Article Type: Biological Flora

Biological Flora of the British Isles: *Sorbus torminalis*

Peter A. Thomas†

School of Life Sciences, Keele University, Staffordshire ST5 5BG, UK

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†Correspondence author. Email: p.a.thomas@keele.ac.uk

Summary

1. This account presents information on all aspects of the biology of *Sorbus torminalis* (L.) Crantz (Wild Service-tree) 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. *Sorbus torminalis* is an uncommon, mostly small tree (but can reach 33 m) native to lowland England and Wales, and temperate and Mediterranean regions of mainland Europe. It is the most shade-tolerant member of the genus in the British Isles and as a result it is more closely associated with woodland than any other British species. Like other British Sorbus species, however, it grows best where competition for space and sunlight is limited. Seedlings are shade tolerant but adults are only moderately so. This, combined with its low competitive ability, restricts the best growth to open areas. In shade, saplings and young adults form a sapling bank,

showing reproduction and extensive growth only when released. *Sorbus torminalis* tolerates a wide range of soil reaction (pH 3.5-8.0) but grows best on calcareous clays and thin soils over limestone.

3. *Sorbus torminalis* is a sexual, diploid, non-apomictic species that has hybridised with a number of other *Sorbus* species to form microspecies. The hermaphrodite flowers are primarily insect pollinated. Seed production is reliable only in warm years, especially at the edge of its range, although even then seed viability is low. The fruits are primarily dispersed by carnivorous mammals. Seeds display embryo dormancy but most will germinate the first spring after falling.

4. This tree is very tolerant of short droughts but only moderately tolerant of frost, hence its southerly and lowland distribution. It faces no particular individual threats although the small size of most populations makes it susceptible to habitat loss and fragmentation, particularly through the loss of open coppiced areas. As a consequence it appears to be declining throughout Britain and Europe despite its wide range of historical uses and the high value of its timber. The extent to which these losses will be offset by increases due to climate change is unknown.

Wild Service Tree or Chequers/Chequer tree. Rosaceae. *Sorbus torminalis* (L.) Crantz (*Crataegus torminalis* L., *Pyrus torminalis* (L.) Ehrh., *Aria torminalis* (L.) Beck., *Torminaria clusii* Roem., *Torminalis clusii* (Roem.) Roberts & Phipps) is usually a subordinate, sub-canopy tree or shrub of temperate deciduous forests, and more rarely a co-dominant canopy tree reaching 30-33 m. Suckers profusely. Crown narrow when shaded but round, ovate with many lateral, angled branches in full sunlight. Bark grey-green to dark brown on young stems, becoming scaly from c. 30 years old (Harper 1981). Shoots initially tomentose, later glabrous, olive-green to brown. Buds ovoid to obtuse, 3-6 mm long, bright green to yellowish, bud scales with scarious margins and sparse white hairs, rarely slightly tomentose otherwise glabrous and viscous. Stipules narrow, linear, glandular ciliate, reaching 12 mm long, falling early. Leaves alternate, very variable in shape: leaves of short shoots are simple, broadly ovoid, deeply lobed; leaves of long shoots less lobed and even more variable. Leaves of short shoots are used for identification: broadly ovate, 5.5-10.0(11) x (4.5)5.0-10.5(12) cm, 0.8-1.3(1.5) times as long as

wide with 7-9 triangular acute to acuminate lobes divided ≤half way to midrib (but variably cut (15)20-60(100)% to the midrib at the centre of the leaf), the lowest two lobes are distinctively divergent, with few veins (4-5 lateral pairs), sparsely tomentose when young becoming glabrous or almost so on the underside, any remaining hairs restricted to the veins, glossy dark green above, greyish-green below; leaf apex acuminate, leaf base rounded, truncate or cordate, rarely broadly cuneate; finely serrate with small strongly asymmetric, forward pointing, appressed teeth; petiole long and slender (15)20-50(58) mm long (Price & Rich 2007; Rich *et al*. 2010). Vivid autumn colour of reds and yellow.

Flowers hermaphrodite; inflorescence a lax corymb of 30-50 flowers, up to 20 cm across, calyx and flower stalks very woolly. Flowers creamy white, 10-13 mm in diameter. Sepals narrowly triangular to deltate, acuminate, sparsely to densely tomentose, sometimes with a few reddish-brown glands on the margins. Petals 4-9 x 4-8 mm, curved, blunt, round, c. 12 stamens as long as the petals, 2-3 styles free to base or joined half to three quarters of the way up. Two carpels each with 1-2 ovules; inferior ovary, in contrast to all other members of the genus *Sorbus* (Pietzarka, Lehmann & Roloff 2009). Fruit a pome with the 2 carpels enclosed by a fleshy hypanthium; 5-10 (20) fruits in a corymb (Oršanić *et al*. 2009). Fruits (8)12-18(20) mm long, obovoid, longer than wide (except smallest fruits which are subglobose), very variable in size within the same corymb (Bednorz 2007a); receptacle hollow at apex, unusual in being brightest before they are ripe: initially reddish-yellow later turning brown with numerous small lenticels, a few large (the density is the highest in any *Sorbus* species; Aldasoro *et al*. 1998); sepals deciduous during fruit ripening. In Poland, most fruits (c. 70%) without hairs, some (23%) with dense hairs and 7% hairless (Bednorz 2007a). The fruits are normally single- seeded but can have up to six. Seeds resemble apple pips, 6-7 x 3-4 mm, obovate, flattened, initially white rapidly turning dark brown upon removal from fruit.

Sorbus torminalis is most readily identified from other Sorbus by the wing-like lobes at the leaf base, long petioles and the distinctive brown fruits with a large number of lenticels in the skin (c. 400 per fruit), a multi-layered cuticle and the low water content (49%) caused by the large number of small sclerids (70 μm in diameter) around the seed (Aldasoro *et al*. 1998). *Sorbus torminalis* also has flavonoids not found in other European *Sorbus* species (McAllister 2005).

In the British Isles, *Sorbus torminalis* is one of only four sexual, diploid, non-apomictic species, out of a total of around 40 native *Sorbus* species (Rich *et al*. 2010). *Sorbus torminalis* shows great variation in leaf morphology across its range but only two forms

appear to be widespread: forma *semitorminalis* (Borbás) Jávorka with leaves finely tomentose below at maturity (possibly correctly known as forma *mollis* Beck – Kovanda 1997), and forma *pinnatifida* (Borbás) Kárpáti with lowest leaf pinnae cut to the midrib (Rich *et al*. 2010). Two other forms have been separated based on extremes of leaf shape: forma *caucasica* Diapulis (= *S. orientalis* Schönbeck-Temesy), which has leaves with hardly any lobes, and forma *perincisa* (Borbás & Fekete) Beck, whose leaves have the lowest pair of lobes completely separated (Kovanda 1997; Aldaroso *et al*. 2004; Bednorz 2006). Kárpáti (1960) used the variability within the species to identify 35 forms of *S. torminalis* based primarily on leaf shape but also fruit shape and leaf indumentum, mostly from Hungary. He stresses that the variability is such that identification of forms requires a large number of leaves observed at the time of fruit ripening.

　　　Sorbus torminalis is strongly associated with woodland in Britain (Pellicer *et al*. 2012), native in a wide range of woods, scrub and hedgerows mostly on clay or limestone. It tends to occur commonly in ancient woodland on calcareous soils, on calcareous rocky outcrops, and most often as a scattered tree in areas where light fluxes are highest such as open deciduous forests and at the edges of rides, clearings or forest margins (Rasmussen & Kollmann 2004a).

I. Geographical and altitudinal distribution

Sorbus torminalis is scattered throughout the lowlands of Wales and England, especially in the Weald and the Wye Valley (Fig. 1), continuing northwards to Northumberland and Westmorland, although its natural northern limit is probably around Morecambe Bay (Rich *et al*. 2010). It is largely absent from Scotland, Ireland, the Isle of Man and the Channel Isles, except as an uncommon introduction.

　　　The native distribution of *S. torminalis* has been obscured by extensive planting for its fruit and wood (Roper 1993). Early planters (e.g. Cook 1679) certainly advocated planting a number of useful species, including *S. torminalis*, as a way of 'thickening woods' from 'running roots'. Regional accounts that take these plantings into account are given by Harper (1981), Lloyd (1977), Pigott (1974) and Wilmott (1977).

　　　Sorbus torminalis is widely distributed throughout lower elevation temperate and Mediterranean zones of Europe (Fig. 2), extending eastwards into the Caucasus Mountains and northern Iran. In the south it extends into the Iberian peninsula, and Morocco and Algeria in northwest Africa in the west, and into eastern Syria and Lebanon in the east (Meusel, Jäger

& Weinert 1965; Demesure-Musch & Oddou-Muratorio 2004; Bednorz & Urbaniak 2005; Pietzarka, Lehmann & Roloff 2009). In the north it extends to the Baltic and is largely absent from Scandinavia except for Denmark.

France sits at the current distribution centre of *S. torminalis* with about 25 million trees, with particularly high densities to the east of Paris in the regions of Champagne-Ardenne and Lorraine, and south to Burgundy and Franche-Comté (Drapier 1993a).

Sorbus torminalis is primarily a lowland species in the British Isles (Roper 1993; Rich *et al.* 2010), with around 80% of occurrences below 150 m and a maximum elevational limit of 338 m in Shropshire (Botanical Society of Britain & Ireland data; Kevin Walker personal communication). At the northern limits of its range in Denmark in mainland Europe it is restricted to below 60 m. Further south, it is found between 300-650 m in the Balkans and Romania (Dinca 2000; Dimitrov & Genova 2008), 175-760 m in the Czech Republic (Maděra, Tichá & Řepka 2013), 100-1000 m in Italy (Rasmussen & Kollmann 2007) and 380-1000 m in Switzerland (Wohlgemuth 1993; Pleines 1994). Elsewhere *S. torminalis* ascends to 720 m in Slovakia, 1250 m in Sicily, 1400 m in Lebanon, 1500 m in the Caucasus Mountains, 2200 m in Turkey and 2300 m in Iran (Kausch-Blecken von Schmeling 1994b; Espahbodi *et al.* 2007b; Paganová 2007; Tabandeh *et al.* 2007; Belletti, Monteleone & Ferrazzini 2008; Saravi *et al.* 2008; Maděra, Tichá & Řepka 2013). In the Moroccan mountains, it is found only between 1300-1800 m (Pietzarka, Lehmann & Roloff 2009).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Sorbus torminalis is a thermophile, with a broad southern continental or submediterranean-suboceanic distribution in Europe (Rodwell 1991; Rasmussen & Kollmann 2008; Fady & Conord 2010). Its requirement for warmth is such that it shares a similar distribution to European oaks and *Sorbus domestica* (Dincă 2000; Pietzarka, Lehmann & Roloff 2009). *Sorbus torminalis* performs best within those areas with a mean annual temperature range of 6.5 to 17 °C, with an optimum of 8.5 °C, and annual precipitation between 600-1500 mm with the optimum >800 mm (Wohlgemuth 1993; Pleines 1994; González, Rey de Viñas & Cisneros 2003; Rasmusen & Kollmann 2004a; Oria de Rueda 2008). In Great Britain, it is largely restricted to areas where mean July temperatures are above 16°C and mean annual ppt is below 1000 mm (Kevin Walker personal communication). It probably evolved in dry, open

woodland and its reproductive performance is strongly affected by climate (Termena 1972). *Sorbus torminalis* is only moderately frost and cold resistant and the northerly distribution is primarily limited by cool summers that reduce successful seed production (Drapier 1993b; Roper 1993). In Britain, abundant fruit is only produced following warm summers, and in cooler years, even in southern Britain, seed production can be very poor (Davis 1976). The southern distribution is undoubtedly limited by drought exacerbated by higher temperatures (Drapier 1993b).

The requirement for warm and dry conditions tends to restrict *S. torminalis* to south facing slopes, particularly at the northern and eastern edge of its range (Dincă 2000) although towards the south edge of its range it occurs primarily on cooler, damper north facing slopes (De Dominicis & Barluzzi 1983). Siles *et al.* (2010) modelled the recovery of vegetation after a fire in *Pinus nigra*, *Quercus ilex* and *Q. faginea* forest in southeast Spain and found that the presence of *S. torminalis* was associated with a southerly aspect, shallow soils and a high rock cover (as were other species tolerant of dry conditions), although altitude and slope were not important. Slope angle only seems to become important on the wettest soils when *S. torminalis* is restricted to the drier, steeper slopes (Wohlgemuth 1993). Similarly, aspect is only important in hot, dry areas such as Iran where it occurs on north and northeast facing slopes (Espahbodi *et al.* 2008). *Sorbus torminalis* is very wind firm and rarely suffers from windthrow (Kausch-Blecken von Schmeling 1994b).

(B) SUBSTRATUM

Sorbus torminalis is tolerant of different soil types, growing on soils of pH 3.5-8.0 (Favre-d'anne 1990; Lanier *et al.* 1990; Savill 1991; Drapier 1993b; García López & Allué Camacho 2006; García-Abad Alonso, Gómez Delgado & Rodríguez Espinosa 2009) although it does increasingly well from slightly acidic to basic soils (Leuschner, Köckemann & Buschmann 2009). It is similarly tolerant of a wide range of soil fertility, coping with soils that are nitrogen deficient to moderately fertile, humus- or loess-enriched (Maděra, Tichá & Řepka 2013) although it performs best on deep fertile soils (Kausch-Blecken von Schmeling 1994b). It can also cope with a wide range of soil moisture although it does best on moderately to very dry soils, sharing a similar requirement to *Taxus baccata*, and is increasingly restricted to dry soils at the eastern end of its range (Grundmann & Roloff 2009; Leuschner, Köckemann & Buschmann 2009). It will survive on soils that are temporarily flooded but avoids permanently waterlogged or peaty soils (Maděra, Tichá & Řepka 2013).

Despite its wide tolerance, *S. torminalis* shows a marked preference for soils derived from clays and from limestone. The best growth of *S. torminalis* is found on deep, nutrient-rich, clays and river valley bottoms where there is a continuous supply of water (Paganová 2007; Maděra, Tichá & Řepka 2013). The contrasting preference for drier calcareous soils is likely due to the greater tolerance of *S. torminalis* to drought than most dominant canopy species (Pietzarka, Lehmann & Roloff 2009).

In Britain, *S. torminalis* is locally abundant on the nutrient-rich Weald, London, Oxford and Barton Clays in southeast England where they are free of superficial deposits of sand or gravel. It is much less common on calacerous Boulder Clay and virtually absent from the Gault Clay of southern England (Roper 1993; Brewis, Bowman & Rose 1996). It occurs much more locally on more acidic damp soils of hilly or undulating gravel terraces where strata produce moist bands. These include the Culm measures of southwest England, Coal Measures Shales, Old Red Sandstone and glacial gravels (Roper 1993), avoiding the driest sandy soils. Cook (1679) noted that *S. torminalis* does not fruit well on "sharp Gravel [free-draining gravel soils], the Fruit naught, and the Tree bear very sadly" compared to clay. This contrasts with its abundance on shallow calcaerous soils over the Magnesian Limestone of Nottinghamshire to South Yorkshire and the Carboniferous limestones of the Peak District, west Shropshire and the Gower Peninsula (Roper 1993). It is also found to a lesser degree on equally dry soils of coastal and inland cliffs, rocky hillsides, land-slips and similar open and disturbed habitat, such as along the Severn Estuary at Chepstow and Lydney, and in the Lower Wye Valley, and sea cliffs of South Wales (Roper 1993). A similar preference for soil types has been found in mainland Europe (Oria de Rueda, Martínez de Azagra & Álvarez 2006; Maděra, Tichá & Řepka 2013).

III. Communities

Sorbus torminalis is mostly a tree of open deciduous woodlands, the edges of rides and clearings, woodland edges (Rasmussen & Kollmann 2004a) and hedgerows in Britain and Germany (Williams, McLaughlin & Harrison 1986; Kausch-Blecken von Schmeling 1993). It is particularly associated with woodland relic hedgerows (species-rich ancient hedges) derived from ash woodland on calcareous soils over clay and limestone (Pollard 1973). It has also been recorded in Shropshire growing on rocks and scree in base-poor lowland *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland (U1; Rodwell 1992) by Lockton &

Whild (2015) and heathland with *Juniperus* scrub on rock outcrops in the Lake District by Halliday (1997).

Despite its need for openness, it is also a common component of old woodlands and Hermy *et al*. (1999) lists it as one of 132 indicator species of old deciduous European woodland. Due to its close association with ancient woodland, *Sorbus torminalis* has frequently been used as an Ancient Woodland Indicator in many areas of Britain (Rose 1999; Kirby 2006) including such Shropshire (Whild 2003), Lancashire and Westmorland (Pigott 1974), Epping Forest (Lloyd 1977), Lincolnshire (Peterken 1983) and Derbyshire (Willmot 1977).

In Britain, *S. torminalis* is a rare component on drier (but still damp) areas of the *Phragmites australis* sub-community of *Alnus glutinosa–Carex paniculata* woodland (W5), along with *Populus tremula*. As such it can be found in the zonation from woodland to swamp primarily in East Anglia and around the meres of Cheshire and Shropshire. It is more common, albeit still as a scarce and scattered tree, in the *Primula vulgaris–Glechoma hederacea* sub-community of *Fraxinus excelsior–Acer campestre–Mercurialis perennis* woodland (W8) in the southeast along with other occasional trees such as *Betula* spp., *Tilia cordata*, *Carpinus betulus* and *Malus sylvestris* (Rodwell 1991; Lockton & Whild (2015). Like these other occasional trees, *S. torminalis* does not usually invade new stands very quickly but can reach a large size (Rodwell 1991). Moreover, like *Tilia cordata*, *S. torminalis* is more frequent along the northwestern side of the community around Morecambe Bay (Pigott & Huntley 1978). On more acid soils, it probably more frequently associated with *Quercus robur-Pteridium aquilinum-Rubus fruticosus* woodland (W10), as reported for Cardiganshire (Chater 2010) and the Birmingham region (Trueman, Poulton & Reade 2013) where its most frequent associates are *Corylus avellana*, *Hyacinthoides non-scripta*, *Quercus robur*, and *Sorbus aucuparia* (Trueman *et al*. 2013).

In continental Europe, *S. torminalis* is typically associated with *Quercus robur*, *Q. petraea*, *Fraxinus excelsior*, *Fagus sylvatica* and *Carpinus betulus* (Rodwell 1991). In western Europe *S. torminalis* occurs primarily in a variety of calcareous beech woodlands, notably Pulmonario–Fagetum melittetosum, hornbeam woodlands, particularly Gallo sylvatici–Carpinetum and Lathyro–Quercetum, pine woodlands such as Molinio–Pinetum sylvestris and Cephalanthero–Pinetum sylvestris, and mixed oak woodlands of the alliance Quercion pubescenti–petraeae (Wohlgemuth 1993; Pleines 1994). In Central Germany, it is also a minor component of mixed deciduous forest (Aceri platanoidis–Tilietum platyphyllos)

dominated by *Fagus sylvatica*, *Tilia* spp. and various *Acer* spp. on loess underlain by limestone (Gebauer, Horna & Leuschner 2012; Seidel *et al*. 2013). It can also occur in tall-shrub communities in the class Rhamno-Prunetea and as a colonist in dry grassland communities in the Festuco-Brometea (Rasmussen & Kollman 2004a).

In Eastern Europe one of the largest concentrations of *S. torminalis* occurs in woodlands of the class Querco–Fagetea. In Poland, Slovakia and the Czech Republic it forms the rare thermophilous association of Sorbo torminalis–Quercetum on acidic soils and is also present in the open, species rich, slightly acidic oak forest Luzulo luzuloidis–Quercetum genistetosum tinctoriae of Poland (Kwiatkowski 2003: Bednorz 2007b; Maděra *et al*. 2012; Szymura 2012). In Slovakia, *S. torminalis* is also a component of the basic soil version of the dry-mesic woodland Corno–Quercetum (Prudič 1998; Roleček 2005).

Further east in northern Turkey in upland mixed woodlands, and in Bulgaria, *S. torminalis* is a defining species of the mesophilous alliance Carpino betuli–Acerion hirkani and associations in the order Querco cerridis–Carpinetalia orientalis in upland mixed woodlands (Velichkov, Zlatanov & Popov 2007; Korkmaz *et al*. 2011). In the mountains of Iran, it is found on west- and southwest-facing slopes between1500-1800 m altitude in a range of beech forests including Carpino–Fagetum, Rusco–Fagetum, Fagetum Oriental and Alno–Fagetum (Espahbodi *et al*. 2007a; Rad & Shafiei 2010). At its south-eastern limit in Lebanon *S. torminalis* is restricted to mixed deciduous forest on limestone at *c*. 1500 m, below the *Cedrus libanii* forest (Rich *et al*. 2010).

Around the Mediterranean, *S. torminalis* is a fairly constant though infrequent species in acidic *Quercus petraea* woodlands in the order Quercetalia robori-petraeae in northern Croatia along with *Fraxinus ornus* (Vukelić, Baričević & Šapić 2010). From here down into northwest Greece, *S. torminalis* is also a rare component of the shrub layer of *Quercus frainetto* and *Q. pubescens* woodlands in the order Quercetalia pubescentis, particularly those that are coppiced (Rackham 2003; Medak 2011). Similarly, in central Italy, it is a minor component of the association Carpino orientalis–Quercetum cerridis (Rosati *et al*. 2010), merging into sub-Mediterranean oak forests dominated by *Quercus pubescens* and *Q. faginea* on calcareous soils (Loidi 2004) and *Q. ilex* in northeast Spain (Sardans & Peñuelas 2007).

IV. Response to biotic factors

Sorbus torminalis is a poor competitor, readily out-competed by other trees, and so usually only reaches its maximum height in open conditions where light fluxes are high

(Wohlgemuth 1993; Collet *et al*. 2008) or where conditions weaken the dominance of other forest trees. For example, seedlings tend to be more abundant on shallow and acidic soils in Central Europe where seedlings of other species are less abundant (Szymura, Szymura & Pietrzak 2014). As such, some regard it as an early- to mid-successional species (Favre-d'anne 1990; Drapier 1993b; Demesure *et al*. 2000b; Hoebee *et al*. 2006; Oddou-Muratorio *et al*. 2006) although, as noted in III, it is also a shade-tolerant, if non-reproducing, component of old woodlands. *S. torminalis* is susceptible to self-competition between root suckers. Rasmussen & Kollmann (2007) found that root sucker density was negatively correlated with stem length, basal diameter and sprout age, suggesting that suckers compete for water, nutrients and particularly light, leading to self-thinning. Competition was higher under low, diffuse light fluxes since here root suckers were taller but thinner, with self-thinning leading to lower sucker density.

