

Biological Flora of the British Isles: *Crataegus laevigata*

Peter A. Thomas¹ | Tomasz Leski² | Nicola La Porta^{3,4} | Monika Dering^{2,5} |
Grzegorz Iszkuło^{2,6}

¹School of Life Sciences, Keele University, Staffordshire, UK; ²Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland; ³IASMA Research and Innovation Centre, Trento, Italy; ⁴The EFI Project Centre on Mountain Forests (MOUNTFOR), Trento, Italy; ⁵Department of Forest Management, Poznań University of Life Sciences, Poznań, Poland and ⁶Institute of Biological Sciences, University of Zielona Góra, Zielona Góra, Poland

Correspondence

Peter A. Thomas

Email: p.a.thomas@keele.ac.uk

Abstract

1. This account presents information on all aspects of the biology of *Crataegus laevigata* (Poir.) DC (Midland hawthorn) (*C. oxyacanthoides* Thuill.) 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 laevigata* is primarily a shade-tolerant shrub or small tree up to 12-m tall of ancient woodlands (of which it is an indicator plant) and occasionally old hedges, usually on heavy clay soils and avoiding limestone and chalk. It is native to central and northern Europe and in the British Isles is native to southeast England, occurring naturally up to the Midlands, hence the common name. It is largely absent naturally from Scotland, Wales and Ireland.
3. Flowers usually have two styles, varying from (rarely) 1 to 5 with an equal number of pyrenes in the fruit, differentiating it from *C. monogyna* with usually one style and pyrene. Pollination is by insects and fruit are dispersed primarily by birds. Fruit has traditionally been used for food, and with the leaves and flowers have a long tradition in herbal medicine.
4. Disturbance and fragmentation have allowed *C. monogyna* to permeate into old woodlands and hybridise with *C. laevigata*. These two species are inter-fertile and barriers to hybridisation are primarily spatial separation thus allowing extensive introgression such that in many parts of Europe, pure *C. laevigata* is becoming scarce.

KEYWORDS

conservation, geographical and altitudinal distribution, germination, mycorrhiza, parasites and diseases, pharmaceuticals, reproductive biology, soils

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

Midland Hawthorn. Rosaceae. *Crataegus laevigata* (Poir.) DC (syn. *C. oxyacanthoides* Thuill., *C. oxyacantha* forma *laevigata* (Poir.) Beck, *C. coriacea* Gand., *C. subinermis* Gand., *C. helvetica* Walo Koch, *C. palmstruchii* Lindm., *C. walokochiana* (Hrabetová-Uhrová) P. Schmidt, *Mespilus laevigata* Poir., *M. oxyacantha* (L.) Crantz, *M. oxyacanthoides* (Thuill.) DC., *M. intermedia* Poir., *M. digyna* Gray, *Oxyacantha vulgaris* (DC.) Roem., *O. obtusata* (DC.) Roem.). A small tree to 8(12) m with a dense, broad, rounded crown but usually an untidy multi-stemmed shrub; trunk not extending far into the crown; branches spreading or ascending, often less rigid than *C. monogyna*, and drooping at the ends. Bark greyish-brown to orange-brown becoming cracked and fissured. Twigs dull greyish-brown, often dense, usually shiny and glabrous sometimes with a few long hairs when young; spines fewer and shorter (6–15 mm) than in *C. monogyna*. Buds 1.1–2.1 mm × 1.2–1.9 mm, ovoid or subglobose, rounded at apex; scales dark brown, ovate, rounded at apex. Leaves alternate, usually coriaceous, shiny dark green above, pale green below, glabrous except for scattered hairs along major veins on both sides when young, usually lacking axillary hair-tufts in the subspecies common in Britain (in contrast to *C. monogyna*), obovate to subrotund, with one to three pairs of obtuse, shallow lobes which rarely reach half-way to the midrib (compared to

(3)5–7 lobes reaching more than one-half cut in *C. monogyna*), lobes usually rounded in outline, wider than long, margin crenate-serrate except in the sinuses, with 6–15 teeth on the basal lobe, the lowest pair of lobes acute; leaves variable in size, those on long shoots usually the largest (1.9–7.2 cm × 1.8–5.1 cm; mean surface area 6,036 mm²) and the most deeply lobed, those on short shoots smaller (2.0–6.0 cm × 1.5–3.2 cm; 6,021 mm²) and those on flowering shoots smaller still (1.3–5.7 cm × 0.9–5.0 cm; 4,267 mm²) and with one or two pairs of lobes or rarely none (Dau, 1941; Figure 1); main veins straight or curved forwards towards leaf tip (curved backwards in *C. monogyna*); leaf base cuneate or rounded, apex acuminate; petiole 6–20 mm; stipules conspicuous on long shoots, leaf-like, 5–10 mm × 1–3 mm, acuminate, unequally incise-serrate.

Flowers usually on short shoots, less commonly on main shoots; in lax 3- to 11-flowered corymbs (up to 16 in *C. monogyna*), 2.5–5.0 cm wide, pedicels 6–30 mm, glabrous or rarely sparsely villous (pubescent in *C. monogyna*); bracts 1.0–5.3 mm × 0.2–0.5 mm, 6–13 times as long as wide, denticulate at margin with 3–16 teeth, caducous; flowers hermaphrodite 15–18 mm in diameter; sepals 5, 0.9–2.8 mm × 1.4–2.6 mm, entire, broadly triangular, as wide as long, margin entire, apex acute; petals 5, white or pale pink with striate papillae,

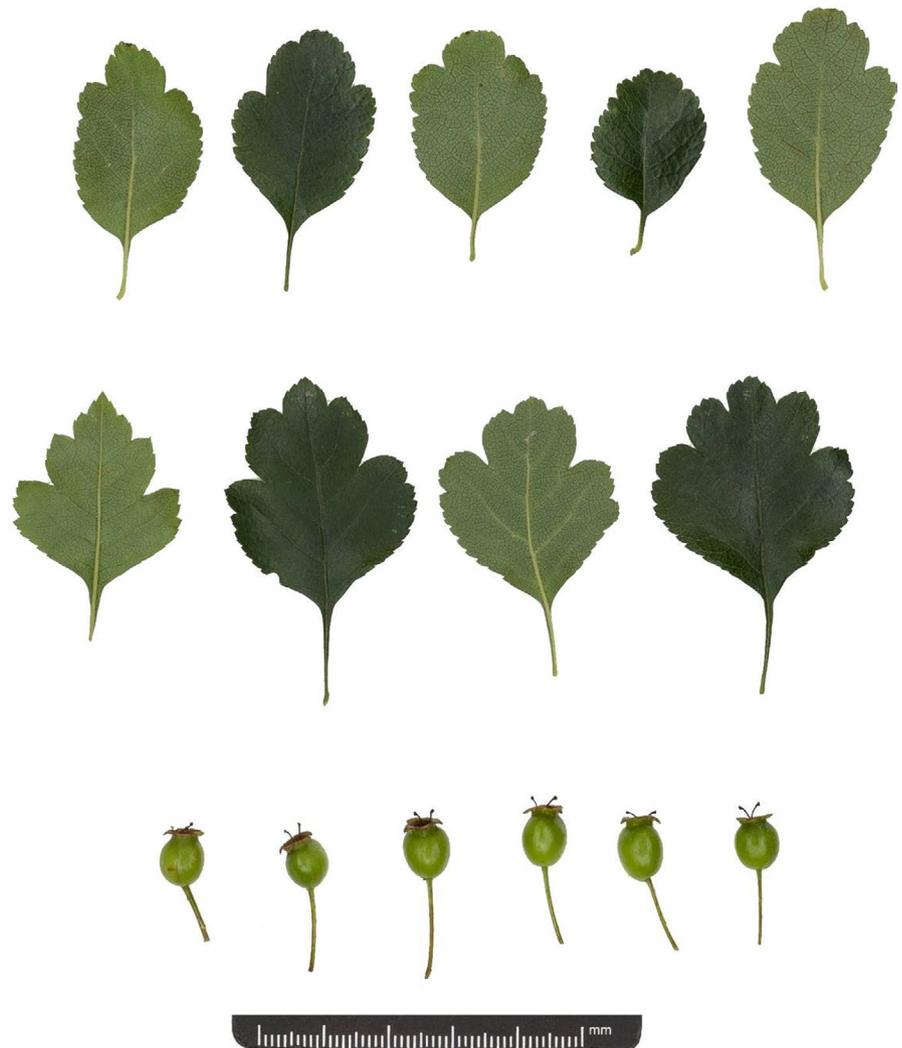


FIGURE 1 Leaves of *Crataegus laevigata* from (top) short shoots and (middle) long shoots. Pale leaves are the underside and darker leaves are the tops of leaves. The bottom row shows unripe fruit each with two styles

5–10 mm × 5–9 mm; hypanthium 3–4 mm, glabrous, rarely villous; stamens 17–22, filaments pale, anthers pink rarely purple; styles mostly 2 but rarely 1 or 3 or even 5 in some flowers (usually 1, occasionally 2 in *C. monogyna*), stigmas yellow. Fruit a subglobose or ellipsoid pome (6)8– to 10(14)-mm diameter, 6- to 12-mm long with a volume of 1.60 cm³, compared to 0.73 cm³ in *C. monogyna* (Eriksson & Ehrlén, 1991), deep red, usually glabrous, without basal protuberances, crowned with persistent recurved or spreading sepals, flesh yellowish. Stones (pyrenes) mostly 2 but matching style number, dorsally and ventro-laterally sulcate, c. 5- to 6-mm long. Williams (1988) noted a slight difference in stone shape between species with *C. monogyna* having a pointed apex and *C. laevigata* with a blunter end probably due to differences in style and stone number. Morphological details compiled from Christensen (1992), Clapham et al. (1987), Dau (1941), Depypere et al. (2006), Sell and Murrell (2014) and Stace (2019).

Crataegus contains 140–265 or even up to 1,200 species (Christensen, 1992), the variability caused by interpreting the effects of extensive hybridisation, apomixis and polyploidy (Dickinson & Campbell, 1991). The genus occurs throughout the temperate areas of the northern hemisphere, but particularly in North America (Fineschi, Salvini, Turchini, Pastorelli, & Vendramin, 2005; Lo, Stefanović, & Dickinson, 2007).

Crataegus laevigata and *C. monogyna* were originally treated as one species, *C. oxyacantha*, by Linnaeus (Clos, 1890). Indeed, nearly all the glabrous or slightly pubescent species in Europe have been called *C. oxyacantha* by regional authors as an aggregate term (Allen, 1981), so that references in the literature can be very confused. As proposed by Byatt (1974), the name *C. oxyacantha* has been formally rejected as ambiguous. The first British Flora in which *Crataegus laevigata* and *C. monogyna* were separated was by Babington (1843), who gave them as varieties but suggested that they might not improbably be distinct species (Pearman, 2017).

In western Europe, *Crataegus laevigata* and *C. monogyna* show low levels of genetic diversity compared to other genera in the Rosaceae based on chloroplast DNA markers (Fineschi et al., 2005). This appears to be because of the four haplotypes identified in the two species, one haplotype was very common in both species with a frequency of 0.75 in *C. laevigata* and 0.85 in *C. monogyna* across the whole geographical range where the two species co-occur. This is commensurate with effective long-range dispersal of seeds by animals and introgression between the two species (introgression ratio 0.83 which will be 1 when the two species are fully introgressed and become in effect one species). Population genetic differentiation based on chloroplast DNA has been found to be higher in *C. laevigata* ($G_{ST} = 0.340$) than *C. monogyna* (0.242) suggesting lower gene flow between populations in the former presumably due to its more restricted habitat in ancient woodlands. Extensive sharing of haplotypes has resulted in a lack of geographic structure, although the most polymorphic populations are those located in central Europe (Fineschi et al., 2005).

Crataegus laevigata has two subspecies, although Sell and Murrell (2014) refer to these as varieties. Subspecies *laevigata* is commoner in the west of its range and in lowlands, and is thus dominant in Britain. It has leaves 15–35 mm, sparsely pubescent or almost glabrous, without

hairs in vein-axils beneath; sepals broadly triangular, about as long as wide; hypanthium glabrous; fruit 8–10 mm, globose (Gosler, 1990; Sell & Murrell, 2014). Subspecies *palmstruchii* (Lindm.) P.D. Sell (*C. palmstruchii* Lindm.) is commoner in mountains and the east although it is sometimes found in Britain in planted hedges where it stands out due to its larger fruits and leaves. It is characterised by leaves 30–50 mm, more densely pubescent on the veins beneath and with tufts of hair in the vein-axils beneath; sepals nearly twice as long as wide; hypanthium hairy; fruit 10–14 mm × 13–15 mm, ellipsoid (do Amaral Franco, 1968; Sell & Murrell, 2014).

