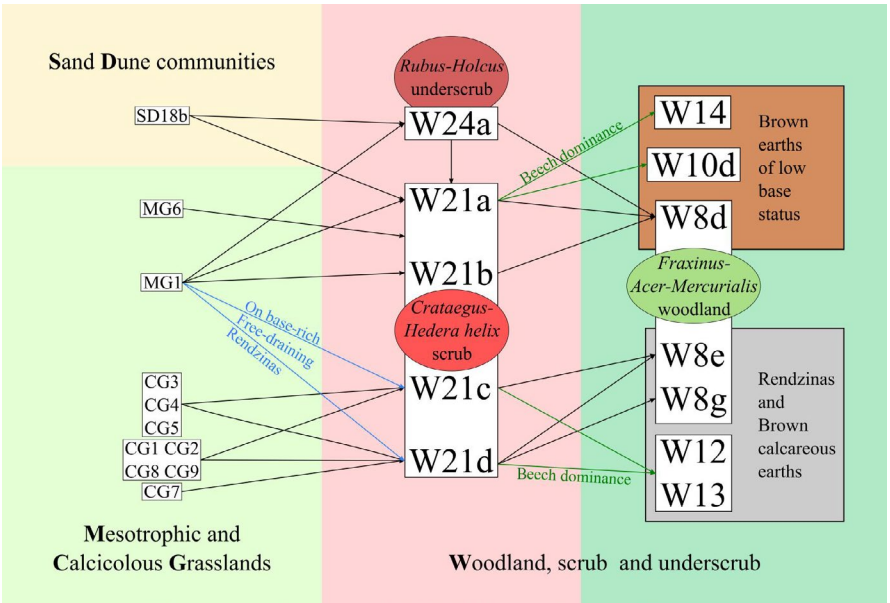

FIGURE 3 Successional sequences including *Crataegus monogyna*. The abbreviations of communities follow Rodwell (1991, 1992, 2000). Subcommunities are indicated by their respective letters. Communities in which only seedlings or small saplings occur are given in smaller font size

TABLE 1 List of species frequently accompanying *Crataegus monogyna* (B = trees, S = shrubs, G = grassland species, W = species of the field layer in woods, F = hygrophilic species, N = nitrophilic species, M = mosses; W21/8/9/7, CG3/4/5, MG1 refer to the respective communities in Rodwell (1991, 1992); K = character of class Querco–Fagetea, O = character of order Prunetalia and V = character of alliance Berberidion refer to the respective communities in Oberdorfer (1978, 1992a, 1992b); CA = Cotoneastro–Amelanchieretum, HB = Hippophao–Berberidetum, Pm = Prunetum mahaleb refer to the respective communities in Schubert et al. (2001), Weber (2003) and Wirth (1993))

	Species	Community code according to Rodwell (1991, 1992)								
B	*Fraxinus excelsior*	W21	W8	W9	W7	CG3	CG4			K
B	*Acer pseudoplatanus*	W21	W8	W9	W7			CG5		K
B	*Fagus sylvatica*	W21	W8	W9	W7			CG5		K
B	*Quercus robur*	W21	W8	W9	W7			CG5		K
B	*Quercus petraea*		W8	W9	W7					K
B	*Carpinus betulus*		W8							K
B	*Prunus avium*		W8							K
B	*Pyrus pyraster*		W8							K
B	*Sorbus torminalis*		W8							K
B	*Sorbus aria*	W21	W8							K
B	*Malus sylvestris*	W21	W8							K
B	*Betula pendula*	W21	W8	W9	W7					
B	*Ulmus glabra*	W21	W8	W9	W7					
B	*Sorbus aucuparia*		W8	W9	W7					
B	*Alnus glutinosa*		W8	W9	W7					
B	*Betula pubescens*		W8	W9	W7					
B	*Populus tremula*		W8	W9						
B	*Salix caprea*		W8		W7					
B	*Pinus sylvestris*			W9						
S	*Hedera helix*	W21	W8	W9	W7					K
S	*Corylus avellana*	W21	W8	W9	W7					K
S	*Sambucus nigra*	W21	W8	W9	W7		CG4	CG5		
S	*Rosa canina*	W21	W8	W9	W7	CG3	CG4			O
S	*Rubus fruticosus* agg.	W21	W8	W9	W7				MG1	O
S	*Prunus spinosa*	W21	W8		W7					O
S	*Crataegus laevigata*	W21	W8							O
S	*Clematis vitalba*	W21	W8					CG5		O
S	*Tamus communis*	W21	W8							O
S	*Euonymus europaeus*	W21								O
S	*Viburnum opulus*		W8		W7					O
S	*Ribes uva-crispa*		W8							O
S	*Rubus caesius*		W8							
S	*Ligustrum vulgare*	W21	W8							V
S	*Viburnum lantana*	W21	W8							V
S	*Cornus sanguinea*	W21	W8							V
S	*Rhamnus cathartica*	W21	W8							V
S	*Acer campestre*	W21	W8							V
S	*Lonicera periclymenum*	W21	W8		W7					
S	*Rosa arvensis*	W21								
S	*Cotoneaster integerrimus*									CA
S	*Cotoneaster tomentosus*									CA
S	*Amelanchier ovalis*									CA

(Continues)

TABLE 1 (Continued)

	Species	Community code according to Rodwell (1991, 1992)								
S	*Juniperus communis*									CA
S	*Hippophae rhamnoides*									HB
S	*Salix eleagnos*									HB
S	*Prunus mahaleb*									Pm
S	*Acer monspessulanum*									Pm
W	*Brachypodium sylvaticum*	W21	W8	W9	W7	CG3			MG1	K
W	*Mercurialis perennis*	W21	W8	W9	W7					K
W	*Melica nutans*		W8							K
W	*Viola reichenbachiana*		W8							K
W	*Dryopteris filix-mas*		W8	W9	W7					K
W	*Ajuga reptans*		W8	W9	W7					
W	*Lamiastrum galeobdolon*		W8	W9	W7					
W	*Primula vulgaris*		W8	W9	W7					
W	*Lysimachia nemorum*		W8	W9	W7					
W	*Ranunculus ficaria*		W8	W9	W7					
W	*Deschampsia cespitosa*		W8	W9	W7					
W	*Athyrium filix-femina*		W8	W9	W7					
W	*Dryopteris dilatata*		W8	W9	W7					
W	*Oxalis acetosella*		W8	W9	W7					
W	*Melica uniflora*		W8	W9						
W	*Rumex sanguineus*	W21	W8							
W	*Arum maculatum*	W21	W8	W9						
W	*Teucrium scorodonia*	W21	W8		W7					
W	*Hyacinthoides non-scripta*	W21	W8	W9	W7					
W	*Viola riviniana*	W21	W8	W9	W7					
W	*Fragaria vesca*	W21	W8	W9	W7					
W	*Circaea lutetiana*	W21	W8	W9	W7					
W	*Anemone nemorosa*	W21	W8	W9	W7					
F	*Juncus effusus*	W21	W8		W7					
F	*Filipendula ulmaria*		W8	W9	W7				MG1	
N	*Alliaria petiolata*		W8							
N	*Glechoma hederacea*	W21	W8		W7					
N	*Geum urbanum*	W21	W8	W9	W7					
N	*Geranium robertianum*	W21	W8	W9	W7					
N	*Silene dioica*	W21	W8	W9	W7					
N	*Galium aparine*	W21	W8	W9	W7				MG1	
N	*Urtica dioica*	W21	W8	W9	W7				MG1	
G	*Heracleum sphondylium*	W21	W8	W9					MG1	
G	*Poa trivialis*	W21	W8	W9	W7				MG1	
G	*Taraxacum* Sect. *Ruderalia*		W8			CG3	CG4	CG5	MG1	
G	*Prunella vulgaris*		W8	W9		CG3	CG4	CG5	MG1	
G	*Arrhenatherum elatius*	W21	W8	W9		CG3	CG4		MG1	
G	*Holcus lanatus*	W21	W8	W9	W7	CG3	CG4	CG5	MG1	
G	*Dactylis glomerata*	W21	W8	W9	W7	CG3	CG4	CG5	MG1	
G	*Origanum vulgare*	W21				CG3	CG4		MG1	
G	*Sanguisorba minor*	W21				CG3	CG4	CG5	MG1	

(Continues)

TABLE 1 (Continued)

	Species	Community code according to Rodwell (1991, 1992)							
G	*Bromus erectus*	W21				CG3		CG5	MG1
G	*Brachypodium pinnatum*	W21					CG4	CG5	
G	*Trisetum flavescens*						CG4	CG5	MG1
G	*Trifolium pratense*					CG3		CG5	MG1
G	*Plantago lanceolata*					CG3	CG4	CG5	MG1
G	*Lotus corniculatus*					CG3	CG4	CG5	MG1
G	*Festuca ovina*					CG3	CG4	CG5	MG1
G	*Campanula rotundifolia*					CG3	CG4	CG5	MG1
G	*Centaurea nigra*					CG3	CG4	CG5	MG1
G	*Knautia arvensis*					CG3	CG4	CG5	MG1
G	*Pimpinella saxifraga*					CG3	CG4	CG5	MG1
G	*Carex flacca*					CG3	CG4	CG5	
G	*Leontodon hispidus*					CG3	CG4	CG5	
G	*Medicago lupulina*					CG3	CG4	CG5	
G	*Cirsium acaule*					CG3	CG4	CG5	
G	*Briza media*					CG3	CG4	CG5	
G	*Koeleria macrantha*					CG3	CG4	CG5	
M	*Atrichum undulatum*		W8	W9	W7				
M	*Eurhynchium striatum*		W8	W9	W7				
M	*Mnium hornum*		W8	W9	W7				
M	*Brachythecium rutabulum*	W21	W8	W9	W7				
M	*Eurhynchium praelongum*	W21	W8	W9	W7				
M	*Plagiomnium undulatum*	W21	W8	W9	W7				

C. monogyna is able to invade a variety of open habitats (Grime et al., 1988). It performs better in establishing from seeds in grazed areas than many other woody species (Linhart & Whelan, 1980), although it is only moderately tolerant to grazing (Klotz et al., 2002) and normally invasion follows a relaxation in grazing pressure (Grime et al., 1988). Its thorn-bearing habit also makes *C. monogyna* a good nurse plant for other woody plants in scrub community succession. Although hawthorn is intolerant to mowing (Klotz et al., 2002), it resprouts after coppicing (Michielsen et al., 2017; Sell & Murrell, 2014) and tends to sucker especially after disturbance (Bass, 1990a). It is also very tolerant to trampling (Klotz et al., 2002). Shrubs of *C. monogyna* are not resistant to fire (Hegi, 1923) and burn readily. They often manage to resprout (Michielsen et al., 2017), but do not benefit from fire in terms of producing seedlings and saplings (Esposito et al., 2014).