Regeneration is also vulnerable to biotic influences. The majority of seeds are usually infertile (VIII(C)) and those that are viable are readily predated by mammals, birds and invertebrates (Termena 1972; Lloyd 1977; Velička 1993; Rich *et al*. 2010). Seedlings and saplings are readily browsed by small mammals, rabbits and ungulates (Harper 1981; Drapier 1993b; Ewald, Zander & Jander 1994; Schüte 2000; Biedenkopf, Ammer & Müller-Starck 2007; Collet *et al*. 2008) and suckers are even more prone to browsing by rodents and deer (Harper 1981; Nicolescu *et al*. 2009). Borchard *et al*. (2011) categorised the defence of *S. torminalis* against large herbivores as very low (2 on a 1-6 scale with *Taxus baccata* being 6), with few chemical defences other than some digestive inhibitors (Ellenberg *et al*. 1991). However, Boulanger *et al*. (2009) stated that in their studies in mixed oak woodland in northeast France, *S. torminalis* individuals 'were always avoided', perhaps due to the abundance of a preferred species of *Cornus* and *Rosa canina*. In contrast, Rasmussen & Kollmann (2007) found that fencing to exclude roe deer (*Capreolus capreolus* L.) resulted in root suckers growing a mean of 3.8 cm in height in one season compared to 0.6 cm outside exclosures. Certainly, a number of authors suggest that browsing is usually severe enough to prevent the natural regeneration of *S. torminalis* (Bednorz 2009; Bednorz, Kaźmierczak & Kaczmarek 2012; Maděra *et al*. 2012).

The loss of traditional woodland management has been suggested as one of the main reasons responsible for *S. torminalis* becoming rarer in Europe over the last century, as with a number of other light-demanding species, mainly as a result of a change from coppicing to

closed high forests (Müller, Ammer & Nüßlein 2000; Szymura 2012); this is discussed in more detail in XI.

V. Response to environment

(A) GREGARIOUSNESS

Sorbus torminalis is extremely non-gregarious, found as spatially isolated, scattered individuals across the whole of its range. Many woodlands have just one individual or clump of root suckers with population size often being fewer than 10 trees and only very rarely over 100 individuals (Pleines 1994; Hoebee *et al.* 2006); for example, in Poland, Bednorz (2007c) found that only 11% of sites (8 out of 73) had >100 *S. torminalis* trees. Population densities are usually in the range of 0.1 to 40 individuals ha^{-1} with most being at the lower end of this range (Pleines 1994; Demesure *et al.* 2000a; Hochbichler 2003; Demesure-Musch & Oddou-Muratorio 2004; Oddou-Muratorio *et al.* 2004; Belletti, Monteleone & Ferrazzini 2008; Dimitrov & Ginova 2008; Aas & Kohles 2011; Maděra *et al.* 2012). Locally high densities are possible, mostly where *S. torminalis* has been cultivated and planted such as in the eastern Weald between Ashford in Kent and Robertsbridge in East Sussex (Roper 1993). In a 130-ha area of coppice-with-standards in southern Austria, Hochbichler (2003) recorded 36 *S. torminalis* trees per hectare (DBH, diameter at breast height, > 7 cm). Possibly more typical is the a well studied population at Monks Wood National Nature Reserve in Huntingdonshire where around 70 individual trees (some up to 20 m tall) have been recorded across 157 ha of ancient ash/oak woodland on Oxford and Boulder Clay since the 1970s (Kevin Walker, personal communication).

On a smaller scale, suckers growing from roots inevitably tend to be clumped. On islands in the Baltic Sea, Rasmussen & Kollmann (2007) found that clumps varied considerably in size from 6 to 207 suckers 100 m^{-2}. Suckers were highly clumped up to a distance of 2.5 m from the trees, reflecting the concentration of suckers around the base of individual trees; at a larger scale the pattern was more random reflecting the pattern between trees. On steep slopes, suckers tended to grow perpendicular to the slope. Bednorz, Kaźmierczak & Kaczmarek (2012) investigated natural regeneration from seed in a population of 597 *S. torminalis* trees in a 1.72 ha fenced plot in north Poland and found seedlings to be similarly clustered.

(B) PERFORMANCE IN VARIOUS HABITATS

Sorbus torminalis has been classified as a forest specialist (de Albuquerque & Rueda 2010) but, given its partial shade tolerance (VI(E)), poor competitive abilities (IV), and its high tolerance of high temperature and drought (V(C)), it is also often found in open situations such as on rocky outcrops. On shallow or rocky soils, where conditions are too harsh for regeneration of other tree species, *S. torminalis* growth may be restricted to patches of suckers no more than 1-2 m high but with some of the densest growth of any habitat, as exemplified on south facing, sandy soils near the Caspian Sea where *S. torminalis* is mixed with *Quercus castaneifolia* (Zare, Tabari & Espahbodi 2002). On rocky outcrops, seed and seedling survival can also be higher due to protection from predators within crevices and cracks (Roper 1993).

On deeper, more nutrient-rich soils, *S. torminalis* performs best in open areas within woodlands such as coppice, the edges of rides, and woodland margins as well as in hedgerows, including wood relic hedges that mark the former boundaries of woodlands (Pollard 1973; Rasmussen & Kollman 2004b; Maděra et al. 2012) and where there is disturbance creating gaps. This is particularly so within oak- and beech-dominated mixed forests (Belletti, Monteleone & Ferrazzini 2008). In more shaded conditions seedlings and suckers can be outcompeted by more competitive species such as oak and beech (Geb, Schmidt & Meyer 2004; Hochbichler 2003; Schrötter 2001) but in less highly shaded conditions they will persist as a sapling bank from 10-20 years of age or as mature trees, showing little annual growth or reproduction until a canopy gap opens up (Kausch-Blecken von Schmeling 1994b; Prudič 1997; Stănescu, Şofletea & Popescu 1997; Hochbichler 2003; Kahle 2004; Rich *et al.* 2010). As such it is rarely a canopy tree in cool western areas of Europe; for example, in mixed oak woodlands in southwest France, *S. torminalis* occurred in 37-54% of 400 m^2 plots as an understory shrub, and only 7% of plots as a canopy tree (Gonzalez, Deconchat & Balent 2009). In a *Quercus petraea* woodland in southwest Germany, Pyttel, Kunz & Bauhus (2013) found that 65% of *S. torminalis* trees were <7 cm DBH, and most were <10 m tall with only occasional trees >20 m and so shorter than the oaks. Further east in more continental conditions *S. torminalis* becomes a more frequent component of the canopy in some types of woodland. In the Czech Republic Maděra *et al.* (2012) found that 34% of *S. torminalis* individuals were co-dominant with the oaks, 3% were dominant and 39% were 'intermediate' or growing towards the canopy; only 22% of the population was classified as shaded but alive. In this study, 35% of trees bore fruit, of these

81% were dominant or co-dominant and the 2% of trees that had the largest number of fruit were always along woodland edges and dominant. Light appears to be important in the regenerative success of *S. torminalis*. At the northern end of its range on islands in the Baltic Sea, root sucker density (ranging from 6 to 207 suckers 100 m^{-2}) and basal diameter were positively correlated with light flux density below the canopy of the mixed deciduous forest (Rasmussen & Kollmann 2007). Suckers were also tallest under high light fluxes due to rapid growth but they were also tall under the lowest light fluxes, presumably due to etiolation. Light is also needed for seed production (VI(E)). However, establishment into woodland gaps can still be limited by its poor competitive ability. Following direct sowing of seeds into meadow vegetation in central France, *S. torminalis* and *Carpinus betulus* were significantly smaller at the end of first growing season (4 cm and 3 cm respectively) than *Prunus avium* (18 cm) and *Quercus petraea* (14 cm). Survival between May and September followed a similar pattern: 23% for *S. torminalis* compared to 6% for *C. betulus* and 37% for *P. avium* (Balandier, Frochot & Sourisseau 2009).

Köckemann (2008) provides evidence that *S. torminalis* occupies a narrower niche at the eastern edge of its range, being increasingly restricted to moderately dry and very dry soils, and also increasingly alkaline soils in the east of its range in Slovakia, than in the centre of its range in central Germany. This restriction in soil types is associated with a corresponding decline in regional abundance of *S. torminalis* from 0.25% cover within Germany to 0.006% within Slovakia. Its ability to cope with, and even require, hot, dry, open conditions is also seen towards the south of its range in north Sardinia: the mortality of planted 1-year-old seedlings of *S. torminalis* was >78% over 12 years, survivors reaching just 35-40 cm high, but this was on a par with the Mediterranean specialist *Quercus ilex* (Schirone, Salis & Vessella 2011). Nevertheless, in the dry southern Balkans, populations of *S. torminalis* under beech were small (<65 individuals) and up to 50% were damaged by dry conditions (Dimitrov & Ginova 2008). Reproduction appears to be better in more continental climates; Rasmussen & Kollmann (2004b) noted poor reproduction in a Danish population while Bednorz, Kaźmierczak & Kaczmarek (2012) found an expanding population in northern Poland.

Genetic diversity in *S. torminalis* is generally high between populations (VIII(A)) but shows a strong decrease with latitude, as it does for many woody species in Europe (Fady & Conord 2010). At the northern edge of the range, diversity between populations is higher (Rasmussen & Kollmann 2008) since gene flow (outbreeding) between populations is

comparatively low due to their long-term isolation from each and higher levels of genetic drift. Populations in Switzerland and parts of Germany show similarly high diversity between populations, also attributed to reproductive isolation of the small populations (generally <100 trees) (Finkeldey *et al*. 2000; Rotach 2000; Biedenkopf, Ammer & Müller-Starck 2007). By comparison, genetic diversity between populations is very low in the centre of its range in France due to larger populations and increased gene flow (Demesure *et al*. 2000a; Oddou-Muratorio *et al*. 2001c).

By contrast, genetic diversity within populations shows a reverse pattern with allelic diversity lower in the north (1.8-4.6 alleles per locus) and in Switzerland (6.4 alleles per locus in a small population) compared to 10.7 alleles per locus in France (Hoebee et al. 2006; Oddou- Muratorio *et al*. 2001b; Rasmussen & Kollmann 2008). This is partly due to greater clonal perennation in the north, and greater outbreeding between populations in the centre but also because the central populations are larger and hold higher genetic variation. However, this geographical pattern tends to be diluted by planting if seeds from a limited number of trees in a stand or from stands with only a few trees are used, lowering the genetic diversity (Biedenkorf *et al*. 2007). The implication for forest management is that isolated populations would benefit from increased connectivity through the restoration or re-creation of landscape corridors (Hoebee *et al*. 2007).

There is no doubt that the frequency and abundance of *S. torminalis* in different habitats has been extensively modified by human planting, certainly on more productive sites with deeper soil in mainland Europe (Szymura 2012). Indeed, most of the large populations in Europe are found where coppice management was practiced until the end of the nineteenth century (Lloyd 1977). The creation of high forests, especially by transformation and conversion of coppice forests into high forests, is often cited as one of the reasons for the decline of *S. torminalis* – see XI. Forest management involving the creation of woodland edges (Maděra *et al*. 2012) and the removal of competing canopy trees (especially beech) and herbaceous species is considered beneficial to *S. torminalis* (Crave 1985; Wilhelm 1993; Wilhelm & Ducos 1996). In southern France, *S. torminalis* has been seen to benefit from plastic tree shelters: after 4 years, trees inside shelters were *c*. 190 cm compared to 130 cm without shelters (Dupraz 1994), although, as with many species, shelters may prove detrimental in shaded conditions due the increased shading (Rodney Helliwell, personal communication). Seedlings are very sensitive to herbicide treatments (Oria de Rueda 2008).

Height growth is generally described as slow, but is often quicker than associated forest species, and reaches a maximum on dry sites where low water availability has a greater debilitating effect on competing species such as *Quercus* spp. and *Fagus sylvatica* (Kausch-Blecken von Schmeling 1994b; Schrötter 2001). Growth also varies across the range of *S. torminalis* from 35-60 cm yr^{-1} in Germany (Kausch-Blecken von Schmeling 1993, 1994b; Schüte 2000) to a mean of 21 cm yr^{-1} in northeast Romania and Moldavia (Sjöman, Nielsen & Oprea 2012). However, age of the tree appears to be a more important determinant of growth, with annual growth rates of between 20-100 cm yr^{-1} in the first 10-18 years, falling to 15-25 cm yr^{-1} at 50 years old and 5 cm yr^{-1} at 70 years old (Crave 1985; Bamberger 1990; Röhrig 1972; Schüte 2001; Kahle 2004). In shaded trees, maximum height is reached within 20-30 years (Sevrin & Keller 1993) but in more open conditions growth continues for 80-100 years (Demesure-Musch & Oddou-Muratorio (2004). In France mean heights have been recorded as 13.4 m at 20-49 years, 15.9 m at 50-79 years and 18.7 m in trees older than 140 years (Sevrin & Keller 1993).

Stem diameter growth varies with competition, and annual ring width may be as low as 1-2 mm in woodland while individuals in the open can have ring widths of 2.5-4.0 mm (Sevrin & Keller 1993; Hochbichler 2003; Kahle 2004; Sjöman, Nielsen & Oprea 2012) although Ramussen (2007) recorded mean tree ring widths of up to 16.1 mm in central Germany. Age is also a large factor in diameter growth. In *Quercus petraea* woodland in southwest Germany, Pyttel, Kunz & Bauhus (2013) found that annual radial increment averaged 1.9-2.2 mm yr^{-1} during the first 8 years after establishment, then decreased to <0.7 mm yr^{-1} at around 25 years and remained constant thereafter. After 50-70 years, diameter growth becomes very small or even appears to cease (Crave 1985; Drapier 1993c). In north Poland, Bednorz, Kaźmierczak & Kaczmarek (2012) found that DBH was most strongly correlated with crown diameter ($r^2 = 0.830$) whereas Pyttel, Kunz & Bauhus (2013) in southwest Germany found a positive relationship between DBH in centimetres and tree height in metres (y = 0.799 x + 1.125, $r^2 = 0.71$), and in north France, Oddou-Muratorio *et al.* (2004) found DBH was related to age: DBH = $16 \times \ln(\text{age}) - 39$ ($r^2 = 0.73$).

Maximum age of *S. torminalis* is highly variable and dependent on growing conditions. At the northern and eastern edges of its main range, trees live for 100-200 years (Haralamb 1967; Stănescu, Şofletea & Popescu 1997; Ramussen 2007), whereas trees in the centre and to the western (oceanic) edge of its range live for 200-300 years (Crave 1985;

Drapier 1993a; Roper 1993; Demesure-Musch & Oddou-Muratorio 2004; Maděra *et al.* 2012) and even up to 400 years (Favre-d'anne 1990; Hurt & Kantor 2004).

(C) EFFECT OF FROST, DROUGHT, ETC.

Seedlings can be damaged by frost but once cold hardened, saplings and older trees can tolerate low winter temperatures (Haralamb 1967; González, Rey de Viñas & Cisneros 2003; Rasmussen 2007) down to -31 to -34 °C (Schüte 2000). However, spring frosts and particularly early autumn frosts can kill unhardened terminal buds leading to forking into two or more co-dominant shoots (Pietzarka, Lehmann & Roloff 2009).

Sorbus torminalis is very tolerant of droughts that last a few months (Haralamb 1967; Ellenberg 1988; González, Rey de Viñas & Cisneros 2003) which it achieves by being isohydric, due to a certain degree through stomatal control (VI(E)). Hydraulic conductivity was measured in northeast Spain at >0.5 mmol m^{-2} MPa^{-1} s^{-1} in July and remained high following a dry period through till August. Stomatal conductance however, dropped from *c.* 0.05 mol H$_2$O m^{-2} s^{-1} in July to <0.01 in August (Martínez-Vilalta *et al.* 2002). But in more intense droughts, Martínez-Vilalta *et al.* (2002) found that it was vulnerable to xylem embolism, similar in degree to *Quercus ilex*, *Acer monspessulanum*, *Arbutus unedo* and *Cistus laurifolius*, loosing >75% of maximum hydraulic conductivity during a summer drought in evergreen oak forest in northeast Spain. Foliar senescence was higher in *S. torminalis* and *A. monspessulanum* than in the other seven species tested. Thus prolonged drought can lead to reduced growth and potentially a greater susceptibility to pests and diseases (Hemery *et al.* 2009).

Sorbus torminalis is tolerant of short-term flooding (Drapier 1993b). Little has been written about the fire tolerance of *S. torminalis* but the thin bark and typical closeness of the canopy to the ground would suggest intolerance by the above-ground portion, but it is highly likely to sucker prolifically after fire. Indeed, Quevedo, Rodrigo & Espelta (2007) found all 36 plants investigated had resprouted after prescribed management fire in northeast Spain.

VI. Structure and physiology
(A) MORPHOLOGY

In open conditions, the crown is rounded, ovate with strong orthotropic development of many lateral, angled branches, while under shade it tends towards being narrow with a main vertical shoot (Barnola, Durand & Parmentier 1993; Drapier 1993c; Sevrin & Keller 1993). The

canopy is composed of a mix of long and short shoots; short shoot spurs can be up to 66 years old. In Britain, there are two main canopy forms: medium to large trees favouring woodland edges on boulder clay, and sprawling multi-stemmed shrubs with no dominant leader, such as found at Monks Wood, Huntingdonshire (Henry Girling, personal communication). Both forms are also seen in mainland Europe with the shrubby form described by Nicolescu *et al*. (2009) as being of 'chandelier' habit with multiple forks and lateral shoots. The upright, single trunked trees are now less frequent due to repeated cutting of the best trees which has led to inferior specimens remaining (Kausch-Blecken von Schmeling & Kellner 2006).

In shade, self-pruning of dead branches is rapid leaving a clean trunk (González, Rey de Vinãs & Cisneros 2003; Oria de Rueda, Martínez de Azagra & Álvarez 2006) but when well spaced in the open, dead branches do not readily fall and brashing of plantations is needed to produce merchantable stems (Crave 1985; Drapier 1993c; Sevrin & Keller 1993). When pruned, few epicormic branches are produced (Lanier *et al*. 1990; González, Rey de Vinãs & Cisneros 2003). The readiness to fork at <3 m, as noted above, and the frequent slight twisting and leaning towards the light is a constraint in the production of veneer and other high quality logs (Drapier 1993c; Sevrin & Keller 1993; Wilhelm 1993; Ramussen 2007). Formative pruning is sometimes necessary to prevent development of the chandelier form (Crave 1985; Drapier 1993c; Wilhelm 1993).

Sorbus torminalis can readily reach 30 m in mainland Europe and even 32-33 m in France and Germany, (Lanier *et al*. 1990; Sevrin & Keller 1993; Kausch-Blecken von Schmeling 1993) and up to 1.0-1.4 m DBH (Drapier 1993a; Kausch-Blecken von Schmeling 1993; Demesure-Musch & Oddou-Muratorio 2004; Kausch-Blecken von Schmeling & Kellner 2006; Oršanić *et al*. 2009). Trees in Britain do not reach such a size but a specimen at Wormley Wood, Broxbourne, Herts was reported in 2011 to be 28.5 m tall, 78 cm DBH with 3 m of clear stem and a canopy diameter of 14 m (Henry Girling, personal communication).

The wood is moderately dense at 640 kg m^{-3} (Safdari *et al*. 2008), similar to birch, and is not durable in contact with the ground (Wagenführ 1996). However, the wood carbon content at 355 kg C m^{-3} is high compared to that of woodland species with dense wood, such as 325 kg C m^{-3} in *Quercus robur* and 320 kg C m^{-3} in *Taxus baccata* (Puhe & Ulrich 2001). There is usually little differentiation between the light-coloured sapwood and heartwood, but the wood becomes redder sometimes with a brown core in older, slow-grown trees (Sevrin, Lachard & Mansouri 1993; Hochbichler 2003) and of less commercial value (Raguin & Boulet-Gercourt 2000). The bark is comparatively thin, decreasing with increasing diameter

from 12 to 8% of log volume (Kahle 2004). Growth ring boundaries are indistinct, as in many diffuse porous woods, but there is sometimes a narrow band of slightly larger pores at the beginning of the early wood (Safdari *et al*. 2008). Vessels are mostly solitary, 939-992 μm long and 20-27 μm wide in late and earlywood, respectively, with higher vessel area in the earlywood (Sevrin, Lachaud & Mansouri 1993); vessels are joined by numerous large (*c.* 7 μm) bordered pits (Lachaud & Maurousset 1996; Pietzarka, Lehmann & Roloff 2009). Physical, mechanical and chemical properties of *S. torminalis* wood are summarised in Wagenführ (1996). Wood structure and growth details are given by Sevrin, Lachaud & Mansouri (1993), Safdari, Sigarody & Ahmed (2011), Lachaud & Mansouri (1993) and Lachaud & Maurousset (1996), and silvicultural management to achieve high value trunks is discussed by Wilhelm (2009).

One year-old seedlings have been seen with a maximum root depth of 32.0 cm (mean 23.1 cm) increasing to 40-60 cm in 2-3 year-old seedlings (Schüte 2000). Once roots reach 50-70 cm in depth, increasingly strong and far-reaching lateral roots create a heart root-system (Herman 1971). On porous soils, roots may reach 1-2 m depth (Schüte 2000).

The most morphologically variable character of *S. torminalis* is leaf shape (Pietzarka, Lehmann & Roloff 2009; Fig. 3). Leaves are more dissected, more pubescent on the underside and generally more variable in outline towards the south and east of its range (Bean 1980; Rich *et al*. 2010). Bednorz (2006) found that leaves had more lobes and a decreasing distance between the second and third lateral veins with increasing distance south in Poland. However, Kárpáti (1960) has pointed out that even within individual trees, leaves vary depending upon the type of shoot and position on the tree. Indeed, Bednorz (2006) observed that leaves were smaller on short shoots compared to long shoots at the top of the tree, but had a longer petiole (mean of 3.72 and 3.50 cm, respectively). On long shoots the angle between the midrib and the vein in the lowest pair of lobes was larger (mean of 71.80° and 66.71° in long and short shoots, respectively) so the bottom lobes project more on long shoots. The base of leaves from short shoots were most often truncate (40% of leaves measured), cordate (33%) or cuneate (27%) while on long shoot leaves were mostly cordate (54%) or truncate (39%) and rarely cuneate (8%). No difference was found in the proportion of leaves with numerous hairs (37-39%), a few hairs (54%) and no hairs (6-9%). Bednorz concluded that leaves on short shoots better characterise interpopulational variability in *S. torminalis*, and are therefore best used for identification. On the strength of this variation it is possible that some forms of *S. torminalis* based on leaf morphology (e.g. forma *perincisa*

(Borbás & Fekete) Beck) and forma *mollis* Beck) encompassed within Bednorz's study may represent normal variation seen in most populations.