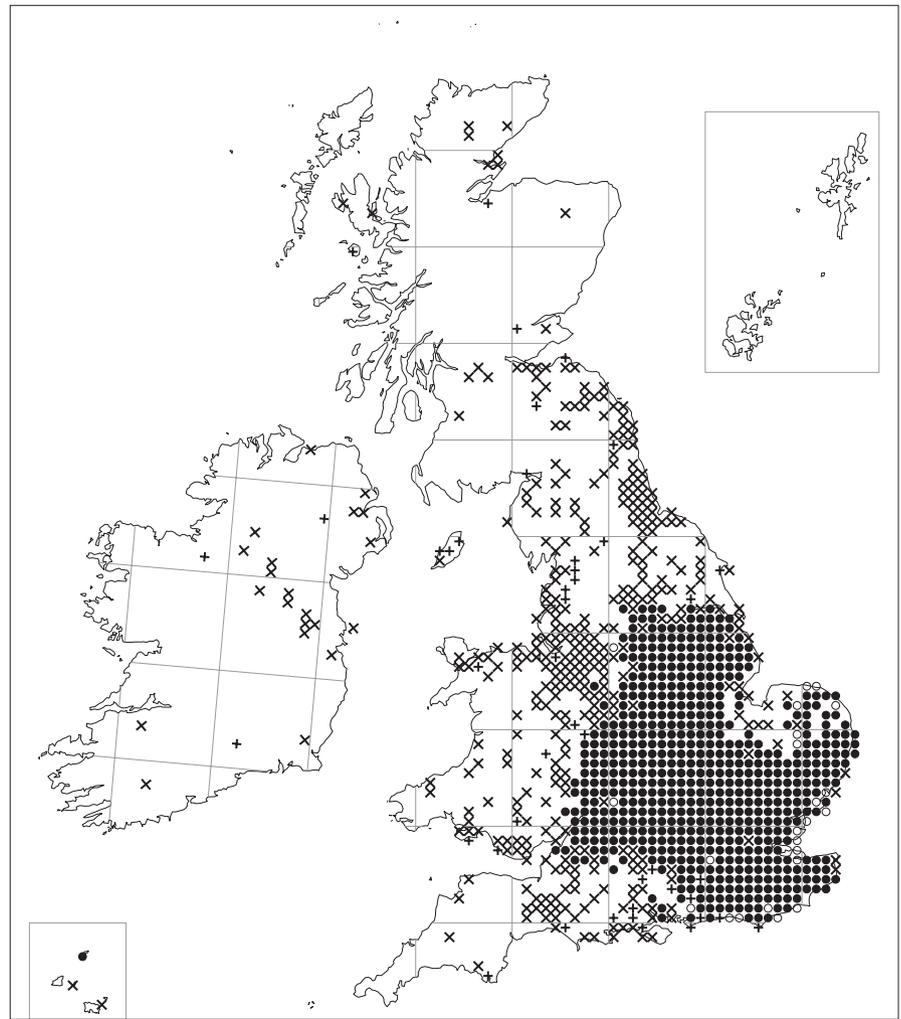
Numerous cultivars of *C. laevigata* and of its hybrid with *C. monogyna* (*C. × media*) have been produced, and most cultivars with pink or red flowers and/or double flowers belong here (Stace, 2019). Notable cultivars include *C. laevigata* 'Rosea Flore Pleno' (double pink flowers), 'Aurea' (yellow fruit, known since 1844; occasionally found in the wild as *C. laevigata* f. *aurea*), 'Auriculata' (large leaves and prominent stipules, known from before 1910) and 'Rosea' (found before 1796, single light pink flowers with white centre; occurs in the wild as *C. laevigata* f. *rosea*). Other cultivars include 'Paulii' (bright carmine flowers), 'Punicea' (flowers single, carmine red with a white centre), 'Candidoplena' and 'Plena' (double flowers, white), 'Gireoudii' (young leaves pink/ white marbled) and 'Xanthocarpa' (fruit yellow), and at least seven cultivars of *C. × media* exist and some of those listed above may in fact belong here (Bartha, 2014; Brown, 1959; Bujarska-Borkowska, 2006; Jablonski, 2017; Phipps et al., 2003; Seneta & Dolatowski, 2000). Notable is 'Paul's Scarlet' (also called 'Coccinea Plena') with double red flowers, which in Britain and North America is regarded as a cultivar of *C. laevigata* that originated as a branch sport in the mid-1880s from *C. laevigata* 'Rosea Flore Pleno' (Baghi et al., 2012; Hillier Nurseries, 2019; Percival & Fraser, 2001) while in mainland Europe it is regarded as *C. × media* 'Paul's Scarlet' (Jablonski, 2017; Schmidt, 2017). Given its reputed origin from 'Rosea Flore Pleno', it is regarded here as a cultivar of *C. laevigata*. Dau (1941) lists further varieties and forms.

Crataegus laevigata is native to Britain, more tolerant of shade than *C. monogyna*, and occurs primarily in ancient woods, wood-borders, old hedgerows and boundary banks on clay soils. It has, however, been extensively planted outside its native range and habitats (Stace et al., 2015).

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

The Midland hawthorn has a more restricted range than *Crataegus monogyna* in the British Isles (Fichtner & Wissemann, 2021) and is most abundant in the south and east of England, occurring naturally up to the Midlands (Figure 2). Its native range extends from Kent, Norfolk and Lincolnshire westwards to Hants (but absent from the New Forest; Brewis et al., 1996), Somerset, Gloucester and into Wales in Gwent and Glamorgan. Further north it is classified as a scattered native in ancient field hedges in Shropshire (Lockton & Whild, 2015) but a rare neophyte in Staffordshire, to the west of the accepted

FIGURE 2 The distribution of *Crataegus laevigata* 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; (x) 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



natural range (Hawksford et al., 2011). Hill, Preston, and Roy (2004) recorded *C. laevigata* as occurring in 597 (21%) of 10-km squares in Great Britain, and 1 square (7%) in the Channel Islands. According to Rackham (2003), the highest ratio of *C. laevigata* to *C. monogyna* (Section 5.2) is to be found on heavy soils in Cambridgeshire, north-west Essex and southwest Suffolk, and 'the best populations' in Britain were to be found in Rivenhall Woods on clay soil in mid-Essex.

Occasional records in Scotland are undoubtedly planted. Druce (1917) found plants near Kirriemuir in Angus in eastern Scotland but recorded that although they were of a good size they 'had the appearance of being planted'. In Ireland it is possible that *C. laevigata* is now an extinct native but it is most likely to be an introduction (Figure 2; Section 10).

Crataegus laevigata is native to western and central Europe as far east as the Czech Republic and Hungary and is almost certainly native in Romania and Ukraine (Figure 3). In the north it extends to southern Sweden, Latvia and Estonia, and in the south into the Pyrenees of Spain and into Italy, most likely including Sicily (Christensen, 1984). It is classified by Preston and Hill (1997) as having a European Temperate range. It is most widespread in the northern central part of its range including Poland (Bujarska-Borkowska, 2006; Oklejewicz et al., 2014) becoming less common at the edges of its range so that it is quite

rare, for example, in Belgium (Depypere et al., 2006). It is an introduced plant in coastal Norway (Gostyńska-Jakuszczyńska & Hrabětová-Uhrová, 1983) and is absent from Greece (Dimopoulos et al., 2016), although Hayek (1927) listed *C. oxyacantha* as one of the parents of *C. x media* (and thus seems to indicate this is *C. laevigata*) and stated that it was then present in Greece and the Aegean Islands.

North American *Crataegus* species were introduced into Europe at an early date (Emerson, 1875) and *C. laevigata* was taken to North America by early European colonists primarily as a hedging plant, where it has rarely become naturalised (Hobbs & Foster, 1990). A naturalised record exists from the Gulf Islands of Washington in North America (Lo et al., 2007; Phipps, 1998) as well as in Canada and eastern United States (Dirr, 1982). *Crataegus laevigata* was introduced into Tasmania and other parts of Australia in the 1800s where it was used for hedging and it now grows naturalised in Victoria, Tasmania, the Adelaide Hills and the tablelands of New South Wales (Lasseigne & Blazich, 2019) and has been declared an injurious weed in a number of Australian states. It has also been reported from Japan, New Zealand, Tanzania and West Africa (Discoverlife, 2020). In India, introduced *C. laevigata* is found in the temperate Himalayas, Kashmir and Himachal Pradesh, at an altitude of 1,800–3,000 m (Lasseigne & Blazich, 2019).

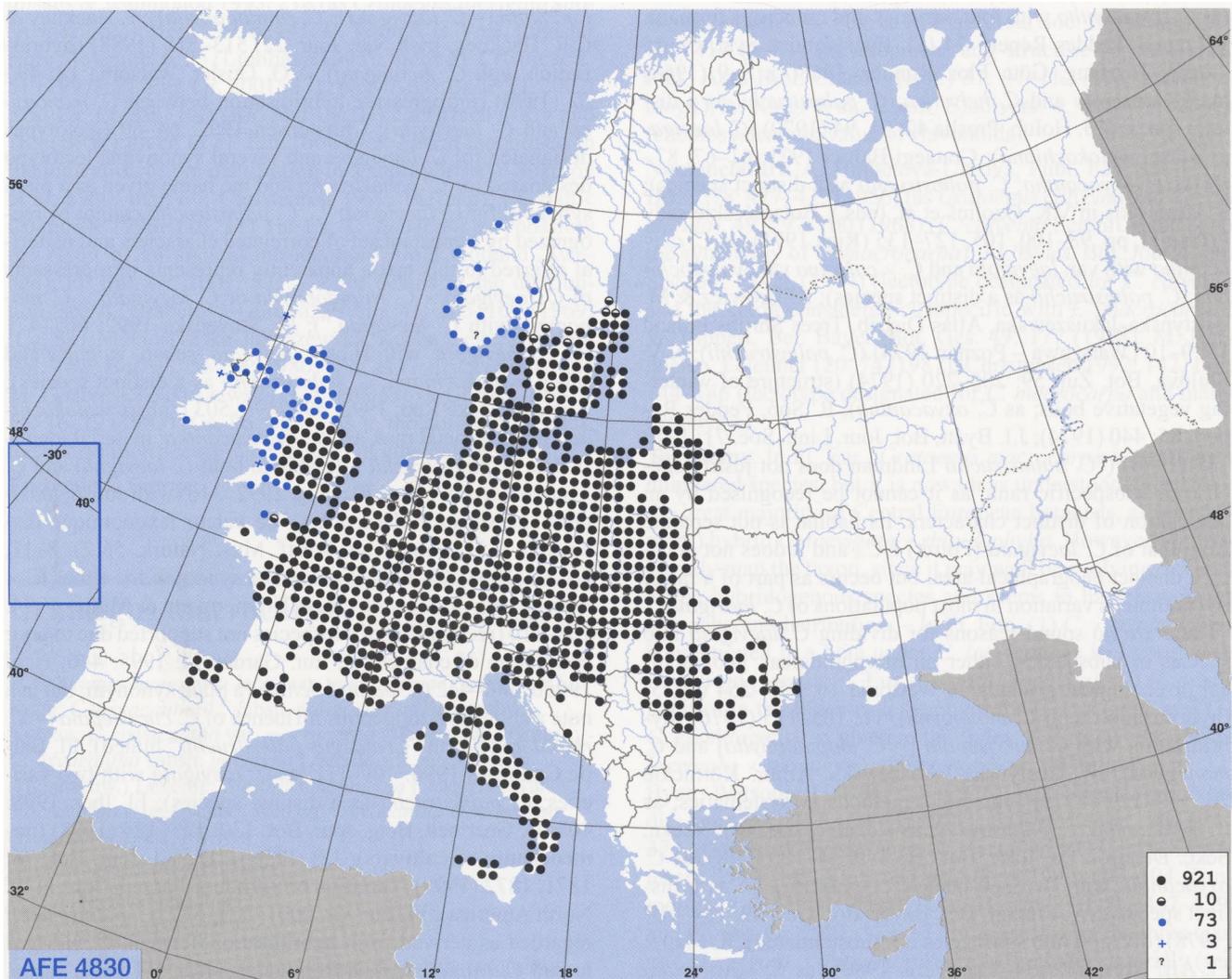


FIGURE 3 Distribution of *Crataegus laevigata* in Europe. Black circles indicate where it is considered native, blue circles where it is introduced. Half-filled circles indicate unknown or uncertain status; + extinct introduction; ? uncertain identification and/or locality. Reproduced from Kurtto et al. (2013), by permission of the Vanamo Biological Society, Helsinki

The altitudinal limit in Europe varies from sea level in the west (Christensen, 1992), reaching 810 m in the Polish Sudetes (Boratyński, 1991; Kosiński, 2007), 860 m in the Eastern Polish Carpathians (Oklejewicz et al., 2014), 785 m in the Czech Republic, 956 m in Slovenia, rising to 1,281 m in the Tatra Mountains in Poland (Gostyńska-Jakuszewska & Hrabětová-Uhrová, 1983; Oklejewicz et al., 2014) and to 1,560 m at Piano Ruggio (Potenza) in Italy (Acta Plantarum, 2020). In comparison, *C. monogyna* reaches over 2,000 m in the Iberian Peninsula (Fichtner & Wissemann, 2021).

2 | HABITAT

2.1 | Climatic and topographical limitations

Crataegus laevigata is a subatlantic species (Christensen, 1992) preferring a cool temperate climate (Humphries & Bradshaw, 1977). Climatic means in Britain correspond to a January mean temperature

of 3.5°C (similar to *C. monogyna*) and July mean temperature of 16.2°C, slightly warmer than for *C. monogyna* (14.7°C), and an annual precipitation 674 mm, drier than *C. monogyna* (1,073 mm; Hill et al., 2004). This is a reflection of the main distribution of *C. laevigata* being in the warmer and drier southeast.

Topography appears to have little direct effect on *C. laevigata* in Britain. In the Polish Carpathians, Oklejewicz et al. (2014) found that *C. laevigata* was less common on north-western slopes than on other aspects, and in the Polish western Sudetes above 500 m it grows primarily on southern exposures (Boratyński, 1991; Kosiński, 2007). However, in the Silesian Foothills, where *C. laevigata* occurred on the greatest number of sites investigated, and lower slopes of the western Sudetes, it was found on slopes of all aspects. In other regions *C. laevigata* occurred at fewer sites and its presence on slopes of different aspect appeared to be random. Slope angle appears unimportant since Gostyńska-Jakuszewska and Hrabětová-Uhrová (1983) record *C. laevigata* in ravines, on the slopes of river valleys, and on escarpments and mountain sides in Poland.

