

Biological Flora of the British Isles: *Ulmus glabra*

Peter A. Thomas¹ | Duncan Stone² | Nicola La Porta^{3,4}

¹School of Life Sciences, Keele University, Staffordshire, UK

²Scottish Natural Heritage, Inverness, UK

³IASMA Research and Innovation Centre, Fondazione Edmund Mach, San Michele a/Adige, Trentino, Italy

⁴The EFI Project Centre on Mountain Forests (MOUNTFOR), San Michele a/Adige, Trentino, Italy

Correspondence

Peter A. Thomas

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

Abstract

1. This account presents information on all aspects of the biology of *Ulmus glabra* Hudson (wych elm) 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. *Ulmus glabra* is a large forest tree, and often an important canopy tree in ancient and semi-natural woodlands. It is primarily native to the north and west of Britain and much of mainland Europe. It is the only elm native to Ireland. It is the most distinct of the British elms in that it rarely suckers and sets abundant viable seed. Although found on limestone screes and cliffs, and hedgerows, it is primarily a woodland tree, especially on moist, basic soils. In many secondary woodlands, it often co-occurs with *Acer pseudoplatanus* and has ecological needs that are similar to *Fraxinus excelsior*.
3. *Ulmus glabra* has clusters of c. 25 hermaphrodite flowers appearing before the leaves on previous year's growth. Seeds are wind-dispersed, falling in April to July, but remain viable for only a few days. Nevertheless, seedling establishment can be abundant. Hybridisation with other northern European elms is common but hybrids are notoriously difficult to identify and therefore probably under-recorded.
4. The health and survival of wych elm in Europe has been seriously compromised since the 1970s due to Dutch elm disease caused by the fungus *Ophiostoma novo-ulmi*, transmitted by elm bark beetles (*Scolytus* spp.). To the south of its Scottish stronghold, many elms are reduced to small trees regrowing from basal sprouts or seeds. These trees tend to be reinfected once trunk diameter exceeds 10 cm. Fortunately for its long-term survival, seed production usually begins a number of years before they are reinfected.

KEYWORDS

communities, conservation, Dutch elm disease, geographical and altitudinal distribution, germination, herbivory, mycorrhiza, reproductive biology

*Nomenclature of vascular plants follows Stace (2010) and, for non-British species, *Flora Europaea*.

Wych elm (mountain elm, Scotch elm). Ulmaceae. *Ulmus glabra* Hudson (*U. montana* With., *U. scabra* Mill., *U. elliptica* C. Koch, *U. podolica* (Wilcz.) Klok., *U. sukaczewii* Andronov) is a deciduous non-suckering tree with a spreading rounded or ovate canopy. Height up to 37–45 m, trunk >200 cm DBH, dividing low-down into long ascending, spreading branches (Medarevic et al., 2011). Bark grey, smooth when young (hence *glabra*), becoming brownish-grey, paler than other elms, furrowed with age. Twigs stout, pendulous, without corky wings; hispid when young becoming smooth and ash-grey to red-brown by the third year. Buds conical, obtuse with dark brown scales, ciliate margins, with rufous hairs on the scales. Leaves alternate, (4)10–11(16) cm × (3)4.5–8(10) cm; more or less pressed against the twig; suborbicular to broadly obovate to elliptic, long-cuspidate, doubly serrate (>130 teeth), apex long-acuminate to cuspidate, usually with three acuminate lobes at a broad apex. These three lobes are specific to *U. glabra* within the genus, particularly on the most vigorous shoots and sprouts, and on the cultivar ‘Cornuta’ (syn. ‘Triserrata’), known in France since 1835 (Fontaine, 1968). Leaves very rough on upperside with scutellate trichomes (Huttunen & Ruonala, 1986), coarsely to finely pubescent beneath; 12–18 pairs of lateral veins often forked (Burton, 2004); asymmetric at base such that the densely villous petiole ≤3 mm is mostly hidden by the long side forming a rounded asymmetrical auricle. Flowers largest of the elms, hermaphrodite, protandrous, appearing before the leaves on previous year’s growth in c. 25-flowered clusters. Pedicel shorter than flowers. Perianth segments connate, usually 4–5 lobed. Anthers purplish red. Fruit a samara 15–20 mm, broadly obovate to elliptical; seed central in fruit (cf. *U. minor* with the seed towards the apex), wing notched at the top (Richens, 1976).