Stomatal density ranges from 171-220 mm^{-2} (Şofletea *et al*. 2005; Čaňová *et al*. 2012) with individual stoma on mature leaves (24 days after bud opening) measuring 29.20 ± 0.50 (SE, *n* = 60) in length and 19.13 ± 0.33 μm wide (Čaňová *et al*. 2012).

Idžojtić, Zebec & Drvodelić (2006) noted some variation in fruit and leaf morphology within populations and greater variation between populations. McAllister (2005) suggests that fruit length is more constant than width in the British Isles and is thus a useful characteristic by which to distinguish between *Sorbus* species but Bednorz (2007a) found that fruit width was more constant than length in Poland despite variable numbers of seeds produced. Other than this, there are few geographic trends in fruit or seed traits, certainly in Poland (Bednorz 2007a, Bednorz *et al*. 2006b).

(B) MYCORRHIZA

Harley & Harley (1987) record *S. torminalis* as being only ectomycorrhizal, unlike other *Sorbus* species native to Britain that are also arbuscular mycorrhizal (AM). However, Moradi *et al*. (2014) observed 51.0-68.5% of 1 cm long root sections to be colonised by AM fungi of unknown species in northern Iran. Lower colonisation of roots by fungi in the autumn (32.4-55.3% of roots) was initially thought to be due to changes in seasonal soil chemistry but no correlation was found between root colonisation and soil chemistry. Similarly AM fungal spore density from soil surrounding the roots (56-81 spores g^{-1} soil) was not correlated to soil chemistry. Wehrelen *et al*. (2009) report on trials to establish the Burgundy truffle (*Tuber uncinatum* Chatin: Ascomycota, Pezizales) as an ectomycorrhizal symbiont on *S. torminalis* in southern China although specific results are not given. *Acaulospora viridis* Palenz., Oehl, Azcón-Aguilar & G.A. Silva (Diversisporales, Glomeromycota), which has formed AM associations with *Sorghum vulgare* and *Trifolium pratense* in pot cultures, has been found within the rhizosphere of *S. torminalis* in Spain and is suspected of forming AM with the tree (Palenzuela *et al*. 2014).

(C) PERENNATION: REPRODUCTION

Sorbus torminalis responds well to coppicing and pollarding (Harper 1981). Suckers are produced profusely from roots in mainland Europe but less so in Britain. Since establishment from seed can be comparatively rare, particularly at the edges of its range and in deep shade,

the majority of established trees in these marginal areas tend to be produced vegetatively from root suckers (Roper 1993; Pleines 1994; Rasmussen & Kollmann 2004b, 2007). Rasmussen & Kollmann (2008) observed that at the northern end of its range in Denmark, 94-100% of trees were of sucker origin. Even in the British Isles where it is weakly suckering it is suggested that many trees originate from suckers, including those in Epping Forest and West Sussex (Evelyn 1664; Lloyd 1977). Propagation from suckers in Britain can be very difficult (Henry Girling, personal communication) but even early planters such as Cook (1679) advocated planting elm, cherry, poplar and *S. torminalis* from "running roots". Nearer the centre of its European range, there is less reliance on suckering (Rameau, Mansion & Dume 1989). On three sites in southwest Germany, with an average of 241 trees taller than 1.3 m, only 43% showed signs of originating from suckers (Pyttel, Kunz & Bauhus 2013). Similarly, in north France, Oddou-Muratorio *et al*. (2004) found that only 8 stems of 185 individuals were from suckers. Demesure-Mush & Oddou-Muratorio (2004) suggested that *S. torminalis* colonises disturbed areas primarily by vegetative suckering. Certainly, repeated suckering allows its long-term persistence in otherwise suboptimal sites (Rasmussen & Kollmann 2007).

Suckers are more shade tolerant than seedlings and grow quickly in height in the first 10–15 years (Crave 1985; Savill 1991) and although the growth slows considerably after this time, the suckers fare better than seedlings in shaded environments under a tree canopy, increasing their relative abundance (Nicolescu *et al*. 2009). Rasmussen & Kollmann (2007) found that the annual mortality of suckers on Baltic Sea islands was 17%, lower than expected for tree seedlings.

Unlike coppice shoots, most suckers grow from trees with intact canopies (Harper 1981), especially when the roots are near the surface or damaged (Drapier 1993c; Wilhelm 1993; Wilhelm & Ducos 1996; Rich *et al*. 2010). Investigation has shown that suckers typically arise from roots 10-15 cm deep on trees older than 10-20 years (Pietzarka, Lehmann & Roloff 2009). The distance of suckers from the parent tree is very variable, but most often within 5-15 m (Germain 1993; K.K. Rasmussen unpubl. data cited in Rasmussen & Kollmann 2004b), more occasionally 25-30 m (Favre-d'anne 1990; Lanier *et al*. 1990; Drapier 1993c; Germain 1993; Hoebee *et al*. 2006) and exceptionally up to 110 m (Lloyd 1977).

Sorbus torminalis can be micro-propagated *in vitro* from shoot tips, axillary buds, nodal segments and embryos (Chalupa 1992; Battut, Grenier & de March 1993; Malá *et al*. 2009, Máchová *et al*. 2009).

(D) CHROMOSOMES

$2n = 34$ (Bailey *et al*. 2008). *Sorbus torminalis* is diploid but tetraploids have been reported from Spain (Aldasoro *et al*. 2004) and a triploid ($2n = 51$) has been recorded in Serbia by Siljak-Yakovlev *et al*. (2010), possibly of hybrid origin since British individuals show a very stable level of ploidy (Pellicer *et al*. 2012). The genome size of *S. torminalis* has been reported as $2C = 1.612 \pm 0.002$ (SD) pg ($1C = 792.180$ Mbp) from English material (Pellicer *et al*. 2012) and $2C = 1.49 \pm 0.02$ (SD) pg ($1C = 728.61$ Mbp) in Bosnia and Herzegovina (Siljak-Yakovlev *et al*. 2010). The genome is slightly larger than that of two other main sexual diploid species, *S. aria* and *S. aucuparia* (Pellicer *et al*. 2012).

(E) PHYSIOLOGICAL DATA

Sorbus torminalis performs best on deep, warm, moist fertile soils but is also tolerant of short droughts (V(C)). However, low water availability and high temperatures reduce growth. Rasmussen (2007) found that annual tree ring growth along a transect from the centre to the northern limit of distribution was negatively correlated to mean monthly summer temperature (July and August) in the previous year, and to spring and summer months in the present year at some sites. This may be attributable to water stress due to increased evapotranspiration. Monthly precipitation was less critical for growth although at some sites there was a positive relationship between spring and summer precipitation of the previous growing season and growth. The highest growth rates were associated with intermediate precipitation, suggesting that water availability is the key in controlling growth. No latitudinal gradients in climatic response were found.

Nutrients are unlikely to be limiting since *S. torminalis* can tolerate a wide range of soil fertility. It is also largely indifferent to soil pH (Drapier 1993b) and is probably fairly resistant to the influence of heavy metal ions. Kol'Tsova (1980) records that *S. torminalis* can accumulate higher levels of heavy metals in the fruits than other species of the genus. David & Gillon (2009) found that the leaf litter had 1.28-1.31% N and 54.7-52.5% C giving a C:N ratio of 40.2 to 42.7, which is fairly typical of other forest trees in France.

Sorbus torminalis is the most shade-tolerant member of the genus in the British Isles with an Ellenberg value for light of 4 whereas all other British *Sorbus* species are 5-7 (Ellenberg 1988). Nevertheless, the light requirement of *S. torminalis* has been variously reported as being shade-demanding (Gonzalez *et al*. 2010), shade tolerant (Müller-Kroehling & Franz 1999; Pyttel, Kunz & Bauhus 2013), partially shade tolerant (Haralamb 1967; Ellenberg 1988; Lanier *et al*. 1990; Fehr 1993; Schütte 2001; Oria de Rueda, Martínez de Azagra & Álvarez 2006; Paganová 2007, 2008), shade intolerant (Evans 1988; Savill 1991; Bednorz 2007b, c; Kotar 2001; Oddou-Muratorio *et al*. 2006; Rich *et al*. 2010; Maděra, Tichá & Řepka 2013) and very shade-intolerant (Belletti, Monteleone & Ferrazzini 2008). This variation can be partially attributed to the fact that *S. torminalis* is more tolerant of shade when young, gradually becoming more light demanding over the first decade of its life (Oršanić *et al*. 2009). Another factor is that the shade classification of *S. torminalis* depends upon whether growth or survival is measured. Pyttel, Kunz & Bauhus (2013) noted that *S. torminalis* rapidly slows its growth at around 8 years, as do many shade-intolerant species. Yet, it can survive in a seedling/sapling bank with limited annual growth with the ability to respond rapidly to release from shade, even when 150 years old (Rasmussen 2007), as do many shade tolerant species.

Pyttel, Kunz & Bauhus (2013) found that mean maximum photosynthesis of sun leaves of understorey trees in southwest Germany (8.53 ± 0.65 (SD) μmol CO_2 m^{-2} s^{-1}) was lower than values reported for other woodland trees. Moreover, values for shade leaves reached 5.96 ± 0.65 μmol CO_2 m^{-2} s^{-1}, similar to the shade-tolerant *Fagus sylvatica*. The light compensation point was at a light flux density of 25.4 μmol PAR m^{-2} s^{-1} for sun leaves and 7.2 μmol m^{-2} s^{-1} for shade leaves. These values are not as low as in *Carpinus betulus*, *Tilia platyphyllos* or *Acer pseudoplatanus* but similar to *Fraxinus excelsior*, *Quercus petraea* and *F. sylvatica* suggesting a partial shade tolerance. The light compensation point was far lower than for shade intolerant *S. domestica*. Dark respiration of shade and sun leaves (-0.73 and -1.57 mol CO_2 m^{-2} s^{-1}, respectively) was higher than in *F. sylvatica* and *T. platyphyllos* and may help explain the slow growth in shade (Pyttel, Kunz & Bauhus 2013). Slow growth appears to be associated with a low photochemical efficiency: chlorophyll a fluorescence was investigated by Čaňová *et al*. (2012) and maximum photochemical efficiency of PSII (F_v/F_m) was 0.797 ± 0.007 (SE, n = 40) – low compared to other *Sorbus* species tested; initial fluorescence ratio (F_v/F_o) was 3.968 ± 0.080 – lowest of the *Sorbus* species tested.

(F) BIOCHEMICAL DATA

A number of phenolic compounds have been isolated from the leaves, inflorescences and fruits of *Sorbus torminalis* including caffeic acid and p-coumaric acid, flavanoids such as vitexin, apigenin, luteolin, quercetin and torminaloside, sterols such as cholesterol, campesterol, stigmasterol and sitosterol, and fatty acids including myristic, palmitic, palmitoleic, stearic, oleic, linoleic and linolenic acids (Tsitsa-Tzardi & Loukis 1991; Tsitsa-Tzardi, Loukis & Philianus 1992; Olszewska & Roj 2011; Hasbal, Yilmaz-Ozden & Can 2015). In the subgenus Torminaria, flavone O-glycosides and the C-glycoside vitexin have also been reported as being unique to *S. torminalis* (Challice & Kovanda 1978). A number of triterpenoids have been identified from the bark (Huneck 1962). Very low levels of abscisic acid (30 nmol l^{-1}) have been measured in phloem exudate, the lowest of any of the 14 tree species tested (Weiler & Ziegler 1981).

VII. Phenology

Leaf-buds begin to swell in March and first leaves develop in early April through to May in older individuals (Pietzarka, Lehmann & Roloff 2009). Flowers within a tree open sequentially from late April into May (Oddou-Muratorio *et al*. 2006) so that flowers from tight bud to those with petals falling are found on the same tree. The flowering period is typically quite short; in eastern Poland it is only 5-14 days per tree (Bednorz & Urbaniak 2005) but synchronous between trees (Klein, Desassis & Oddou-Muratorio 2008). Fruit ripens rather late, occasionally from late July but usually from September though to November and fruits may still be on the tree in January (Snow & Snow 1988; Bednorz & Urbaniak 2005; Rich *et al*. 2010). Leaves show autumn colouration in mid-September to October with leaf fall from early October to the middle of November (Bednorz & Urbaniak 2005). As with many trees, temperature rather than precipitation is the main driver of annual variation in phenology, at least in Poland (Bednorz & Urbaniak 2005).

In trees under the shade of a canopy, shoot elongation has been reported to occur in late May, early June with a second but smaller burst of growth in September/October with no discernible growth in the 2.5 months between (Barnola, Durand & Parmentier 1993).

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

Flowering begins comparatively early in life and occurs in trees <10 years old (Demesure-Musch & Oddou-Muratorio 2004) although abundant and frequent seed production does not starts until trees reach 15-30 years old with good seed years occurring every 2-3 years (Haralamb 1967; Favre-d'anne 1990; Savill 1991; Oršanić *et al*. 2009; Pietzarka, Lehmann & Roloff 2009). Not all trees flower every year; in Switzerland, Hoebee *et al*. (2007) noted that 50-70% of trees flowered in any one year. Pollen production is related to tree size (particularly high in trees ≥50 cm DBH which physically hold more flowers) and is also high in dominant and woodland edge trees under reduced competition (Odduo-Muratorio *et al*. 2005).

Flowers are pollinated by insects (Hymenoptera, Diptera and Coleoptera), mostly small flies but the large and open flowers attract other generalist pollinators such as beetles and bees including bumblebees (Prat & Daniel 1993; Demesure-Musch & Oddou-Muratorio 2004; Rasmussen & Kollmann 2004b; Oddou-Muratorio *et al*. 2006). Pollen dispersal is aided by sequential flowering within a corymb. Pollen grains are elliptic, 22-40 μm in diameter, 3(4)-colporate, and of medium size compared to other species within the genus (Bednorz *et al*. 2005). Pollen viability is affected by both temperature and humidity (Termena 1972) and was found by Price & Rich (2007) to vary around England between 50 and 100%, with a mean of 75%.

Outcrossing is the predominant mating system, due to high self-incompatibility and high abortion rates of any inbred seeds produced; apomixis is rare (Wojciechowski & Bednorz 2000; Rasmussen & Kollmann 2004b; Klein, Desassis & Oddou-Muratorio 2008). The rate of self-fertilisation is usually low, from 0-2% with variation between mother trees (Demesure-Musch & Oddou-Muratorio 2004; Rasmussen & Kollmann 2004b; Oddou-Muratorio, Klein & Austerlitz 2005) although selfing becomes more common in isolated stands, reaching 2-29% in two Swiss stands with a maximum individual selfing rate of 54% in small, isolated stands (Hoebee *et al*. 2007).

As expected from a largely out-breeding tree, *S. torminalis* has been found to be genetically diverse within and between populations with strong gene flow (Bednorz & Krzakowa 2002; Bednorz, Myczko & Kosiński 2004, 2006; Demesure *et al*. 2000a; Hoebee *et al*. 2006, 2007; Oddou-Muratorio *et al*. 2001a, 2004, 2006; Rasmussen & Kollmann 2004b, 2007; Oddou-Muratorio, Klein & Austerlitz 2005; Angelone *et al*. 2007; Espahbodi *et*

al. 2008). *Sorbus torminalis* in Britain has a lower genetic diversity than the other two common sexually reproducing diploid species, *S. aria* and *S. aucuparia* (Proctor, Proctor & Groenhof 1989; Chester *et al*. 2007) and lower than *S. torminalis* in mainland Europe: Chester *et al*. (2007) identified seven different plastid DNA types in Britain (shared with French and Spanish populations) compared to the 25 haplotypes identified through Europe by Oddou-Muratorio *et al*. (2001a). In areas with scattered populations, gene flow has inevitably been found to be lower between populations (Bednorz, Myczko & Kosiński 2006) and subject to greater genetic drift and loss of genetic diversity (Kučerová *et al*. 2010) – see V(B).

Demesure-Musch & Oddou-Muratorio (2004) found that pollen exchange shows two main patterns: preferential mating between neighbouring trees from local pollen dispersal with a mean of 6 pollen donors providing the pollen cloud around a given tree, and also long-distance pollen movement of up to 2.5 km. This is consistent with social bees providing local pollen movement with some (especially bumblebees) flying long distances. Modelling by Austerlitz *et al*. (2004) concluded that the dispersal of *S. torminalis* pollen decreased more slowly than exponential with distance from the tree, suggesting that long distance pollen dispersal is likely. Paternity analysis confirms that long-distance pollen dispersal of up to 2.2 km is possible (Oddou-Muratorio *et al*. 2003) although the average distance is *c*. 750 m, with a median distance of *c*. 500 m and an average effective number of pollen donors per maternal adult of 10 (range 1-23) (Oddou-Muratorio, Klein & Austerlitz 2005, Oddou-Muratorio *et al*. 2008). Long distance pollen dispersal from outside the population was found to be 37-39% for a large Swiss stand (Hoebee *et al*. 2007) and 40% for a large stand in France (Oddou-Muratorio, Klein & Austerlitz 2005). However, in smaller and more isolated stands this was reduced to 4% but still demonstrates that this small amount of pollen had travelled 1.25-6 km (Hoebee *et al*. 2007). Wirth *et al*. (2005) suggests that up to 5% of *S. torminalis* pollen had been transported >6 km.

From microsatellite studies in a mixed oak stand in north France, Klein, Desassis & Oddou-Muratorio (2008) found that male reproductive success of 172 *S. torminalis* trees was affected by distance between trees (reducing the population to an effective size of 122 'pollen donors') and variability in pollen production between trees (reducing the effective population to 53 trees). Conversely, for female success, isolated trees received a greater diversity of pollen and more long-distance pollen, seemingly because they attracted pollinators from a wider range who had visited more pollen-producing trees. Very isolated trees, however, had

poorer seed production presumably due to lower visitation by pollinators. Less isolated trees tended to be pollinated by fewer, more local trees. Moreover, when competition for pollinators was strong in a French population, the attractiveness of an individual to pollinators, determined by the size of the canopy and number of flowers, resulted in larger trees received a greater diversity of pollen (Oddou-Muratorio *et al*. 2006). They also found that 30% of seeds within a single fruit were found to share the same father and 11% of seeds in different fruits on the same tree (Oddou-Muratorio *et al*. 2006). Both pollen- and seed-mediated gene flow are equally important in propagating the genes of *S. torminalis*; (Oddou-Muratorio *et al*. 2001, 2004) give the pollen/seed migration ratio as 2.21, one of the lowest found in woody plants suggesting that rare long-distance dispersal of pollen and seed are equally important in determining genetic diversity. Petit *et al*. (2003) used chloroplast DNA to track gene flow through seeds, and for *S. torminalis* genetic distance between populations (G_{ST}) was 0.33, similar to the understorey species *Crataegus monogyna* and *Rubus* spp., higher than in light, wind-dispersed seeds of *Salix caprea* (0.09) but much lower than in *Quercus* sp. (0.84) and *Fraxinus excelsior* (0.86). Others have measured G_{ST} as low as 0.13 (Prat & Daniel 1993; Oddou-Muratorio *et al*. 2001b; Bednorz & Krzakowa 2002).

(B) HYBRIDS

Sorbus torminalis is the diploid female parent of hybrids in the subgenus Tormaria, including *S*. x *decipiens* (=*S*. x *tomentella* Gand., *S*. x *vagensis* Wilmott), *S. latifolia* (Lam.) Pers., *S*. x *confusa* Gremli, *S*. x *semiincisa* Borbas and *S*. x *eximia* Kovanda, caused by introgression of *S. aria* into *S. torminalis* (Sell 1989; Prat & Daniel 1993; Aas *et al*. 1994; Rudow & Aas 1997; Fay *et al*. 2002; Chester *et al*. 2007; Price & Rich 2007; Rich *et al*. 2010; Robertson *et al*. 2010; Pellicer *et al*. 2012; Stace, Preston & Pearman 2015), and another hybrid of *S. porrigentiformis* E.F. Warb. *sensu lato* introgressed into *S. torminalis* (Rich *et al*. 2014). *Sorbus rupicola* (Syme) Hedl. x *S. torminalis* could also exist due to the occurrence of both species in close proximity on limestones in northern England (Stace, Preston & Pearman 2015). In central Germany, Leinemann *et al*. (2010) found hybridization occurred in both directions, and in France 75% of hybrids have *S. torminalis* as the father (Oddou-Muratorio *et al*. 2001b). The hybrids have lower pollen and seed fertility than the parents and they do not appear to backcross with the parents (Price & Rich 2007) though there is evidence of minor backcrossing with *S. torminalis* in France (Oddou-Muratorio *et al*. 2001b).

Sorbus torminalis has also been identified as the female parent of *S. bristoliensis* Wilmott, breeding with a member of the *S. aria* aggregate (Wilmott 1934; Nelson-Jones, Briggs & Smith 2002; Chester *et al*. 2007), which is likely given the geographic overlap between both parents and the hybrid (Proctor & Groenhof 1992). A number of other microspecies in Britain have been suggested to have *S. torminalis* as a parent on the evidence that they contain flavone O-glycosides, otherwise unique to *S. torminalis*; these include *S. decipiens* (Bechst.) Irmisch in Petzold & Kirchner and *S. devoniensis* E. F. Warb. (Sell 1989). In other cases (for example, *S.* x *houstoniae* Rich) these would require unreduced (i.e. diploid) *S. torminalis* gametes and unbalanced subgenus *Aria* male gametes and these have not been recorded in *Sorbus* (Robertson, Newton & Ennos 2004).

Sorbus intermedia, native to the Baltic region, is considered a tetraploid triple hybrid between *S. aucuparia*, *S. aria* and *S. torminalis* (Nelson-Jones, Briggs & Smith 2002). *Sorbus cordigastensis* N. Mey has been reported by Aas & Kohles (2011) as a hybrid of *S. aria* and *S. torminalis* in Bavaria. In the Czech Republic, various hybrid apomictic triploids are reported that involve *S. torminalis*, including *S. omissa* Velebil, *S. bohemica* Kovanda, *S. portae-bohemicae* M. Lepší, P. Lepší, Vít et Boublík, *S. milensis* M. Lepší, K. Boublík, P. Lepší et P. Vít and *S. albensis* M. Lepší, Boublík, P. Lepší et Vít (a hybrid between *S. danubialis* (Jáv.) Prodan and *S. torminalis*), *S. eximia* Kovanda (between *S. aria* or *S. danubialis* and *S. torminalis*) and *S. barrandienica* Vit, M. Lepsi et P. Lepsi (Jankun & Kovanda 1987, 1988, Lepší et al. 2009, Velebil 2012, Vít, Lepší,& Lepši 2012). Németh (2012, 2015) also reports *S. barabitsii* Cs. Németh and *S. polgariana* Cs. Németh in northwest Hungary as triploid hybrids involving *S. torminalis*. Mikoláš (1996) reports the apomictic triplod *S. dolomiticola* Mikoláš sp. nov. arising as a hybrid between *S. torminalis* and *S. sanubialis* (Jáv.) Prodan agg. in eastern Slovakia.