2.2 | Substratum

Crataegus laevigata will grow on a wide range of soils, including siliceous (Clos, 1890) and moderately acid soils (Christensen, 1992). Humphries and Bradshaw (1977) noted that when planted on derelict land material, *C. laevigata* is tolerant of the range of soil acidity including alkaline materials, and will tolerate a range of soil moisture. However, within its natural range, *C. laevigata* is most common on loam and clay soils, particularly where heavy (Clapham et al., 1987; Rackham, 2003). This tends to restrict it to the clay soils of the English midlands and the Weald of southeast England but avoiding clay with flints (Byatt, 1975). It is also largely absent from the surrounding chalk, oolitic and limestone soils (Gosler, 1990). This is reflected in the pH Ellenberg indicator value for Britain of 7, indicative of weakly acid to weakly basic conditions and not on very acid or basic soils (Hill et al., 2004).

3 | COMMUNITIES

Crataegus laevigata is an ancient woodland indicator species in central-southern and southeast England, including East Anglia but not the southwest of Dorset or Avon (Rose, 1999). The Midland hawthorn is a member of W8 *Fraxinus excelsior*–*Acer campestre*–*Mercurialis perennis* woodland on calcareous mull soils mixed with the more abundant *Corylus avellana* (Rodwell, 1991). Particularly good examples can be found around Hatfield Forest, Essex (Rackham, 2003). In the northwest (such as the *Geranium robertianum* and the *Teucrium scorodonia* subcommunities), the hawthorn present tends to be *C. monogyna* but in the south-eastern subcommunities *C. laevigata* is the most frequent, particularly in the older, less disturbed stands. This includes the *Deschampsia cespitosa* subcommunity and south-eastern examples of the *Anemone nemorosa* subcommunity. Nevertheless, *C. laevigata* is still infrequent and of low abundance, scattered among the more dominant *Corylus avellana* and *Acer campestre*. It is rarely found in the *Hedera helix* subcommunity of the south probably because many of the sites tend to be recent secondary stands with *C. monogyna* instead.

Midland hawthorn is also an infrequent member on the lower base-status soils of W10 *Quercus robur*–*Pteridium aquilinum*–*Rubus fruticosus* woodland, mostly found in the older stands of the warmer and drier southeast in the *Anemone nemorosa* subcommunity, and more rarely in the *Hedera helix* subcommunity where, again, it tends to be replaced by *C. monogyna* (Rodwell, 1991).

On base-rich soils in the southeast, *C. laevigata* is a very rare component of W21 *Crataegus monogyna*–*Hedera helix* scrub, mainly because this community is mostly seral in nature. Midland hawthorn is most likely to occur close to long-established woodlands in the *Mercurialis perennis* subcommunity (Rodwell, 1991).

Wetter fen peat in alder carr may also very occasionally support *C. laevigata* (Wheeler, 1980), specifically, W5 *Alnus glutinosa*–*Carex paniculata* woodland may occasionally include *C. monogyna* and very rarely *C. laevigata* (Rodwell, 1991).

While *C. monogyna* invades more open habitats such as southerly calcicolous grasslands (Rodwell, 1992) and is found as occasional saplings in SD18 *Hippophae rhamnoides* dune scrub (Rodwell, 2000), *C. laevigata* is always absent from these. However, it can persist in old hedges (particularly where the hedge is a remnant of former woodland or part of a parish boundary) such as around Monks Wood, Cambridgeshire in association with *Corylus avellana*, *Cornus sanguinea*, *Acer campestre*, *Sorbus torminalis* and *Euonymus europaeus*, and herbs characteristic of old hedges such as *Hyacinthoides non-scripta* and *Anemone nemorosa*, and to a lesser extent *Mercurialis perennis* (Pollard, 1973; Tallowin, 1970).

In mainland Europe, *C. laevigata* is often present but not dominant in pedunculate oak–hornbeam forest and in Lowland beech forest of southern Scandinavia and north-central Europe (San-Miguel-Ayanz et al., 2016). In Dalby Söderskog, southern Sweden, *C. laevigata* forms a shrub layer with *Corylus avellana* and saplings of *Fraxinus excelsior* and *Ulmus glabra* under a canopy of *Quercus robur*, *Fraxinus excelsior* and elm with some invasion of *Acer platanoides* (Leemans, 1992). Hazel and hawthorn have been decreasing since 1916 as secondary succession has progressed.

In Poland, *C. laevigata* grows in open mixed-deciduous woodland, usually hornbeam-beech or beech of the class *Querco*–*Fageteta* and occurs usually in communities of the orders *Fagetalia* and *Quercetalia pubescentis* (Oberdorfer, 1949). But it also occurs singly or in small clumps in oak–hornbeam or oak–elm forests, and in marshy meadows with willows and poplars. It is also frequent on the edges and rides of undisturbed forests and in more open habitats such as xerophilous scrub on hills, ravines and river valleys and up onto mountain sides (Gostyńska-Jakuszevska & Hrabětová-Uhrová, 1983; Oklejewicz et al., 2014). In the Czech Republic and Slovakia, it is found in similar communities but is seldom in deep woodland shade. As such it is found only in thinned *Querco*–*Carpinetum*, an association of the *Quercion pubescentis*, usually as sterile trees (Gostyńska-Jakuszevska & Hrabětová-Uhrová, 1983).

4 | RESPONSE TO BIOTIC FACTORS

Crataegus laevigata is more tolerant of shade than *C. monogyna*, and in undisturbed woodland *C. laevigata* will dominate. It will also dominate in the deep shade of overgrown coppice (Rodwell, 1991). But if disturbance allows in more light, or woodland is left as a hedgerow remnant, then *C. monogyna* and the hybrid *C. × media* can rapidly colonise and *C. laevigata* decreases in frequency (Bradshaw, 2006; Peterken, 1976; Rackham, 2003). It is unclear whether this is due to biotic competition between the species, the unsuitability of environmental abiotic conditions for *C. laevigata*, or both. This is further muddied by the introgression between the two species (Section 8.2) reducing the frequency of pure *C. laevigata*.

In the understorey of old woodlands, *C. laevigata* coppices well (Peterken, 1976) and can form large stools (Rackham, 1975). This, and its shade tolerance, favours *C. laevigata* and allows it to persist in a maintained coppice system (Byatt, 1975). *Crataegus laevigata* is

generally resistant to browsing. It is highly palatable to deer and livestock but only for a few weeks in spring before the spines harden (Rackham, 2003).

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

Crataegus laevigata is sometimes locally more frequent than *C. monogyna* in undisturbed woodlands (Clapham et al., 1987) but is nearly always found as isolated individuals in most of the communities in which it is found (Rackham, 2003), usually separated by many metres. In Poland, *C. laevigata* grows mostly as isolated individuals or in small groups (Gostyńska-Jakuszczyńska & Hrabětová-Uhrová, 1983), supported by detailed studies in the Polish Sudetes and the Carpathians (Kosiński, 2007; Oklejewicz et al., 2014).

5.2 | Performance in various habitats

As a shrub indicative of Ancient woodland (Rackham, 2003) it performs well in deep shade. Leemans (1992), modelling forest succession in southern Sweden, used a maximum leaf area index (LAI) of 2.1 for *C. laevigata* (similar to *Corylus avellana* but lower than all the forest trees used e.g. LAI 5.0 for *Fagus sylvatica*), suggesting that it copes with shade by forming fewer layers of leaves than canopy trees and can approach a monolayer. Leemans (1992) also used a maximum growth rate of 0.60 m/year (fairly high compared to other species modelled: 0.47 m/year in *Acer platanoides* to 0.75 m/year in *Fraxinus excelsior*). Rahman et al. (2015) planted *Crataegus laevigata* 'Paul's Scarlet' in the harsher conditions of urban streets of Manchester and monitored it for 6 years after planting. They showed a rate of growth of c. 0.3 m in height, 0.6 cm in DBH and a 20 cm increase in crown diameter. During this time it sequestered c. 140 kg CO₂ per tree, corresponding to 38 kg C (Rahman et al., 2015). These growth parameters were not significantly different from that of the other four species used: *Sorbus arnoldiana* 'Schouten', *Prunus* 'Umineko', *Pyrus calleryana* and *Malus* 'Rudolph', all commonly planted in urban areas. However, LAI (c. 2.7 in May and 2.4 in July) was significantly higher in *C. laevigata* than *Sorbus*, *Prunus* and *Malus* (Rahman et al., 2015) suggesting that *C. laevigata* can be plastic in its response to open conditions.

In open habitats of hedge and scrub in southeast England, fruit production was significantly poorer in *C. laevigata* (a mean of 0.5 on a scale of 0 no fruit and 5 heavily fruiting) than in *C. monogyna* (4.07). However, *C. monogyna* showed a significant reduction in fruit production in woodland (3.36) while *C. laevigata* fruited significantly better in woodland (3.28) than in the open. In both woodland and open habitats, fruit production of the hybrid was intermediate to the two parental species (Gosler, 1990). The fruiting of both species, but particularly *C. laevigata*, was reduced with increasing herbivore damage to the leaves. Gosler (1990) concluded

that *C. laevigata*, being adapted to the lower insect diversity of woodlands, had evolved fewer defences against herbivory than *C. monogyna*.

Van Hooff (1983) suggested, perhaps unsurprisingly, that the presence of *C. laevigata* litter has a positive effect on earthworm *Lumbricus terrestris* numbers compared to beech litter since the latter is less readily attacked by micro-organisms and therefore less palatable to earthworms.

5.3 | Effect of frost, drought, etc

Despite the woodland habitat and heavy soils of *C. laevigata*, it is likely to be periodically exposed to drought, and may be susceptible when it is. Glenz et al. (2006) list *C. laevigata* as having a very low tolerance to flooding, similar to that of *Ilex aquifolium* and *Quercus petraea*, and is thus susceptible to winter waterlogging on clay soils.

Hill et al. (2004) stated that *C. laevigata* is intolerant of saline sites, and so similar to *C. monogyna*. However, Percival and Fraser (2001) found that *C. laevigata* 'Paul's Scarlet' was the most tolerant species to salt damage (by dipping leaves into salt solutions up to 9% salt.) of six *Crataegus* taxa tested, all common to urban areas (see Section 6.5). For *C. laevigata* no difference in chlorophyll fluorescence was found between salt solutions of 2%–9% (Fv/Fm, ratio of variable and maximum fluorescence, indicative of the quantum efficiency of Photosystem II, and thus a measure of stress) while other taxa showed a decline with increasing salt solution. Leaves were also frozen in a separate experiment: treatments began at 10°C, and leaves were chilled at 2°C/hr, frozen to a set temperature for 4 hr and then warmed at the same rate back to 10°C. The Fv/Fm ratio was significantly higher (indicating the plants were under less stress) than controls when leaves were frozen at –1 and –3°C, simulating a light and 'standard' frost (Fv/Fm 0.797, 0.810 respectively) but lower at –7°C (0.566). *Crataegus laevigata* was classified as comparatively sensitive to frost compared to the other taxa tested.

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

When grown together in the shaded conditions of a woodland or coppice, the two species of *Crataegus* native to Britain respond with a different morphology. *Crataegus laevigata* produces spreading branches near to the ground with its leaves in a monolayer in response to the low light levels. By contrast, *C. monogyna* grows vertically with tall, thin stems into the woodland canopy, shedding its lower branches, and with leaves orientated in different directions like 'a lavatory brush chasing the light' (Bradshaw, 2006). In more open conditions, *C. laevigata* will produce a mix of long and short flowering shoots, and look more similar to *C. monogyna* (Fichtner & Wissemann, 2021). Leaf morphology is variable (see introductory paragraphs).

Crataegus laevigata tends to form large basal stools after coppicing, more so than *C. monogyna* (Rackham, 2003). A trunk up to 8 m in height and 75 cm DBH is the usual maximum (Sell & Murrell, 2014). The largest current individual of *C. laevigata* is recorded in Wojanow, Lower Silesia Province, Poland at 11 m height and 65.6 cm DBH. Several others taller than 7 m are known in the Czech Republic, Germany and Austria (Monumental Trees, 2020).

The roots of *C. laevigata* tend to be shallow and small in extent compared to the crown as befits a species growing in a woodland understorey. This makes it generally unsuitable for growing in avenues or roadsides as it is less wind-firm than other common urban species (Dau, 1941). The wood is similar to that of other *Crataegus* species and that of *Pyrus*, being reddish-white, diffuse porous and comparatively dense at 0.81–0.88 g/cm³ (Dau, 1941).

Stomata are present only on the lower leaf surface. Salisbury (1928) gave a mean stomatal density for British plants of 147/mm², with a range of 93–192/mm², in comparison in *C. monogyna* to a mean of 154 (range 93–225)/mm². However, more recent measurements yielded a mean of 108 ± 22.3/mm² (SD, range 92–168) for Worcestershire material and a mean 96 ± 20.5/mm² (SD, range 60–136) for west-central Polish material collected 33 km south of Kórnik.