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

Crataegus monogyna can exist as a solitary tree or produce stands ranging from open to dense scrub. Good et al. (1990) found stand densities in Snowdonia National Park, Wales, varying between 49 and 79 individuals per ha depending on sheep stock numbers. Such more or less monospecific stands are especially characteristic for secondary succession. Although it sometimes suckers and sprouts, its gregariousness is generally driven by the spatial distribution of the dispersed seeds. There is no evidence of dispersing animals caching the seeds in high density clusters. In Australia, Bass et al. (2006) calculated a slow population growth rate of 1.1 by modelling with modified Leslie transition matrices. In planted areas, including hedges, hawthorn is variably gregarious, obviously depending on the whims of each planting scheme. Old hedges of the medieval are much more diverse than recent ones largely through natural colonization and species turnover.

5.2 | Performance in various habitats

A study by Grubb et al. (1999) measured heights of young shrubs in an experimental garden in southern England after initial damage by a plague of rabbits for 12 years. The mean increment of height for *C. monogyna* was *c.* 37 cm/year. In a comparative study by Willoughby et al. (2007), hawthorn was planted among 16 mostly native species (*Acer campestre*, *Alnus glutinosa*, *Alnus incana*, *Acer saccharinum*, *Betula pendula*, *Corylus avellana*, *Cornus sanguinea*, *Euonymus europaeus*, *Fraxinus excelsior*, *Malus sylvestris*, *Prunus avium*, *Populus tremula*,

Quercus robur, *Rhamnus cathartica*, *Salix caprea* and *Tilia cordata*) on different sites to check performance in afforestation. The mean increment in height and thickness was about fourfold higher on good-quality agricultural land with moist, rich, fine and coarse loamy soil over Triassic keuper marls than on restored low-grade agricultural pasture with moderately dry, medium, fine to coarse reddish loam over carboniferous shale with coal measures and beds of sandstone. The authors regard *C. monogyna* suitable for the former site with >80% survival but an average growth lower than for the site, where *P. tremula* and *P. avium* showed the best results, while only *F. excelsior* had a better survival rate on the latter site. Jones et al. (2001) tested performances of nine provenances (one local, four British and four continental European commercial ecotypes) on two sites with two treatments in all combinations. Growth performance was better on either lowland than upland sites, or when fenced or mulched. Their findings for annual growth rates of height were 30.63 ± 0.52 cm (mean ± *SD*) and 8.44 ± 0.52 cm for lowland and upland sites, respectively, and 3.45 ± 0.07 cm and 1.60 ± 0.07 cm for annual width growth respectively. On South Island, New Zealand, Williams and Buxton (1986) calculated annual growth rates of height and stem diameter in natural sites varying from 10 to 31 cm and 3.0 to 4.8 mm respectively.

Like most of its accompanying woody hedge species (Section 3), *C. monogyna* is a more or less light-demanding plant. In the open, it comes into full flower, but shaded by other plants, for example inside woods, it will produce fewer or even no flowers (Grime et al., 1988).

5.3 | Effect of frost, drought, etc.

5.3.1 | Frost

Dirr (2010) ranked *C. monogyna* in zone 4 in the USDA cold hardiness rating, indicating the species withstands an average annual minimum temperature down to −30°C. Looking at the effect of spring frosts after the great May frosts of 1935 Day and Peace (1946) state that *C. laevigata* (reported as *C. oxyacantha* L.) was not very much damaged by late frosts, although it appeared softer than hornbeam or birch. The authors received one report of severe damage to seedlings, in which many were killed, and a few reports of damage to the blossoms only. These findings may presumably also apply to *C. monogyna*. The freezing temperature of the xylem sap is −6.1 ± 0.8°C in winter and −5.5 ± 0.2°C in early spring (Lintunen et al., 2015). The authors also found the smallest diameter shrinkage in *C. monogyna* among the species *Ginkgo biloba*, *Carpinus betulus*, *Sorbus aucuparia*, *Malus baccata*, *Pterocarya fraxinifolia* and *Quercus palustris*.

5.3.2 | Drought

C. monogyna is more resistant to drought than the other mid-European species of the genus (Hegi, 1923). Despite that summer dryness causes earlier leaf abscission starting in July with a mean leaf longevity of 164 days (Mediavilla & Escudero, 2003). Due to low stomatal sensitivity to both the decrease in soil water supply and the increase in air dryness, the shrub species *C. monogyna* and *Pyrus bourgaeana* may suffer irreversible leaf damage, in contrast to other deciduous or evergreen trees (*Quercus faginea*, *Q. pyrenaica*, *Q. ilex* subsp. *ballota* and *Q. suber*) studied on the Iberian Peninsula (Mediavilla & Escudero, 2003).

5.3.3 | Flooding

Frye and Grosse (1992) tested the effect of flooding 10 cm above soil surface on 1-year-old seedlings for 120 days during the growing season. They reported a decrease in growth in height (22.8 ± 2.93 to 14.7 ± 2.22 cm) and in stem diameter (2.3 ± 0.2 to 1.2 ± 0.2 mm). In this study, only *Quercus robur* and *Fraxinus excelsior* were not significantly retarded in height growth, while showing a significant increase in diameter growth. In the following year of recovery, *C. monogyna* showed increased growth in height compared to the control group. Only *Taxodium distichum* and *Salix purpurea* were able to gain height. While hawthorn showed no effect on stem diameter growth, that in *T. distichum*, *Q. robur*, *Q. palustris*, *Betula nigra* and *Tilia cordata* increased.

5.3.4 | Salinity

Despite the Ellenberg value for salt (*S*) being zero (Ellenberg et al., 2001), *C. monogyna* grows in dunes and coastal communities and reacts to exposure to salt (NaCl) in different ways. Responses range from toleration to severe adverse effects, depending on amount and the method of application of sodium chloride. Thompson and Rutter (1986) tested the effect of applying water with different salt concentrations (4, 8, 16 and 32 g/L) as spray or irrigation water. Although some young shoots died in the spraying treatment the total new biomass increased by a mean of 36% over all concentrations compared to the control. In the irrigation treatment *C. monogyna* did suffer from solutions of 4 or 8 g/L with 10%–20% mortality, respectively, but survivors did not show significant change in biomass. With higher concentrations the results became severe with death rates from 70% to 100% for 16 and 32 g/L respectively. Rodwell (1991) considers *C. monogyna* less tolerant to salt than *Prunus spinosa*.

5.3.5 | Pollutants

Hawthorn has a moderate sensitivity to SO_2 and HF and is only slightly sensitive to NH_3 (Däßler, 1991) but shows foliar injuries due to a strong impairment by O_3 at concentrations below the European threshold AOT40 (Novak et al., 2003). Fruit yield is heavily reduced by the herbicide metsulfuron-methyl (Kjaer et al., 2006).

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Crataegus monogyna is normally more of a shrub than a tree. Apical growth and a more tree-like shape may be suppressed by either disturbance when young or competition for light with other plants. The European height record is 18.4 m found in Keighley, England (Monumental Trees) and the widest girth was measured at 3.9 m in Crawley (Sussex), England (The Tree Register, 2011). A DBH of 1.85 m and a maximum crown width of 11 m was found in Kaarst and Neuss, Germany respectively (Deutsche Dendrologische Gesellschaft, 2019). Troll (1984) described four types of shoots: long shoots with leaves, short shoots bearing leaves or forming leafless thorns between 1 and 2.4-cm length and leafy intermediate shoots of 10-cm length ending with a thorn. The long shoots are monopodial; the short shoots are sympodial and alternately along a long shoot (Bartels, 1993). While the thorns grow sylleptically from the mid part of a long shoot, that is, during the same vegetation period as the long shoot bearing them, the leafy short shoots grow proleptically, that is, from lateral meristems in the axils of leaves or thorns with an intervening period of dormancy. The mode of branching is strongly affected by number, time and orientation of pruning, but total shoot length is not (Bannister & Watt, 1995). The authors found a cut applied horizontally in summer resulted in fewer but longer shoots, whereas a cut applied vertically in summer produced more thorn-tipped shoots. A vertical cut in winter resulted in longer shoots than one in summer and reduced the number which were thorn-tipped.

The wood shows distinct rings (Schweingruber & Landolt, 2010) without any heartwood (Bartels, 1993). It is diffuse porous but fine-grained, pale reddish, hard and heavy (Grosser, 2007). Reported wood densities vary from 0.61 to 0.88 g/cm^3 (Crivellaro & Schweingruber, 2013; Grosser, 2007; Grubb et al., 1999). Vessels appear to be predominantly solitary or clustered with a density of 100–200 per mm^2 with a mean tangential diameter of earlywood vessel lumina of <20 μm in twigs and 50–100 μm in stems (Crivellaro & Schweingruber, 2013). Young periderm has a grey-yellowish shine with narrow horizontal lenticels developing into an irregular small-scaled bark after 12–15 years (Bartels, 1993).

C. monogyna has a far-reaching and deep tap-root system (Bartels, 1993; Kutschera & Lichtenegger, 2013). In a study on excavated individuals, Kárász (2006) measured maximum root spread and penetration lengths. We calculated from these data mean annual horizontal and vertical increases of about 10 and about 3 cm respectively.

Leaf morphology displays considerable environmental plasticity (Gosler et al., 1994) and it also differs enormously between long and short shoots, as do the stipules. Leaves on short shoots are heteromorphic in their leaf succession. Laminae are smaller and less deeply lobed at the base of a short shoot and become larger (1.0–5.7 × 0.8–6.0 cm) with 1–3 pairs of lobes at the shoot's apex. Leaves on long shoots are slightly larger (2.2–6.2 × 2.2–6.4 cm) and more deeply lobed or even nearly dissected. Oliver (1999) shows actual compound leaves on long shoots. The lobes are frequently horizontally spreading and bear two to 16 teeth. Their stipules are conspicuous, often leaf-like and ± regularly serrate. Prior to abscission in autumn, the leaves turn yellow-orange. Taking the broad variation in some morphological traits into account, particularly from heteroblasty and heterophylly, reliable identification therefore requires short shoots and fertile material, and preferably collections of both flowers and fruit.