A rare hybrid between *S. torminalis* and *Malus sylvestris* has been described, named x *Malosorbus florentina* (Zucc.) Browicz (=*Sorbus* x *florentina* (Zucc.) Hedlund), native to Greece (Christensen 1995), although Qian *et al*. (2008) gives convincing evidence that this is a species in its own right (*Malus florentina* (Zuccagni) C.K. Schneid.).

(C) SEED PRODUCTION AND DISPERSAL

Climatic conditions affect the ability of *Sorbus torminalis* to produce flowers, fruit and viable seed. Even under optimal warm and dry conditions in Britain most trees only produce fruit every other year. Under less optimal conditions, particularly at the edge of its range, it fruits

even less frequently (Roper 1993). In Switzerland and Croatia good seed years have occurred 2-3 years apart (Barengo, Rudow & Schwab 2001; Oršanić *et al.* 2006, 2009) falling to every 25 years in northern Poland (Conwentz 1895). At the northern end of its range, flowering is common but few mature fruits are produced (Rasmussen & Kollmann 2007). As is common in the Rosaceae, Rasmussen & Kollmann (2004b) observed 75-85% abortion of immature fruits during the first 8 weeks after pollination.

Fruits become darker as they ripen and soften after bletting, usually by frost (Snow & Snow 1988). In England, the number of fertile seed per fruit was found to vary from 1.37 ± 0.13 (SE, *n* = 27) in the Wye Valley to 2.63 ± 0.17 (*n* = 30) in Leigh Woods near Bristol, with an overall mean of 1.9 ± 0.076 (*n* = 174) (Price & Rich 2007). In Staffordshire, the norm is 1 seed per fruit, but samples of fruits from 3 different trees in 2014 showed 8-15% of fruits with 2 seeds and 2-3% with 3 seeds (but which were all shrivelled and non-viable). Similar norms have been found across the range of *S. torminalis*, from Spain to Iran (Herrera 1987; Espahbodi *et al.* 2007a) but higher numbers have been reported; up to 4 seeds per fruit in Italy (Belletti, Monteleone & Ferrazzini 2008) and occasionally 5-6 in Poland and Switzerland (Bednorz 2007a; Hoebee *et al.* 2007). Warm summers lead to more abundant fruit and more seeds per fruit (Davis 1976). As an example, the number of seeds per fruit was found in Switzerland to depend upon spring weather; Hoebee *et al.* (2007) found 1.28 ± 0.16 (SE, *n* unstated) seeds per fruit in 2001 but only 0.6 ± 0.17 in 2002 following a cold, wet spring that year. This may also explain why Rasmussen & Kollmann (2004b) found a higher number of seeds per fruit at the centre of the range of *S. torminalis* compared to the north edge of its range (2.2 ± 0.07 and 1.9 ±0.07 – SE, *n* unstated – respectively).

Fresh mass of fruit varied from 765 mg in Spain (Herrera 1987; Aldasoro *et al.* 1998) to 990-1170 mg in Denmark (Rasmussen & Kollmann 2004b) and1240 mg (range 890-1710 mg, *n* = 4000) in Iran (Espahbodi *et al.* 2007a). Dry fruit mass in Spain varied from 345-390 mg, giving a fruit moisture content of 49-59% (Herrera 1987; Aldasoro *et al.* 1998). Espahbodi *et al.* (2007a) noted that in Iran, fruit mass was negatively correlated with DBH. Rasmussen & Kollmann (2004b) recorded that fruits resulting from outbreeding (as opposed to experimentally self-pollinated) yielded slightly heavier fruits.

Sorbus torminalis seeds are some of the biggest in the genus, similar in size to *S. aria* (Bednorz, Myczko & Kosiński 2006). Published dry seed mass values are extremely variable but a mean seed dry mass of 20-21 mg appears typical (Herrera 1987; Aldasoro *et al.* 1998). Espahbodi *et al.* (2007a) noted a positive correlation between mean sound seed mass and

mean fruit mass in Iran, but found no correlation between seed size and percentage germination. In Croatia, fruits were seen to increase in length with altitude (226-499 m) but seed mass remained constant (Oršanić *et al*. 2009). By contrast, Rasmussen & Kollmann (2004b) observed that while fruits at the centre of the range of *S. torminalis* were smaller than those from the range edge, the seeds were larger. The smaller fruits from the centre of the range were suggested to be due to complete maturation here and so lower starch content.

Fruit are dispersed primarily by carnivorous mammals such as red fox *Vulpes vulpes* (L.), badger *Meles meles* (L.) and stone marten *Martes foina* (Erxleben) (Herrera 1989; Demesure-Musch & Oddou-Muratorio 2004) aided by other animals such as wild boar (Conwentz 1895) and domestic pigs and cattle (Roper 1993). In southeast Spain, a mean of 10.9 ± 12.4 (SD) seeds of *S. torminalis* per scat were found in the scats of the above carnivores by Herrera (1989). Of 556 seed recovered only 5.2% were damaged. Herrera (1987, 1989) observed that large, scented, fibrous fruits that fall to the ground when ripe are readily eaten by carnivores despite being low in protein and minerals. This included species such as *Juniperus oxycedrus, Ficus carica* and *Sorbus domestica* in addition to *S. torminalis*. The abundant sclereids and high fruit fibre content help protect the seeds during their passage through the gut (Herrera 1989).

Although a number of bird such as redwing (*Turdus iliacus* L.), song thrush (*T. philomelos* Brehm), blackbird (*T. merula* L.) and robin (*Erithacus rubecula* L.) are known to feed on the fruits of *S. torminalis* (Snow & Snow 1988; Herrera 1984, 1989), endozoochorous dispersal of seeds is likely to be ineffective. In southeast Spain, for example, Herrera (1984) found that <20% of large-sized fruit from plants such as *Ruscus aculeatus, Juniperus oxycedrus, Rosa canina* and *Sorbus torminalis* were taken by birds. In this study, *S. torminalis* fruits were taken only by blackbirds and these formed just 1.5% of their diet. At the northern edge of the range of *S. torminalis* in Denmark, 75% of fruits simply fell from the tree and only 20% were presumed to be taken by birds (K.K. Rasmussen unpubl. data cited in Rasmussen & Kollmann 2004b). Various causes for poor dispersal by birds have been suggested, including that the brown colouration of the fruits is not attractive to birds, especially in comparison to brighter fruits carried nearer the ground as in *Crataegus monogyna* (Snow & Snow 1988). Moreover, at the north of its range *S. torminalis* fruit ripens comparatively late and most frugivorous passerines have migrated by this time (Rasmussen & Kollmann, 2004a). In this context, seed dispersal by birds may improve with the higher temperatures and longer growing season due to climate change. A further factor limiting bird

dispersal is that many of the seeds are taken by seed predators, particularly bullfinches (*Pyrrhula pyrrhula* (L.)) and to a lesser extent marsh tits (*Poecile palustris* (L.)), leaving the shredded skins and pulp attached to the tree (Snow & Snow 1988). Some limited dispersal by birds does, however, appear to happen; in France, seedlings of *S. torminalis* are common underneath large oaks presumably because this is where thrushes roost after feeding on *S. torminalis* fruits (S. Oddou-Muratorio, personal observation cited in Oddou-Muratorio *et al.* 2004).

Most seed is dispersed over short distances. In France, established seedlings were found at a mean distance of 174 m from the mother tree, with genetically related clumps of *S. torminalis* 150-300 m in radius. But some seeds disperse much further since 17% of seedlings in the centre of the 470 ha forest originated from outside the stand (Demesure-Musch & Oddou-Muratorio 2004; Oddou-Muratorio *et al.* 2004).

The morphology of fruits and seeds of *S. torminalis* are described by Aldaroso *et al.* (2004), Maciejewska-Rutkowska & Bednorz (2004), Debnorz *et al.* (2006b) and Bednorz (2007a), and development and ontogeny of the fruit epidermis is discussed by Bednorz & Wojciechowicz (2009).

(D) VIABILITY OF SEEDS: GERMINATION

Few fully formed seeds are produced and the viability of seed collected is usually low; Wilmott (1977) found that only 5% of seed tested in Derbyshire were fertile. However, viability of sorted sound seed can easily be >60% and reach 94-97% (Muller & Laroppe 1993; Oršanić *et al.* 2006; Var, Bekci & Dinçer 2010). *Sorbus torminalis* seeds have a deep embryo dormancy, aided by chemical inhibition from the seed coat, that can be overcome by moist stratification at 2-3 °C for 3 months (Devillez 1979; Devillez, Fraipont & Tissot 1980), resulting in most seeds germinating within four months (Var, Bekci & Dinçer 2010) although more uniform germination was obtained by alternating two-week periods at 3 °C and 20 °C followed by 18-20 weeks at 3 °C (Muller & Laroppe 1993). Under the long, cold conditions of continental winters, germination takes place in the spring following seed production but in Britain two or more years may elapse before dormancy is broken, allowing germination (Roper 1993). Delayed germination has also been found in hot dry climates. In Iran, Espahbodi *et al.* (2007a) found 42% germination in 2000 and 14% germination the following year. By contrast, for seeds sown in 2001, germination was 20% and 26% the year after, showing that the lower the first year germination, the higher the delayed germination. At

higher altitudes in Croatia, seeds were more dormant and required a longer period of stratification (Oršanić *et al*. 2009). Seeds will germinate in the dark following stratification (Winkler 1999) and so may benefit from burial. In northern Iran, burial of seeds up to 1.5-3.5 cm deep increased emergence (Espahbodi *et al*. 2002). This effect was not found when the soil was covered with a mulch which suggests that burial better improves water supply to the seed or young pre-emergent seedling under hot and dry conditions. Certainly, Takos & Efthimiou (2003) found that letting seeds 'dry considerably' in Greece between collection in mid-October and sowing in December resulted in <1% germination, and Röhrig (1972) noted that germination was highest when seed was in contact with the better water supply of mineral soil or thin leaf litter. Nevertheless, seeds can cope with some drying since germination of *S. torminalis* was found to be similar after two years whether stored at 4 °C or -5 °C and 7, 8 or 10% moisture (Muller & Laroppe 1993). Dormancy can be re-induced by exposure of hydrated seeds to 20-25 °C (Muller & Laroppe 1993). Further details of seed storage, sowing depth and other *in vivo* recommendations can be found in Barnola, Durand & Parmentier (1993), Drapier (1993b), Kausch-Blecken von Schmeling (1993), Muller & Laroppe (1993) and Kausch-Blecken von Schmeling & Kellner (2006).

Germination is improved if the fruit is removed from around the seeds prior to sowing (Cook 1679; Roper 1993; Yagihashi, Hayashida & Miyamoto 1998). Muller & Laroppe (1993) found germination decreased by >50% if fruit were left intact, although Röhrig (1972) reported good germination when intact whole fruits were sown immediately after harvest in October. Espahbodi *et al*. (2007b) found genetically fixed differences in germination and early performance between seed from trees growing at 1600-1800 m and at 2100-2300 m altitude *c*. 16 km apart in Iran. Trees from the lower site showed significantly lower seedling emergence (38%) than the higher site (45%). Survival of 1-year-old seedlings transplanted into a common garden at 1500 m was the opposite, being significantly higher in seedlings from the lower site (89.7%) than the higher (80.5%). Seedlings from the lower site were also larger after two years as measured by root collar diameter (10.98 mm lower site, 9.54 mm upper), height (52 cm lower, 41 cm upper) and they also had more branches (8.4 lower site, 4.9 upper). Espahbodi *et al*. (2007a) also found that DBH of the parent tree affected germination. The highest germination rate (43%) over two years was in seed from trees 25-35 cm diameter.

(E) SEEDLING MORPHOLOGY

Seedlings of *Sorbus torminalis* have two small, oval cotyledons (Fig. 4). The primary leaves are similar to the later true leaves, but initially without the characteristic lobing (Amann 2004). The root system starts with a rapidly developing taproot and by the time the cotyledons are expanded, the taproot can be 8-14 cm long (Schüte 2000).

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

As noted in IV, seedlings and saplings of *S. torminalis* are readily browsed by small mammals, rodents and deer. Thrushes feed to a certain extent on fruits, and bullfinches and marsh tits are known seed predators (VIII(C)).

Sorbus torminalis is fairly resistant to insect pests (Chalupa 1992) but a number of mites in the family Eriophyidae are found on *S. torminalis* in Britain (Table 1) notably *Eriophyes torminalis* and *Phytoptus pyri* var. *torminalis* that are restricted to *S. torminalis*. An extensive list of mites feeding on *S. torminalis* in Hungary is given by Ripka (2010, 2011) and Ripka & Szabó (2010).

Insects recorded feeding on *S. torminalis* in the British Isles are given in Table 1. A variety of chalcid wasps (Hymenoptera, Tenthredinidae) affect *S. torminalis*. Most notable is *Torymus druparium* that can result in excellent seed trees only rarely setting any viable seed (Henry Girling, personal communication). The pear shoot sawfly *Janus compressus* (Fabricius) (Hymenoptera, Cephidae) can cause inconsequential withering of *S. torminalis* shoots (Coello *et al*. 2013). A number of aphids (Hemiptera, Aphididae) found on *S. torminalis* is restricted to the Rosaceae or *Sorbus* (Table 1). *Aphis pomi* De Geer is also common in Hungary (Ripka 2001) and aphids of the genus *Dysaphis* are frequently observed in mainland Europe at the beginning of the summer, sometimes in large number, and are linked to extensive premature leaf fall (Lanier 1993b). These include the wild service aphid *Dysaphis aucupariae* (Buckton) that forms reddish to yellowish rolled or twisted pseudogalls on the leaves (Lanier 1993b). A number of leaf miners (Lepidoptera, micro-moths) are found on *S. torminalis* (Table 1), notably *Stigmella torminalis* that is restricted to *S. torminalis* in the Malvern Hills, the type location (Emmet 1976). *Phyllonorycter leucographella* (Zeller) (Lepidoptera, Gracillariidae) is also an occasional leaf miner in Poland (Walczak, Baraniak & Jerzak 2010).

(B) PLANT PARASITES

Sorbus torminalis will support the epiphytic hemiparasite mistletoe *Viscum album* (Turker, Yıldırım & Karakas 2012) but *S. torminalis* has not been reported as a host in the British Isles despite a number of national surveys. A list of fungi and slime moulds associated with *S. torminalis* in the British Isles is given in Table 2. *Phyllosticta sorbi* Westend. var. *torminalis* (Ascomycota, Botryosphaeriales) was also recorded on fading leaves of *S. torminalis* by Grove (1935). Badurowa & Badura (1968) list a number of fungi (primarily Phycomycota and Ascomycota) found on *S. torminalis* leaves in southeast Poland, and Andrianova (2001) a number of fungal parasites on *S. torminalis* in the Ukraine. Czeczuga *et al.* (2009) reports on 26 species of aquatic fungi found on seeds of *S. torminalis* in Poland.

(C) PLANT DISEASES

Sorbus torminalis is prone to infection by fungal diseases (Drapier 1993b) including *Armillaria* spp., which can be fatal (Draper 1993c). European canker of apple (*Nectria galligena*) and apple scab (*Venturia inaequalis*) use *S. torminalis* as a minor host (Table 2; Kausch-Blecken von Schmeling 2000). Species of *Verticillium* Nees (Ascomycota, Incertae sedis) cause wilting and dieback of branches of *S. torminalis* (Butin 1989). *Sorbus* species are important hosts of fireblight (*Erwinia amylovora* (Burrill): Proteobacteria, Enterobacteriales) in the warmer climate of the Mediterranean and will certainly include *S. torminalis* (Anon 2013).

X. History

Sorbus was a representative of a warm temperate mesophyte flora that was widespread as early as the Tertiary period. Fossil species of the Torminaria group have been found in southwest and central China from the Miocene and Pliocene (Gabriëlian 1978) and it is likely that *S. torminalis* evolved in dry, open woodlands (Gabriëlian 1961). There are possible records of *S. torminalis* in the British Isles from the warm Hoxnian Interglacial *c.* 130 000 years BP (Godwin 1975) although, like most other woody species, it will have retreated to refugia further south in Europe during the last glaciation. Evidence from chloroplast DNA haplotype distribution suggests that *S. torminalis* survived in a number of different refugia across Europe (Demesure-Musch & Oddou-Muratorio 2004). As the climate warmed at the start of the Holocene, *S. torminalis* is thought to have slowly re-colonised along warmer river valleys avoiding wetlands (Roper 1993) particularly in the warmer period between 8000-

5000 years BP when it reached as far north as southern Sweden (Kutzelnigg 1995). *Sorbus torminalis* is widely held to be one of the later tree species to arrive in the British Isles (Roper 1993) and like other thermophiles (II(A)) will have survived cooler periods along woodland edges and on steep south-facing slopes where competition was reduced (Kollmann 1997; Rasmussen & Kollmann 2004b).

Due to the tree's comparative scarcity, there are no more than sporadic records of its pollen during the Holocene. It is known to have been present in the British Isles since the Neolithic around 5900 BP (Godwin 1975) and indeed pollen has been found at Roudsea Woods, Cumbria in mid-Flandrian deposits (6680-5150 BP). It became extinct here in the last century (Baker 1885; Birks 1982) but other populations remain on the limestones to the east around the northern edge of Morecambe Bay (Kevin Walker, personal communication). *Sorbus torminalis* charcoal has been recovered from the Iron Age hill fort at Maiden Castle, Dorset (Salisbury & Jane 1940) but there are doubts as to whether the wood was of local origin (Godwin 1975).

There are suggestions that its distribution in some parts of Europe was enhanced by its introduction for its fruits (Roper 1993). However, the genetic diversity across Europe is consistent with extensive local pollen movement and occasional long-distance dispersal, and although it was extensively planted, shows little evidence of long-distance movement by humans (Demesure-Musch & Oddou-Muratorio 2004).

USES

Sorbus torminalis was formerly widely coppiced possibly due to its ability to readily sucker rather than for the value of its wood. The wood has been widely used for firewood and charcoal (Phillips 1821; Drapier 1993a, c; Demesure-Musch & Oddou-Muratorio 2004). However, other native species are better in both respects and this may account for *S. torminalis* being rarer than it might otherwise be. In central Europe it was frequently planted as a standard tree in coppice systems for its valuable larger pieces of timber (Müller *et al*. 2000) and is regarded as the most important forestry tree within the genus *Sorbus*. It was also planted on shooting estates for its fruits (Conwentz 1895). A review of the use of *S. torminalis* in forestry is given by Nicolescu *et al*. (2009) and in agroforestry by Guitton (1994).

The timber of *S. torminalis* has a fine yellow colour with an attractive sheen (Henry Girling, personal communication) and although it is now little used in Britain, in central

Europe it is one of the most highly priced timbers and in great demand (Drapier 1993b; Franke, Dagenbach & Hauff 1990; Uthoff 2002; Demesure-Musch & Oddou-Muratorio 2004). Indeed, in 1900 at the Paris World Exhibition, *S. torminalis* was voted the most beautiful wood in the world (Düll 1959). It has been used for fine furniture, musical instruments, measuring instruments, arrows, and for veneers, wood-carving and turnery, and was sometimes dyed and used as an ebony substitute (Germain 1993; Lanier 1993a; Kausch-Blecken von Schmeling 1994b; Klumpp & Kiristis 1998; Kausch-Blecken von Schmeling & Kellner 2006; Rich *et al*. 2010). It was also widely used for making rifle and crossbow stocks across Europe including Britain, and for cogs since it shrinks little and does not split on drying (Evelyn 1664; Roper 1993). It has also been used for the main screw of wine presses (Kausch-Blecken von Schmeling & Kellner 2006).

The fruits are high in vitamin C and have been used as food, particularly once bletted (Sowerby & Sowerby 1878), often treated in a similar way to the medlar (*Mespilus germanica*). In Germany the fruit was macerated in a sweet and sour porridge (Düll 1959) and has been also been processed into jellies and conserves (Facciola 1998); the fruits have also been eaten raw (Mustafa *et al*. 2012). Seeds were eaten in Lower Saxony certainly since the 15th century (Hellwig 1997). However, the main culinary use of the fruits has been to make drinks. There is a long economic history of use of the 'chequers' fruit to make a form of cider. The name possibly derived from the fruits' use to brew an alcoholic drink or flavour spirits, formerly drunk in Chequers Inns, particularly in the Weald and Kent, where a chequer board was hung outside to advertise its presence (Mabey 1996). They have also been used to make wine, brandy and vinegar (Facciola 1998).

The astringent tannins in the fruits have been used to settle *tormina* or colic (Grigson 1955), hence the specific name. The fruits have also been used against cholera and dysentery, and as anti-diarrhoeal, diuretic, anti-inflammatory, anti-diabetic, vasoprotective, broncho- and vasorelaxant medicines, and also as antioxidant agents (Grigson 1955; Tsitsa-Tzardi & Loukis 1991; Tsitsa-Tzardi, Loukis & Philianus 1992; Klumpp & Kiristis 1998; Tuzlacı & Erol 1999; Rivera *et al*. 2005; Kültür 2007; Pietzarka, Lehmann & Roloff 2009) although they have lower antioxidant properties than fruits of many trees including the much more widespread *Sorbus aucuparia* (Serteser *et al*. 2009; Olszewska 2011). In Turkey, *S. torminalis* leaves have been eaten boiled to treat diabetes and colic (Kültür 2007) and a decoction as an expectorant (Tuzlacı & Erol 1999). Despite the abundant uses, the name,

'service', is not an indication of its usefulness but rather is derived from the Latin *Sorbus*, via 'serves', the plural of 'serve' from Old English 'syrfe' (Grigson 1955).

XI. Conservation

Sorbus torminalis is by its nature an uncommon tree in most places; for example, it is one of the rarest trees in Germany making up <1% of the forest area (Schüte 2001). In some areas it has apparently increased in frequency, such as in England and Scotland between the two periods 1930-1960 and 1987-88 (Rich & Woodruff 1996) although this may be due to improved knowledge of the distribution of the species due to targeted surveys (Roper 1993). Indeed, it is more likely to have declined in many British woods due to the cessation of coppice and ride management, which has been shown to increase shading in British woodlands since the 1940s and consequently reduce the abundance of more light-demanding species (Keith *et al*. 2009). There is also evidence that it is becoming rarer in some areas such as eastern France, starting in 1988 (Allegrini, Giard & Mariel 1993), and central Europe (Drapier 1993b; Ewald, Zander & Jander 1994). It has also been suggested that particularly tall trees of good form are being preferentially harvested and not replaced (Henry Girling, personal communication), leading to the species becoming increasingly shrubby.