6.2 | Mycorrhiza

Data on the mycorrhizal status of *C. laevigata* are scarce and mostly come from research conducted over 50 years ago. Based on these reports, Harley and Harley (1987) recognised *C. laevigata* as a species colonised by both arbuscular and ectomycorrhizal mycorrhiza fungi. This is supported by research by Dominik (1957, 1963) and Kovács and Szigetvári (2002) finding ectomycorrhizal fungi on *C. monogyna*. However, data from recent publications on the mycorrhizal status of trees (Brundrett & Tedersoo, 2019, 2020) suggest that trees of the genus *Crataegus* form only arbuscular mycorrhiza, and the authors state that the relationship of *Crataegus* with ectomycorrhizal fungi should be regarded as an error. To add evidence to this, the mycorrhizal status of *C. laevigata* growing on two sites in Poland was investigated. The colonization of the roots by arbuscular fungi was confirmed by observing the occurrence of hyphae, appressoria, and vesicles (Figure 4). No ectomycorrhizas were found in the analysed samples although this does not rule out ectomycorrhizal

fungi elsewhere. Fine roots of *C. laevigata* were also colonised by dark septate endophytes.

6.3 | Perennation: Reproduction

Crataegus laevigata is normally a non-clonal phanerophyte (Hill et al., 2004) although it may occasionally spread locally by the layering of branches. For all practical purposes, spread is primarily by seed. Flowering starts at around 15 years of age, or 15 years after coppicing, similar to *C. monogyna* (Gosler, 1990). *Crataegus* species in general are easily propagated by grafting and budding (Bonner & Karrfalt, 2008). As with *C. monogyna*, *C. laevigata* lives for more than a century (Gosler, 1990). However, the oldest known *C. laevigata* trees, in Nový Oldřichov, Czech Republic and in Alsfeld, Germany, are 170 ± 20 years old, compared to a 670-year-old *C. monogyna* at Bouquetot, France (Monumental Trees, 2020).

6.4 | Chromosomes

$2n = 34$ (Stace, 2019). There is no evidence of polyploidy in Europe (Gladkova, 1968; Talent & Dickinson, 2005) but a tetraploid has been recorded from Washington State, USA (Lo et al., 2007). The hybrid between *C. laevigata* and *C. monogyna* (Section 8.2) has the same number of chromosomes as *C. laevigata* (Stace, 2019).

Diploid genome size (2C DNA) has been measured at 1.40 ± 0.13 pg which is at the lower end of the world-wide list of hawthorns and medlars studied (range 1.4–1.65 pg, midpoint 1.525 pg) and smaller than that of *C. monogyna* which ranges from 1.46 to 2.17 pg (Talent & Dickinson, 2005). Length of chromosomes is 0.6–1.1 µm in *C. laevigata*, shorter than in *C. monogyna* at 1.1–1.7 µm (Ptak, 1986).

6.5 | Physiological data

The Ellenberg indicator value in Britain for light is 5 for *C. laevigata*, indicating a semi-shade plant, rarely in full light, but generally with more than 10% relative illumination when trees are in leaf, compared to 6 in the more light-demanding *C. monogyna* (Hill et al., 2004). This matches the light compensation point which was calculated by

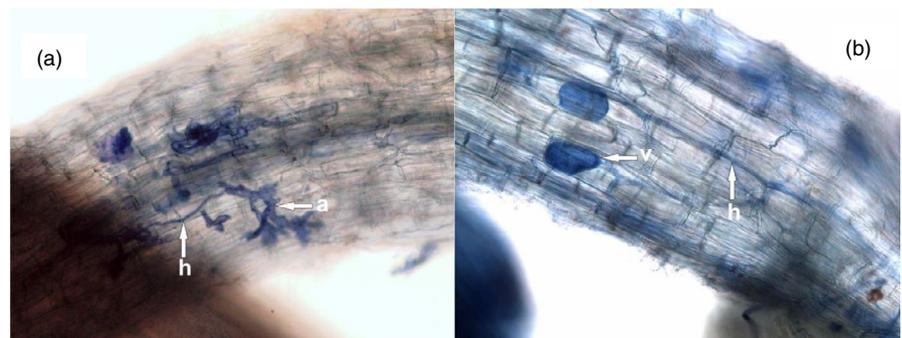


FIGURE 4 Arbuscular fungi in the roots of *Crataegus laevigata* showing (a) an appressorium and (b) vesicles (h – hyphae; a – appressorium; v – vesicles). Photographs by Tomasz Leski

Leemans (1992) to be $46.3 \mu\text{mol m}^{-2} \text{s}^{-1}$, similar to *Quercus robur* and *Acer platanoides* but higher than *Fagus sylvatica*, *Corylus avellana* and *Ulmus* sp. Chlorophyll amounts measured in southwest Slovakia in July and August were: chlorophyll *a* 7.99–8.10 g/kg dry wt, chlorophyll *b* 2.43–2.97 g/kg, with a ratio of 2.69–3.38 (Masarovičová & Eliáš, 1981). Total chlorophyll was the lowest of the eight shrubs tested from oak-hornbeam forest (e.g. chlorophyll *a* and *b*, were 11.54 and 4.34 g/kg, respectively, in *Cornus mas*). However, when calculated per unit of leaf area, this amounted to chlorophyll *a* 0.30–0.33 g/m² and chlorophyll *b* of 0.10–0.11 g/m² for *C. laevigata* which was very similar to that of the other eight species tested (*Prunus avium*, *Cornus mas*, *Euonymus europaeus*, *E. verrucosus*, *Hedera helix*, *Ligustrum vulgare*, *Sorbus torminalis* and *Ulmus campestris*) tested under forest understorey conditions (Masarovičová & Eliáš, 1981). This was explained by the correlation of chlorophyll amount with leaf mesophyll structure such as thickness of the palisade and spongy parenchyma, and chloroplast number (Masarovičová & Eliáš, 1981). Similar figures for total chlorophyll content were measured in *C. laevigata* 'Paul's Scarlet' which were c. 29 mmol/cm² in May increasing to 38 mmol/cm² in July with a ratio of chlorophyll *a*:*b* of c. 3.6 in May reducing to c. 2.8 in August (Rahman et al., 2015). This was similar to other species tested growing in urban conditions.

The net photosynthesis rate (NPR) of *Crataegus* sp. in Michigan, USA was c. $7.0 \mu\text{mol m}^{-1} \text{s}^{-1}$, similar to *Cornus racemosa* and *Juglans nigra* and significantly lower than *Prunus serotina* and *Elaeagnus umbellata* ($9.7 \mu\text{mol m}^{-1} \text{s}^{-1}$). Hawthorn exhibited lower NPR rates at higher light fluxes, but was able to fix carbon more efficiently than all other species, except *C. racemosa* (Ritsema & Dornbos II, 2006). These data suggest that while hawthorn has a significant competitive advantage in low to moderate light fluxes, it may be inferior in environments where high levels of light are able to penetrate the leaf canopy. In an *in vitro* study, the growth of *Crataegus laevigata* 'Paul's Scarlet' (recorded as *C. oxyacantha* cv. Paul's Scarlet) was modified by altering either the spectral quality or the level of irradiance received by shoot cultures, which were otherwise maintained under uniform medium and plant growth regulator (PGR) conditions. In such conditions, 'Paul's Scarlet' shoots were tolerant of a wide range of irradiances and only shoot extension was inhibited at the highest level tested, while leaf chlorophyll content was unaffected (Marks & Simpson, 1999).

The Ellenberg indicator values in Britain for soil moisture is 5, indicating that it prefers soils of average dampness, which is similar to many other plants (Hill et al., 2004). *Crataegus laevigata* 'Paul's Scarlet' planted in urban streets of Manchester had a mean mid-day leaf water potential of c. -1.7 MPa in May and -1.5 MPa in July, and stomatal conductance of c. 180 and 230 mmol H₂O m⁻² s⁻¹ in May and July, respectively, which were relatively low compared to other species tested. Despite this, the high LAI of 'Paul's Scarlet' compared to the other trees in this study (LAI 2.1, see Section 5.2) led to high evapotranspirational cooling such that the energy loss for *C. laevigata* was c. 240 W/m^2 per tree. This was significantly lower than for *Pyrus calleryana* (c. 460 W/m^2) but higher than the other two species tested (Rahman et al., 2015).

The Ellenberg indicator value in Britain for soil nitrogen availability is 5, indicative of sites of intermediate fertility (Hill et al., 2004), so slightly less fertile soils than required by *C. monogyna* (6). Kopinga and van den Burg (1995) measured N and P concentrations in leaves of *C. laevigata* growing under different conditions in the Netherlands and considered N to be deficient at 15–18 g/kg dry mass and normal at 19–22 g/kg. Similarly, P was considered deficient at 1.2–1.5 g/kg and normal at 1.4–1.6 g/kg. These are similar levels to those in *C. monogyna* but lower than many trees planted in urban areas, so they concluded that *C. laevigata* is undemanding in its nutrient requirements. Rahman et al. (2015) measured nutrient concentrations in leaves: N 2.32%, P 0.21% K 1.03%, Ca 2.32%, Mg 0.21%, Al 45.30 µg/g, B 31.20 µg/g, Co 0.60 µg/g, Cu 7.00 µg/g, Fe 136.40 µg/g, Mn 26.80 µg/g, Mo 0.50 µg/g, Na 238.30 µg/g, Ni 1.70 µg/g and Zn 27.20 µg/g. Chapman (1931) measured metal concentrations equivalent to 0.20 mg/L of MnO and 12.3 mg/L of Fe₂O₃ in the sap extracted from *C. laevigata* wood.

Crataegus laevigata accumulates heavy metals in its roots and leaves at concentrations comparable to other shrubs planted on contaminated soil in Russia (*Berberis vulgaris*, *Sambucus racemosa* and *Rosa cinnamomea*): Cu 84.2/100.2 mg/kg (leaves/roots); Ni 10.5/11.3 mg/kg; Zn 64.2/112.5 mg/kg; Pb 2.35/7.36 mg/kg; Cd 0.13/3.07 mg/kg (Timofeeva et al., 2017).

6.6 | Biochemical data

Total phenolic content of *Crataegus laevigata* (1,288 mg/100 g fresh mass) and total phenolic acids (964 mg/100 g) were similar to *C. monogyna* and higher than seven other shrub species tested, and was thought to make them more attractive to birds (Witczak et al., 2014). Karar and Kuhnert (2015) investigated the phenolic compounds in *C. laevigata* and listed 54 compounds found in leaves and 47 in flowers (compared to 38 and 41, respectively, in *C. monogyna*). The identified compounds included chlorogenic acids and other phenolic acids, proanthocyanidins, flavonoid glycosides, flavonoid aglycones and their derivatives. Phenolic concentration and antioxidant activity is usually higher in buds than in shoots but is significantly affected by phenological stage and sampling location (Feroli et al., 2020).

The phenolic chlorogenic acid has been found in the fruit and leaves of all hawthorn species investigated including *C. laevigata* (Liu, 2012), and the related caffeic acid was found in the leaves of *C. laevigata* by Svedström et al. (2006). Ursolic and oleanolic acids are also prominent. Total flavonoid content was found to range between 3 and 19 g/kg dry mass (mean 12 g/kg) in the flowering tops (flowers and leaves) of 150 samples of wild European hawthorn belonging to *C. monogyna*, *C. laevigata* and their hybrids (Peschel et al., 2008). Total flavonoids in leaves, involved in protection from herbivory, have been measured at 245 mg/kg dry mass, dominated by proanthocyanidins at 40.6 g/kg in *C. laevigata* from Slovenia (Škerget et al., 2005). The total flavonoid contents in flowers of *C. laevigata* was shown to be the highest of 10 *Crataegus* species tested (Mudge et al., 2016; Preedy & Watson, 2014). Comparable figures for

proanthocyanidins were reported from Finland (Svedström, Vuorela, Kostiaainen, Huovinen, et al., 2002; Svedström, Vuorela, Kostiaainen, Tuominen, et al., 2002) in leaves, 16 g/kg dry mass; flowers, 12 g/kg and fruit, 2 g/kg. In *C. laevigata*, other flavonoids include catechin, epicatechin, procyanidin B-2, rutin (0.3% dry mass), hyperoside (12.9%), vitexin (0.9%), isovitexin (2.5%), isoquercitrin (6.0%), quercetin (0.1–10.5 mg/g dry mass in flowers; 241 mg/kg in leaves) and apigenin (1.9–12.8 mg/g in flowers; 3.95 mg/kg dry mass in leaves; Lamaison & Carnat, 1990; Ringl et al., 2007; Škerget et al., 2005; Yang & Liu, 2012). Clear differences in flavonoid composition and concentration were found in leaves and flowers of 15 Eurasian and American *Crataegus* species but not in triterpenes (Khokhlova et al., 2020). Vitexin and its derivatives are of a higher concentration in the leaves of European species (*C. laevigata* and *C. monogyna*) while rutin (quercetin-3-O-rutinoside) is significantly more concentrated in the leaves of North American species (*C. douglasii* Lindl. and *C. okanaganensis*; J. B. Phipps & O'Kennon) leaves (Lund et al., 2020). Flavonoid glycosides and aglycones found in *C. monogyna*, *C. laevigata*, *C. pentagyna*, *C. nigra* and *C. azarolus* were identified as kaempferol-3-O-neohesperidoside, hyperoside (quercetin-3-O-galactoside), crataegide (quercetin-3'-O-arabinoside), spiraeoside (quercetin-4'-O-glucoside), rutin, quercetin-3-O-rhamnosylgalactoside, sexangularetin-3-O-glucoside, sexangularetin-3-O-neohesperidoside and sexangularetin-3-O-(6"-O-malonyl)- β -D-glucoside (Petereit & Nahstedt, 2005). The absence of the flavonoids isoorientin, orientin, 8-methoxykaempferol-3-O-glucoside and 4"-acetyl-vitexin-2"-O-rhamnoside from *C. laevigata* was thought by Prinz et al. (2007) to offer a diagnostic test for separating this species from *C. monogyna*.