Leaf abscission leaves single scars of v-form with three bundle marks as the stipules are adnate to the petiole (Hecker, 2008). Hawthorn leaves are bifacial with an upper epidermis of polygonal cells, palisade cells in one row with possibly a second row of smaller cells and spongy mesophyll of loosely arranged cells and a lower epidermis (Upton et al., 2011). In 109 individuals in Spain, Mediavilla et al. (2001) measured the mean thickness of leaves at 233 ± 5.16 μm (mean ± *SD*) with proportions of 40.7% palisade layer, 34.1% spongy mesophyll, 21.9% epidermis and 3.2% cuticle. The anomocytic stomata of 42 μm in length occur only on the abaxial (underside) leaf surface (Upton et al., 2011). Stomatal spacing is 83.0 ± 16.2 μm (Mediavilla et al., 2001) and their density is said to vary from 140 per mm^2 (Salisbury, 1927) to 154 per mm^2 (Kelly & Beerling, 1995). The authors presented in a subsequent study a range of 90 ± 22 stomata/mm^2 (Beerling & Kelly, 1997). In comparison to the findings of Salisbury (1927), they found a significant decrease in stomatal density in the 20th century which was mainly related to the increase in atmospheric CO_2. Unicellular covering trichomes can be present primarily at the margin and along veins (Upton et al., 2011). They occur in different lengths with the longer one (up to 500–600 μm) along the veins.

6.2 | Mycorrhiza

The roots of *C. monogyna* show both arbuscular and ectotrophic mycorrhiza (Harley & Harley, 1987 and the literature cited therein). In a study of root-associated fungi in sandy grassland of the Great Hungarian Plain, Kovács and Szigetvári (2002) found hawthorn solidly colonized throughout the sample area with more than 75% of the root length colonized with endomycorrhiza. Maremmani et al. (2003) discovered ectomycorrhizal associations of hawthorn in Brijuni National Park, Croatia. Dominik (1963) found the level of ectomycorrhiza of *Crataegus* saplings not affected by shade in his field studies. Three *Entoloma* (reported as the respective species of *Rhodophyllus* Quél.) species, *E. aprile* (Britz.) Sacc., *E. clypteatum* (L.) P. Kumm. and *E. sepium* (Noull.-Dass.) Richon & Roze, were reported as ectomycorrhizal fungal associates of different *Crataegus* species (Becker, 1956 as cited in Trappe, 1962), whereas *Cenococcum graniforme* (Sow.) Ferd. & Winge was mentioned as specific ectomycorrhizal associate of *C. monogyna* (Dominik, 1957 as cited in Trappe, 1962). *Scutellospora armeniaca* Błaszkowski was reported as a fungal partner of arbuscular mycorrhiza with *C. monogyna* in Poland (Błaszkowski, 1992). Recently Brundrett and

Tedersoo (2019, 2020) have questioned the mycorrhizal research conducted over 50 years ago for misinterpretation and consider that the genus *Crataegus* forms arbuscular mycorrhiza only (see also Thomas et al., 2021).

6.3 | Perennation: Reproduction

Phanerophyte. Reproduction is primarily by seeds, as sexual reproduction yields a large number of drupaceous pomes. Vegetative reproduction by root suckers (Hegi, 1923) is seldom seen but occurs more frequently after coppicing or disturbance. Propagation through cuttings from the current year's shoots taken in early summer is possible (Schuck, 2005). In nurseries both sexual and asexual propagation techniques are used (Lasseigne & Blazich, 2008). In horticulture, propagation from seeds is important to produce root-stocks for grafting of cultivars and related fruit genera (Bush et al., 1991; Dirr & Heuser, 2006). Micropropagation can be an alternative to current propagation practices. Iapichino and Airò (2009) tested axillary shoot proliferation and rooting of in vitro cultures on Murashige and Skoog agar medium. They found the highest rate of shooting in the presence of 4.44 μM benzyladenine and 2.46 μM indole-3-butyric acid in the medium and a rooting percentage of 52% was obtained on medium with 4.90 μM indole-3-butyric acid with a survival rate of 80% after potting.

Depending on the environmental conditions, individuals of *C. monogyna* grow vegetatively for 5–8 years prior to first flowering. The probably oldest known individual stands at the Cemetery of Bouquetot, France, having been planted in *c*. AD 1360 (Monumental Trees). However, individuals of *C. monogyna* typically can have a longevity of more than 70 years (Bass, 1990a).

6.4 | Chromosomes

The basic chromosome number of the genus *Crataegus*, like many other pomoid Rosaceae, is $n = 17$ (Moffett, 1931a, 1931b; Sax, 1931, 1932). *C. monogyna* is reported to be a diploid species with different chromosome numbers of 32, 34 and 51 (Sell & Murrell, 2014). However, $2n = 32$ given by Meyer (1915) and Longley (1924) are apparently miscounts (Muniyamma & Phipps, 1979b) and $2n = 51$ by Gladkova (1968) may be based on a similar looking hybrid with a triploid species. Unlike other *Crataegus* species in Europe or northern America, there is no evidence for triploid individuals in this species, so $2n = 34$ is accepted (Bradshaw, 1975a; Byatt et al., 1977; Do Amaral Franco, 1968; Gustafsson, 1947).

The 2C DNA amount was reported as 1.52 ± 0.11 pg by Talent and Dickinson (2005) for material from field collections in Ontario, Canada and Oregon, United States. Siljak-Yakovlev et al. (2010) confirmed this value of 1.52 ± 0.04 pg with samples from Serbia. Considering also the data presented by Siljak-Yakovlev et al. (2010), who proposed that all *Crataegus* species have an amount of *c*. 0.75 pg/n, the value of 23.8 pg provided by Grime et al. (1988) may be completely wrong; the authors record 'no data' later (Grime et al., 2007).

6.5 | Physiological data

Kollmann and Reiner (1996) used 14–15 week old seedlings to measure gas exchange rates under greenhouse conditions. The rate of cellular respiration (in the dark) doubled from −0.65 ± 0.06 μmol m^{-2} s^{-1} at 15°C to −1.30 ± 0.10 μmol m^{-2} s^{-1} at 25°C, in accordance with van't Hoff's rule. The light compensation point was 9.3 μmol m^{-2} s^{-1} at 15°C. Manzanera and Martínez-Chacón (2007) measured a light-saturated assimilation rate of 24.62 ± 2.33 μmol m^{-2} s^{-1} under natural conditions in a restored riparian forest around Madrid, Spain. They also provide a net assimilation rate per area (A_{area}) of 4–8 μmol m^{-2} s^{-1}. A slightly higher value (12.8 ± 0.52 μmol m^{-2} s^{-1}) and a net assimilation rate per mass (A_{mass}) of 104.1 ± 5.9 nmol g^{-1} s^{-1} was measured by Mediavilla et al. (2001) from naturally grown individuals around Salamanca, Spain. The transpiration rate (E) was given as *c*. 2–4(9) mmol m^{-2} s^{-1} (Manzanera & Martínez-Chacón, 2007). Values provided for stomatal conductance (g_s) range from *c*. 50 to 100 mmol m^{-2} s^{-1} (Manzanera & Martínez-Chacón, 2007) to 0.21 ± 0.014 mol m^{-2} s^{-1} (Mediavilla et al., 2001) and *c*. 260–335 mmol m^{-2} s^{-1} (Herbst et al., 2007). The ratio of assimilation rate to stomatal conductance, that is, the intrinsic water use efficiency (IWUE), was calculated to be 65.0 ± 2.9 μmol/mol by Mediavilla et al. (2001) and *c*. 80–90 μmol/mol by Manzanera and Martínez-Chacón (2007). With a N concentration per unit area (N_{area}) of 2.46 ± 0.10 g/m^2 and a N concentration per unit mass (N_{mass}) of 19.6 ± 0.78 mg/g provided by Mediavilla et al. (2001) they computed 5.20 ± 0.31 μmol g^{-1} s^{-1} for the photosynthetic nitrogen-use efficiency (PNUE). Herbst et al. (2007) conducted sap flux density measurements of hawthorn shrubs from a hedgerow near Swindon, United Kingdom. The sap flux density of 0.04–0.05 kg m^{-2} s^{-1} in mid-June can be explained as a function of stem diameter and the fraction of leaves exposed to the open air. Rodríguez-Calcerrada et al. (2015) measured stem CO_2 efflux rates in Spain under natural conditions and found strong positive correlations between the sapwood parenchyma proportion and CO_2 efflux expressed per unit of stem surface area (E_{s5}), sapwood volume (E_{v5}), sapwood mass (E_{m5}) and sapwood nitrogen mass (E_{n5}), except for sapwood parenchyma volume (E_{p5}).

6.6 | Biochemical data

Crataegus monogyna contains a range of flavonoids, biogenic amides and triterpenic acids in leaves, flowers and fruit (Braun & Frohne, 1987). By contrast, no alkaloids or saponins were detected in the similar *C. laevigata* (Dau, 1941), but the pseudosaponin tormentosid is present in this species (Steinegger & Peters, 1966). Very unusually for Rosaceae, neither of the cyanogenic compounds,

amygdalin or prunasin, is found in *Crataegus* (Hegnauer, 1973). The main triterpenic acids are oleanolic acid and ursolic acid, occurring as components of cuticular waxes on leaves and fruit (Hegnauer, 1973). There has been misleading information, for example, on supposed crataegolic acid, which was found to be a mixture of the former ones (Bersin & Müller, 1951). Witczak et al. (2014) measured total phenolic content of fruit at 1,473.5 mg per 100 g fresh weight containing 1,012.4 mg phenolic acids and 102.0 mg flavonoids. Among the flavonoids, the flavonols are quercetin and its derivatives hyperoside (quercetin-3-*O*-galactoside), and rutin (quercetin-3-*O*-rutinoside) as well as vitexin and vitexin-2″-*O*-rhamnoside as flavones (Rehwald et al., 1994). The latter also appears as the monoacetate form (Fisel, 1965). Along with orientin, isoorientin and 8-methoxykaempferol-3-*O*-glucoside, this is a relevant chemotaxonomical marker of *C. monogyna* as these compounds are lacking in *C. laevigata* (Prinz et al., 2007) although Rehwald et al. (1994) did not detect 4‴-acetylvitexin-2″-*O*-rhamnoside in their study. The class of proanthocyanidins contains the monomers (+)-catechin, (−)-*epi*-catechin and oligo- to polymeric forms (Petereit & Nahrstedt, 2005; Thompson et al., 1972; Weinges, 1961, 1964; Weinges et al., 1968). Such phenolic compounds have an antioxidant activity and help to avoid oxidative damage caused by free radicals (Kirakosyan et al., 2003; Rakotoarison et al., 1997; Zhang et al., 2001). The effect of different types of stress on the production of secondary metabolites such as flavonol-type substances and flavonoid constituents was tested by Kirakosyan et al. (2004). They found chilling to 4°C and drought increase antioxidative capacities. Levels of vitexin-2″-*O*-rhamnoside, 4‴-acetylvitexin-2″-*O*-rhamnoside, hyperoside and quercetin rose with cold stress while continuous water deprivation increased the productivity of chlorogenic acid, (+)-catechin and (−)-*epi*-catechin. Flooding as complete immersion of pots for 10 days and simulated herbivory caused no major increases in levels of polyphenolics. Besides sucrose, glucose and fructose *C. monogyna*, like other Rosaceae, uses the sugar alcohol sorbitol for the transport of fixed carbon (Hegnauer, 1973). The content of sorbitol in leaves decreases from May to September (Fung & Herrebout, 1988). The fruit contain high amounts of pectin, carotene, ascorbic acid (vitamin C) and thiamine (vitamin B_1; Timmermann & Müller, 1998) and about 2%–3% catechins (Zepernick et al., 1983). Lacking starch as storage compound the seeds contain protein and fatty acids, specifically oleic acid, linoleic acid and about 10% saturated fatty acids, particularly palmitic and stearic acids (Eckey, 1954; Hilditch & Williams, 1964; all cited in Hegnauer, 1973) and (α)-Tocotrienol (Zlatanov & Ivanov, 1999).