Few European countries consider *S. torminalis* to be in need of conservation efforts (Lefèvre *et al*. 2012) for example in Great Britain where it has been classified as Least Concern using IUCN threat criteria (Cheffings & Farrell 2005). Nevertheless, it is considered as Endangered or Near Threatened in the north of its range, central Germany and the Czech Republic (Stoltze & Pihl 1998; Pietzarka, Lehmann & Roloff 2009; Úradníček *et al*. 2010) and in Poland it has been protected by law since 1946 (Bednorz 2007c), as one of the rarest trees in the country (Szymura 2012), and state bodies are actively engaged in *in situ* and *ex situ* conservation (Zwierzyński & Bednorz 2012).

The main threats to *S. torminalis* are considered to be woodland clearance (reducing population size and increasing fragmentation), increased browsing, especially by deer, and, most importantly, changing management practices. As noted in VI(E), many authors consider that the decline in coppicing with a concomitant rise in denser high forest has led directly to large-scale population decline of *S. torminalis*, increased fragmentation and reduced reproduction (Röhrig 1972; Franke, Dagenbach & Hauff 1990; Drapier 1991; Kausch-Blecken von Schmeling 1994a; Kleinschmit 1998; Müller *et al*. 2000; Oddou-Muratorio *et al*. 2004; Oddou-Muratorio, Klein & Austerlitz 2005; Angelone *et al*. 2007; Rasmussen

2007; Paganová 2007; Rasmussen & Kollmann 2007, 2008; Collet *et al*. 2008; Pietzarka, Lehmann & Roloff 2009) and will continue to decline without silvicultural intervention (Favre-d'anne 1990; Lanier *et al*. 1990; Drapier 1993b; ONF 1999; Démesure *et al*. 2000; Schüte 2001; Hochbichler 2003; Collet *et al*. 2008; Pyttel, Kunz & Bauhus 2013). Pyttel, Kunz & Bauhus (2013) counter this charge by stating that *S. torminalis* is shade tolerant (see VI(E)) and as it readily persists below a canopy of other trees, the loss of coppice is not a serious threat to *S. torminalis*. Moreover, *S. torminalis* has in the past been common in coppiced woodlands not so much because it needs the open conditions but because it can readily spread in coppice through suckering, aided by the skidding of logs damaging roots and stimulating suckering (Wilhelm 1993), and has undoubtedly been planted in the past for this reason. Perennation is by suckers in the shade: in southwest Germany, Pyttel, Kunz & Bauhus (2011) found frequent recruitment, (primarily by suckering) over the past 80 years in deep shade. However, despite tolerating shaded conditions vegetatively, reduced reproduction by seed in the shade is a long-term issue, and is being adversely affected by a reduction in open coppiced woodland across Europe. Moreover, the low competitiveness of the species reduces its ability to colonise new sites (Bednorz 2007c) and this, together with the high cost of seeds (Jacobée 1993), has limited its planting, despite frequent calls for it to be used more extensively in forestry (Drapier 1993d; Fehr 1993; Kausch-Blecken von Schmeling 1994a; Demersure *et al*. 2004; Espabodi *et al*. 2007b) and in "biocorridors" (Úradnícek 2010). In non-coppiced areas, *S. torminalis* would benefit from woodland thinning (Müller, Ammer & Nüßlein 2000), especially when under the most competitive species such as beech, in effect simulating conditions previously found in coppicing (Kleinschmit 1998) and naturally at woodland edges.

Increasing isolation of local populations, particularly at the northern end of its range may limit gene flow with the risk of losing genetic diversity (Bednorz 2007c). This can be countered by planting seed collected from as wide a range of parent trees within a provenance as possible to ensure maximum genetic diversity (Wirth *et al*. 2005; Biedenkpof *et al*. 2007) although this will dilute genetic uniqueness in these populations especially if done indiscriminately with stock of unknown provenance, as is happening in central Europe (Belletti, Monteleone & Ferrazzini 2008). These isolated populations should be supported by specific habitat management plans (Rasmussen & Kollmann 2008) and in Poland, Bednorz (2009) suggests that conservation measures should include establishment of reserves to

protect the 'best' of the 84 isolated populations and the establishment of clonal archives and seed orchards to protect the 'best' genotypes.

Climate change may benefit *S. torminalis* due to it being more drought tolerant than its main competitors such as *Fagus sylvatica* (Paganová 2007) but migration northwards and eastwards may be limited due to poor seed production amongst widely spaced individuals and poor seed dispersal (Hemery *et al*. 2009).

Acknowledgements

References

Aas, G., Maier, J., Baltisberger, M. & Metzger, S. (1994) Morphology, isozyme variation, cytology and reproduction of hybrids between *Sorbus aria* (L.) Crantz and *S. torminalis* (L.) Crantz. *Botanica Helvetica*, **104**, 195-214.

Aas, G. & Kohles, M. (2011) Verbreitung, Häufigkeit und Verjüngung von *Sorbus cordigastensis* (Kordigast-Mehlbeere) in der nördlichen Frankenalb. *Tuexenia*, **31**, 59-71.

Aldaroso, J.J., Aedo, C., Garmendia, F.M., Del La Hoz, F.P. & Navarro, C. (2004) Revision of *Sorbus* subgenera Aria and Torminaria (Rosaceae – Maloideae). *Systematic Botany Monographs*, **69**, 1-148.

Aldasoro, J.J., Aedo, C., Navarro, C. & Muñoz Garmendia, F. (1998) The Genus *Sorbus* (Maloideae, Rosaceae) in Europe and in North Africa: morphological analysis and systematics. *Systematic Botany*, **23**, 189-212.

Alford, D.V. (1984) *A Colour Atlas of Fruit Pests: Their Recognition, Biology and Control*. Wolfe Publishing, London, UK.

Allegrini, C., Giard, D. & Mariel, M. (1993) Perpétuer et améliorer la ressource locale en alisiers: un projet Haut-Saônois. *Revue Forestière Française*, **45**, 383-387.

Amann, G. (2004) *Bäume und Sträucher des Waldes*. Neumann-Neudamm Verlag, Melsungen, Germany.

Andrianova, T.V. (2001) Phyllotrophic mitosporic fungi of "Cape Mart'ian" nature reserve (Ukraine, Crimea). *Mikologiya i Fitopatologiya*, **35**, 1-10.

Angelone, S., Hilfiker, K., Holderegger, R., Bergamini, A. & Hoebee, S.E. (2007) Regional population dynamics define the local genetic structure in *Sorbus torminalis*. *Molecular Ecology*, **16**, 1291-1301.

Anon (2013) PM 7/20 (2) *Erwinia amylovora*. *EPPO Bulletin*, **43**, 21–45.

Austerlitz, F., Dick, C.W., Dutech, C., Klein, E.K., Oddou-Muratorio, S., Smouse, P.E. & Sork, V.L. (2004) Using genetic markers to estimate the pollen dispersal curve. *Molecular Ecology*, **13**, 937–954.

Badurowa. M. & Badura, L. (1968) A comparative study on the occurrence of microscopic fungi on leaves and needles from different species of trees growing within the Reserve "Kamień Śląski". *Ekologia Polska - Seria A*, **16**, 253-260.

Bailey, J.P., Kay, Q.O.N., McAllister, H. & Rich, T.C.G. (2008) Chromosome numbers in *Sorbus* L. (Rosaceae) in the British Isles. *Watsonia*, **27**, 69-72.

Baker, J.G. (1885) *A Flora of the English Lake District*. George Bell & Sons, London, UK.

Balandier, P., Frochot, H. & Sourisseau, A. (2009) Improvement of direct tree seeding with cover crops in afforestation: Microclimate and resource availability induced by vegetation composition. *Forest Ecology and Management*, **257**, 1716-1724.

Bamberger, U. (1990) Ergebnisse des Elsbeer-Herkunftsversuchs im Kaiserstuhl. *Allgemeine Forst Zeitschrift*, **45**, 817–818.

Barengo, N., Rudow, A. & Schwab, P. (2001) *Förderung seltener Baumarten auf der Schweizer Alpennordseite.* Swiss Agency for Environment, Forests and Landscape and Eidgenössische Technische Hochschule, Zürich, Bern, Switzerland.

Barnola, P., Durand, P. & Parmentier, C. (1993) Recherches préliminaires sur la croissance et la morphogenèse de l'alisier torminal. *Revue Forestière Française*, **45**, 261-278.

Battut, A., Grenier, E. & de March, G. (1993) Micropropagation de *Sorbus torminalis* L. *Revue Forestière Française*, **45**, 284-288.

Bean, W.J. (1980) *Trees and Shrubs Hardy in the British Isles* (8th edn). Murray, London.

Bednorz, L. (2006) Morphological variability of leaves of *Sorbus torminalis* (L.) Cratz in Poland. *Acta Societatis Botanicorum Poloniae*, **75**, 233-243.

Bednorz, L. (2007a) Morphological variability of fruits and seeds of *Sorbus torminalis* in Poland. *Dendrobiology*, **57**, 3-14.

Bednorz, L. (2007b) The wild service tree *Sorbus torminalis* (L.) Crantz in plant communities of Poland. *Dendrobiology*, **57**, 49-54.

Bednorz, L. (2007c) Conservation of genetic resources of *Sorbus torminalis* in Poland. *Dendrobiologia*, **58**, 3-7.

Bednorz, L. (2009) Jak chronić jarząb brekinię (*Sorbus torminalis*) w polskich lasach? [How to protect wild service tree (*Sorbus torminalis*) in Polish forests?] *Sylwan*, **153**, 354-360.

Bednorz, L., Kaźmierczak, K. & Kaczmarek, L. (2012) Analyses of spatial structure and selected measures of growth of *Sorbus torminalis* in Forest District Jamy (northern Poland). *Dendrobiology*, **67**, 59-65.

Bednorz, L. & Krzakowa, M. (2002) Phosphoglucose isomerase (PGI) polymorphism in *Sorbus torminalis* (L.) Crantz. *Acta Societatis Botanicorum Poloniae*, **71**, 121-124.

Bednorz, L., Maciejewska-Rutkowska, I., Wrońska-Pilarek, D. & Fujiki, T. (2005) Pollen morphology of the Polish species of the genus *Sorbus* L. *Acta Societatis Botanicorum Poloniae*, **74**, 315-322.

Bednorz, L., Myczko, L. & Kosiński, P. (2004) Isozyme polymorphism and genetic structure of the population of *Sorbus torminalis* (L.) Crantz from the Bytyń Forest (Poland). *Journal of Applied Genetics*, **45**, 321–324.

Bednorz, L., Myczko, L. & Kosiński, P. (2006) Genetic variability and structure of the wild service tree (*Sorbus torminalis* (L.) Crantz) in Poland. *Silvae Genetica*, **55**, 197-202.

Bednorz, L. & Urbaniak, A. (2005) Phenology of the wild service tree (*Sorbus torminalis* (L.) Crantz) in Poznań and Wielkopolski National Park. *Dendrobiology*, **53**, 3-10.

Bednorz, L., Walkowiak, R., Maciejewska-Rutkowska,I. & Moliński, K. (2006b) Seed variability of the Polish species of the genus *Sorbus* (Rosaceae). *Dendrobiology*, **55**, 3-9.

Bednorz, L. & Wojciechowicz, M.K. (2009) Development of the multilayered epidermis covering fruit of *Sorbus torminalis* (Rosaceae). *Dendrobiology*, **62**, 11-16.

Belletti, P., Monteleone, I. & Ferrazzini, P. (2008) A population genetic study in a scattered forest species, wild service tree [*Sorbus torminalis* (L.) Crantz], using RAPD markers. *European Journal of Forest Research*, **127**,103-114.

Biedenkopf, S., Ammer, C. & Müller-Starck, G. (2007) Genetic aspects of seed harvests for the artificial regeneration of wild service tree (*Sorbus torminalis* [L.] Crantz). *New Forests*, **33**, 1-12.

Biological Records Centre (2016) Database of Insects and their Food Plants. http://www.brc.ac.uk/dbif/ (accessed 12 April 2017).

Birks, H.J.B. (1982) Mid Flandrian forest history of Roudsea Wood National Nature Reserve, Cumbria. *New Phytologist*, **90**, 339-354.

Borchard, F., Berger,H.-J., Bunzel-Drüke, M. & Fartmann, T. (2011) Diversity of plant–animal interactions: Possibilities for a new plant defense indicator value? *Ecological Indicators*, **11**, 1311–1318.

Boulanger, V., Baltzinger, C., Saïd, S., Ballon, P., Picard, J.-F. & Dupouey, J.-L. (2009) Ranking temperate woody species along a gradient of browsing by deer. *Forest Ecology and Management*, **258**, 1397-1406.

Brewis, A., Bowman, P. & Rose, F. (1996) *The Flora of Hampshire*. Harley Books, Colchester, UK.

British Mycological Society (2016) The Fungal Records Database of Britain and Ireland. http://www.fieldmycology.net/FRDBI/FRDBI.asp (accessed 12 April 2017).

Butin, H. (1989) *Krankheiten der Wald- und Parkbäume. Diagnose, Biologie, Bekämpfung. 2. überarbeitete und erweirterte Auflage*. Georg Thieme Verlag, Stuttgart, Germany.

Campbell, C.S. & Dickinson, T.A. (1990) Apomixis, patterns of morphological variation, and species concept in subfam. Maloideae (Rosaceae). *Systematic Botany*, **15**, 124-135.

Čaňová, I., Ďurkovič, J., Hladká, D. & Lukáčik, I (2012) Changes in stomatal characteristics and photochemical efficiency during leaf development in six species of *Sorbus*. *Photosynthetica*, **50**, 635-640.

Challice, J.S. & Kovanda, M. (1978) Chemotaxonomic survey of the genus *Sorbus* in Europe. *Naturwissenschaften*, **65**, 111–112.

Chalupa, V. (1992) Micropropagation of European mountain ash (*Sorbus aucuparia* L.) and wild service tree [*Sorbus torminalis* (L.) Cr.]. In: Bajaj, Y.P.S. *Biotechnology of Agriculture and Forestry 18, High-Tech and Micropropagation II*. Springer, Berlin, Germany, pp 211-226.

Chater, A.O. (2010) *Flora of Cardiganshire*.Cambrian Printers, Aberystwyth, UK.

Cheffings, C.M. & Farrell, L. (2005) *The Vascular Plant Red Data List for Great Britain. Species Status 7*. Joint Nature Conservation Committee, Peterborough, UK.

Chester, M., Cowan, R.S., Fay, M.F. & Rich, T.C.G. (2007) Parentage of endemic *Sorbus* L. (Rosaceae) species in the British Isles: evidence from plastid DNA. *Botanical Journal of the Linnean Society*, **154**, 291-304.

Christensen, K.I. (1995) ×*Malosorbus florentina* (Zuccagni) Browicz. In: The Red Data Book of Rare and Threatened Plants of Greece (ed. Phitos, D., Strid, A., Snogerup, S. & Greuter W.) World Wide Fund for Nature, XX, pp. 358-359. [abstract on web]

CIE (1969) *Distribution Maps of Pests, No. 87*. CAB International, Wallingford, UK.

Coello, J., Becquey, J., Ortisset, J.P., Gonin, P., Baiges, T. & Piquè, M. (2013) *Ecology and Silviculture of the Main Valuable Broadleaved Species in the Pyrenean Area and Neighbouring Regions*. Ministry of Agriculture, Livestock, Fisheries, Food and Natural Environment, Government of Catalonia & Catalan Forest Ownership Centre, Catalonia, Spain.

Collet, C., Piboule, A., Leroy, O. & Frochot, H. (2008) Advance *Fagus sylvatica* and *Acer pseudoplatanus* seedlings dominate tree regeneration in a mixed broadleaved former coppice-with-standards forest. *Forestry*, **81**, 135-150.

Cook, M. (1679) *The Manner of Raising, Ordering; and Improving Forest and Fruit-Trees*. Printed for P. Parker, London.

Crave, M.F. (1985) Un frutier meconnu: l'alisier torminal. *Forêt Entreprise*, **28**, 14–20.

Czeczuga, B., Muszyńska, E., Godlewska, A. & Mazalska, B. (2009) Aquatic fungi and fungus-like organisms growing on seeds of 131 plant taxa. *Nova Hedwigia*, **89**, 451-467.

David, J.-F. & Gillon, D. (2009) Combined effects of elevated temperatures and reduced leaf litter quality on the life-history parameters of a saprophagous macroarthropod. *Global Change Biology*, **15**, 156-165.

Davis, T.A.W. (1976) The wild service in Pembrokeshire and South Cardiganshire. *BSBI Welsh Bulletin*, **25**, 4-6.

de Albuquerque, F.S. & Rueda, M. (2010) Forest loss and fragmentation effects on woody plant species richness in Great Britain. *Forest Ecology and Management*, **260**, 472-479.

De Dominicis, V, & Barluzzi, C. (1983) Coenological research on macrofungi in evergreen oak woods in the hills near Siena (Italy). *Vegetatio*, **54**, 177-187.

Demesure, B., Le Guerroué, B., Lucchi, G., Prat, D. & Petit, R.-J. (2000a) Genetic variability of a scattered temperate forest tree: *Sorbus torminalis* L. (Crantz). *Annals of Forest Science*, **57**, 63-71.

Demesure-Musch, B. & Oddou-Muratorio, S. (2004) *EUROFORGEN Technical Guidelines for Genetic Conservation and Use: Wild Service Tree* (Sorbus torminalis). International Genetic Resource Institute, Rome, Italy.

Demesure, B., Oddou, S., Le Guerroué, B., Lévèque, L., Lamant, T. & Vallance, M. (2000b) L'alisier torminal: une essence tropicale qui s'ignore? *Bulletin Technique de l'Office National des Forets*, **39**, 51–63.

Devillez, F. (1979) Influence de la stratification sur les graines et les fruits de *Sorbus aria* (L.) Crantz, *S. aucuparia* L. et *S. torminalis* (L.) Crantz. *Bulletin de la Classe des Sciences Académie Royale de Belgique, 5E Serie*, **65**, 312-329.

Devillez, F., Fraipont, J. & Tissot, M. (1980) Comportement des embryons isolés de *Sorbus aria* (L.) Crantz, de *S. aucuparia* L. et de *S. torminalis* (L.) Crantz en fonction de leurs positions sur le milieu de culture et des prétraitements appliqués aux graines. *Bulletin de la Classe des Sciences Académie Royale de Belgique, 5E Serie*, **66**, 162-182.

Dimitrov, I. & Genova, F. (2008) Investigations on the distribution and health status of *Sorbus torminalis* (L.) Crantz. in Preslavska Mountain. *Forest Science*, **2**, 37-45.

Dinca, L. (2000) Elsbeere in Rumänien. *Corminaria*, **14**, 28.

Drapier, N. (1991) À propos de la protection de l'alisier de Fontainebleau et des essences forestières en general. *Revue Forestière Française*, **43**, 501-506.

Drapier, N. (1993a) Connaissance du genre *Sorbus*. Les *Sorbus* en France: caractères botaniques et généralités. *Revue Forestière Française*, **45**, 207-215

Drapier N. (1993b) Écologie de l'alisier torminal, *Sorbus torminalis* (L.) Crantz. *Revue Forestière Française*, **45**, 229-243.

Drapier, N. (1993c) Recherche d'éléments de sylviculture pour l'alisier torminal. *Revue Forestière Française*, **45**, 321–334.

Drapier N. (1993d) Écologie et intérêt sylvicole de divers *Sorbus* en France. *Revue Forestière Française*, **45**, 345-354.

Düll, R. (1959) *Unsere Ebereschen und ihre Bastarde*. A. Ziemsen Verlag, Wittenberg, Germany.

Dupraz, C. (1994) Le chêne et le blé: l'agroforesterie peut-elle intéresser les exploitations Européennes de grandes cultures? *Revue Forestière Française*, **46**, 84-95.

Ellenberg, H. (1988) *Vegetation Ecology of Central Europe* (4th edn). Cambridge University Press, Cambridge, UK.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1991) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, **18**, 1-248.

Emmet, A.M. (1976) Nepticulidae. *The Moths and Butterflies of Great Britain and Ireland, Vol. 1.* (ed. Heath, J.) Harley, Books, Colchester, UK, pp. 171-267.

Emmet, A.M., Watkinson, I.A. & Wilson, M.R. (1985a) Lyonetiidae. *The Moths and Butterflies of Great Britain and Ireland, Vol. 2. Cossidae -Heliodinidae* (ed. Heath, J. & Emmet, A.M.), pp. 212-239. Harley, Books, Colchester, UK.

Emmet, M.A., Watkinson, I.A. & Wilson, M.R. (1985b) Gracillariidae. *The Moths and Butterflies of Great Britain and Ireland, Vol. 2. Cossidae -Heliodinidae* (ed. Heath, J. & Emmet, A.M.), pp. 244-362. Harley, Books, Colchester, UK.

Espahbodi, K., Mirzaei-Nadoushan, H., Emadian, S.F.A., Sabbagh, S. & Ghasemi, S. (2002) The effect of sowing depth and soil protection for seed germination of service tree (*Sorbus torminalis* in a mountainous nursery. *Iranian Journal of Natural Resources*, **55**, 47-55.

Espahbodi, K., Hosseini, S.M., Mirzaie–Nodoushan, H., Tabari, M., Akbarinia, M. & Dehghan-Shooraki, Y. (2007a) Tree age effects on seed germination in *Sorbus torminalis*. *Bulgarian Academy of Sciences, General and Applied Plant Physiology*, **33**, 107-119.

Espahbodi, K., Mirzaie–Nodoushan, H., Tabari, M., Akbarinia, M., Jalali, S.G. & Hosseini, S.M. (2007b) Seed source effects on seed emergence, seedling survival and growth on wild service (*Sorbus torminalis*) seedlings. *International Journal of Agriculture and Biology*, **9**, 426-430.

Espahbodi, K., Mirzaie-Nodoushan, H., Tabari, M., Akbarinia, M., Dehghan-Shuraki, Y. & Jalali, S.G. (2008) Genetic variation in early growth characteristics of two populations of wild service tree (*Sorbus torminalis* (L.) Crantz) and their interrelationship. *Silvae Genetica*, **57**, 340-348.

Evans, J. (1988) *Natural Regeneration of Broadleaves*. Forestry Commission Bulletin 78, HMSO, London, UK.

Evelyn, J. (1664) *Sylva*. Jo. Martin & Ja. Allestry, London.

Ewald, C., Zander, M. & Jander, A. (1994) Die Elsbeere (*Sorbus torminalis* [L.] Crantz) in Brandenburg. *Der Wald*, **44**, 232-235.

Facciola, S. (1998) *Cornucopia II: A Source Book of Edible Plants*. Kampong, Vista, California, USA.

Fady, B. & Conord, C. (2010) Macroecological patterns of species and genetic diversity in vascular plants of the Mediterranean basin. *Diversity and Distribution*, **16**, 53-64.