Stress applied to 1-year-old *C. laevigata* seedlings in the form of drought (not watering pots for 10 days at 25°C and light at 400–1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) increased the levels of epicatechin and hyperoside but reduced the levels of acetyl-vitexin and vitexin. Cold stress (4°C for 10 days with controls at 25°C) increased levels of vitexin, epicatechin, hyperoside, quercetin and acetyl-vitexin; in the case of the last of these it almost doubled from 6.525 ± 0.482 to 12.130 ± 0.845 mg/g dry mass (*SD* assumed; Kirakosyan et al., 2003, 2004). Interestingly, stress by flooding (complete immersion of pots for 10 days) and simulated herbivory (cutting off half of each leaf) produced no such increases.

Total concentrations of medically active compounds (organic acid, phenolic acid, terpene and hydroxycinnamic acid) have been measured in *C. laevigata* at 6.1–7.5 mg/g in flowers and 3.6–8.9 mg/g in leaves (Lamaison & Carnat, 1990; Svedström et al., 2006).

The sesquiterpenes, caryophyllene and humulene, were identified in volatile organic compound emissions of *C. laevigata* 'Paul's Scarlet' from flowers (15.1 and 4.4 ng $\text{C g}^{-1} \text{hr}^{-1}$ respectively) and from leaves after flowering (4.0 and 0.5 ng $\text{C g}^{-1} \text{hr}^{-1}$ respectively). This was 100–1,000 times less at flowering than in the other species tested (*Aesculus carnea*, *Gleditsia triacanthos* and a *Malus* species). A third sesquiterpene, farnesene, and the monoterpene limonene were also detected in emissions of *C. laevigata* after flowering (Baghi et al., 2012). By contrast, no alkaloids or saponins were detected in *C. laevigata*

by Dau (1941) but the pseudosaponin tormentosid was identified by Steinegger and Peters (1966). Crystals of oxalic acid are found in all parts of the plant, and in the leaves form 0.065% dry mass (Dau, 1941).

7 | PHENOLOGY

Flowering occurs in *Crataegus laevigata* from April to June, and more towards the end of this period at the north of its range in Sweden (Eriksson & Ehrlén, 1991). This gives the local name in southeast England of 'Whitsun rose' (Brown, 1959). The average start of flowering in the Netherlands was 17 May between 1940–1968 and 1 May between 2001–2010 (van Vliet et al., 2014). Flowers appear before the leaves are fully developed (Dau, 1941; Sell & Murrell, 2014) and earlier in shrubs than in trees. *Crataegus laevigata* comes into leaf earlier than *C. monogyna*, and into flower c. 8 to 14 days earlier (Lockton & Whild, 2015; Stace et al., 2015) but there is a 40% overlap in flowering time with *C. monogyna*, hence the hybrid between the two—see Section 8.2 (Stace et al., 2015). In Danish glasshouses, plants bloomed for 12 days with individual flowers lasting 8 days (Christoffersen & Brander, 1990). Fruit are present and can ripen from June to November (Christensen, 1992; Clapham et al., 1987; Dau, 1941) although this may be as late as mid-August to November in Sweden (Eriksson & Ehrlén, 1991). Fruit ripening occurs at the same time as in *C. monogyna*.

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Crataegus laevigata is hermaphroditic and flowers are readily produced even in shaded conditions (Rackham, 2003). There is no evidence of apomixis (Gosler, 1989). Flowers are protogynous, as in all *Crataegus* species. The anthers of the outermost stamens release pollen a day or two after the flower opens, and the filaments curve inwards on warm days so self-pollination appears possible (Dau, 1941). However, *C. laevigata* is largely self-incompatible, as are all *Crataegus* species. Bradshaw (1971) investigated the effect of hybridisation on fruit set and found that in a series of crosses between *C. laevigata* and *C. monogyna* (Section 8.2) that 30%–59% of flowers setting fruit resulted from inter- or intraspecific cross-pollination but self-pollination in only 2%.

In bright weather, the stamens spread wide and nectar is produced. Nectar concentration has been found to vary in *C. x media* in southern England from c. 10% sucrose by weight in the early morning (before 8 a.m.) to >50% through the main part of the day, with peaks of up to 80% sucrose as relative humidity increases towards evening and it is likely to be similar in *C. laevigata*. The cause behind this relationship is largely unknown but may be due to flower morphology influencing the internal microclimate. However, total sugar available per flower was highest in the early morning at c. 500–1,250 μg , dropping to c. 200 μg by mid-morning, staying constant into the

evening (Corbet et al., 1979). Pollination is by insects, particularly various species of Hymenoptera and Diptera (Gosler, 1990) that are attracted by the nectar and the unpleasant smell (to humans) of the flowers resulting from trimethylamine production, which is also present in the leaves (Dau, 1941).

The alfalfa leafcutter bee, *Megachile rotundata* (Fab.) has been seen to act as a pollinator in glasshouse trials in Denmark (Christoffersen & Brander, 1990). Bee-pollinated plants produced 269 fruits and control plants just one fruit, indicating the dependence on insect pollination for fruit production. Pollen of *C. laevigata* has high viability (96%–98%) and grains have a mean length of 36.5 µm, range 29–46 µm (Section 10; Byatt et al., 1977).

8.2 | Hybrids

The most common hybrid (Table 1) is between *Crataegus laevigata* and *C. monogyna*, producing *C. × media* Bechst. (*C. × ovalis* Kitt., *C. intermixta* (Wenzig) Beck) although Zaráš-Januszkiewicz (2008) suggest that the last is a hybrid between *C. monogyna* and *C. × macrocarpa*. Sell and Murrell (2014) regard it as a species in its own right (*C. media* Brechst.). The hybrid is formed where the range of the two species overlap and is intermediate in morphology to the parents (Bradshaw, 1971; Byatt, 1975; Williams, 1988) and in flavonoid content (Gosler, 1981). Both species are obligate outbreeders, inter-fertile and pollen of the hybrid shows no reduction in fertility (Bradshaw, 1971) and so there is high introgression (Bradshaw, 1953, 1971; Byatt, 1975). It thus seems that the natural barrier to hybridisation is spatial separation (Stace, 1975). In undisturbed woodlands hybridisation is usually low, but disturbance has allowed *C. monogyna* to spread more effectively into woodlands and woodland margins, facilitating hybridisation.

TABLE 1 Putative hybrids of *Crataegus laevigata* (= *C. l.*)

Parents	Hybrid	References
Hybrids with species of sect. <i>Crataegus</i>	Intrasectinal hybrids	
Hybrids with species of ser. <i>Crataegus</i>	Intraserial hybrids	
<i>C. l.</i> (Poir.) DC. × <i>C. monogyna</i> Jacq.	<i>C. × media</i> Bechst.	2, 3, 6, 7, 9
<i>C. l.</i> (Poir.) DC. × <i>C. rhipidophylla</i> Gand.	<i>C. × macrocarpa</i> Gand. s. str.	7, 8, 9
<i>C. l.</i> (Poir.) DC. × <i>C. lindmanii</i> Hrabětová	<i>C. × calycina</i> Peterm.	7
<i>C. l.</i> (Poir.) DC. × <i>C. microphylla</i> Koch	<i>C. × hafniensis</i> Christensen	5, 7
Hybrids with different genera	Intergeneric hybrid	
<i>C. l.</i> (Poir.) DC. × <i>Mespilus germanica</i> L. (= <i>Crataegus germanica</i> (L.) O. Kuntze)	× <i>Crataemespilus grandiflora</i> (Sm.) E.G. Camus	1, 4, 9, 10

Note: 1. Browicz (1970); 2. Bradshaw (1975); 3. Byatt (1975); 4. Byatt et al. (1977); 5. Jablonski (2017); 6. Lippert (1978); 7. Christensen (1992); 8. Oklejewicz et al. (2014); 9. Stace, Preston, and Pearman (2015); 10. Phipps (2016).

The hybrid is frequent across Europe throughout the native range of *C. laevigata* (Oklejewicz et al., 2013; Vakarelov & Tashev, 2007), often mixed with *C. laevigata* in woodlands and with *C. monogyna* or both parents in hedges (Stace et al., 2015). In southeast England in the former county of Middlesex, Williams (1988) noted that *C. monogyna* occurred in 213 hedges, *C. × media* in 134 and *C. laevigata* in 18 hedges. The hybrid also occurs in wooded riverbanks, dismantled railway lines, scrub and gravel-pits (Stace et al., 2015). It also appears to be favoured by coppicing and Gosler (1990) considered that when coppicing is abandoned, the hybrid drops in frequency over time.

In many places in Britain the hybrid is more frequent than *C. laevigata*, especially towards the edge of its native range in Hampshire (Brewis et al., 1996) and parts of North Wiltshire (Gillam, 1993) but even within the central area of its British range, as in parts of Essex (Jermyn, 1974). The hybrid can also be more abundant than either parent, and certainly more so than *C. laevigata*, in old hedges (James, 2009) but also in younger hedges from the Parliamentary Enclosures although in these it is likely to have been planted (Tarpey & Heath, 1990). In Ireland where *C. laevigata* was introduced after possible extinct (Section 10) the hybrid is frequent in old hedges, presumed to be from imported English nursery stock (Hackney & Hackney, 1988) and has spread from hedges into scrub on Umbra Dunes, Co. Londonderry.

The higher abundance of the hybrid may be due to it being better adapted to disturbed and changing habitats than *C. laevigata* (Depypere et al., 2006; Thomaes & Vander Mijnsbrugge, 2001). In southeast England, Byatt (1975) found that the hybrids on lighter soils were nearer to *C. monogyna* while the spread of morphology was much broader and included more *C. laevigata* characters on heavier soils. This may be due to *C. monogyna* being naturally more abundant on lighter soils and so being more available for backcrossing, and hybrids more resembling *C. laevigata* being out-competed due to less suitable environmental and soil conditions. So introgressed are the two species in southeast England that Byatt (1975) suggested that while pure *C. monogyna* can be found, pure *C. laevigata* has effectively ceased to exist, and the concept of the two species here is 'largely irrelevant' (Gosler, 1990). The hybrid is also frequent in mainland Europe, possibly also at the expense of *C. laevigata*. However, Byatt (1976) identified relatively pure populations of *C. laevigata* in large forests near Nancy, France, presumed to have survived due to the large size of the woodlands and lack of fragmentation.

Byatt (1975) found that a higher proportion of the hybrids are closer morphologically to *C. monogyna* than *C. laevigata*. In Britain, hybrids derived from *C. laevigata* subsp. *laevigata* and *C. monogyna* subsp. *nordica* have cuneate leaves, with three to five subacute, subentire lobes extending three quarters of the way to the midrib, almost straight main veins, flowers 10–14 mm in diameter, triangular-acute sepals 1.5–2 × 2 mm, villous hypanthium and 1–2 styles. Plants derived from *C. monogyna* subsp. *monogyna* differ in having leaves with the lobes extending not more than half-way to the midrib, serrulate in their apical half, flowers 12–16 mm in diameter, broadly triangular sepals and glabrous hypanthium (do Amaral Franco, 1968). In mainland Europe *C. × media* can be difficult to separate from *C. × macrocarpa* (Christensen, 1982).

Other accepted hybrids with *C. laevigata* are listed in Table 1. Some others, including several multiple hybrids have been suggested by Christensen (1982), Gostyńska-Jakuszczyńska and Hrabětová-Uhrová (1983), Oklejewicz et al. (2013), Bartha (2014) and Jablonski (2017) but their acceptance as valid nothospecies is questionable.

The intergeneric hybrid \times *Crataegospilus grandiflora* (Smith) Camus (Table 1) was regarded by Byatt et al. (1977), on the basis of the work by Smith (1805), as being a hybrid between *Crataegus laevigata* \times *Mespilus germanica*. If *Mespilus* were to be subsumed into *Crataegus* as *Crataegus germanica* (L.) O. Kuntze, as is recommended by Talent et al. (2008), this would become another *Crataegus* hybrid. The resulting hybrid is intermediate between the two parents. There are no reliable records of this from the wild but it is available as an ornamental from nurseries. Phipps (2016) states that mature small trees of this hybrid have been planted along suburban roads in Harborne, Birmingham. Pollen has a viability of c. 5% (Byatt et al., 1977) and so this hybrid is effectively infertile. Another intergeneric hybrid \times *Pyrocrataegus williei* Dan. (*C. laevigata* \times *Pyrus communis*) may also exist (Bartha, 2014).

A number of graft hybrids or chimeras have been produced by grafting *Mespilus germanica* onto *Crataegus laevigata* or *C. monogyna*, and utilising the chimera growth from the graft union. Two cultivars of +*Crataegospilus dardarii* Simon-Louis ex Bellair are known: 'Dardarii', with a morphology nearer to that of the medlar, and 'Jules d'Asnièresii', more similar to hawthorn (Byatt et al., 1977). Another graft hybrid, in which medlar was apparently grafted onto *C. laevigata* was described by Seeliger (1926) as +*Crataegospilus lungei*.