7 | PHENOLOGY

Budburst of *C. monogyna* has been recorded between mid-March and mid-April, depending on altitude and provenance (Jones et al., 2001; Vander Mijnsbrugge et al., 2015). In Britain flowering starts from late April to end of May (Gyan & Woodell, 1987a). Using a 35-year dataset, Jeffree (1960) identified the mean start of flowering as 13 May ± 8 days (mistakably referred to as *C. oxyacantha*). In a consecutive study with a 58-year dataset Sparks et al. (2000) clarified the ambigous usage of *C. oxyacantha* as *C. monogyna* and came to the same result with the earliest −19 days and the latest +16 days. In Central Europe, hawthorn is listed to flower in the *Sorbus aucuparia–Galium odoratum* phase at the end of mid spring (Dierschke, 1995), which is during May and June. In a more Mediterranean climate flowering begins earlier in April (Browicz, 1972; Guitián & Fuentes, 1992) and at more oceanic sites as early as February. In general, flowering appears about 1–2 weeks later than in *C. laevigata* (Clapham et al., 1989; Hegi, 1923).

A second blooming during winter is seen in *C. monogyna* 'Biflora' (forma *praecox*), famously known as the Holy Thorn of Glastonbury according to the legend of Joseph of Arimathea (Sell & Murrell, 2014).

Anthesis is at maximum between 10.2 and 18°C air temperature and is inhibited by rain (Percival, 1955). The obvious correlation of budburst and flower opening with spring temperature is supported by the data of Vander Mijnsbrugge and Janssens (2019). As for budburst, Vander Mijnsbrugge et al. (2015) showed an influence of altitude and provenance on the date of flowering, which lasts for about 2 weeks. Guitián et al. (1992) observed a mean of 3 weeks of flowering for hawthorns in Northern Spain. Fruit ripening starts in August and has finished by late September. Studies of fruit production by 16 common woody species over 14 years in the United Kingdom show that hawthorn is one of the three least variable species, with little evidence of mast years (T.H. Sparks, unpubl. data). Guitián (1998) summarized the literature on fruiting phenology as being more affected by climate than it is a function of latitude. His data on *C. monogyna* do not support the adaptive delay hypothesis of fleshy-berry bearing species ripening earlier with arrival of the southward travelling migratory disperser birds.

Leaf senescence and leaf fall were modelled by Vander Mijnsbrugge and Janssens (2019) for different provenances of hawthorn across Europe, ranging from around early October to late November.

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Hawthorn features flowers on any side of the individual but with significantly more on western sides than on eastern sides (Sparks & Croxton, 2007). The flowers of *C. monogyna* are hermaphroditic and protogynous and have five, rarely four or six, petals (Knuth, 1898). Macreight (1837) describes the aestivation of petals as quincuncial or spirally imbricate, where two petals are outside all others, two are inside all others, and the fifth is outside on one margin and inside on the other. However, they also appear cochleate or spirally twisted, where one petal is outside all others, one petal is inside all others, and three are outside on one margin and inside on the

other (A. Fichtner, pers. obs.). On the day of anthesis, the petals bend outwards and soon reveal the mature stigma. During the next 2 days, the stamens expand until they are erect to suberect before the outermost anthers begin first to dehisce and are laced with pollen. In doing so, they change colour from pink-purplish to yellowish-brown (Godet, 1984). After anthesis flowers keep blooming for 5 days (Gyan & Woodell, 1987b) and attract pollinators in two ways: visually by the well-developed white petals, and by a foetid scent. Pollinators are rewarded with nectar and pollen (Ehlers, 1960). Broughton and Wright (1998) discovered a change of petal colour from white in the previous years to coral pink and deep carmine red among hawthorns of an old hedgerow in north-east Essex. Flowering until June, the latest flowers reverted to the normal white colour again. This sequence might be unique but colour changes seen elsewhere could be caused by a light-induced production of anthocyans. This change in colour did not seem to distract pollinators as fruit-set was very high.

Pollen release takes place from 7 a.m. to 5 p.m. without any peak period in *C. monogyna* (Percival, 1955). The pollen is of the *Crataegus*-type (Reitsma, 1966). The grains are tricolporate, striate, without a tectate operculum, and with fine, doubled, curved and short vallae, distributed as parallel pairs (Fægri et al., 1989). Data of length and diameter range from 23.5 to 35.4 μm and 23.8 to 36.9 μm (Eide, 1981) and 30 to 44 μm and 24 to 40 μm, respectively, with a prolate-spheroidal to subprolate shape (Wrońska-Pilarek et al., 2013). The pattern of the exine varies considerably (Byatt, 1976 as cited in Lippert, 1995). *Crataegus* species may be identified by their pollen grains. In a comparative study of *C. laevigata*, *C. monogyna*, *C. rhipidophylla*, and their spontaneous hybrids *C.* × *media*, *C.* × *subsphaerica* and *C.* × *macrocarpa* Gand. s.l. in Poland Wrońska-Pilarek et al. (2013) showed differences in Erdtman's (1952) pollen shape classes and relief. As *C. azarolus* L. and *C. monogyna* form a morphologically homogenous palynological group in Lebanon they can only be distinguished by size (Chakass et al., 2008).

The nectar is secreted by a ring of nectaries in the receptacle (Clapham et al., 1989), whose anatomy is described in Weryszko-Chmielewska and Konarska (1996). The amount of secretion varies diurnally with a decrease in the morning and a recovery in the afternoon, so the sugar concentration increases during the day as temperature increases and relative humidity decreases, ranging between 36% and 70% (Gyan & Woodell, 1987b). In terms of amount of sugar per flower during a day the actual reward averages 0.15 mg. The nectar is composed of sucrose and eight amino acids, of which alanine, arginine and proline are dominant, with additional leucine, lysine, threonine, tyrosine and only traces of aspartic acid (Gyan & Woodell, 1987b). In addition, it contains the yellow-coloured quercetin (Hegi, 1923) and has a scent of herring brine, due to a trimethylamine component (Kugler, 1970). This disgusting smell attracts especially diptera fond of putrefying substances, such as muscids and tachinids, but also anthophilous diptera such as syrphids (hoverflies), as well as coleoptera and hymenoptera (Clapham et al., 1989; Knuth, 1898; Lippert, 1995). Among the latter are mostly apids like the honey bee *Apis mellifera* (L.), mining bees *Andrena barbilabris* (Kirby), *A. labiata* Fabricius, *A. scotica* Perkins (=*A. jacobi* Perkins), *A. synadelpha* Perkins, *A. varians* (Kirby) and the mason bee *Osmia cornuta* (Latreille; Westrich, 1989, 2018). The bumblebees, *Bombus terrestris* L., *B. lucorum* L. and *B. pratorum* L., are listed by Gyan and Woodell (1987a), along with *Volucella* spp., *Eristalis* spp. and other small- and medium-sized hoverflies.

As a result of the species' RNase-based gametophytic self-incompatibility (Nettancourt, 1977; Raspé & Kohn, 2002), xenogamic cross-pollination by insects should be the rule, whereas self-pollination only occurs at failure of outcrossing (Knuth, 1898). Guitián and Fuentes (1992) and Guitián et al. (1992) report different flower to fruit conversion rates from 20% to 50% under natural conditions and a fruit-set limited by lack of pollinator activity. Gyan and Woodell (1987a) found autogamy with a flower to fruit conversation rate of 82% and Guitián and Fuentes (1992) observed 20% after manual self-pollination. However, further research on the questions of reproduction seems necessary, as in an ongoing study with self- and cross-pollination by hand of different *Crataegus* species, neither autogamy nor geitonogamy have been detected (A. Fichtner, unpubl. data).

While fresh mass of fruit yield is significantly lowered by higher cutting frequencies the percentage of dry matter content remains unaffected (Croxton & Sparks, 2002). There is no evidence for mast events in *C. monogyna*. Sallabanks (1992) showed higher fitness for larger and/or older plants through producing more fruit, suggesting that growing as big and as quickly as possible by delaying fruiting until later in life is an optimal fruiting strategy for hawthorn.

8.2 | Hybrids

Agamospermy and apomixis are common in *Crataegus* (Campbell et al., 1991; Dickinson & Campbell, 1991; Dickinson & Phipps, 1986; Muniyamma & Phipps, 1984). As part of the breeding strategy apomixis results in polyploidy in *Crataegus* (Campbell et al., 1991; Smith & Phipps, 1988a, 1988b; Wells & Phipps, 1989). Such polyploids occur together with sexual diploids in North America, where apomixis has been proved (Lo, et al., 2009; Muniyamma & Phipps, 1979a; Talent & Dickinson, 2007a). In Europe the genus *Crataegus* consists of some sexual species mixed with pseudogamous apomicts. Hellwig (2006) claimed apomixis to be irrelevant in Thuringia although no experimental work on pseudogamy appears to have been done yet in Europe (Sell & Murrell, 2014). Despite being ecologically separated, European hawthorns still hybridize in contact zones increasingly caused by human influence, for example, through deforestation and habitat fragmentation. Moreover, the introduction of non-local species leads to a whole new set of putative hybrids. The morphology of the descendants of such hybridization events is normally intermediate between that of the parents (Christensen, 1992a; Lippert, 1978; Schmidt, 1981). As these primary hybrids may be fertile, there may be backcrossings with the parents leading to a reduction of the morphological and ecological differentiation between the parent species (Hellwig, 1997).