Favre-d'anne, E. (1990): *L'Alisier Torminal (*Sorbus torminalis *Crantz): Synthèse Bibliographique, Recherche sur la Densité du Bois*. Ecole Nationale du Génie Rural, des Eaux et des Forêts (ENGREF), Nancy, France.

Fay, M.F., Gernandt, D.S., Cowan, R.S., Kitchen, M.A.R., Kitchen, C. & Rich, T.C.G. (2002) Parentage of an unknown member of the *Sorbus latifolia* (Lam.) Pers. group. *Watsonia* **24**: 91–100.

Fehr, R. (1993) La place de l'alisier torminal *Sorbus torminalis* (L.) Crantz dans la gestion d'un domaine forestier public en Suisse. *Revue Forestière Française*, **45**, 371-374.

Finkeldey, R., Mátyás, G., Sperisen, C. & Bonfils, P. (2000) Strategien zur Auswahl forstlicher Genreservate in der Schweiz. *Forest Snow and Landscape Research*, **75**, 137-152.

Franke, A., Dagenbach, H. & Hauff, U. (1990) Erhaltung und Nachzucht seltener einheimischer Baumarten in Baden-Württemberg. *Allgemeine Forst Zeitschrift*, **45**,166–168.

Gabrielian, E.T. (1961) The genus *Sorbus* L. in Turkey. *Notes from the Royal Botanic Garden, Edinburgh*, **23**, 483-496.

Gabriėlian, Ė.T. (1978) *Service Trees (*Sorbus*) of Western Asia and the Himalayas*. Botanicheskiĭ Institut, Akademiia nauk Armianskoĭ SSR, Yerevan, Armenia.

García López, J.M. & Allué Camacho, C. (2002) *Flora Ilustrada del Centro y Norte de la Península Ibérica*. Exlibris Ediciones, Madrid, Spain.

García-Abad Alonso, J.J., Gómez Delgado, M. & Rodríguez Espinosa, V.M. (2009) Cartografía detallada de plantas vasculares, en un sector de la Alta Alcarria, Guadalajara. Utilidad en la detección de enclaves naturales de interés. *Lazaroa*, **30**, 161-175.

Geb, M., Schmidt, W. & Meyer, P. (2004) Das Mittelwaldprojekt Liebenburg—Entwicklung der Bestandesstruktur. *Forst und Holz*, **59**, 567–573.

Gebauer, T., Horna, V. & Leuschner, C. (2012) Canopy transpiration of pure and mixed forest stands with variable abundance of European beech. *Journal of Hydrology*, **442-443**, 2-14.

Germain, B. (1993) Regeneration d'alisier torminal. Un réseau de placettes à 30 km de Notre-Dame de Paris en forêt régionale de Ferrières (Seine-et-Marne). *Revue Forestière Française*, **45**, 335-342.

Godwin, H. (1975) *History of the British Flora*, 2nd edn. Cambridge University Press, Cambridge, UK.

González, G.M., Rey de Vinãs, I.C. & Cisneros, O. (2003) *Manual de Selvicultura para Plantaciones de Especies Productoras de Madera de Calidad.* Mundi-Prensa, Madrid, Spain.

Gonzalez, M., Deconchat, M. & Balent, G. (2009) Woody plant composition of forest layers: the importance of environmental conditions and spatial configuration. *Plant Ecology*, **201**, 305-318.

Gonzalez, M., Ladet, S., Deconchat, M., Cabanettes, A., Alard, D. & Balent, G. (2010) Relative contribution of edge and interior zones to patch size effect on species richness: An example for woody plants. *Forest Ecology and Management*, **259**, 266-274.

Grigson, G. (1955) *The Englishman's Flora*. Phoenix House, London, UK.

Grove, W.B. (1935) *British Stem- and Leaf-Fungi (Coelomycetes). A Contribution to our Knowledge of the Fungi Imperfecti Belonging to the Sphaeropsidales and Melanconiales. Volume 1. Sphaeropsidales, to the end of the Sphaerioideae which have Colourless or Nearly Colourless Spores*. Cambridge University Press, Cambridge, UK.

Grundmann, B.M. & Roloff, A. (2009) Use of forest tree species under climate change. In: *Crop Plant Resistance to Biotic and Abiotic Factors* (ed. by Feldmann, F., Alford, D.V. & Furk, C.) Deutsche Phytomedizinische Gesellschaft, Braunschweig, Germany, pp. 53-65.

Guitton, J.-L. (1994) Essais de plantations agroforestières en Corse du Sud. *Revue Forestière Française*, **46**, 96-101.

Halliday, G. (1997) *A Flora of Cumbria: Comprising the Vice-counties of Westmorland with Furness (v.c.69), Cumberland (v.c.70) and parts of North-west Yorkshire (v.c.65) and*

North Lancashire (v.c. 60). Centre for North-West Regional Studies, University of Lancaster, Lancaster, UK.

Haralamb, A. (1967) *Cultura Speciilor Forestiere* (3ʳᵈ edn.). Editura Agro-Silvică, Bucharest, Romania.

Harley, J.L. & Harley, E.L. (1987) A check-list of mycorrhiza in the British Flora. *New Phytologist*, **105** (suppl.), 1-102.

Harper, G. (1981) Wild service in Hertfordshire and Middlesex. *Transactions of the Hertfordshire Natural History Society and Field Club*, **28(4)**, 17-26.

Hasbal, G., Yilmaz-Ozden, T. & Can, A. (2015) Antioxidant and antiacetylcholinesterase activities of *Sorbus torminalis* (L.) Crantz (wild service tree) fruits. *Journal of Food and Drug Analysis*, **23**, 57-62.

Hellwig, M. (1997) Plant remains from two cesspits (15th and 16th century) and a pond (13th century) from Göttingen, southern Lower Saxony, Germany. *Vegetation History and Archaeobotany*, **6**, 105-116.

Hemery, G.E., Clark, J.R., Aldinger, E., Claessens, H., Malvolti, M.E., O'Connor, E., Raftoyannis, Y., Savill, P.S. & Brus, R. (2009) Growing scattered broadleaved tree species in Europe in a changing climate: a review of risks and opportunities. *Forestry*, **83**, 65-81.

Herman, J. (1971) *Šumarska Dendrologija*. Stanbiro, Zagreb, Croatia.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C. & Lawesson, J.E. (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, **91**, 9-22.

Herrera, C.M. (1984) A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs*, **54**, 1-23.

Herrera, C.M. (1987) Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecological Monographs*, **57**, 305-331.

Herrera, C.M. (1989) Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. *Oikos*, **55**: 250-262.

Hochbichler, E. (2003) Die Elsbeere (*Sorbus torminalis* Crantz) im Weinviertel (Niederösterreich). *Forst und Holz*, **58**, 647–653.

Hoebee, S.E., Arnold, U., Düggelin, C., Gugerli, F., Brodbeck, S., Rotach, P. & Holderegger, R. (2007) Mating patterns and contemporary gene flow by pollen in a large

continuous and a small isolated population of the scattered forest tree *Sorbus torminalis*. *Heredity*, **99**, 47–55.

Hoebee, S.E., Menn, C., Rotach, P., Finkeldey, R. & Holderegger, R. (2006) Spatial genetic structure of *Sorbus torminalis*: The extent of clonal reproduction in natural stands of a rare tree species with a scattered distribution. *Forest Ecology and Management*, **226**, 1-8.

Huneck, S. (1962) Triterpene. III. Die Anwendung von gewachsenem Aluminiumoxyd als selbsttragendes Adsorbens in der Diinnschichtchromatographie von Triterpenen. *Journal of Chromatography*, 7, 561-564.

Hurt, V. & Kantor, P. (2004) Jeřáb břek (*Sorbus torminalis* (L.) Crantz.), opomíjená cenná listnatá dřevina a její význam na Krivoklátsku. [The wild service tree (Sorbus torminalis L. Crantz.) - the neglected valuable hardwood species and its significance in Křivoklátsko area (Central Bohemia).] (ed. Anon) *Conference Proceedings: Woody plants and forest soil – biological melioration and its uses*. Kostelec nad Černými lesy, Prague, Czech Republic, pp. 40-48.

Idžojtić, M., Zebec, M. & Drvodelić, D. (2006) Varijabilnost populacija brekinje u kontinentalnom dijelu Hrvatske prema morfološkim obilježjima lišća i plodova. (The variability of wild service tree populations in the continental part of Croatia according to morphology of leaves and fruits.) *Glasnik za Šumske Pokuse*, **5**, 305-314.

Jacobée, F. (1993) Base génétique des récoltes d'alises dans le quart nord-ouest de la France. Solution propose. *Revue Forestière Française*, **45**, 388-394.

Jankun, A. & Kovanda, M. (1987) Apomixis and origin of *Sorbus bohemica* (Embryological studies in *Sorbus* II). *Preslia*, **59**, 187–230.

Jankun, A. & Kovanda, M. (1988) Apomixis at the diploid level in *Sorbus eximia* (Embryological studies in *Sorbus* III). *Preslia*, **60**, 193–213.

Kahle, M. (2004) *Untersuchungen zum Wachstum der Elsbeere (*Sorbus torminalis *[L.] Crantz) am Beispiel einiger Mischbestände in Nordrhein-Westfalen*. Landesanstalt für Ökologie, Bodenordnung und Forsten, Recklinghausen, Germany.

Kárpáti, Z. (1960) Die *Sorbus* – Arten Ungarns und der angrenzenden Gebiete. *Feddes Repertorium*, **62**, 71-331.

Kausch-Blecken von Schmeling, W. (1993) Efforts en faveur de l'alisier torminal (et du cormier) en Allemagne. *Revue Forestière Française*, **45**, 357-363.

Kausch-Blecken von Schmeling, W. (1994a) Förderung von Elsbeere und Speierling mit Diplomarbeiten. *Allgemeine Forst Zeitschrift*, **49**, 1449–1450.

Kausch-Blecken von Schmeling, W. (1994b) *Die Elsbeere (*Sorbus torminalis *Crantz.)*. Verlag Kausch, Bovenden, Germany.

Kausch-Blecken von Schmeling, W. (2000) *Der Speierling. 2. Auflage*. Eigenverlag W.K.-B. von Schmeling, Bovenden, Germany.

Kausch-Blecken von Schmeling, W. & Kellner, T. (2006) *Die Elsbeere. Stiftung Landesbank Baden Württemberg: Natur und Umwelt (Hrsg.): Naturschutz im Kleinen*. Heft 27. Stuttgart, Germany.

Keith, S.A., Newton, A.C., Morecroft, M.D., Bealey, C.E. & Bullock, J.M. (2009) Taxonomic homogenisation of woodland plant communities over 70 years. *Proceedings of the Royal Society, Series B,* **276**, 3539-3544.

Kirby, K. (2006) Table of Ancient Woodland Indicator plants (AWIs). In: *The Wild Flower Key*. (ed. Rose, F.) , pp. 558-561 Penguin, London, UK.

Klein, E.K., Desassis, N. & Oddou-Muratorio, S. (2008) Pollen flow in the wild service tree, *Sorbus torminalis* (L.) Crantz. IV. Whole interindividual variance of male fecundity estimated jointly with the dispersal kernel. *Molecular Ecology*, **17**, 3323-3336.

Kleinschmit, J. (1998) Erhaltung und Nutzung wertvoller Edellaubbaumarten. *Forst und Holz*, **53**, 515-519.

Klumpp, R. & Kiristis, T. (1998) The genus *Sorbus* in Austrian Forestry. In: *The Conservation Status of* Sorbus *in the UK*. (eds. Jackson A. & Flanagan, M.) , pp. 48-50 Royal Botanic Gardens, Kew, Surrey, UK.

Köckemann, B. (2008) Abundance, Niche Breadth and Stress in the Centre and at the Border of the Distribution Range. A Macroecological Study on Abundant and Rare Tree Species. PhD thesis, Georg-August-Universität, Göttingen, Germany.

Kollmann, J. (1997) Hypotheses on the regeneration niche of fleshy-fruited species in natural forest gaps and edges in central Europe. *Verhandlungen-Gesellschaft fur Ökologie*, **27**, 85–91.

Kol'Tsova, M.A. (1980) Content of trace elements in fruit of different mountain ash species. *Biologicheskii Zhurnal Armenii*, **33**, 95-99.

Korkmaz, H., Engin, A., Kutbay, H.G. & Yalçin, E. (2011) A syntaxonomical study on the scrub, forest, and steppe vegetation of the Kızılırmak valley. *Turkish Journal of Botany*, **35**, 121-165.

Kotar, M. (2001) Höhenwachstum der Elsbeere und des Speierlings. *Corminaria*, **16**, 19–22.

Kovanda, M. (1984) A new hybridogeneous *Sorbus*. *Preslia*, **56**, 169-172.

Kovanda, M. (1997) Observations on *Sorbus* in Southwest Moravia (Czech Republic) and adjacent Austria II. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich*, **134**, 305-316.

Kučerová, V., Honec, M., Paule, L., Zhelev, P. & Gömöry, D. (2010) Genetic differentiation of *Sorbus torminalis* in Eastern Europe as determined by microsatellite markers. *Biologia*, **65**, 817-821.

Kutzelnigg, H., 1995. *Sorbus torminalis*. *Illustrierte Flora von Mitteleuropa*. (Ed. G. Hegi), pp. 343–349. Parey, Berlin, Germany.

Kwiatkowski, P. (2003) Podgórska ciepłolubna dąbrowa brekiniowa *Sorbo torminalis-Quercetum* na Pogórzu Złotoryjskim. [Submontane thermophilous oak-wild service forest *Sorbo torminalis-Quercetum* in Złotoryja foothills.] *Fragmenta Floristica et Geobotanica Polonica*, **10**, 175-193.

Lachaud, S. & Mansouri, A. (1993) Reprise d'activite du cambium et xylogenèse chez l'alisier torminal. *Revue Forestière Française*, **45**, 279-283.

Lachaud, S. & Maurousset, L. (1996) Occurrence of plasmodesmata between differentiating vessels and other xylem cells in *Sorbus torminalis* L. Crantz and their fate during xylem maturation. *Protoplasma*, **191**, 220-226.

Lanier, L. (1993a) Le boom sur le marché de l'alisier torminal. *Revue Forestière Française*, **45**, 319–320.

Lanier, L. (1993b). Les maladies de l'alisier torminal. *Revue Forestière Française*, **45**, 343–344.

Lanier, L., Rameau, J.-C., Keller, R., Joly, H.-I., Drapier N. & Sevrin E. (1990) L'alisier torminal *Sorbus torminalis* (L.) Crantz. *Revue Forestière Française*, **42**, 13–34.

Lefèvre, F., Koskela, J., Hubert, J., Kraigher, H., Longauer, R., Olrik, D.C., Schüler, S., Bozzano, M., Alizoti, P., Bakys, R., Baldwin, C., Ballian, D., Black-Samuelsson, S., Bednarova, D., Bordács, S., Collin, E., De Cuyper, B., De Vries, S.M.G., Eysteinsson, T., Frýdl, J., Haverkamp, M., Ivankovic, M., Konrad, H., Koziol, C., Maaten, T., Paino, E.N., Oztürk, K., Pandeva, I.D., Parnuta, G., Pilipovič, A., Postolache, D., Ryan, C., Steffenrem, A., Varela, M.C., Vessella, F., Volosyanchuk, R.T., Westergren, M., Wolter, F., Yrjänä, L. & Zariņa, I. (2012) Dynamic

conservation of forest genetic resources in 33 European countries. *Conservation Biology*, **27**, 373-384.

Leinemann, L., Kahlert, K., Arenhövel, W., Voth, W. & Hosius, B. (2010) Insights into genetic variation patterns in the genus *Sorbus* in Thuringia. *Allgemeine Forst und Jagdzeitung*, **9/10**, 169- 174.

Lepší, M., Vít, P., Lepší, P., Boublík, K. & Kolář, F. (2009) *Sorbus portae-bohemicae* and *Sorbus albensis*, two new endemic apomictic species recognized based on a revision of Sorbus bohemica. *Preslia*, **81**, 63-89.

Lepší, M., Vít, P., Lepší, P., Boublík, K. & Suda, J. (2008) *Sorbus milensis*, a new hybridogenous from northwestern Bohemia. *Preslia*, **80**, 229–244.

Leuschner, C., Köckemann, B. & Buschmann, H. (2009) Abundance, niche breadth, and niche occupation of Central European tree species in the centre and at the margin of their distribution range. *Forest Ecology and Management*, **258**, 1248–1259.

Lloyd, E.G. (1977) The Wild Service Tree *Sorbus torminalis* in Epping Forest. *The London Naturalist*, **56**, 22-28.

Lockton, A. & Whild, S. (2015) *The Flora and Vegetation of Shropshire*. Shropshire Botanical Society, Shrewsbury, UK.

Loidi, J. (2004) Südwesteuropäische sommergrüne Laubmischwälder. *Tuexenia*, **24**, 113-126.

Máchová, P., Malá, J., Cvrčková, H. & Dostál, J. (2009) Optimalizace mikropropagace jeřábu břeku. [Optimalization of wild service tree micropropagation.] *Zprávy Lesnického Výzkumu*, **54**, 218-222.

Maciejewska-Rutkowska, I. & Bednorz, L. (2004) SEM and stereoscope microscope observations on the seeds of the Polish species of the genus *Sorbus* L. (Rosaceae). *Acta Societatis Botanicorum Poloniae*, **73**, 294-300.

Maděra, P., Kohoutek, M., Šenfeldr, M. & Řepka, R. (2012) The population structure and regeneration of *Sorbus torminalis* in Hádecká planinka National Nature Reserve (Czech Republic). *Dendrobiology*, **68**, 63-68.

Maděra, P. Tichá, S. & Řepka (2013) Distribution and ecological requirements of *Sorbus torminalis* (L.) Crantz in the Czech Republic. *Dendrobiology*, **69**, 59-68.

Malá, J., Máchová, P., Cvrčková, H., Karady, M., Novák, O., Mikulík, J., Hauserová, E., Greplová, J., Strnad, M. & Doležal, K. (2009) Micropropagation of wild service tree

(*Sorbus torminlais* [L.] Crantz): the regulative role of different aromatic cytokinins during organogenesis. *Journal of Plant Growth Regulation*, **28**, 341-348.

Mabey, R. (1996) *Flora Britannica*. Sinclair-Stevenson, London, UK.

McAllister, H. (2005) *The Genus* Sorbus*: Mountain Ash and Other Rowans*. Royal Botanic Gardens, Kew, Richmond, UK.

Martínez-Vilalta, J., Prat, E., Oliveras, I. & Piñol, J. (2002) Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia*, **133**, 19-29.

Medak, J. (2011) Šume pitomog kestena s prasećim zeljem (*Aposeri foetidae-castanetum sativae* ass. nova) u Hrvatskoj [Forests of sweet chestnut with odorous pig-salad (*Aposeri foetidae-castanetum sativae* ass. nova) in Croatia]. *Šumarski List*, **135**, 5-24.

Meusel, H., Jäger, E. & Weinert, E. (1965) *Vergleichende Chorologie der Zentraleuropäischen Flora*. Veb Gustav Fischer Verlag, Jena, Germany.

Mikoláš, V. (1996) *Sorbus dolomiticola* Mikoláš, a new hybridogenous species of the genus *Sorbus* s.l. from eastern Slovakia. *Thaiszia*, **6**, 1-12.

Moradi, M., Shirvany, A., Matinizadeh, M., Etemad, V., Naji, H.R., Abdul-Hamid, H. & Sayah, S. (2014) Arbuscular mycorrhizal fungal symbiosis with *Sorbus torminalis* does not vary with soil nutrients and enzyme activities across different sites. *iForest – Biogeosciences and Forestry*, **8**, 308-313.

Muller, C. & Laroppe, E. (1993) Conservation et germination des semences. *Revue Forestière Française*, **45**, 253-260.

Müller, S., Ammer, C. & Nüßlein, S. (2000) Analyses of stand structure as a tool for silvicultural decisions – a case study in a *Quercus petraea – Sorbus torminalis* stand. *Forstwissenschaftliches Centralblatt*, **119**, 32-42.

Müller-Kroehling, S. & Franz, C. (1999) Elsbeere und Speierling in Bayern. Bemühungen um ihren Erhalt, Anbau, Waldbau und Holzverwertung. *Corminaria*, **12**, 3–8.

Mustafa, B., Hajdari, A., Pajazita, Q., Syla, B., Quave, C.L. & Pieroni, A. (2012) An ethnobotanical survey of the Gollak region, Kosovo. *Genetic Resources and Crop Evolution*, **59**, 739-754.

Nelson-Jones, E.B., Briggs, D. & Smith, A.G. (2002) The origin of intermediate species of the genus *Sorbus*. *Theoretical and Applied Genetics*, **105**, 953-963.

Németh, Cs. (2012) Two new *Sorbus* (Rosaceae) species from the Bakony Mts, Hungary. *Acta Botanica Hungarica*, **54**, 131-144.

Németh, Cs. (2015) *Sorbus pelsoensis* (*Sorbus* subgenus *tormaria*), a new species from the surroundings of Lake Balaton, Hungary. *Studia Botanica Hungarica*, **46**, 49–60.

Nicolescu, V.N., Hochbichler, E., Coello Gomez, J., Ravagni, S. & Giulietti, V. (2009) Ecology and silviculture of wild service tree (*Sorbus torminalis* (L.) Crantz): A literature review. *Die Bodenkultur*, **60**, 35-44.

Oddou-Muratorio, S., Aligon, C., Decroocq, S., Plomion, C., Lamant, T. & Mush-Demesure, B. (2001b) Microsatellite primers for *Sorbus torminalis* and related species. *Molecular Ecology Notes*, **1**, 297–299.

Oddou-Muratorio, S., Demesure-Musch, B., Pélissier, R. & Gouyon, P.-H. (2004) Impacts of gene flow and logging history on the local genetic structure of a scattered tree species, *Sorbus torminalis* L. Crantz. *Molecular Ecology*, **13**, 3689-3702.

Oddou-Muratorio, S., Guesnet, D., Ozdemir, E. Petit, R.J. & Demesure, B. (2001c) Patterns of seed dispersal in a scattered forest tree species (*Sorbus torminalis*) based on multi-scale investigation of population genetic structure for chloroplast DNA. In: Müller-Starck, G. & Schubert, R. (eds) Genetic Response of Forest Systems to Changing Environmental Conditions. Springer, Dordrecht, pp 271–280

Oddou-Muratorio, S., Houot, M.-L., Demesure-Musch, B. & Austerlitz, F. (2003) Pollen flow in the wildservice tree, *Sorbus torminalis* (L.) Crantz. I. Evaluating the paternity analysis procedure in continuous populations. *Molecular Ecology*, **12**, 3427-3439.

Oddou-Muratorio, S. & Klein, E.K. (2008) Comparing direct vs. indirect estimates of gene flow within a population of a scattered tree species. *Molecular Ecology*, **17**, 2743-2754.