8.3 | Seed production and dispersal

The fruit of *C. laevigata* are usually larger than those of *C. monogyna* (see introductory section) and heavier. The mean fresh mass of fruit in Swedish *C. laevigata* was 0.817 ± 0.111 g (SD) compared to 0.476 ± 0.061 g in *C. monogyna* (Eriksson & Ehrlén, 1991). However, this appears to vary with growing conditions since in southern England fresh fruit mass was measured at 0.49 g in *C. laevigata*, compared to 0.63 g in *C. monogyna* (Snow & Snow, 1988). Moisture content of the fruit pulp is 68%–77% (Eriksson & Ehrlén, 1991; Snow & Snow, 1988; Toncheva et al., 2016). Total pulp carbohydrate content has been measured in Bulgaria at $5.9 \pm 0.1\%$ (assumed to be SD), monosaccharide content $5.2 \pm 0.2\%$ and total sugar content $0.7 \pm 0.1\%$ (Toncheva et al., 2016). This is lower than total carbohydrate content found in Sweden (11.1%) by Eriksson and Ehrlén (1991) who also measured N content at 0.59% and lipid content at 1.4%. Carbohydrate levels in Bulgaria were lower than in *Cornus mas*, *Vaccinium myrtillus* and *V. vitis-idaea* but fruit were still considered to be nutritious (Toncheva et al., 2016). Trace elements, measured in unpolluted sites in Serbia and Bulgaria, appear quite variable: Cr 72 $\mu\text{g}/\text{kg}$, Ni 110 $\mu\text{g}/\text{kg}$, Pb 114 $\mu\text{g}/\text{kg}$, Mo 1.49 mg/kg, Zn 1.3–17.3 mg/kg, Fe 10–273 mg/kg, Mn 3–25 mg/kg, Cu 1.3–8.0 mg/kg and Cd 0.09–0.16 mg/kg (Randjelovic et al., 2014; Toncheva et al., 2016). Randjelovic et al. (2014) in Serbia found that these concentrations were low compared to what was in the soil, and concentrations in the

fruit was similar to *Cornus mas* and *Prunus spinosa*. It was concluded that the fruit are non-toxic, and pose no hazard to animals (including humans) eating them (Ehrlén & Eriksson, 1993; Randjelovic et al., 2014).

Fruit of *C. laevigata* in Sweden took 106 days to develop (cf. 89 days in *C. monogyna*), individual ripe fruit persisted for 64.4 days, somewhat less than the 107.3 days of *C. monogyna*, and trees held ripe fruit for a mean of 82 days, compared to 150 days in *C. monogyna* (Eriksson & Ehrlén, 1991). Fruit of *C. laevigata* contain a mean of 2.1–2.8 seeds (Eriksson & Ehrlén, 1991; Snow & Snow, 1988). Mean seed mass has been measured at 60–68 mg, smaller than *C. monogyna* at 97–130 mg (Eriksson & Ehrlén, 1991; Snow & Snow, 1988). No soil seed bank exists in *C. laevigata* (Thompson et al., 1997).

Dispersal of seeds is primarily by frugivorous birds. In Britain this is likely to be similar to *C. monogyna* in Wytham Woods, Oxfordshire: blackbird *Turdus merula* L., fieldfare *T. pilaris* L., redwing *T. iliacus* L. and song thrush *T. philomelos* Brehm plus to a lesser extent, wood pigeon *Columba palumbus* L. (Sorensen, 1981). Seeds ingested by birds can pass through the gut, as in blackbirds, or be regurgitated as by song thrushes (Christensen, 1992). Woodruffe-Peacock (1919) also lists the following as eating the pulp and thus potentially some of the larger species would also disperse the seeds: goldfinch *Carduelis carduelis* (L.), black grouse *Lyrurus tetrix* L., pheasant *Phasianus colchicus* L., mistle thrush *Turdus viscivorus* L., long-tailed tit *Aegithalos caedatus* (L.), marsh tit *Poecile palustris* (L.), waxwing *Bombycilla garrulus* (L.), and in deep snow conditions stock dove *Columba oenas* L., red grouse *Lagopus lagopus scotica* (Latham), grey ('common') partridge *Perdix perdix* (L.) and red-legged partridge *Alectoris rufa* (L.).

In Poland, fruit of hawthorns are eaten by many bird species from the genus *Turdus* such as redwing, song thrush, fieldfare, ring ouzel *T. torquatus* L., mistle thrush and particularly the blackbird (Wojtatowicz & Pietrzykowska, 2018). The European robin *Erithacus rubecula* L. and black redstart *Phoenicurus ochruros* (S. G. Gmelin) have also been seen feeding on *Crataegus* species (Wojtatowicz & Pietrzykowska, 2018). In the Polish Carpathians, the fruit flesh of *Crataegus* species including *C. laevigata* are eaten by many bird species including redpoll *Carduelis flammea* (L.), greenfinch *Chloris chloris* (L.), rook *Corvus frugilegus* L., hazel grouse *Tetrastes bonasia* (L.), blackcap *Sylvia atricapilla* (L.), crested tit *Lophophanes cristatus* (L.), blue tit *Cyanistes caeruleus* (L.), marsh tit, golden oriole *Oriolus oriolus* (L.), wood pigeon and waxwing. Fruit are also periodically eaten by overwintering bramblings *Fringilla montifringilla* L. (Oklejewicz et al., 2014). Hawthorn stones have been reported in droppings of crane, presumably the common crane *Grus grus* (L.) by Dau (1941) and in the faeces of bears and ungulates (Christensen, 1992).

Secondary spread of *C. laevigata* and other *Crataegus* species by birds and animals is also possible. Woodruffe-Peacock (1919) reported a peregrine falcon *Falco peregrinus* Tunstall striking a 'ring dove', presumed to be the wood pigeon, and the hawthorn stones contained in the crop being scattered over frosty ground. He also reported that stoats would carry caught blackbirds underground, so that the seeds contained in their crops and gut are deposited somewhat below-ground. However, these may be too deep to be considered as successful dispersal. Woodruffe-Peacock (1919) also reports that *Crataegus* seed is

'carried by millions down our becks, and is the commonest seed found in their alluviums, but never to live, so far as I have been able to observe'.

8.4 | Viability of seeds: Germination

Seed cutting tests immediately after extracting the stones from the fruit in Poland by Bujarska-Borkowska (2006) gave a viability of 70%–80%. Seeds of European hawthorns including *C. laevigata* are orthodox (surviving desiccation) and can be dried to 9%–13% moisture without loss of viability (Bujarska-Borkowska, 2006). However, without scarification seeds may not germinate till 18 months or even the third growing season after production (Dau, 1941). Stones of *C. laevigata* have been fed to turkeys to encourage germination a year earlier than non-scarified seeds (DeCandolle, 1825). Other early attempts at breaking dormancy involved burying whole fruit in damp sand and storing for a year in a cellar before planting the following autumn (Dau, 1941).

The dormancy of *Crataegus laevigata* seeds has been overcome by stratifying in a moist medium for a warm phase of alternating 20/30°C for 16/8 or 24/24 hr, respectively, for 16 to 20 weeks. This was followed by a cold phase at 3°C for 16–18 weeks by which time the radicles were appearing. Suitable germination conditions following this were at 3°C for 16 hr and then 15 or 20°C for 8 hr (Bujarska-Borkowska, 2006). The stratified seeds germinated vigorously in 3–5 weeks and all seedlings emerged under these conditions within 4–6 weeks of sowing. Germination rates increased from 2%–4% before stratification to 87% (3/20°C) to 94% (3/15°C). If the warm phase was shortened to 8 weeks and the cold phase maintained at 16 weeks, seed germination dropped to between 15% (with a warm phase of 15/25°C for 16/8 hr) and 46% (warm phase constant at 25°C; Bujarska-Borkowska, 2006).

Seeds could also be chemically scarified in concentrated sulphuric acid for 2 or 3 hr, followed by soaking in water for 24 hr, then warm stratification at 27.5°C for 4 weeks and cold stratification at 3°C for 19–21 weeks. The same germination conditions as above yielded germination rates of 77%–87%, similar to cold stratification. Chemical scarification thus allows the warm period to be shorted from 16–20 weeks to just 4 weeks with only slightly lower germination rates (Bujarska-Borkowska, 2006). Dau (1941) recommended a similar treatment in putting 'well-dried seeds' into concentrated sulphuric acid for three hours, followed by warm stratification at 25°C for three weeks. This suggests two dormancy mechanisms: a hard seed coat, alleviated by scarification, and a physiological requirement for low temperatures (stratification), followed by warmer temperatures.

Seed germination after stratification or scarification can be stopped by partial desiccation. Desiccation to 10%–13% moisture content and storage at –3°C for 12 months reduced seed germination only slightly to 71% (Bujarska-Borkowska, 2006).

8.5 | Seedling morphology

Germination is epigeal. Seedling development is shown in Figure 5. Cotyledons are 12–17 mm long and 4.5–6.0 mm wide, elongated

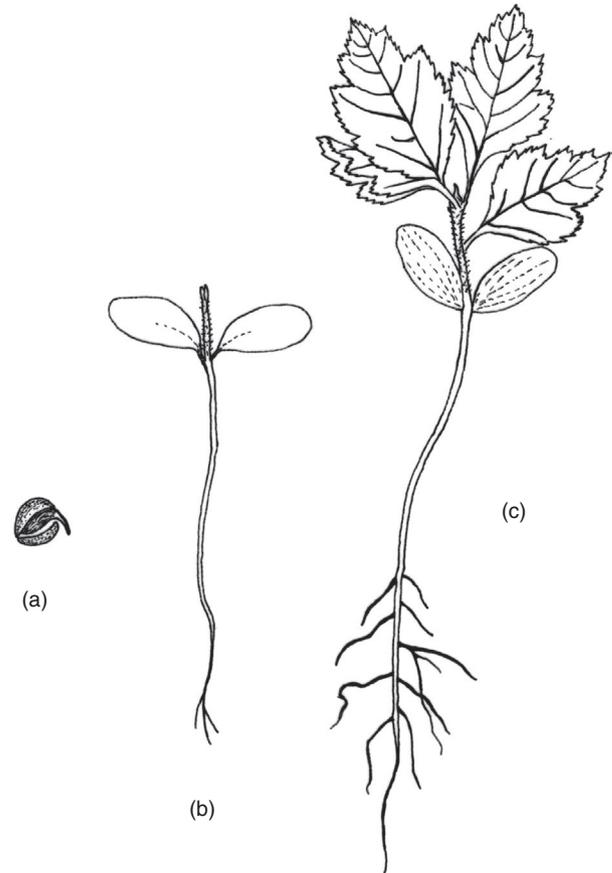


FIGURE 5 Seedling development of *Crataegus laevigata* at 1 day, c. 3 weeks and c. 6 weeks. Based on drawings from Król (1972) and Bartha (2014) and photographs by Barbara Bujarska-Borkowska

elliptically, on a very short petiole or almost sessile, narrowed at the base, evenly rounded at the apex or slightly retuse; they have three or five visible veins. The adaxial surface of cotyledons is green, the abaxial surface light green; both surfaces are hairless. The epicotyl is 8- to 12-mm long, densely covered with sharp hairs. The first true leaves are 15- to 25-mm long and 10- to 14-mm wide, ovate-elliptic, narrow at the base, wedge-shaped converging to the petiole, pointed at the apex, leaf margin double serrated, three- or five-lobed blade on short, winged petioles. The leaf blade is green on the adaxial surface and glabrous; the abaxial surface is brighter with hairs primarily on the veins. Stipules are small, up to 3-mm long, very variable. The radicle develops into a taproot with thin, short, thread-like lateral roots (Król, 1972).

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

Invertebrates associated with *Crataegus laevigata* in Britain are listed in Table 2. It is highly likely that the majority of species, if not all, associated with *C. monogyna* (Fichtner & Wissemann, 2021) are also found on *C. laevigata* and the hybrid between the two. A range of other mites is also found in Hungary on *C. laevigata* including

TABLE 2 Invertebrates recorded from *Crataegus laevigata* in Britain. Nomenclature follows that of the Database of Insects and their Food Plants (DBIF, 2020)

Species/classification	Ecological notes	Source
Acari		
Eriophyoidea		
<i>Aceria crataegi</i> (Canestrini)	Small galls on both leaf surfaces	8
<i>Eriophyes calciobius</i> Nalepa	Galls on swollen, unopened buds	8
<i>Phyllocoptes goniothorax</i> (Nalepa)	Galls on leaf underside or leaf margin	8
Hemiptera		
Aphididae		
<i>Aphis pomi</i> De Geer	Galling; leaf tips curled over	8
<i>Dysaphis crataegi</i> -group	Red gall on leaf	8
<i>D. ranunculi</i> (Kaltenbach)	Leaf curling gall like an upturned boat	8
<i>Rhopalosiphum insertum</i> (Walker)	Galling; leaf-lobes inrolled	8
Tingidae		
<i>Physatocheila smreczynskii</i> China	On many woody Rosaceae	4
Lepidoptera		
Coleophoridae		
<i>Coleophora coracipennella</i> (Hübner)	Larvae on <i>Prunus</i> and <i>Crataegus</i> ; boring in buds	6
Geometridae		
<i>Abraxas grossulariata</i> (L.)		4
<i>Agriopsis aurantiaria</i> (Hubner)	Larvae; many deciduous trees and some shrubs	4
<i>A. marginaria</i> (F.)	Larvae; many deciduous trees and shrubs	4
<i>Alcis repandata</i> (L.)	Larvae; many trees, shrubs and some herbs	4
<i>Biston betularia</i> (L.)	Larvae; many deciduous trees, shrubs and herbs	4
<i>Campaea margaritata</i> (L.)	Larvae; many deciduous trees and shrubs	4
<i>Colotois pennaria</i> (L.)	Larvae; many deciduous trees, shrubs and some herbs	4
<i>Ectropis bistortata</i> (Goeze)	Larvae, on a range of trees and shrubs	4
<i>Electrophaea corylata</i> (Thunberg)	Larvae; deciduous trees	4
<i>Erannis defoliaria</i> (Clerck)	Larvae, wide range of trees and shrubs	4
<i>Eupithecia exiguata</i> (Hubner)	Larvae; many deciduous trees, shrubs and some herbs	4
<i>Hemithea aestivaria</i> (Hubner)	Larvae; many deciduous trees	4
<i>Hypomecis punctinalis</i> (Scop.)	Larvae; deciduous trees	4
<i>Lomographa bimaculata</i> (F.)	Larvae; Rosaceae trees	4
<i>L. temerata</i> (Denis & Schiffermuller)	Larvae; deciduous trees	4
<i>Lycia hirtaria</i> (Clerck)	Larvae, on a range of trees and shrubs	4
<i>Odontopera bidentata</i> (Clerck)	Larvae; many deciduous trees and shrubs	4
<i>Operophtera brumata</i> (L.)	Larvae on many woody plants	3
<i>Opisthograptis luteolata</i> (L.)	Larvae; mostly Rosaceae trees	4
<i>Parectropis similaria</i> (Hufn.)	Larvae; deciduous trees	4
<i>Phigalia pilosaria</i> ([D.&S.])	Larvae; on a range of deciduous trees and shrubs	4
<i>Theria primaria</i> (Haworth)	Larvae; mostly Rosaceae trees	4
Gracillariidae		
<i>Phyllonorycter oxyacanthae</i> (Frey)	Leaf mining larvae on <i>C. laevigata</i> and <i>C. monogyna</i>	2
Lymantriidae		
<i>Lymantria monacha</i> (L.)	Larvae; many trees and shrubs	4
Mompidae		
<i>Blastodacna hellerella</i> (Duponchel)	Larvae; fruit; <i>Crataegus</i> , <i>Malus</i> and <i>Prunus</i> spp.	4