TABLE 2 Putative hybrids of *Crataegus monogyna* (=*C. m.*)

Parents	Hybrid	References
Hybrids with species of **sect. *Crataegus***	**Intrasectional** hybrids	
Hybrids with species of **ser. *Crataegus***	**Intraserial** hybrids	
C. m. Jacq. × *C. laevigata* (Poir.) DC.	*C.* × *media* Bechst.	1, 4, 6, 8, 9, 10, 16
C. m. Jacq. × *C. rhipidophylla* Gand.	*C.* × *subsphaerica* Gand. s.str.	8, 9, 10, 11, 12, 14, 16
C. m. Jacq. × *C. lindmanii* Hrabětová	*C.* × *domicensis* Hrabětová	8, 9, 10
C. m. Jacq. × *C. meyeri* Pojarkova	*C.* × *armena* Pojarkova	2, 10
C. m. Jacq. × *C. nevadensis* Christensen	*C.* × *inexpectans* Christensen	14
C. m. Jacq. × *C. heterophylla* Flüggé		17
Hybrids with species of **ser. *Orientales*** (Zabel ex. Schneid.) Pojarkova	Hybrids of **nothoser. *Orientaegus*** Christensen	10
C. m. Jacq. × *C. azarolus* L.	*C.* × *sinaica* Boiss.	10, 12, 13, 14
C. m. Jacq. × *C. heldreichii* Boiss.	*C.* × *killinica* Christensen	10, 11
C. m. Jacq. × *C. orientalis* Pallas ex Bieb.	*C.* × *albanica* Pojarkova	10, 11
Hybrids with species of **ser. *Pentagynae*** (Schneid.) Rus.	Hybrids of **nothoser. *Crataegynae*** Christensen	10
C. m. Jacq. × *C. pentagyna* Waldst. & Kit ex Willd.	*C.* × *rubinervis* Lange (=*C. dipyrena* Pojarkova)	2, 10, 12, 14
Hybrids with species of **ser. *Tanacetifoliae*** Christensen	Hybrids of **nothoser. *Crataegifoliae*** Christensen	10
C. m. Jacq. × *C. tanacetifolia* L.	*C.* × *yosgatica* Christensen	10, 12, 14
	Intersectional hybrids	
Hybrids with species of **sect. *Sanguineae*** Zabel ex. Schneid.	Hybrids of **nothosect. *Crataeguineae*** Christensen	10
C. m. Jacq. × *C. nigra* Waldst. & Kit.	*C.* × *lambertiana* Lange	10
Hybrids with species of **sect. *Coccineae*** Loud.	Hybrids of **nothosect. *Coccitaegus*** Christensen & Dickinson	15
C. m. Jacq. × *C. punctata* Jacq.	*C.* × *ninae-celottiae* Christensen & Dickinson	15
Hybrids with species of **sect. *Douglasia*** Loud.	Hybrids of **nothosect. *Crataeglasia*** Christensen & Dickinson	15
C. m. Jacq. × *C. suksdorfii* (Sarg.) Kruschke	*C.* × *cogswellii* Christensen & Dickinson	15
Hybrids with different 'genera'	'Intergeneric' hybrid	
C. m. Jacq. × *Crataegus germanica* (L.) O. Kuntze	×*Crataemespilus gillotii* Beck	1, 3, 5[a], 7, 16, 17

Note: 1. Hegi (1923); 2. Pojarkova (1939); 3. Browicz (1970); 4. Bradshaw (1975a); 5. Bradshaw (1975b); 6. Byatt (1975); 7. Byatt et al. (1977); 8. Lippert (1978); 9. Schmidt (1981); 10. Christensen (1992a); 11. Christensen (1992b); 12. Dönmez (2004); 13. Albarouki and Peterson (2007); 14. Christensen and Zieliński (2008); 15. Christensen et al. (2014); 16. Stace et al. (2015); 17. Phipps (2016).

[a]Bradshaw (1975b) applied × *Crataemespilus grandiflora* (Sm.) E.G. Camus for this sexual medlar-hawthorn hybrid, which refers to *C. laevigata* as the hawthorn-parent (Byatt et al., 1977).

In the British Isles, *Crataegus monogyna* hybridizes most notably with the other native species, *C. laevigata*, (Thomas et al., 2021). However, in its natural range and where it has been introduced, *C. monogyna* hybridizes freely with other *Crataegus* species. The taxonomic status of these hybrids as nothospecies, nothosubspecies or nothovarieties is debatable (Schmidt, 2017c) and, for some crosses, depends also on the acceptance of the constitution of '*C. rhipidophylla*'. In Table 2 we present a system adopting the members of *C. rhipidophylla* s.l. (i.e. *C. rhipidophylla* Gand. and *C. lindmanii* Hrabětová) as species (Schmidt, 2017a) and medlar, formerly treated as genus *Mespilus*, as *Crataegus germanica* (L.) O. Kuntze (Lo et al., 2007; Talent et al., 2008).

The unstable graft-chimera +*Crataegomespilus dardarii* Simon-Louis ex Bellair is of horticultural origin only (Byatt et al., 1977; Hegi, 1923; Schneider, 1906). The first and best-known example was developed as a graft of *C. germanica* on *C. monogyna* at the nursery of Simon-Louis in Bronvaux near Metz, France. Depending on the number of epidermal layers there are two cultivars (Bergann & Bergann, 1984; Fitschen et al., 1994): +*Crataegomespilus dardarii* 'Dardarii' with one layer of medlar, resembling *C. germanica* and +*Crataegomespilus dardarii* 'Asnieresii' with two layers of medlar resembling *C. monogyna*. Byatt et al. (1977) came to the conclusion of 'dynamic rather than static random arrangements of parental tissues' leading to a series of transitional stages in different branches on individuals.

As it is the parent of many hybrids, with occasional introgression (Byatt, 1975; Fineschi et al., 2005), the term 'compilo-species' (Harlan & Wet, 1963) has been applied to *C. monogyna* by Christensen (1992a).

8.3 | Seed production and dispersal

There are typically five to eight fruits per corymb, each drupaceous pome bearing one nutlet (Bojňanský & Fargašová, 2007). Khadivi-Khub et al. (2015) provided data on number of nutlets ranging from one to four (mean 3.11) in Iran. These counts have to be regarded with suspicion as the pictures of leaves, fruit and nutlets of the studied plants presented suggest that some were probably incorrectly allocated to *C. monogyna*. Each nutlet holds one seed enclosed in a lignified endocarp that may act to protect the seed and to retard germination (Bewley & Black, 1982). The presence of an endosperm was denied by Ascherson and Graebner (1906) but was described for *Crataegus* species by Aldasoro et al. (2005) and Talent and Dickinson (2007b). The seeds show embryo dormancy (Dickinson, 1985).

Mean fruit mass has been measured as 675.4 mg for fresh and 294.7 g for dried fruit, respectively, resulting in 171.0 mg per dried pulp and 123.7 mg per dry seed (Herrera, 1987). The thousand-seed weight varies with authorities from 55 g (Hrynkiewicz-Sudnik et al., 1987 as cited in Bujarska-Borkowska, 2002) to 98 g (Royal Botanic Gardens Kew, 2019) and 280 g (Kheloufi et al., 2019).

The flesh of the fruit contains starch and is mealy without any special flavour. Specific pulp constituents are provided in Table 3. Although it is not really poisonous it contains some slightly toxic compounds such as saponins (Rossiiskaya et al., 1989) so only a small number of fruit are consumed by an individual each time (Barnea et al., 1993). Therefore, they can remain on the trees for more than 9 months (Bass, 1990a) representing, in case of need, a food supply for overwintering that lasts all winter (Barnea et al., 1993). On the other hand, birds consistently reject fruit infested by insects (Manzur & Courtney, 1984).

Because of their bright red colour, fruit are easily detected and eaten by resident and migrating birds and to a lesser extent by mammals. Dispersal is mostly endozoochorous. The intestinal passage does not affect the seeds (Kollmann, 1994). Among the main avian dispersers are Starlings (*Sturnus vulgaris* L.), Robins (*Erithacus rubecula* L.) and Woodpigeons (*Columba palumbus* L.), along with a larger number of members of the thrush family such as Blackbirds (*Turdus merula* L.), Song Thrushes (*Turdus philomelos* Brehm), Mistle Thrushes (*Turdus viscivorus* L.), Redwings (*Turdus iliacus* L.) and Fieldfares (*Turdus pilaris* L.; Snow & Snow, 1988). Guitián and Fuentes (1992) list additionally Eurasian Blackcap (*Sylvia atricapilla* (L.)). Smaller birds like Blue Tits (*Cyanistes caeruleus* (L.)), Common Chiffchaff (*Phylloscopus collybita* (Vieillot)), Bullfinch (*Pyrrhula pyrrhula* (L.)), Common Chaffinch (*Fringilla coelebs* L.) and Greenfinches (*Chloris chloris* (L.)) are reported as pulp-predators (Guitián & Fuentes, 1992; Turček, 1961 as cited in Snow & Snow, 1988). In North America, the American Robin (*Turdus migratorius* L.) prefers the fruit of the introduced *C. monogyna* to those of a native congener (Reichard et al., 2001; Sallabanks, 1992) and in Australia the native Pied Currawong (*Strepera graculina* (Shaw)) disperses the seeds over distances of more than 1,000 m (Bass, 1990a). Mammal dispersers include hares (*Lepus timidus* L.), red foxes (*Vulpes vulpes* (L.); Bonn & Poschlod, 1998; Turček, 1967) and goats (*Capra hircus* L.; Delibes et al., 2017). The Australian native mammal Brush-tailed possum (*Trichosurus vulpecula* (Kerr)) eats the fruit and defecates the seeds up to 50-m away (Bass, 1990b). Due to these vectors, seeds may be distributed more than 300 m (Carlo et al., 2013) and this may explain different *Crataegus* species in one stand (Lippert, 1995).

Guitián and Fuentes (1992) reported the powerfully billed Hawfinch (*Coccothraustes coccothraustes* (L.)) as a seed predator. As reviewed by Bonn and Poschlod (1998) much post-dispersal predation takes place, for example, by mice (Herrera, 1984). Isolated nutlets are less favoured by rodents than whole fruit with pulp because of their stony endocarp (Kollmann et al., 1998).

TABLE 3 Pulp constituents of *C. monogyna* expressed in relation to dry mass of pulp except for WCF (Herrera, 1987)

Lipids (%)	2.3
Protein (%)	2.5
Fibre (%)	20.5
NSC (%)	72.4
WCF (%)	56.4
Ash (%)	4.3
Ca (g/kg)	4.4
Mg (g/kg)	0.6
P (g/kg)	0.5
K (g/kg)	12.5
Na (g/kg)	0.3
Fe (mg/kg)	28
Mn (mg/kg)	3
Zn (mg/kg)	6
Cu (mg/kg)	4

Abbreviations: NSC, non-structural carbohydrate; WCF, water content of the whole fruit (seeds plus pulp).