Oddou-Muratorio, S., Klein, E.K. & Austerlitz, F. (2005) Pollen flow in the wildservice tree, *Sorbus torminalis* (L.) Crantz. II. Pollen dispersal and heterogeneity in mating success inferred from parent–offspring analysis. *Molecular Ecology*, **14**, 4441-4452.

Oddou-Muratorio, S., Klein, E.K., Demesure-Musch, B. & Austerlitz, F. (2006) Real-time patterns of pollen flow in the wild-service tree, Sorbus torminalis (Rosaceae). III. Mating patterns and the ecological maternal neighborhood. *American Journal of Botany*, **93**, 1650-1659.

Oddou-Muratorio, S., Petit, R. J., Le Guerroue, B., Guesnet, D. & Demesure, B. (2001a). Pollen- versus seed-mediated gene flow in a scattered forest tree species. *Evolution*, **55**, 1123-1135.

Olszewska, M.A. (2011) In vitro antioxidant activity and total phenolic content of the inflorescences, leaves and fruits of *Sorbus torminalis* (L.) Crantz. *Acta Poloniae Pharmaceutica - Drug Research*, **68**, 945-953.

Olszewska, M.A. & Roj, J.M. (2011) Phenolic constituents of the inflorescences of *Sorbus torminalis* (L.) Crantz. *Phytochemistry Letters*, **4**, 151–157.

ONF (1999) Le conservatoire génétique des arbres forestiers. *Bulletin Technique de l'Office National des Forêts*, **38**, 9–11.

Oria de Rueda, J.A. (2008) *Guía de Árboles y Arbustos de Castilla y León*. Ediciones Cálamo, Palencia, Spain.

Oria de Rueda, J.A., Martínez de Azagra, A. & Álvarez, A. (2006) Botánica forestal del género *Sorbus* en España. *Investigaciones Agrarias: Sistemas y Recursos Forestales (2006),* **Fuera de Serie**, 166-168.

Oršanić, M., Drvodelić, D., Anić, I. & Mikac, S. (2006) Morphological-biological properties of fruit and seed of the genus *Sorbus* (L.) species. *Periodicum Biologorum*, **108**, 693–706.

Oršanić, M., Drvodelić, D., Jemrić, T., Anić, I. & Mikac, S. (2009) Variability of morphological and biological characteristics of wild service tree (*Sorbus torminalis* (L.) Crantz) fruits and seeds from different altitudes. *Periodicum Biologorum*, **111**, 495–504.

Paganová, V. (2007) Ecology and distribution of *Sorbus torminalis* (L.) Crantz in Slovakia. *Horticultural Science*, **34**, 138-151.

Paganová, V. (2008) Ecological requirements of wild service tree (*Sorbus torminalis* [L.] CRANTZ.) and service tree (*Sorbus domestica* L.) in relation with their utilization in forestry and landscape. *Journal of Forest Science*, **54**, 216-226.

Palenzuela, J., Azcón-Aguilar, C., Barea, J.-M., Alves da Silva, G. & Oehl, F. (2014) *Acaulospora viridis*, a new species in the Glomeromycetes from two mountain ranges in Andalucía (Spain). *Nova Hedwigia*, **99**, 71–82.

Pellicer, J., Clermont, S., Houston, L., Rich, T.C.G. & Fay, M.F. (2012) Cytotype diversity in the *Sorbus* complex (Rosaceae) in Britain: sorting out the puzzle. *Annals of Botany*, **110**, 1185-1193.

Peterken, G.F. (1983) Wild service-tree in central Lincolnshire. *Transactions of the Lincolnshire Naturalists' Union*, **20**, 158-162.

Petit, R.J., Aguinagalde, I., de Beaulieu, J.-L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi, S., Grivet, D., Lascoux, M., Mohanty, A., Müller-Starck, G., Demesure-Musch, B., Palmé, A., Martín, J.P., Rendell, S. & Vendramin, G.G. (2003) Glacial refugia: hotspots but not melting pots of genetic diversity. *Science*, **300**, 1563-1565.

Phillips, H. (1821) *Pomarium Britannicum: an Historical and Botanical Account of Fruits Known in Great Britain. 2ⁿᵈ edition.* T. and J. Allman, London.

Pigott, C.D. (1974) The wild service-tree in Lancashire and Westmorland. *Nature in Lancashire*, **4**, 40-43.

Pigott, C.D. & Huntley, J.P (1978) Factors Controlling the Distribution of *Tilia cordata* at the Northern Limits of its Geographical Range. I. Distribution in North-West England. *New Phytologist*, **71**, 429-441.

Pietzarka, U., Lehmann, M. & Roloff, A. (2009) *Sorbus torminalis* (L.) Cratz, 1763. *Enzyklopädie der Holzgewächse, Handbuch und Atlas der Dendrologie* (eds. Roloff, A., Weisgerber, H., Lang, U. & Stimm, B.) Wiley, Weinheim, Germany, pp. 1-16.

Pleines, V. (1994) Comportement écologique et sylvicole de l'alisier torminal dans quatre régions de Suisse. *Revue Forestière Française* , **46**, 59-68.

Pollard, E. (1973) Hedges: VII. Woodland relic hedges in Huntingdon and Peterborough. *Journal of Ecology*, **61**, 343-352.

Prat, D. & Daniel, C. (1993) Variabilité génétique l'Alisier torminal et du genere *Sorbus*. *Revue Forestière Française*, **45**, 216–228.

Price, D.T. & Rich, T.C.G. (2007) One-way introgressive hybridisation between *Sorbus aria* and *S. torminalis* (Rosaceae) in southern Britain. *Watsonia*, **26,** 419-432.

Proctor, M.C.F. & Groenhof, A.C. (1992) Peroxidase isoenzyme and morphological variation in *Sorbus* L. in South Wales and adjacent areas, with particular reference to *S. porrigentiformis* E. F. Warb. *Watsonia*, **19**, 21–37.

Proctor, M.C.F., Proctor, M.E. & Groenhof, A.C. (1989) Evidence from peroxidase polymorphism on the taxonomy and reproduction of some *Sorbus* populations in south-west England. *New Phytologist*, **112**, 569-575.

Prudič, Z. (1997) Wuchsleistung und Konkurrenzbeziehungen von Elsbeere und Speierling. *Corminaria*, **7**, 9–12.

Prudič, Z. (1998) Růst a rozšíření jeřábu oskeruše a břeku v Moravských Karpatech. (Growth and distribution of *Sorbus domestica* L. and *Sorbus torminalis* (L.) Crantz in the Moravian Carpathians). *Lesnictví*, **44**, 32-38.

Puhe, J. & Ulrich, B. (2001) *Global Climate Change and Human Impacts on Forest Ecosystems: Postglacial Development, Present Situation and Future Trends in Central Europe*. Springer, Heidelberg, Germany.

Pyttel, P., Kunz, J. & Bauhus, J. (2011) Age and growth of wild service tree (*Sorbus torminalis* (L.) Crantz) in former oak coppice forests in southwest Germany. Maaten-Theunissen M, Spiecker H, Gärtner H, Helle G, Heinrich I (Eds.) (2011): TRACE - Tree Rings in Archaeology, Climatology and Ecology, Vol. 9. GFZ Potsdam, Scientific Technical Report STR 11/07, Potsdam, p. 64 - 70.

Pyttel, P., Kunz, J. & Bauhus, J. (2013) Growth, regeneration and shade tolerance of the Wild Service Tree (*Sorbus torminalis* (L.) Crantz) in aged oak coppice forests. *Trees*, **27**, 1609-1619.

Qian, G.-Z., Liu, L.-F., Hong, D.-Y. & Tang, G.-G. (2008) Taxonomic study of *Malus* section *Florentinae* (Rosaceae). *Botanical Journal of the Linnean Society*, **158**, 223–227.

Quevedo, L., Rodrigo, A. & Espelta, J.M. (2007) Post-fire resprouting ability of 15 non-dominant shrub and tree species in Mediterranean areas of NE Spain. *Annals of Forest Science*, **64**, 883–890.

Rackham, O. (2003) *Ancient Woodland*. Castlepoint, Dalbeattie, UK.

Rad, J.E. & Shafiei, A.B. (2010) The distribution of ecological species groups in Fagetum communities of Caspian forests: Determination of effective environmental factors. *Flora*, **205**, 721-727.

Raguin, F. & Boulet-Gercourt, b. (2000) L'alisier torminal et le cormier en Allemagne. *Forêt Entreprise*, *132*, 17–18.

Rameau, J.C., Mansion, D. & Dume, G. (1989) *Flore Forestière Française, Tome I: Plaines et Collines*. Institut pour le Développement Forestier, Paris, France.

Rasmussen, K.K. (2007) Dendroecological analysis of a rare sub-canopy tree: Effects of climate, latitude, habitat conditions and forest history. *Dendrochronologia*, **25**, 3-17.

Rasmussen, K.K. & Kollmann, J. (2004a) Defining the habitat niche of Sorbus torminalis from phytosociological relevés along a latitudinal gradient. *Phytocoenologia*, **34**, 639-662.

Rasmussen, K.K. & Kollmann, J. (2004b) Poor sexual reproduction on the distribution limit of the rare tree *Sorbus torminalis*. *Acta Oecologica*, **25**, 211–218.

Rasmussen, K.K. & Kollmann, J. (2007) Genetic diversity, spatial patterns, and growth of root sprouts in a temperate tree at the northern distribution limit. *Écoscience*, **14**, 250–258

Rasmussen, K.K. & Kollmann, J. (2008) Low genetic diversity in small peripheral populations of a rare European tree (*Sorbus torminalis*) dominated by clonal reproduction. *Conservation Genetics*, **9**, 1533–1539.

Rich, T.C.G., Green, D. Houston, L., Lepší, M., Ludwig, S. & Pellicer, J. (2014) British *Sorbus* (Rosaceae): six new species, two hybrids and a new subgenus. *New Journal of Botany*, **4**, 2-12.

Rich, T.C.G., Houston, L., Robertson, A. & Proctor, M.C.F. (2010) *Whitebeams, Rowans and Service Trees of Britain and Ireland. A Monograph of British and Irish* Sorbus *L.* BSBI Handbook No. 14, Botanical Society of the British Isles, London, UK.

Rich, T.C.G. & Woodruff, E.R. (1996) Changes in the floras of England and Scotland between 1930-1960 and 1987-1988: The BSBI Monitoring Scheme. *Biological Conservation*, **75**, 217-229.

Ripka, G. (2001) New data to the knowledge of the aphid fauna of Hungary (Homoptera: Aphidoidea). *Acta Phytopathologica et Entomologica Hungarica*, **36**, 81-87.

Ripka, G. (2007) Checklist of the eriophyoid mite fauna of Hungary (Acari: Prostigmata: Eriophyoidea). *Acta Phytopathologica et Entomologica Hungarica*, **42**, 59-142.

Ripka, G. (2010) A new *Calepitrimerus* species and new gall mite records from Hungary (Acari: Prostigmata: Eriophyoidea). *Acta Phytopathologica et Entomologica Hungarica*, **45**, 383-389.

Ripka, G. (2011) New *Quercus*-feeding *Brevulacus* species, redescription of *Rhyncaphytoptus cerrifoliae* Farkas and new eriophyoid mite records from Hungary (Acari : Prostigmata : Eriophyoidea). *Acta Phytopathologica et Entomologica Hungarica*, **46**, 129-138.

Ripka, G. & Szabó, Á. (2010) Additional data to the knowledge of the mite fauna of Hungary (Acari: Mesostigmata, Prostigmata and Astigmata). *Acta Phytopathologica et Entomologica Hungarica*, **45**, 373-38.

Rivera, D., Obon, C., Inocencio, C., Heinrich, M., Verde, A., Fajardo, J. & Llorach, R. (2005) The ethnobotanical study of local mediterranean food plants as medicinal resources in southern Spain. *Journal of Physiology and Pharmacology*, **56** (Suppl. 1), 97-114.

Robertson, A., Rich, T.C.G., Allen, A.M., Houston, L., Roberts, C., Bridle, J.R., Harris, S.A. & Hiscock, S.J. (2010) Hybridization and polyploidy as drivers of continuing evolution and speciation in *Sorbus*. *Molecular Ecology*, **19**, 1675-1690.

Robertson, A., Newton, A.C. & Ennos, R.A. (2004) Breeding systems and continuing evolution in the endemic Sorbus taxa on Arran. *Heredity*, **93**, 487–495.

Rodwell, J.S. (1991) *British Plant Communities*, Vol. 1 *Woodlands and Scrub*. Cambridge University Press, Cambridge, UK.

Rodwell, J.S. (1992) *British Plant Communities*, Vol. 3 *Grasslands and Montane Communities*. Cambridge University Press, Cambridge, UK.

Röhrig, E. (1972) Die Nachzucht der Elsbeere (*Sorbus torminalis* L.). *Forst und Holzwirt*, **27**, 401-403.

Roleček, J. (2005) Vegetation types of dry-mesic oak forests in Slovakia. *Preslia*, **77**, 241–261.

Roper, P. (1993) The distribution of the Wild Service Tree, *Sorbus torminalis* (L.) Crantz, in the British Isles. *Watsonia*, **19**, 209-229.

Rosati, L., Fipaldini, M., Marignani, M. & Blasi, C. (2010) Effects of fragmentation on vascular plant diversity in a Mediterranean forest archipelago. *Plant Biosystems*, **144**, 38-46.

Rose, F. (1999) Indicators of ancient woodland: the use of vascular plants in evaluating ancient woodland for nature conservation. *British Wildlife*, **10**, 241-251.

Rotach, P. (2000) Zur Gefährdung seltener Baumarten in der Schweiz: Grundsätzliche Überlegungen, Situationsanalyse und zwei Fallbeispiele. *Forest Snow and Landscape Research*, **75**, 267-284.

Rudow, A. & Aas, G. (1997) *Sorbus latifolia* s.l. in Central Northern Switzerland: Distribution, site and population biology. *Botanica Helvetica*, **107**, 51-73.

Safdari, V., Ahmed, M., Palmer, J. & Baig, M.B. (2008) Identification of Iranian commercial wood with hand lens. *Pakistan Journal of Botany*, **40**, 1851-1864.

Safdari, V., Sigarody, M.R.N. & Ahmed, M. (2011) Identification of fibers of woody and non-woody plant species in pulp and papers. *Pakistan Journal of Botany*, **43**, 2127-2133.

Salisbury, E.J. & Jane, F.W. (1940) Charcoals from Maiden Castle and their significance in relation to the vegetation and climatic conditions in prehistoric times. *Journal of Ecology*, **28**: 310-325.

Saravi, A.T., Tabari, M., Espahbodi, K., Nodoushan, H.M. & Enayati, B. (2008) Phenotypic correlation between selected characters of parent trees and progenies in Wild Service Tree (*Sorbus torminalis* L. Crantz). *Asian Journal of Plant Sciences*, **7**, 579–583.

Sardans, J. & Peñuelas, J. (2007) Drought changes phosphorus and potassium accumulation patterns in an evergreen Mediterranean forest. *Functional Ecology*, **21**, 191–201.

Savill, P.S. (1991): *The Silviculture of Trees used in British Forestry*. CAB International, Wallingford, UK.

Schirone, B., Salis, A. & Vessella, F. (2011) Effectiveness of the Miyawaki method in Mediterranean forest restoration programs. *Landscape and Ecological Engineering*, **7**, 81-92.

Schrötter, H. (2001) Vogelkirsche, Spitzahorn und Elsbeere: Drei wertvolle Baumarten in Mecklenburg-Vorpommern im Abseits. *Forst und Holz*, **56**,188–196

Schüte, G. (2000) *Waldbauliche in-situ und ex-situ Verjüngungskonzepte für die Elsbeere (*Sorbus torminalis *[L.] Crantz).* Forschungszentrum Waldökosysteme, University of Göttingen, Germany.

Schüte, G. (2001) Jugendwachstum und Schattentoleranz vegetativer Verjüngungen der Elsbeere (*Sorbus torminalis* Crantz). *Forst und Holz*, **56**, 11–15

Seidel, D., Leuschner, C., Scherber, C., Beyer, F., Wommelsdorf , T., Cashman, M.J. & Fehrmann, L. (2013) The relationship between tree species richness, canopy space exploration and productivity in a temperate broad-leaf mixed forest. *Forest Ecology and Management*, **310**, 366-374.

Sell, P.D. (1989) The *Sorbus latifolia* (Lam.) Pers. aggregate in the British Isles. *Watsonia*, **17**, 385-399.

Serteser, A., Kargioğ, M., Gök, V., Bağci, Y., Özcan, M. & Arslan, D. (2009) Antioxidant properties of some plants growing wild in Turkey. *Grasas y Aceites*, **60**, 147-154.

Sevrin, E. & Keller, R. (1993) Étude de la qualité technologique du bois d'alisier torminal: relations avec la sylviculture et le sol. *Revue Forestière Française*, **45**, 299–316.

Sevrin, E., Lachaud, S. & Mansouri, A. (1993) Anatomie du bois de l'alisier torminal. *Revue Forestière Française*, **45**, 289-298.

Siles, G., Alcántara, J.M., Rey, P.J. & Bastida, J.M. (2010) Defining a target map of native species assemblages for restoration. *Restoration Ecology*, **18**, 439-448.

Siljak-Yakovlev, S., Pustahija, F., Šolić E.M., Bogunić, F., Muratović, E., Bašić, N., Catrice, O. & Brown, S.C. (2010) Towards a genome size and chromosome number database

of Balkan flora: C-values in 343 taxa with novel values for 242. *Advanced Science Letters*, **3**, 190–213.

Sjöman, H., Nielsen, A.B. & Oprea, A. (2012) Trees for urban environments in northern parts of Central Europe – a dendroecological study in north-east Romania and Republic of Moldavia. *Urban Ecosystems*, **15**, 267-281.

Snow, B. & Snow, D. (1988) *Birds and Berries*. Poyser, Calton, UK.

Şofletea, N., Târziu, D., Spârchez, G. & Curtu, L. (2005) Indicatori fenotipici ai cireşului sălbatic (*Prunus avium* L.) şi sorbului (*Sorbus torminalis* (L.) Cr.) în funcţie de condiţiile stationale şi de arboret. [Phenotypic indicators for wild cherry (*Prunus avium* L.) and wild service tree (*Sorbus torminalis* (L.) Cr.) with site conditions and stand characteristics. In: Lucrările Sesiuni Ştiinţifice Pădurea şi Dezvoltarea Durabilă. (ed. Ignea, G.) Universitatea Transilvania, Braşov, Romania, pp. 47-52.

Sowerby, J. & Sowerby, J.E. (1878) *English Botany* (3rd edn.) George Bell & Sons, London, UK.

Stace, C. (2010) *New Flora of the British Isles* (3rd edn.) Cambridge University Press, Cambridge, UK.

Stace, C.A., Preston, C.D. & Pearman, D.A. (2014) *Hybrid Flora of the British Isles*. Botanical Society of Britain and Ireland, Bristol, UK.

Stănescu, V., Şofletea, N. & Popescu, O. (1997) *Flora Forestieră Lemnoasă a României*. Editura Ceres, Bucharest, Romania.

Stoltze, M. & Pihl, S. (1998) *Rødliste 1997 over Planter og Dyr i Danmark*. Miljø- og Energiministeriet, Danmarks Miljøundersøgelser og Skov- og Naturstyrelsen, Copenhagen, Denmark.

Szymura, T.H. (2012) How does recent vegetation reflects previous systems of forest management? *Polish Journal of Ecology*, **60**, 859-862.

Szymura, T.H., Szymura, M. & Pietrzak, M. (2014) Influence of land relief and soil properties on stand structure of overgrown oak forests of coppice origin with *Sorbus torminalis*. *Dendrobiology*, **71**, 49-58.

Tabandeh A., Tabari M., Nadoushan H.M., Espahbodi K. (2007) Heritability of some characteristics of *Sorbus torminalis* seedling. *Pakistan Journal of Biological Sciences*, **10**, 2760–2763.

Takos, I.A. & Efthimiou, G.S. (2003) Germination results on dormant seeds of fifteen tree species autumn sown in a northern Greek nursery. *Silvae Genetica*, **52**, 67-71.

Termena, B.K. (1972) Effect of meteorological conditions on the blooming and fruit bearing of *Sorbus torminalis* in Bukovina. *Ukrayins'kyi Botanichnyi Zhurnal*, **29**, 609-613.

Trueman, I., Poulton, M. & Reade, P. (2013) *Flora of Birmingham and the Black Country*. Pisces Publications, Newbury, UK.

Tsitsa-Tzardi, E. & Loukis, A. (1991) Constituents of *Sorbus torminalis* fruits. *Fitoterapia*, **62**, 282-283.

Tsitsa-Tzardi, E., Loukis, A. & Philianos, S. (1992) Constituents of *Sorbus torminalis* leaves. *Fitoterapia*, **63**, 189–190.

Turker, A.U., Yıldırım, A.B. & Karakas, F.P. (2012) Antitumor and antibacterial activities of *Viscum album* L. grown on different host trees. *Spatula DD*, **2**, 229-236.

Tuzlacı, E. & Erol, M.K. (1999) Turkish folk medicinal plants. Part II: Eğirdir (Isparta). *Fitoterapia*, **70**, 593-610.

Úradnícek, L., Maděra, P., Tichá, S. & Koblížek, J. (2010) *Woody Plants of the Czech Republic*. Lesnická práce, Kostelec nad Cernými lesy, Czech Republic.

Uthoff, P. (2002) Achtung, Sorbus! *Allgemeine Forstzeitschrift für Waldwirtschaft und Umweltvorsorge*, **57**, 585-586.

Var, M., Bekci, B. & Dinçer, D. (2010) Effect of stratification treatments on germination of *Sorbus torminalis* L. Crantz (wild service tree) seeds with different origins. *African Journal of Biotechnology*, **9**, 5535-5541.

Velebil, J. (2012) *Sorbus omissa*, a new endemic hybridogenous species from the lower Vltava river valley. *Preslia*, **84**, 375-390.

Velichkov, I., Zlatanov, T. & Popov, G. (2007) Response of the native deciduous tree vegetation in 'Byala reka' State Forest (eastern Balkan Range) to clear cutting and reforestation with conifers. *Silva Balcanica*, **8**, 5-15.

Velička, M. (1993) Dnešní výzkum původních dřevin na severovýchodní Moravě. *Časopis Slezského zemského muzea v Opavě. Série A: Vědy přírodní*, **42**,187-191.

Vít, P., Lepší, M. & Lepši, P. (2012) There is no diploid apomict among Czech *Sorbus* species: a biosystematics revision of *S. eximia* and discovery of *S. barrandienica*. *Preslia*, **84**, 71-96.