(Continues)

TABLE 2 (Continued)

Species/classification	Ecological notes	Source
<i>Spuleria flavicaput</i> (Haworth)	Larvae; webbing, boring, <i>Crataegus</i> spp.	4
Nepticulidae		
<i>Ectoedemia atricollis</i> (Stainton)	Mining larvae; range of Rosaceae trees	4
<i>Stigmella crataegella</i> (Klimesch)	Mining larvae; <i>Crataegus</i> species	5
<i>S. oxyacanthella</i> (Stainton)	Mining larvae; range of Rosaceae trees	4
Noctuidae		
<i>Agrochola circellaris</i> (Hufnagel)	Larvae; leaves, flowers, fruits; range of trees and shrubs	4
<i>Allophyes oxyacanthae</i> (L.)	Larvae; mostly Rosaceae trees and shrubs	4
<i>Amphipyra pyramidea</i> (L.)	Larvae; many deciduous trees and shrubs	4
Nolidae		
<i>Nola cucullatella</i> (L.)	Larvae; Rosaceae trees	4
Pieridae		
<i>Aporia crataegi</i> (L.)	Larvae, on many woody Rosaceae and herbs	4
Yponomeutidae		
<i>Argyresthia bonnetella</i> (L.)	Larvae; buds, leaves; mostly Rosaceae trees	4
<i>Paraswammerdamia lutarea</i> (Haworth)	Larvae; stem mining, leaf webbing; Rosaceae trees	4
<i>Yponomeuta evonymellus</i> (L.)	<i>Prunus padus</i> is main host but larvae survive on <i>C. laevigata</i>	7
<i>Y. padella</i> L.	Pest of apples; larvae common on <i>C. laevigata</i> in southeast	7, 9
Coleoptera		
Buprestidae		
<i>Agrilus sinuatus</i> (Olivier)	Larvae common on <i>C. laevigata</i> in Gloucestershire and Herefordshire	1
Curculionidae		
<i>Anthonomus bituberculatus</i> Thomson	Galls on buds	8
<i>A. pedicularius</i> (L.)	Galls on ovaries	8
Diptera		
Cecidomyiidae		
<i>Contarinia anthobia</i> (F. Löw)	Galls on flowers	8
<i>Dasineura crataegi</i> (Winnertz)	Galls on leaves and buds; on many <i>Crataegus</i> spp.	4, 8
<i>D. oxyacanthae</i> Rübssaamen	Galls on flowers	8
Tephritidae		
<i>Anomoia purmunda</i> (Harris)	Larvae mining fruits/seeds; on many woody Rosaceae	4

Note: 1. Alexander (1990); 2. Askew (1980); 3. Cheng (1970); 4. DBIF (2020); 5. Emmet (1976); 6. Gosler (1990); 7. Menken et al. (1992); 8. Redfern et al. (2002); 9. Thorpe (1930).

Aculops crataegumplicans (Cotte) (= *Eriophyes crataegumplicans* Cotte: Acari, Eriophyoidea) which creates galls on the upper leaf surface (Zozma & Kovács, 2001), *Cheletogenes ornatus* (Canestrini et Fanzago) (Acari, Cheyletidae), *Hemisarcoptes baldensis* Fain et Ripka (Acari, Hemisarcoptidae), *Michaelopus corticalis* (Michael) (Acari, Acaridae) and *Eupalopsis maseriensis* (Canestrini et Fanzago) (Acari, Eupalopsellidae). The last of these is also found on *C. monogyna* (Ripka et al., 1999). *Calepitrimerus crataegi* Malandraki, Petanović & Emmanouel (Acari: Eriophyidae) has been found on found on *C. laevigata*, *C. monogyna* and *C. orientalis* Pall (presumed to be *C. orientalis* Pall. ex Bieb.) in Greece and Serbia (Malandraki et al., 2004).

Southwood (1961) identified 131 species of Lepidoptera and Coleoptera and a total of 149 insect species on the two hawthorn

species in Britain, with no differentiation between them (compared to 237 and 284 species, respectively, on oak species). The moth *Coleophora coracipennella* (Hubner—Table 2) burrows into flower buds to feed on pollen. A survey by Gosler (1990) showed that as many as 20% of flowers of *C. laevigata* in an Oxfordshire woodland had been sterilised by the moth, and Gosler concluded that this reduced fruit production of *C. laevigata* more than in *C. monogyna*. In addition to the Lepidoptera included in Table 2, Buszko (1987) also noted *Stigmella crataegella* (Klimesch) (Lepidoptera, Nepticulidae) mining leaves on *C. laevigata* and *C. monogyna* in Poland. This species is known from Britain on *Crataegus* species and it thus most likely to include *C. laevigata* (Emmet, 1976).

Syntomaspis druparum Boh. (Hymenoptera, Torymidae), the apple-seed Chalcid, is a common pest of apples in North America, but in

New Zealand it does not attack apples and rather has been found in the seeds of *C. laevigata* and *C. crus-galli* (Gourlay, 1930).

Apple maggot fly, *Rhagoletis pomonella* (Walsh), (Diptera: Tephritidae), the larvae of which are an important pest of apple flesh in North America, has also been found to be common in *C. laevigata* fruit on the west coast of North America (Yee & Goughnour, 2008). In Britain, the gall midge larvae (*Dasyneura crataegi*—Table 2) induces leafy galls on shoots of *Crataegus* species in July which are sometimes associated with fireblight infections (Billing et al., 1974).

The field mouse, *Apodemus sylvaticus* (L.) as well as hawfinch *Coccothraustes coccothraustes* (L.), greenfinch *Chloris chloris* (L.) and nuthatch *Sitta europaea* L. have been seen opening the stones of hawthorns to eat the seeds (Dau, 1941; Heymer, 1966; Woodruffe-Peacock, 1919). Since *C. monogyna* seeds are eaten by bullfinches *Pyrrhula pyrrhula* (L.) (Matthews & Flegg, 1980) and since these are woodland as well as hedge birds, it is expected that they also feed on *C. laevigata*.

9.2 | Plant parasites and epiphytes

Bartha (2014) recorded *Viscum album* subsp. *album* as occurring frequently on *C. laevigata* in mainland Europe. A number of epiphytic lichens are found on the bark of *Crataegus laevigata*. In northeast Poland this includes *Evernia prunastri* (L.) Ach., *Hypogymnia physodes* (L.) Nyl., *Parmelia sulcata* Taylor (Ascomycota, Lecanorales), and *Physcia adscendens* (Fr.) H. Olivier, *P. caesia* (Hoffm.) Fürnröhr, *P. dubia* (Hoffm.) Lettau and *Xanthoria parietina* (L.) Th. Fr (Ascomycota, Teloschistales) (Matwiejuk & Korobkiewicz, 2012). These are all found on a variety of deciduous trees and all are found in Britain and so could occur on *C. laevigata* in Britain. The slime mould *Reticularia lycoperdon* Bull. (Amoebozoa, *Incertae sedis*) has also been found on the bark of *C. laevigata* (British Mycological Society, 2020).

9.3 | Plant diseases

Apple chlorotic leafspot virus (CLSV) (Kitrinoviricota, Tymovirales), a common virus on fruit trees was detected in 27 of 109 hawthorns made up of *C. laevigata*, *C. monogyna* and their hybrid sampled through Great Britain (Sweet, 1980). European hawthorns, including *C. laevigata*, are highly susceptible to fireblight *Erwinia amylovora* (Burrill) Winslow (Proteobacteria, Enterobacterales) (Zeller, 1979), especially *C. laevigata* 'Rosea Flore Pleno' and 'Paul's Scarlet' (Paulin et al., 1992). These may act as reservoirs of infection for apple and pear trees (Billing, 1981; Billing et al., 1974), although it is likely that *C. laevigata* is less important than *C. monogyna* due to its lower prevalence in hedges and woodland edges. *Erwinia billingiae* (likely to be strain Eb661) causes infections on many Rosaceae trees, including *C. laevigata* (Mergaert et al., 1999).

Bartha (2014) lists fungal diseases and parasites of *C. laevigata* in mainland Europe, and Table 3 gives its fungal associates in Britain. Hawthorn leaf blight, producing spots and larger lesions on leaves,

TABLE 3 Fungi (by Phylum and Order) associated with *Crataegus laevigata*. Details of these can be found in the Fungal Records Database of Britain and Ireland (British Mycological Society, 2020). Nomenclature follows this database

Species/classification	Ecological notes
Ascomycota	
Botryosphaerales	
<i>Camarosporium</i> Schulzer sp.	
<i>Oththia spiraeae</i> (Fuckel) Fuckel	Dead twigs; range of woody plants
Capnodiales	
<i>Cladosporium epiphyllum</i> (Pers.) Mart.	Leaves; range of plants
<i>Mycosphaerella oxyacanthae</i> Jaap	Living leaves of <i>Crataegus</i> spp.
<i>M. slaptioniensis</i> D. Hawksw. & Sivan.	Dead wood of <i>Crataegus</i> spp.
Chaetosphaerales	
<i>Chaetosphaeria myriocarpa</i> (Fr.) C. Booth	Dead wood; range of woody plants
Coronophorales	
<i>Nitschkia cupularis</i> (Pers.) P. Karst.	Decorticated wood
Diaporthales	
<i>Cytospora oxyacanthae</i> Rabenh.	Dead twigs, dried fruit; mostly on <i>C. laevigata</i>
<i>Diaporthe crataegi</i> (Curr.) Fuckel	Dead branch
Erysiphales	
<i>Podosphaera clandestina</i> var. <i>clandestina</i> (Wallr.) Lévl.	Living leaves
<i>Phyllactinia mali</i> (Duby) U. Braun	Living leaves
Heliotales	
<i>Diplocarpon mespili</i> (Sorauer) B. Sutton	Living leaves; range of shrubs
<i>Hyaloscypha hyalina</i> (Pers.) Boud.	Dead twigs; range of woody species
<i>Lachnum fasciculare</i> Velen.	
<i>L. pudibundum</i> (Qué.) J. Schröt.	Dead twigs; range of woody species
<i>Mollisia ligni</i> (Desm.) P. Karst.	Dead wood; range of woody species
<i>Monilinia johnsonii</i> (Ellis & Everh.) Honey	Leaves and fruit
<i>Neodasyscypha cerina</i> (Pers.) Spooner	Rotting wood
<i>Strossmayeria basitricha</i> (Sacc.) Dennis	Dead wood; range of trees
Hypocreales	
<i>Dialonectria episphaeria</i> (Tode) Cooke	Twigs, rotten wood; mostly on <i>Crataegus</i> spp.
<i>Nectria cinnabarina</i> (Tode) Fr.	Fallen wood; common

(Continues)

TABLE 3 (Continued)

Species/classification	Ecological notes
Hysteriales	
<i>Gloniopsis praelonga</i> (Schwein.) Underw. & Earle	Dead attached branch
Incertae sedis	
<i>Cytosporina crataegi</i> Allesch.	One record, on <i>C. laevigata</i>
<i>Cyrtidula hippocastani</i> (DC.) R.C. Harris	Twig
<i>Hysterium angustatum</i> Alb. & Schwein.	Wood; range of trees
<i>Myxosporium Link sp.</i>	
Pleosporales	
<i>Melanomma pulvis-pyrius</i> (Pers.) Fuckel	Common on a range of plants
Rhytismatales	
<i>Lophodermium foliicola</i> (Fr.) P.F. Cannon & Minter	Dead leaves; mostly <i>Crataegus</i> spp.
Taphrinales	
<i>Taphrina crataegi</i> Sadeb.	Yellowish or reddish blisters on leaves of <i>C. laevigata</i> and <i>C. monogyna</i>
Xylariales	
<i>Coryneopsis microsticta</i> Grove	Stem; range of woody species
<i>Diatrype disciformis</i> (Hoffm.) Fr.	Dead wood; range of trees
<i>D. stigma</i> (Hoffm.) Fr.	Common
<i>Discostroma corticola</i> (Fuckel) Brockmann	Stems; range of shrubs
<i>Eutypa flavovirens</i> (Pers.) Tul. & C. Tul.	Leaves; range of plants
<i>Eutypella prunastri</i> (Pers.) Sacc.	Fallen dead wood
<i>E. scoparia</i> (Schwein.) Ellis & Everh.	Bark; wide range of plants
<i>Hypoxylon rubiginosum</i> (Pers.) Fr.	Dead branches
<i>Nemania confluens</i> (Tode) Laessøe & Spooner	Wood; range of trees
<i>Xylaria oxyacanthae</i> Tul. & C. Tul.	On fallen and buried fruit of <i>C. laevigata</i> and <i>C. monogyna</i>
Basidiomycota	
Agaricales	
<i>Agaricus altipes</i> (F.H. Møller) Pilát	Leaf litter and soil beneath tree
<i>Calocybe gambosa</i> (Fr.) Donk	Leaf litter and soil beneath tree
<i>Entoloma clypeatum</i> f. <i>clypeatum</i> (L.) P. Kumm.	Grassy soil below trees
Phallales	
<i>Phallus impudicus</i> var. <i>impudicus</i> L.	Mossy soil below tree
Polyporales	
<i>Bulbillomyces farinosus</i> (Bres.) Jülich	Dead wood