8.4 | Viability of seeds: Germination

Under natural conditions seeds of *C. monogyna* usually start germinating in the second spring after seed-set (Flemion, 1938 as cited in Lasseigne & Blazich, 2008) and can take up to 6 years to germinate (Christensen, 1992a); thus they require cold stratification to break embryo dormancy (Brinkman, 1974 as cited in Lasseigne & Blazich, 2008). Increasing temperatures during spring will induce secondary dormancy if the seeds have not germinated after their cold stratification during winter (Bujarska-Borkowska, 2002). Therefore, according to Phipps (1998; pers. comm. as cited in Lasseigne & Blazich, 2008) and Davies et al. (2017), a double dormancy of embryo and endocarp dormancy can be postulated for *C. monogyna*.

For propagation purposes, fruit are collected best in October when they are fully ripe, either readily from the ground or hand-picked from the plants (Brinkman, 1974 as cited in Lasseigne & Blazich, 2008). To store seeds, fruit need to be either dried at

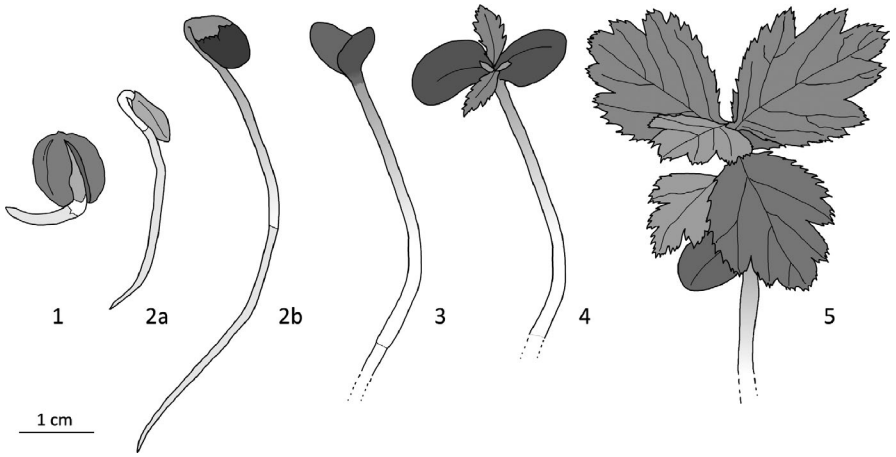

FIGURE 4 Seedlings of *Crataegus monogyna* at (1) 5–7, (2a) 10–12, (2b) 15, (3) 20, (4) 25–30 and (5) 45–50 days after germination. Drawings by Dr. Theresa Reimann from pictures provided by Dr. Abdenour Kheloufi

room temperature to a moisture content of about 10% (Bujarska-Borkowska, 2002) or macerated and floated to remove the pericarp (Munson, 1986). After air-drying, the seeds should be stored under refrigerated conditions to remain viable for 2 to 3 years (Dirr & Heuser, 2006). St. John (1982), however, noted decreased seed viability after storage for 2 years. This may be the reason why no persistent seed bank in nature has been reported (Grime et al., 1988), although Kheloufi et al. (2019) found 20%–25% of seeds dormant and only about 5% dead after cold stratification under natural-like conditions.

To overcome seed dormancy, manifold methods are published. Deno (1993) found a germination rate of 55% after a cold-warm-cold-warm-cold cycle of 3 months each at 21°C or 4°C respectively. A germination rate of 80% was gained after acid scarification and cold stratification at 2–4°C (St. John, 1982). The ground-breaking study of Bujarska-Borkowska (2002) lists different thermal regimes of pre-treatments which led to a germination rate of 90%: Fully ripe fruit dried to a moisture content of 10% at room temperature should experience 16 weeks at 25°C or cyclical 20–30°C, the latter at either 16 + 8 or 24 + 24 hr per day followed by 14–18 weeks at 3°C.

8.5 | Seedling morphology

Germination is epigeal and the cotyledons are green, ovate and fleshy. The first leaves are smaller and less dissected compared to the subsequent ones (Lippert, 1995). Seedling morphology is shown in Figure 4. The seedlings may reach heights of 40 cm after one year (Köpp, 1987 as cited in Schuck, 2005).

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

Its thorns render *C. monogyna* relatively unpalatable and, therefore, not a preferred diet of grazing mammals, though donkeys (*Equus asinus asinus* L.; Lamoot et al., 2005) and, in winter, Highland cattle (*Bos primigenius taurus* L.; Lamoot et al., 2005) in Belgium, sheep (*Bos ovis* L.) in North Wales (Good et al., 1990) and feral goats (*Capra hircus* L.) in Somerset (Smith & Bullock, 1993) were found to graze on *C. monogyna*-containing dune scrub. *C. monogyna* also has had reduced cover due to grazing by Przewalski's horses (*Equus ferus przewalskii* Poljakow) and red deer (*Cervus elaphus* L.; Hanauer et al., 2012). Bushes may persist in a heavily grazed state at 30–50 cm height, as they are too thorny to be finished off by grazing animals, and seem stuck in this state because the young shoots are eaten down when they emerge above the thorny mass (C.D. Preston, pers. comm.). Seedlings and young, non-thorny plants are grazed by the European rabbit (*Oryctolagus cuniculus* (L.)) which led to proliferation of hawthorn scrub after introduction of myxomatosis in the 1950s (Thomas, 1960). The foliage is reported to be relatively unpalatable to garden snails (*Cornu aspersum* (Müller)), but serves a large insect fauna (Wratten et al., 1981). A list of associated insects, their food sources and their preferences is given in Table 4. Further information is available from Biological Records Centre (2019) and Ellis (2001 ongoing). The Palaearctic and *Crataegus*-exclusive psyllid *Cacopsylla peregrina* (Foerster) was introduced to North America probably with nursery root-stocks and is potentially injurious to the native *Crataegus* flora (Wheeler & Stoops, 2001). Edwards and Wratten (1985) suggest a mechanism of inducible defence against foliar predation by insects for *C. monogyna*.

9.2 | Plant parasites

Figure 5 shows the only recorded higher plant parasite of hawthorn from Europe, *Viscum album* L. (Buhr, 1964; Kubus, 1998). Among other *Crataegus* taxa, *C. monogyna* serves also as a host for *Viscum* outside Europe (Mehrvarz et al., 2012). An unconfirmed report as host of *Loranthus europaeus* Jacq. in Slovakia is reported in Krasylenko et al. (2019) and for *Loranthus grewingkii* Boiss. & Buhse in Iran (Shavvon et al., 2012). Hawthorn serves as host for endemic *Ileostylus micranthus* (Hook.f.) Tiegh. in New Zealand (Herbarium, 2000).

TABLE 4 Arthropods associated with *Crataegus monogyna*, with their food source and preference. Non-exclusive ones are presented in parentheses

		References
Gall mites (**Acari**)		
Eriophyidae		
Calepitrimerus armatus (Canestrini)	Leaves; *Crataegus*	1, 9
Eriophyes calycobius (Nalepa)	Leaf buds; Rosaceae	3, 9
Eriophyes crataegi (Canestrini)	Leaves; *Crataegus*	3, 9
Phyllocoptes goniothorax (Nalepa)	Leaves; *Crataegus*	1, 3, 9
Tetranychidae		
Tetranychus viennensis Zacher	Leaves; woody Rosaceae	4, 12
Gall midges (**Diptera**)		
Cecidomyiidae		
Contarinia anthobia (Löw)	Floral buds; *Crataegus*	3, 9
Dasineura crataegi (Winnertz)	Tips of shoots; *Crataegus*	1, 3, 4, 9
Dasineura oxyacanthae Rübsaamen	Floral buds; *Crataegus*	3, 9
Resseliella crataegi (Barnes)	Cambium; *Crataegus*	3, 9
Tephritidae		
Anomoia purmunda (Harris)	Fruit; *Berberis* and Rosaceae	7, 9
Aphids (**Hemiptera**)		
Aleyrodidae		
Asterobemisia carpini (Koch)	Polyphagous	9
Siphoninus phillyreae (Haliday)	Polyphagous	9
Aphididae		
Aphis fabae Scopoli	Polyphagous; 2° e.g. *Crataegus*	9
Aphis gossypii Glover	Polyphagous	9
Aphis pomi deGeer	On Rosaceae, mainly Maleae	3, 9
Aphis spiraecola Patch	Polyphagous	9
Dysaphis angelicae (Koch)	1° *Crataegus*; 2° *Angelica*	3, 9
Dysaphis apiifolia (Theobald)	1° *Crataegus*; 2° Apiaceae	3
Dysaphis crataegi (Kaltenbach)	1° *Crataegus*; 2° Apiaceae	3, 9
Dysaphis laserpitii (Börner)	1° *Crataegus*; 2° *Laserpitium*	3, 9
Dysaphis lauberti (Börner)	1° *Crataegus*; 2° Apiaceae	3, 9
Dysaphis ranunculi (Kaltenbach)	1° *Crataegus*; 2° *Ranunculus*	3, 9
Ovatus crataegarius (Walker)	1° Maleae; 2° Lamiaceae	9
Ovatus insitus (Walker)	1° Maleae; 2° *Lycopus*	9
Prociphilus pini (Burmeister)	1° *Crataegus*; 2° Pinaceae	3, 9
Rhopalosiphum oxyacanthae Schrank	1° woody Rosaceae; 2° Poaceae	1, 3, 9
Aphrophoridae		
Philaenus spumarius (Linnaeus)	Rarely on suckers	3
Cicadellidae		
Anoplotettix fuscovenosus (Ferrari)	Endemic	1
Edwardsiana crataegi (Douglas)	Leaves; endemic	1, 12
Coccidae		
Eulecanium tiliae (Linnaeus)	Polyphagous on woody plants (Rosaceae)	9
Palaeolecanium bituberc. (Signoret)	Polyphagous on woody plants (Rosacaeae)	9
Parthenolecanium corni (Bouché)	Polyphagous on woody plants	9
Pulvinaria hydrangeae Steinweden	Polyphagous on trees	9
Diaspididae		
Lepidosaphes ulmi (Linnaeus)	Polyphagous on woody plants (Rosaceae)	9
Pseudococcidae		
Phenacoccus aceris (Signoret)	Polyphagous on woody plants	9
Psyllidae		
Cacopsylla affinis (Löw)	Leaves; Rosaceae (*Crataegus*)	9
Cacopsylla crataegi (Schrank)	Leaves; Rosaceae (*Crataegus*)	4, 9
Cacopsylla melanoneura (Foerster)	Leaves; Rosaceae (*Crataegus*)	3, 7, 9
Cacopsylla peregrina (Foerster)	Leaves, buds, flowers, petioles; *Crataegus*	3, 7, 9
Sawflies (**Hymenoptera**)		
Tenthredinidae		
Caliroa cerasi (Linnaeus)	Leaves; Rosaceae	11
Micro-moths (**Lepidoptera**)		
Bucculatricidae		
Bucculatrix bechsteinella (Bechstein & Scharfenberg)	Leaf-miner; Maleae (*Crataegus*)	1, 9
Coleophoridae		
Coleophora chiclanensis Hering	Leaf-miner; *Crataegus monogyna*	9
Coleophora hemerobiella (Scopoli)	Leaf-miner; Rosaceae	9