Vukelić, J., Baričević, D. & Šapić, I. (2010) Nomenclatural-phytocoenological analysis of the association *Potentillo micranthae-Quercetum petraeae* ass. nova in Croatia. *Hacquetia*, **9**, 5-17.

Wagenführ, R. (1996) *Holzatlas* (4th edn.) Fachbuchverlag, Leipzig, Germany.

Walczak, U., Baraniak, E. & Jerzak, E. (2010) Host range of an invasive moth, *Phyllonorycter leucographella*. *Journal of Applied Entomology*, **134**, 714-717.

Weiler, E.W. & Ziegler, H. (1981) Determination of phytohormones in phloem exudate from tree species by radioimmunoassay. *Planta*, **152**, 168-170.

Wehrlen, L., Chevalier, G., Besancon, G. & Frochot, H. (2009) Truffle cultivation-forestry: a new strategy to produce the Burgundy truffle (*Tuber uncinatum* Chatin). *Acta Botanica Yunnanica*, **16** (suppl.), 97-99.

Whild, S. (2003) Ancient Woodland Indicators in Shropshire. *Shropshire Botanical Society Newsletter* (spring 2003), 18-19.

Wilhelm, G.J. (1993) L'alisier torminal dans les forêts limitrophes de la Lorraine, de la Savre et du Palatinat. *Revue Forestière Française*, **45**, 364-370.

Wilhelm, G.J. (2009) Gérer l'alisier dans les peuplements mélangés. [Managing service trees in mixed populations.] *Forêt-Entreprise*, **184**, 31-35.

Wilhelm, G.J. & Ducos, Y. (1996) Suggestions pour le traitement de l'alisier torminal en mélange dans les futaies feuillues sur les substrats argileux du nord-est de la France. *Revue Forestière Française*, **48**, 137–143.

Williams, L.R., McLaughlin, J. & Harrison, T.G. (1986) Hedgerows surviving in suburban Kingsbury England UK. *London Naturalist*, **66**, 35-39.

Willmot, A. (1977) *Sorbus torminalis* (L.) Crantz in Derbyshire. *Watsonia*, **11**, 339-344.

Wilmott, A.J. (1934) Some interesting British *Sorbi*. *Proceedings of the Linnean Society of London*, **146**, 73–79.

Winkler, M. (1999) Anzucht von Elsbeer-und Speierlingspflanzen. *Corminaria*, **12**, 11.

Wirth, L.R., Hoebee, S.E., Arnold, U., Düggelin, C., Brodbeck, S., Rotach, P., Gugerli, F. & Holderegger, R. (2005) Ausbreitung der Elsbeerpollen. Destination unbekannt? *Corminaria*, **23**, 3-5.

Wohlgemuth, T. (1993) Répartition et affinités phytosociologiques de *Sorbus torminalis* (L.) Crantz en Suisse. *Revue Forestière Française*, **45**, 375-381.

Wojciechowski, A. & Bednorz, L. (2000) Estimation of mating-compatibility of the wild service tree (*Sorbus torminalis* (L.) Crantz) by observing pollen tube germination. *Journal of Applied Genetics*, **41**, 253-258.

Yagihashi, T., Hayashida, M. & Miyamoto, T. (1998) Effects of bird ingestion on seed germination of *Sorbus commixta*. *Oecologia*, **114**, 209-212.

Zare, H., Tabari, M. & Espahbodi, K. (2002) Ecological characteristics on quantitative condition of *Sorbus torminalis* (a case study in the northern forests of Iran). International Congress of Ecology. Seoul, Korea, August, p 11–18.

Zwierzyński, J. & Bednorz, L. (2012) Regional programme of conservation and restitution of *Sorbus torminalis* in the territory of the regional directorate of the state forests in Piła in 2010-2013. *Nauka Przyroda Technologie*, **6**, paper 42.

Table 1. Acari and insects recorded living on *Sorbus torminalis* in the British Isles

Species/classification	Ecological notes	Source
Acari		
Eriophyidae		
Eriophyes arianus (Canestrini)	Galling	11
E. pyri (Pagenstecher)	Galling, primarily on *Pyrus* and *S. aucuparia*	11
E. sorbi (Canestrini)	Galling, primarily on *S. aucuparia*	4, 9
E. torminalis Nalepa	Forms brown wart-like pustules on the leaves of *S. torminali*s	11
Phyllocoptes sorbeus (Nalepa)	Galling, primarily on *S. aucuparia*	11
Phytoptus pyri Pagenstecher	Common on Rosaceae, larvae and adults	2
P. pyri var. *torminalis* Nalepa	Restricted to *S. torminalis*, larvae and adults	2
Hemiptera		
Aphididae		
Aphis pomi DeGeer	Primarily a pest of *Malus*	3
Dysaphis aucupariae (Buckton)	Leaves, restricted to *Sorbus*	2
D. plantaginea (Passerini)	Leaf rolling, restricted to *Sorbus* and *Malus*	2
Rhopalosiphum insertum (Walker)	Flowers, leaves, *S. torminalis* a major host	2
Hymenoptera		
Tenthredinidae		
Caliroa cerasi (L.)	Sawfly larvae skeletonizing leaves, primarily Rosaceae	2
Torymus druparum Boheman	Wasp larvae on fruits and seeds, on Rosaceae; infestation can be heavy	2, 8, 10
T. varians (Walker)	Wasp larvae on fruits and seeds, on Rosaceae	2
Lepidoptera (macro-moths)		
Cossidae		
Cossus cossus (L.)	Wide range of hosts	2
Zeuzera pyrina (L.)	Wide range of hosts	2
Geometridae		
Colotois pennaria (L.)	Larvae, wide range of hosts	2
Opisthograptis luteolata (L.)	Larvae, primarily Rosaceae	2

Operophtera brumata (L.)	Larvae, wide range of hosts	2
Noctuidae		
Cosmia trapezina (L.)	Larvae on leaves	2
Lepidoptera (micro-moths)		
Gracillariidae		
Parornix anglicella (Stainton)	Leaf miner on Rosaceae	2, 7
P. scoticella (Stainton)	Leaf miner on *Sorbus torminalis*	6
Phyllonorycter cydoniella (Denis & Schiffermuller)	Leaf miner on Rosaceae	2, 7
P. mespilella (Hubner)	Leaf miner on Rosaceae	2, 7
Lyonetiidae		
Bucculatrix crataegi Zeller	Leaf miner	6
Lyonetia clerkella (L.)	Leaf miner, primarily on Rosaceae	2
Nepticulidae		
Stigmella mespilicola (Frey)	Leaf miner on *Sorbus*	2
S. torminalis (Wood)	Leaf miner restricted to *S. torminalis*	2, 5
Ectodemia bradfordi Emmet	Adult found on *S. torminalis* and mined fallen leaf suggests it is a food plant	5
Yponomeutidae		
Argyresthia conjugella Zeller	Leaf miner on *Sorbus* and *Malus*	2
Yponomeuta padella (L.)	Widespread on Rosaceae	2
Coleoptera		
Attelabidae		
Rhynchites caeruleus (Degeer)	Larvae on shoots; found on other Rosaceae	2
R. cupreus (L.)	Adults, primarily on *Prunus* and *Sorbus* spp.	2
Curculionidae		
Anthonomus chevrolati Desbrochers	Restricted to Rosaceae	2
A. conspersus Desbrochers	Restricted to Rosaceae	2
Magdalis ruficornis (L.)	Vegetative buds and leaves on Rosaceae	2
Scolytus mali (Bechstein)	Wide range of hosts	2
S. rugulosus (Müller, P.W.J.)	Wide range of hosts	2
Xyleborus dispar (Fabricius)	Primarily a pest of *Pyrus*	1
Diptera		
Cecidomyiidae		
Contarinia sorbi Kieffer	Galling, restricted to *Sorbus*	1

Sources: 1, Alford (1984); 2, Biological Records Centre (2016); 3, CIE (1969); 4, Drapier (1993c); 5, Emmet (1976); 6, Emmet, Watkinson & Wilson (1985a); 7, Emmet, Watkinson & Wilson (1985b); 8, Harper (1981); 9, Lanier (1993b); 10, Rich *et al*. (2010); 11, Ripka (2007).

Table 2 Fungi and Slime moulds associated with *Sorbus torminalis* in the British Isles. Data and nomenclature from the British Mycological Society (2016)

Species/classification	Ecological notes
Ascomycota	
Capnodiales	
Septoria sorbi (Ces.) Fuckel	Fallen leaf
Helotiales	
Hymenoscyphus caudatus (P. Karst.) Dennis	Dead leaves
H. fructigenus (Bull.) Fr.	Old seeds
Lachnum niveum (R. Hedw.) P. Karst.	Fallen branch
Hypocreales	
Gibberella baccata (Wallr.) Sacc.	Bark
Nectria galligena Bres.	Bark
Lecanorales	
Punctelia subrudecta (Nyl.) Krog	Fallen wood
Pezizales	
Peziza micropus Pers.	Bark
Pleosporales	
Spilocaea sp. Fr.	
Venturia inaequalis (Cooke) G. Winter	Dying leaves
Sordariales	
Bombardia bombarda (Batsch) J. Schröt.	Bark
Stemonitida	
Enerthenema papillatum (Pers.) Rostaf.	Bark
Xylariales	
Daldinia concentrica (Bolton) Ces. & De Not.	Wood
D. fissa Lloyd	Wood
Basidiomycota	
Agaricales	
Agrocybe praecox (Pers.) Fayod	Soil
Amanita pantherina (DC.) P. Kumm.	Soil
Ampulloclitocybe clavipes (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys	Soil
Armillaria gallica Marxm. & Romagn.	Wood and soil
Clitocybe nebularis (Batsch) P. Kumm.	Soil
Crepidotus cesatii (Rabenh.) Sacc.	Fallen dead twig
Inocybe flavella P. Karst.	Wood under tree
Pholiota squarrosa (Weigel) P. Kumm.	Fallen wood, stump

Pleurotus cornucopiae (Paulet) Rolland   Standing tree
Auriculariales
Auricularia mesenterica (Dicks.) Pers.   Stump
Hymenochaetales
Inonotus hispidus (Bull.) P. Karst.   Living wood
Phellinus igniarius (L.) Quél.   Living tree
Pucciniales
Ochropsora ariae (Fuckel) Ramsb.   Living leaves
Polyporales
Aurantiporus fissilis (Berk. & M.A. Curtis) H. Jahn   Wood
Phlebia radiata Fr.   Fallen wood
Polyporus leptocephalus (Jacq.) Fr.   Fallen wood
Russulales
Lactarius subdulcis (Pers.) Gray   Wood
Russula nigricans (Bull.) Fr.   Soil and leaf litter
Stereum rugosum (Pers.) Fr.   Living branch
Thelephorales
Thelephora terrestris Ehrh.   Living trunk
Trechisporales
Brevicellicium olivascens (Bres.) K.H. Larss. & Hjortstam   Dead attached branch
Tremellales
Tremella mesenterica Retz.   Fallen wood

Amoebozoa
Echinostelida
Echinostelium fragile Nann.-Bremek.   Living bark
E. minutum de Bary   Bark
Stemonitida
Paradiacheopsis solitaria (Nann.-Bremek.) Nann.-
Bremek.   Living bark
Trichiida
Arcyria cinerea (Bull.) Pers.   Bark
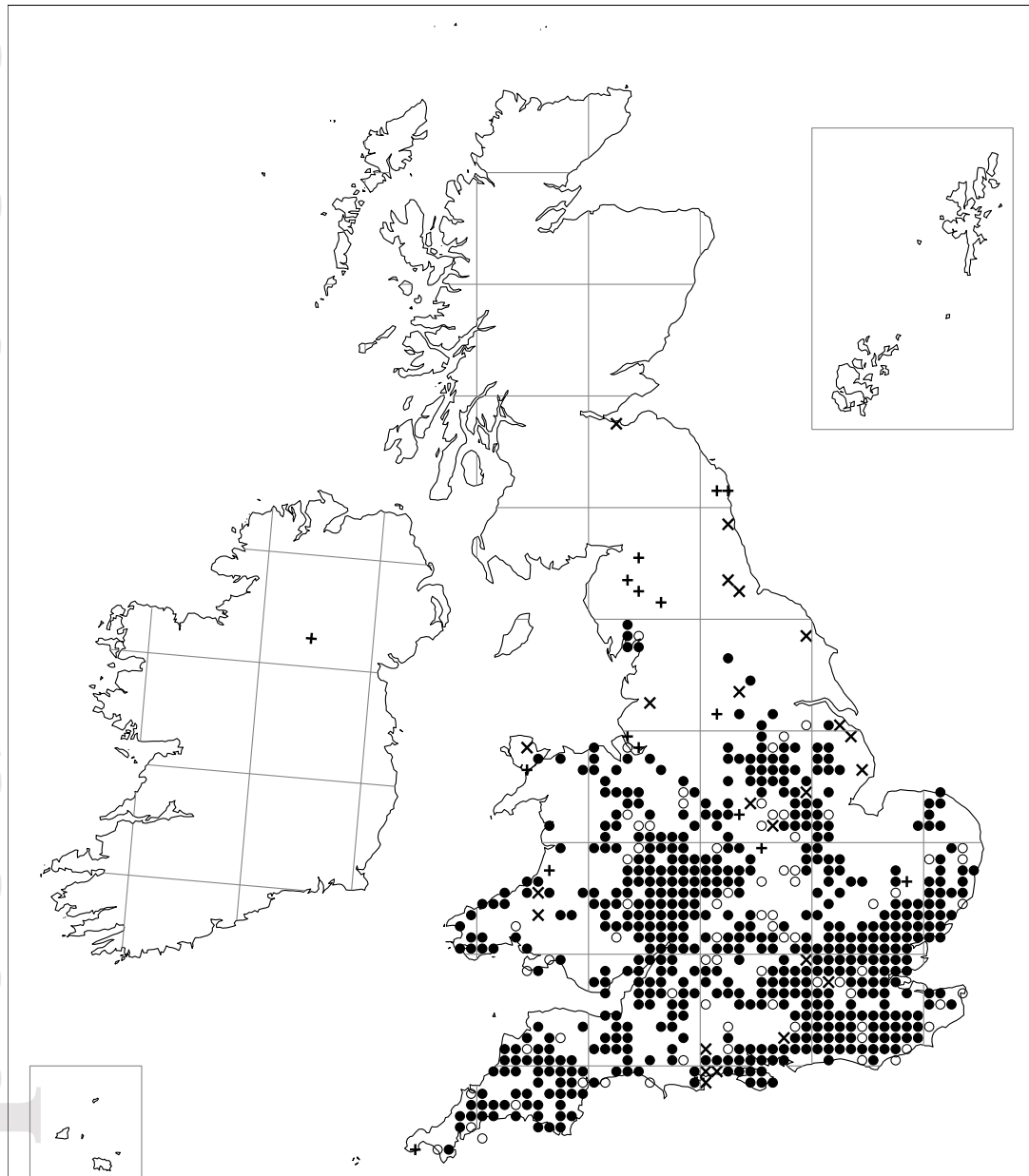*A. pomiformis* (Leers) Rostaf.   Bark

Figures

Fig. 1 The distribution of *Sorbus torminalis* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (●) native 1970 onwards; (O native pre 1970; (+) non-native 1970 onwards; (**x**) 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.
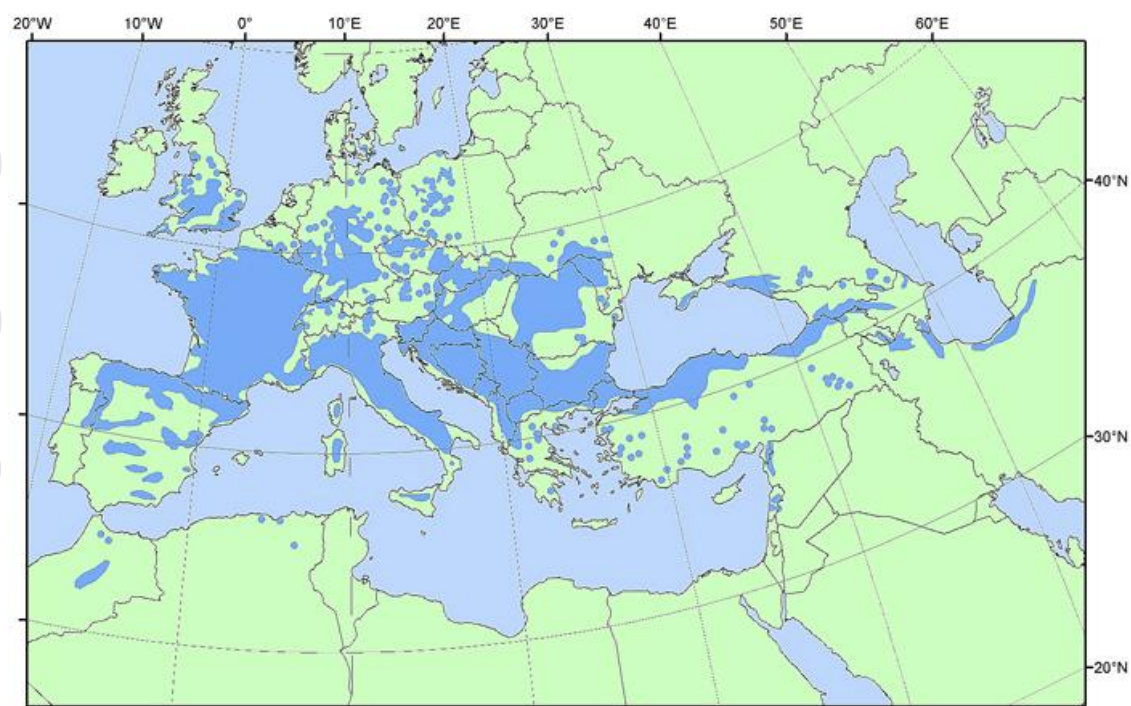
Fig. 2 The natural distribution area of *Sorbus torminalis* in Europe. Map courtesy of EUFORGEN (European Forest Genetic Resources Programme; www.euforgen.org).
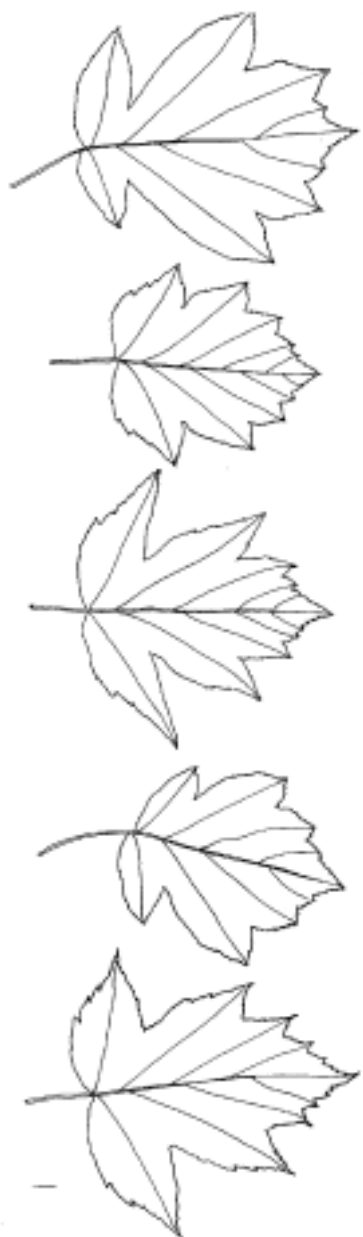
Fig. 3 Examples of the variation in leaf shape found between different trees of *Sorbus torminalis*. Scale bar, 1 cm. From Rich *et al.* (2010).
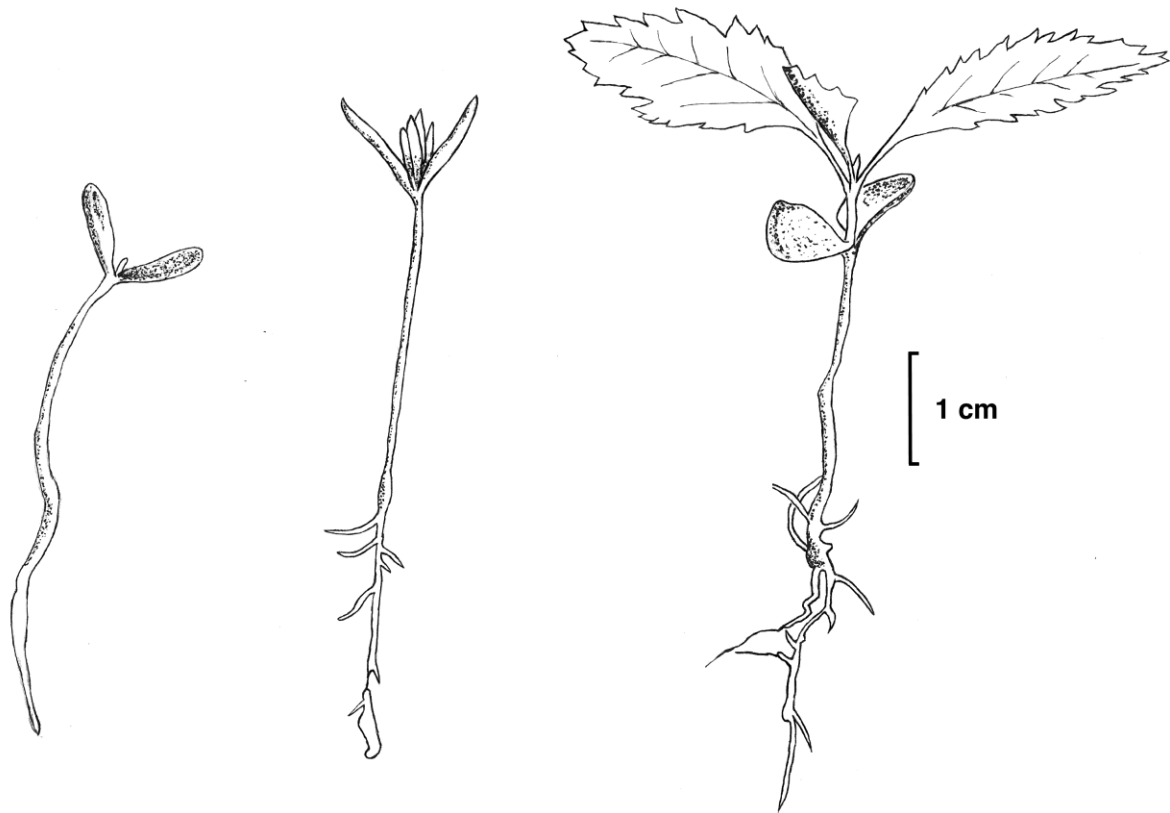
Fig. 4 Seedlings of *Sorbus torminalis* growing under parent trees at Keele University, UK, excavated approximately (a) 1, (b) 2 and (c) 6 weeks after the first appearance of the seedlings above ground.