(Continues)

TABLE 3 (Continued)

Species/classification	Ecological notes
<i>Byssomerulius corium</i> (Pers.) Parmasto	Dead branches
<i>Trametes pubescens</i> (Schumach.) Pilát	Live wood
Puccinales	
<i>Gymnosporangium clavariiforme</i> (Jacq.) DC	Leaves and branches
<i>G. confusum</i> Plowr.	Leaves
Russulales	
<i>Lactarius vellereus</i> (Fr.) Fr.	Leaf litter below trees

an aesthetic nuisance, is caused by *Entomosporium thumenii* (Cooke) Sacc. (Ascomycota, Heliotales) on *Crataegus* species including *C. laevigata*. Control has been achieved by three applications of 5 ppm cycloheximide fungicide at 14-day intervals, which gave 90%–95% foliage retention compared with only 2%–8% in the untreated controls (Strong, 1960). On heavier soils of the Kentish Weald with a relatively high mean temperature, *Monilinia cydoniae* (Schellenb.) Whetzel (= *Sclerotinia cydoniae* Schellenb.) (Ascomycota, Heliotales) forms dark brown, almost black, blotches on *C. laevigata* leaves. It is particularly prevalent on *C. laevigata* and may be confined to this host (Wormald & Harris, 1938). *Diploccarpon mespili* (Sorauer) B. Sutton (= *Entomosporium mespili* Höhn.) (Ascomycota, Heliotales) causes a similar disease and *C. laevigata* has been found to be more susceptible than other hawthorns in the USA (Anon, 2015). *Nectria cinnabarina* (Ascomycota, Hypocreales) is found on dead wood in Britain (Table 3), but *C. laevigata*, in common with many other trees, is also a host of *Neonectria ditissima* (Tul. & C. Tul.) Samuels & Rossman (= *Nectria gallegena* Bres.) which causes cankers on apple trees (Flack & Swinburne, 1977). Several *Gymnosporangium* species (Basidiomycota, Puccinales; Table 3) produce rusts on the leaves of *C. laevigata* (Muskett & Malone, 1980; Wilson & Bisby, 1954). *Gymnosporangium globosum* (Farl.) Farl. causes similar problems in the American northwest although *C. laevigata* is said to be resistant (Tisserat & O'Mara, 2001). *Heterobasidion annosum* (Fr.) Bref. (Basidiomycota, Russulales), a common root disease, can be found on *C. laevigata* (Wilson, 1927).

10 | HISTORY

Dau (1941) discussed the presence of *Crataegus* in Europe in the Tertiary and Synnott (1978) the Quaternary fossil records of *Crataegus* from Ireland but none of the records differentiates between *C. monogyna* and *C. laevigata* (Godwin, 1975). Lo and Donoghue (2012) used chloroplast DNA to reconstruct lineages and dated the split of *C. laevigata* and *C. monogyna* to around 10 mya. Most of the abundant postglacial records are from charcoal (Godwin, 1975), and macrofossils of wood and charcoal of the two species are indistinguishable, as generally are the seeds. Pollen grains of *C. laevigata* and

C. monogyna are similar but can be differentiated statistically based on the following set of partially overlapping characters: *C. laevigata* pollen is primarily spheroidal (49.3% of grains) and oblate-spheroidal (20.7%), 28–40 µm in diameter and striate with low relief, whereas *C. monogyna* has primarily elongated grains, prolate-spheroidal (50.7%) to subprolate (33.3%), 30–44 µm in diameter and striate with perforations and usually high relief (Byatt et al., 1977; Wrońska-Pilarek et al., 2013) but this does not appear to have been applied to palaeontological studies and is unlikely to be feasible in practice (Chakass et al., 2008).

Hawthorn has been common in woodlands since the Mesolithic period. Most of the prehistoric evidence for hawthorn is for *C. monogyna* although *C. laevigata* may have been overlooked through poor identification (Rackham, 2003). Certainly, every cultural period from Neolithic to Norman times contains records of hawthorn, often numerous (Godwin, 1975). It is likely that *C. monogyna* was the commonest species during this period since it is a better pioneer species in an opening landscape.

There has been some dispute over whether *C. laevigata* is native in Ireland (Section 1). Mature specimens have been found in Co. Cork and Dublin in southern Ireland and in Co. Antrim and Co. Down in the north (Hackney, 1986; Hackney & Hackney, 1988; O'Mahony, 1973) including a herbarium record for the hybrid (*C. × media*) from 1895 (Synnott, 1978). Synnott concluded that these specimens could have been chance sowings by birds but the existence of older records of at least the hybrid suggests that *C. laevigata* may have been native in Ireland but became extinct through introgression with *C. monogyna* aided by clearance of oak woodlands during the 18th and 19th centuries, despite no fossil evidence. Since many of the specimens are found in hedges, Hackney (1986) reached the conclusion that *C. laevigata* was introduced through planting stock acquired, presumably from English nurseries, as part of the Parliamentary Enclosures.

Gutermann (2011) contended that the species name should be spelt *levigata* based on DeCandolle's (1825) publication; however, a close interpretation of the printing by Christensen and Talent (2012) confirms that *laevigata* is correct. The name *Crataegus* comes from the Greek *κράταιγος* (*cràtaigos*) derived from *κρατύς* (*cratùs*) meaning strength or possibly hurdle and *αἴξ* (*àix*) goat (probably referring to a fence to contain goats) or handle, management (from the strength of the wood) or sharp tip (from the thorns); *laevigata* derives from *levigo/laevigo* smooth, make smooth (Acta Plantarum, 2020; Pojarkova, 1939).

10.1 | Uses

Hawthorn wood, including *C. laevigata*, has been used to make handles and walking sticks because of its high density and even grain. Bark and roots were used to give a yellow or brown dye, and bark has been used for tanning in, for example, Algiers (Dau, 1941). Eberly (1989) gives further insights into the folklore of hawthorn although it is not clear which information refers to *C. laevigata*.

Fruit has been widely used fresh and for making fruit juices, jams, teas and a form of brandy in Europe (Dau, 1941; Randjelovic et al., 2014). Fruit were often reserved for invalids, and in many parts of Europe they were dried for winter use as they are high in vitamin C; ripe fruit contain 5 mg of ascorbic acid per gram (Meiling, 1937). Roasted stones have been used as a coffee substitute (Dau, 1941). In the past, hawthorn, including *C. laevigata*, was commonly used in various Italian regions for hedging between plots (Lavenir, 1899). Currently, the need of movement of mechanical agricultural vehicles has led to the almost total disappearance of hawthorn hedges (Pignatti, Guarino, & La Rosa, 2017). *Crataegus laevigata* was assessed to be a potentially compatible dwarfing rootstocks for pears including clones of *Pyrus communis*, *P. calleryana* Decne., *P. fauriei* C.K. Schneid. and also *Amelanchier* spp., *Sorbus* spp., *Mespilus germanica* and *×Pyronia*, a hybrid of *Pyrus* and *Cydonia* (Lombard, 1989).

10.2 | Pharmaceutical uses

Crataegus laevigata, along with other hawthorns, has been used in herbal medicine since the Greek physician, Dioscorides, in the first century (Ju, 2005) who called *Crataegus* 'Oxuakantha' (Hobbs & Foster, 1990). The European Pharmacopoeia and the American Herbal Pharmacopoeia allow for the use of *C. laevigata*, *C. monogyna*, their hybrids and a number of less common species, in the preparation of phytomedicines. It meets the minimum required level of 1.5% flavonoids, expressed as the compound hyperoside equivalents for leaf and flower material and 1.0% procyanidins expressed as cyanidin chloride equivalents for fruit (AHP & Therapeutic Compendium, 1999a, 1999b; The Council of Europe, 2004; United States Pharmacopoeial Convention, 2011). It is thus a common herbal medicine used for a wide number of different complaints using primarily the unripe and ripe fruit but also stems, flowers and dried leaves (Gary et al., 2012; Vaughn, 2015). Dau (1941) believed that *C. laevigata* was more effective in herbal medicine than *C. monogyna*.

More than 150 bioactive molecules have been identified in hawthorn. Traditionally, hawthorn, including *C. laevigata*, has been used most widely to treat asthma, diabetes, neurasthenia and nervous tension, and various digestive problems, but also kidney and bladder stones, fever, pleurisy, insomnia, anxiety and depression. It also has been suggested to be useful against radiation effects, the development of cataracts and obesity, as a protective and therapeutic agent against HIV, Alzheimer's disease, ageing and cancer (Nazhand et al., 2020). The active ingredients are polyphenols (Section 6.6), particularly proanthocyanidins (catechin and epicatechin) and flavonoids, particularly quercetin, hyperoside, vitexin, isovitexin and rutin (Dalli, Colomer, et al., 2011; Edwards et al., 2012; Rohr, 1999).

More recently it has been used for the treatment of various cardiovascular diseases such as high cholesterol (Dalli, Colomer, et al., 2011; Littleton et al., 2013; Littleton, Miller, & Hove, 2012), platelet anti-aggregation (Dalli, Vallés, et al., 2011), tachycardia,

hypertension and arteriosclerosis (Guo et al., 2008; Holubarsch et al., 2008; Long et al., 2006; Rajendran et al., 1996; Schmidt et al., 1994; Schröder et al., 2003; Swaminathan et al., 2010; Tadić et al., 2008; Tassell et al., 2010; Tauchert, 2002; Walker et al., 2006; Wang et al., 2013; Zapfe, 2001; Zick et al., 2009). For example, treatment for 8 weeks with an aqueous ethanol extract from fresh fruits of *C. laevigata* and *C. monogyna*, corresponding to a daily dose of 6.4 mg of procyanidins and 12.7 mg total phenolic compounds, significantly improved the exercise ability of patients with congestive heart failure (Degenring et al., 2003). In a recent promising study, *C. laevigata* was shown to be a useful stimulator of stem cells for cardiomyogenesis and angiogenesis (Halver et al., 2019).

Studies have also reported that extracts of *C. laevigata* are beneficial as an antioxidant, (Cuevas-Durán et al., 2017; Kirakosyan et al., 2003). The antioxidant properties of *C. laevigata* are due to the high total content of phenols (Feroli et al., 2020), but also to proanthocyanidins, flavones and flavonols (Škerget et al., 2005). The therapeutic properties of *C. laevigata* as an anti-inflammatory and antimicrobial agent were also proved (Arya et al., 2012; Dalli et al., 2008; Periera da Silva et al., 2000; Tadić et al., 2008) as well as reduced hypoglycaemia in rats (Alaghawani & Naser, 2013) and improved pulmonary hypertension in chickens (Ahmadipour et al., 2019). In tinctures of *C. laevigata*, flavonoid concentration declines within 2–3 months while procyanidins are stable for more than 9 months (Bilia et al., 2007). *Crataegus laevigata* appears to have minimal side effects at recommended dosages, although 'high' doses can cause hypotension and sedation leading to bradycardia, respiratory depression and eventually cardiac arrest (Arya et al., 2012).

11 | CONSERVATION AND MANAGEMENT

The frequency of *Crataegus laevigata* in Britain has changed little within the main part of its native range since 1962 but this may partly be due to it being widely planted around Britain both within and outside its native range, reflected in the location of new records. Moreover, *C. laevigata* can be easily confused with the hybrid *C. × media* and some new records may be for the hybrid (Braithwaite et al., 2006; Preston et al., 2002). Hidden behind this it is likely that pure *C. laevigata* is in decline, certainly in the southeast, due to disturbance and fragmentation of woodland habitat allowing *C. monogyna* to encroach, encouraging hybridisation (Section 8.2) and replacement of *C. laevigata*. Byatt (1975) went so far as to suggest that pure *C. laevigata* may disappear altogether as introgression increases. A similar problem has been identified in other European countries including Belgium and Poland by Oklejewicz et al. (2013). Paradoxically perhaps, *C. × media* is considered a rare species in Bulgaria at the southeast extent of the native range of *C. laevigata* and should be included in the Red Data Book of Bulgaria as being in need of legal protection (Vakarelov & Tashev, 2007). *Crataegus laevigata* is included in the Red List of the Vascular Plants of Luxembourg though with a threat category

of Least Concern, together with *C. monogyna* and *C. rhipidophylla* (Colling, 2005).

In some European countries, there has previously been a requirement to remove flowers from all hawthorns (since flowers are the entry point for the fireblight bacterium—Section 9.3) and the removal of plants that are infected with fireblight from near pear and apple orchards to help protect them from the disease (Schouten, 1992). This was a short-lived exercise and was likely to have less effect on *C. laevigata* due to its woodland habitat and greater distance from orchards than *C. monogyna*.

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