(Continues)

TABLE 4 (Continued)

		References
Coleophora potentillae Elisha	Leaf-miner; Rosaceae	9
Coleophora serratella (Linnaeus)	Leaf-miner; polyphagous on woody plants	9
Coleophora siccifolia Stainton	Leaf-miner; polyphagous on woody plants	9
Coleophora spinella (Schrank)	Leaf-miner; woody Rosaceae (*Crataegus*)	9
Coleophora trigeminella Fuchs	Leaf-miner; woody Rosaceae	9
Gelechiidae		
Recurviara nanella (Denis & Schiffermüller)	Leaf-miner; woody Rosaceae	9
Gracillariidae		
Parornix anglicella (Stainton)	Leaf-miner; woody Rosaceae (*Crataegus*)	1, 9
Phyllonorycter corylifoliella (Hübner)	Leaf-miner; woody Rosaceae	9
Phyllonorycter oxyacanthae (Frey)	Leaf-miner; Maleae (*Crataegus*)	1, 9
Phyllonorycter sorbi (Frey)	Leaf-miner; woody Rosaceae	9
Lyonetiidae		
Leucoptera malifoliella (O Costa)	Leaf-miner; woody plants (Rosaceae)	9
Lyonetia clerkella (Linnaeus)	Leaf-miner; woody plants (Rosaceae)	9
Lyonetia prunifoliella (Hübner)	Leaf-miner; woody plants	9
Nepticulidae		
Ectoedemia atricollis (Stainton)	Leaf-miner; woody plants (*Crataegus*)	9
Stigmella crataegella (Klimesch)	Leaf-miner; *Crataegus*	9
Stigmella hybnerella (Hübner)	Leaf-miner; Maleae (*Crataegus*)	9
Stigmella oxyacanthella (Stainton)	Leaf-miner; woody Rosaceae (*Crataegus*)	9
Stigmella paradoxa (Frey)	Leaf-miner; *Crataegus*	9
Stigmella perpygmaeella (Doubleday)	Leaf-miner; *Crataegus*	9
Stigmella regiella (Herrich-Schäffer)	Leaf-miner; *Crataegus*	1, 9
Pyralidae		
Acrobasis advenella (Zincken)	Leaf-miner; Maleae	5, 7, 9
Sesiidae		
Synanthedon myopaeformis (Borkhausen)	Leaf-miner; Maleae	9
Yponomeutidae		
Argyresthia bonnetella (Linnaeus)	Leaf-miner, buds; woody plants (Rosaceae)	1, 5
Argyresthia curvella (Linnaeus)	Buds; *Malus* (*Crataegus*)	5
Paraswammerdamia nebulella (Goeze)	Leaf-miner; Maleae	5, 7, 9
Scythropia crataegella (Linnaeus)	Leaf-miner; woody Rosaceae	9
Yponomeuta padella (Linnaeus)	Leaf-miner; woody Rosaceae	10, 12
Momphtidae/Elachistidae		
Blastodacna hellerella (Duponchel)	Fruit; woody Rosaceae	1, 12
Spuleria flavicaput (Haworth)	Endemic	1, 12
Tortricidae		
Ancylis achatana (Denis & Schiffermmüller)	Leaves, woody Rosaceae	5, 7, 9
Acleris rhombana (Denis & Schiffermmüller)	Buds, leaves, woody Rosaceae	5, 7, 9
Cydia janthinana (Duponchel)	Fruit; woody Rosaceae	1, 7, 12
Hedya nubiferana (Haworth)	Leaves, woody plants	5, 7, 9
Macro-moths (**Lepidoptera**)		
Lasiocampidae		
Trichiura crataegi (Linnaeus)	Leaves; woody plants	10, 12
Drepanidae		
Cilix glaucata (Scopoli)	Leaves; woody Rosaceae	10, 12
Lymantriidae		
Orgyia recens (Hübner)	Leaves; woody plants	10, 12
Geometridae		
Operophtera brumata (Linnaeus)	Leaves; woody plants	4, 10, 12
Noctuidae		
Allophyes oxyacanthae (Linnaeus)	Leaves; woody Rosaceae	10, 12
Butterflies (**Lepidoptera**)		
Lycaenidae		
Thecla betulae (Linnaeus)	Leaves; woody plants	6
Nymphalidae		
Argynnis paphia (Linnaeus)	Leaves; Violaceae and Rosaceae	2
Nymphalis polychloros (Linnaeus)	Leaves; woody plants	8
Pieridae		
Aporia crataegi (Linnaeus)	Leaves; woody Rosaceae	2, 6

(Continues)

(Continues)

TABLE 4 (Continued)

		References
Beetles (**Coleoptera**)		
Attelabidae		
Neocoenorrhinus pauxillus (Germar)	Leaves; woody Rosaceae	9
Buprestidae		
Trachys minutus (Linnaeus)	Leaf-miner; woody plants	9
Curculionidae		
Anthonomus bituberculatus Thomson	Floral buds; woody Rosaceae	9
Anthonomus chevrolati Desbrochers	Leaves; endemic	1, 12
Anthonomus pedicularius (Linnaeus)	Floral buds; *Crataegus*	3, 9
Anthonomus spilottus Redtenbacher	Leaves; Maleae	9
Rhamphus oxyacanthae (Marsham)	Leaf-miner; woody Rosaceae (*Crataegus*)	9
Rhamphus subaeneus Illiger	Leaf-miner; *Crataegus*	9

Note: 1. Hegi (1923); 2. Allan (1949); 3. As cited in Buhr (1964); 4. Menzinger and Sanftleben (1980); 5. Dreyer (1981); 6. Blab and Kudrna (1982); 7. Dreyer (1984); 8. Heath et al. (1984); 9. Ellis (2001 ongoing); 10. As cited in Schuck (2005); 11. Pasiecznik (2008); 12. Biological Records Centre (2019).



FIGURE 5 *Viscum album* on a *Crataegus monogyna* host in Nuremberg, Germany (Photo: André Fichtner)

TABLE 5 Fungi (by order) associated with *Crataegus monogyna* including those found on soil or litter below the trees, or those found solely on dead wood. Nomenclature follows the Fungal Records Database of Britain and Ireland (British Mycological Society, 2019)

	Ecological notes	References
Ascomycota		
Capnodiales		
Mycosphaerella crataegi Johanson ex Oudem.	Leaves	1
Diaporthales		
Diaporthe crataegi Fuckel	Twigs	1, 7
Togninia crataegi (Mouton) Berl.	Twigs	1
Erysiphales		
Phyllactinia mali (Duby) U. Braun	Leaves	5, 6, 7
Podosphaera clandestina (Wallr.) Lév.	Leaves, young shoots	1, 2, 4, 5, 6, 7
Helotiales		
Diplocarpon mespili (Sorauer) B. Sutton	Leaves	4, 7
Lachnum spp.	Twigs	1
Pezicula aurantiaca Rehm	Twigs	1
Pleosporales		
Fenestella crataegi (Niessl) Jaklitsch & Voglmayr	Twigs	1
Taphrinales		
Taphrina crataegi Sadeb.	Leaves, young shoots, peduncles	1, 2, 5, 7
Venturiales		
Venturia crataegi Aderh.	Leaves	1, 4, 7
Incertae sedis		
Myriellina cydoniae (Desm.) Höhn.	Leaves	4
Basidomycota		
Agaricales		
Calocybe gambosa (Fr.) Donk	Soil	7
Chlorophyllum rachodes (Vittad.) Vellinga	Soil	7
Clitocybe nebularis (Batsch) P. Kumm.	Soil	7
Entoloma aprile (Britz.) Sacc.	Soil	7
Entoloma clypeatum (L.) P. Kumm.	Soil	7
Entoloma sepium (Noull.-Dass.) Richon & Roze	Soil	7
Lepista nuda (Bull.) Cooke	Soil	7
Mycena galericulata (Scop.) Gray	Soil	7
Tubaria dispersa (Pers.) Singer	Soil	7
Tubaria furfuracea (Pers.) Gillet	Soil	7

(Continues)

TABLE 5 (Continued)

	Ecological notes	References
Geastrales		
Geastrum triplex Jungh.	Soil	7
Helotiales		
Monilinia johnsonii (Ellis & Everh.) Honey	Fruit	7
Hymenochaetales		
Fuscoporia ferruginosa (Schrad.) Murrill	Wood	7
Pezizales		
Mitrophora semilibera (DC.) Lév.	Soil	7
Verpa conica (O.F. Müll.) Sw.	Soil	7
Polyporales		
Trametes versicolor (L.) Lloyd	Twigs	7
Pucciniales		
Gymnosporangium clavariiforme (Wulfen) DC.	Leaves, young shoots, fruit; aecia	1, 2, 5, 6, 7
Gymnosporangium clavipes Cooke & Peck	Fruit; aecia	4
Gymnosporangium confusum Plowr.	Leaves, young shoots, fruit; aecia	1, 2, 5, 7
Russulales		
Stereum hirsutum (Willd.) Pers.	Twigs	7
Stereum rugosum Pers.	Twigs	7
Xylariales		
Diatrype stigma (Hoffm.) Fr.	Twigs, branches	7
Xylaria hypoxylon (L.) Grev.	Wood	7

Note: 1. Hegi (1923); 2. As cited in Buhr (1964); 3. Sharma and Koul (1984); 4. As cited in Schuck (2005); 5. Klenke and Scholler (2015); 6. Kruse (2019); 7. British Mycological Society (2019).

Corticolous lichens appear as epiphytes. Besides the maritime sunburst lichen, *Xanthoria parietina* (L.) Th. Fr., species preferring an acid substratum with a low pH of 3–4 are to be found on hawthorn (Smith et al., 2009).

9.3 | Plant diseases

In contrast to other woody species *C. monogyna* is affected by a huge number of diseases (Kehr & Butin, 2003 as cited in Schuck, 2005). An overview of fungal associates is provided in Table 5. A noteworthy and harmful disease is fire blight, induced by the bacterium *Erwinia amylovora* (Burrill) Winslow et al. (Lippert, 1995). Introduced from the United States to Europe (southern England) in 1957 (Crosse et al., 1958), this disease spread across the continent (France 1978, Switzerland 1989, Germany 1990, Yugoslavia 1990). It attacks woody Rosaceae and causes the withering and necrosis of shoots, flowers, leaves and fruit, as well as cankers on the branches (Moricca et al., 2018). Because of its sometimes epidemic extent, fire blight is dreaded among owners of orchards and is notifiable in several countries, for example, in the United Kingdom since November 1987 (The Plant Health (Great Britain) Order 1987, 1987) and in Germany since June 1988 (Verordnung zur Bekämpfung der Feuerbrandkrankheit, 1985). Equivalent laws are effective in Austria, Switzerland and autonomous South Tyrol in Italy to protect traditional orchard meadows. In addition to a natural resistance to fire blight of some hawthorns native to North America, Korba et al. (1998) found one out of 63 seedlings to be highly resistant to fire blight. This individual plant was not infected after 34 oculations in three growing seasons. This seedling was identified as *C. monogyna* but having some characteristics of *C. laevigata*.

Similar to fire blight, pruning with non-disinfected tools as well as the technique of clipping itself intensifies attacks of powdery mildew (*Podosphaera clandestina* (Wallr.) Lév.; Khairi & Preece, 1978). Furthermore, *C. monogyna* may be infected by a MLO (mycoplasma-like organism) leading to shorter shoots linked with leaf-size reduction and chlorotic leaf-colour (Seemüller & Lederer, 1988). Otto and Winkler (1995) detected infections of rootlets by actinomycota on both its own soil and soil already infected with apple replant disease.

10 | HISTORY

Based on molecular phylogenetic reconstruction of apples and their relatives, the genus *Crataegus* evolved during the Eocene before 40 mya as sister to *Amelanchier* and its segregates *Malacomeles* and *Peraphyllum*, and the split of *C. germanica* and *Crataegus* s.str. is dated in the Oligocene before 30 mya (Lo & Donoghue, 2012). Although lacking sample material of the least derived form of hawthorns, East Asian *C. scabrifolia* (Franchet) Rehder, the biogeographic analyses of Lo, et al. (2009) indicate, from both the maximum likelihood and the maximum parsimony criteria, Eastern North America and Europe as the most recent common areas for all *Crataegus* species. From there, the two major lineages spread in Eurasia and North America. According to differences in chromosome base numbers and their recent geographical distribution, El-Gazzar and Badawi (1977) divided the genus *Crataegus* into two subgenera, the Eurasian clade of *C.* subgen. *Crataegus* with a base number of 17 and characteristic deeply divided leaves and the North American clade, *C.* subgen. *Americanae* El-Gazzar with a base number of 16 and less deeply divided leaves (El-Gazzar, 1980). Recent work by Ufimov and Dickinson (2020) suggest five subgenera adding *C.* subgen. *Sanguineae* Ufimov, *C.* subgen. *Mespilus* (L.) Ufimov and T.A. Dickinson, and *C.* subgen. *Brevispinae* (Beadle) Ufimov and T.A. Dickinson, of which the last two are monotypic. Christensen (1992a) groups the European representatives in sect. *Crataegus* with the characteristic feature of intercalary veins of leaves ending in sinuses. Lo and Donoghue (2012) date the split of *C. monogyna* and its closest relatives *C. laevigata* and *C. songarica* K. Koch to about 10 mya. The oldest fossil records are pyrenes of *Crataegus*, doubtfully of *C. monogyna* found at Baggotstown, Limerick and Gort, Galway in western Ireland and Clacton, Essex,

England. A younger record from Wretton, Norfolk, England is a leaf identification. All records are dated in the Middle Pleistocene, during Hoxnian interglacial substages II, III and IV and Ipswichian interglacial substages I, II, III respectively (Godwin, 1984). There is no evidence of presence during glacial stages for the whole genus, but it is supposed to have returned readily to the British Isles if it was excluded in these periods (Godwin, 1984). The oldest subfossil evidence for *C. monogyna* on the British Isles at Ballybetagh, Dublin, Ireland is dated in the Boreal (Flandrian zone V; Godwin, 1984) and the one on continental Europe at Hornstaad-Hörnle, Germany is dated in the late Atlantic (Flandrian zone VII; Rösch as cited in Sebald et al., 1992).

Collinson (1989) reported a rise of *C. monogyna* in the early Sub-Boreal due to the clearance and creation of farmland by immigrant people of Neolithic culture and the plant's resistance to grazing. In the Neolithic, hedges are known to have been used as natural fences to exclude livestock from the fields and were used as food supply (Groenman-van Waateringe, 1975 as cited in Ellenberg et al., 2010). Hence, hawthorn was planted extensively across the continent as part of wind-break hedges and on clearance cairns (Hegi, 1923). An ideal hedge for these purposes has an A-shape of 2-m height. A special form of hedges are the 'knicks' of Central European lowlands (Weber, 2003). Hawthorn among other shrubs was planted and either bent down and interwoven or partially cut down and laid crosswise to keep stock enclosed. For this purpose, it was even introduced by settlers in Australia (Bass, 1990a). As planting material has been grown from cuttings or uniform seeds in nurseries, hedgerows may be genetically uniform for long distances. However, planted shrubs may have been derived from diverse locations and the local genotypes seem no longer to be grown in Britain (Sell & Murrell, 2014). Whereas Schwarz (1899) surprisingly considered *C. monogyna* to be less frequent than *C. laevigata*, *C. monogyna* is now the most frequent species of hawthorn across Europe and its natural distribution remains somewhat unclear (Batkó, 1946). In periods of agricultural depression, *C. monogyna* has been the major colonist of abandoned, agriculturally marginal, heavy clay, arable land and pasture in eastern England and such stands are illustrated by Tansley (1939); they tend to be cleared when prosperity returns. The extent of hedges declined dramatically in the 20th century when they were cut down either for farmland consolidation or to reduce the risk of epidemic spreading of fire blight (Lippert, 1995).

Individual hawthorns are mentioned as landmarks in Anglo-Saxon boundary charters, most of which date from the 10th century, and in Wiltshire they are mentioned twice as frequently as any other tree or shrub (Grose, 1947). The first botanical reference to hawthorn in Britain is the mention in Turner's (1562). *Herball* of 'our common hawthorn' (Pearman, 2017); Turner also mentions the thorn at Glastonbury that is green all winter.

10.1 | Uses

Being a 'common and abundant wild species with a wide distribution area', hawthorn is not only an object in the European ethnomedicinal flora (Pardo-de-Santayana et al., 2015), but also used in many other ways. Regarding its medicinal uses *C. monogyna* homeopathic remedies such as infusions or tonic extracts made from leaves, flowers and fruit—*Folia Crataegi cum floribus* and *Fructus Crataegi*—are applied in case of cardiovascular diseases (Lippert, 1995). As a treatment of chronic congestive heart failure stage II, as defined by the New York Heart Association, its usage is supported by clinical data and the support of cardiac and circulatory functions data (World Health Organization, 2002 and the literature cited therein). *Crataegus* extracts show the following effects: positive inotrope (increasing the strength of heart contractions), negative bathmotrope (decreasing the excitability of the heart) and positive dromotrope (increasing the conduction velocity in the AV node; Wichtl & Loew, 2009 and the literature cited therein). As advantage they do not show severe side effects like other cardiac glycosides (e.g. toxicity of glycosides retrieved from common and woolly foxglove). As part of folk medicine, with support of neither experimental nor clinical data, hawthorn is used as an antispasmodic agent in the treatment of asthma, diarrhoea, gall bladder disease and uterine contractions, and as a sedative for the treatment of insomnia (World Health Organization, 2002 and the literature cited therein).

A light brown or yellow dye for garments was yielded by decocting leaves, bark and roots (Pojarkova, 1939). *C. monogyna* is suitable for living fences as it tolerates clipping very well. Clipped twigs and branches were used in graduation towers to enrich the salinity (Ehlers, 1960) and due to its density and hardness the wood was used for lathe work, tool handles, sticks, etc. (Pojarkova, 1939). Among the variation of this species, there are several horticulturally selected forms for ornamental purpose (Jablonski, 2020; Krüssmann, 1976). *C. monogyna* is a preferred stock for grafting other slow growing pomoid Rosaceae (apple, pear, quince, medlar, Japanese medlar; Pojarkova, 1939; Schretzenmayr & Hermann, 1990). Fresh fruit have been used for stewed fruit and jelly or as part of fruit cakes or were fed to pigs (Düll & Kutzelnigg, 2016; Pojarkova, 1939; Schuck, 2005). In time of need they were also dried and milled to extend flour (Düll & Kutzelnigg, 2016). This use is testified to by several regional German vernacular names of *Crataegus* species, for example, 'Mehlkübeli' (Bavarian Franconia), 'Mâelfässer' (Thuringia) and 'Mehlfässli' (Switzerland; Hegi, 1923). Roasted pyrenes have replaced coffee (Witt, 1995 as cited in Schuck, 2005).

11 | CONSERVATION AND MANAGEMENT

Crataegus monogyna is classified as of 'Least Concern' on the IUCN red list in Europe (Rivers et al., 2017). However, as a component of hedges it suffered from their condemnation in the 1840s 'for taking up so much land, making the use of machinery difficult, acting as weed magazines and asylums of pests, impoverishing the soil and preventing the free circulation of air' (Sheail, 2005). Although opinions have changed since, hedges are still locally threatened by either farmland consolidation (Schubert et al., 2001) or mismanagement and neglect. Bannister and Watt (1994, 1995) summed up that hedgerow management originated from the understanding of growth stimulation of woody shrubs by repeated cuttings while

uncut shrubs will naturally grow more tree-like than getting bushy. The principal methods of cutting are 'plashing' (laying), coppicing and trimming (Churchward & Shea, 2005 and the literature cited therein). A variety of techniques for each method is available and these occur in various combinations. Most hedges are cut by flails. Although hawthorn branches are likely more damaged by them than by finger-bar cutters or circular saws, this technique favours branching further from the cut end (Semple et al., 1994). The ideal shape of hedges is controversial, for example, Maclean (1992) considered the formation of mulch by accumulation of trimmings at the bottom of a flat-topped hedge as detrimental to wildlife and thus favoured an A-shaped or rectangular hedge with a chamfered top, while Deane (1989) and others considered that an A-shaped hedge may be detrimental to insects. Although the A-shape is not self-shading, ground flora may be shaded out.

An unpublished study by Hooper (1992; as cited in Barr & Stuart, 2005) concluded three points for wildlife and landscape benefiting by hedge management: (a) management to produce as large a volume of woody growth as is compatible with farming operations; (b) hedge bottom management to produce an herbaceous, grassy strip about a metre wide on either side; and (c) hedge-top management to allow sapling trees to grow. As part of the majority of hedges, hawthorn provides important nesting shelter for many species of bird through its dense thorny foliage and serves as a food plant for more than 100 insect species. Furthermore, hawthorns produce pollen and nectar for pollinating insects and provide abundant fruit as food, especially for thrushes over a long period, lasting into winter.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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