In the first complete chloroplast genomic sequencing study of the Ulmaceae, the genus *Ulmus* appears to be close, in order of distance, to Cannabaceae, Moraceae, Rosaceae, Juglandaceae and Salicaceae (Zuo et al., 2017). *Ulmus* contains 20–45 species, mostly north temperate, concentrated in Eurasia and the mountains of tropical Asia; three species extend into the tropics (Caudullo & de Rigo, 2016; Richens, 1983). Heybroek (1976) defined five sections within *Ulmus*, plus one *incertae sedis*. *Ulmus glabra* is within the section Madocarpus, with *U. minor*, *U. procera*, *U. japonica* (Rehd.) Sarg. (= *Ulmus davidiana* var. *japonica* Redh.), *U. elliptica* Koch, *U. rubra* Muhl., *U. wilsoniana* Schneid. and *U. pumila* L. Within this section, *U. glabra* belongs to the series *Ulmus* together with *U. laciniata* (Tr.) Mayr (NE Asia), *U. bergmanniana* Schn. (China C), *U. uyematsui* Hay (Taiwan) and *U. wallichiana* Planch (Himalayas). However, the classification of elms has for many years been contentious (e.g. Armstrong & Sell, 1996; Heybroek, 1976; Melville, 1975, 1978; Richens, 1980, 1983; Richens & Jeffers, 1985) with between one and seven broad groups in Britain. Rackham (2003) described *Ulmus* as the most critical genus in the British flora, adding that species and varieties are a distinction in the human mind rather than a measured degree of genetic variation. This diversity of opinion comes from the wide variation of form in British elms, aided by multiple hybrids, a lack of internal sterility barriers, and the ability to sucker in some, resulting in large areas of one clone. There has also been disagreement over

the importance of different morphological characters in separating species. In the words of Armstrong and Sell (1996), “[a]ll this has left a legacy of taxonomic incalitrance exacerbated by the vociferous disagreements of the two former elm specialists, R. Melville and R.H. Richens, so that elms are usually overlooked or regarded with despair.” Melville firmly believed that elms in the British Isles have hybridised freely and consequently named many taxa while Richens recognised just *U. glabra* and *U. minor* and a hybrid between them, *U. x hollandica*. In an attempt to move away from this debate, Rackham (1986) classified elms based on their origin: fashion elms (plantsmen’s varieties), traditional elms (linked to a geographical area) and evolution elms (very local elms different from the other two types). Armstrong and Sell (1996) later separated out a group with large leaves, flower-clusters and fruits (including *U. glabra*, *U. vegeta* and *U. hollandica*), those with small, narrow leaves (*U. minor*, *U. plotii*) and those with small, wide leaves (*U. procera*, *U. coritana*). Similarly, Jeffers (1996, 1999), using the leaf collection of R.H. Richens, separated out the same main groups based on leaf parameters. More recently, Sell and Murrell (2018) have recognised 57 species of elm native to the British Isles, including splitting wych elm (*U. scabra*) from the northern wych elm (*U. glabra*). Nevertheless, in nearly all classifications, including *Flora Europaea*, three main species are recognised: *Ulmus glabra*, *U. minor* and *U. procera*. *Ulmus glabra* has been shown to be morphologically and genetically distinct from other European elms (Coleman, Hollingsworth, & Hollingsworth, 2000; Čurn et al., 2014; Hollingsworth, Hollingsworth, & Coleman, 2000; Petrokas & Baliuckas, 2014; Richens & Pearce, 1984) and can be separated from non-European elms by chloroplast DNA barcoding (Gravendeel, Eurlings, & Heijerman, 2009) although hybrids lead to some genetic overlap (Goodall-Copestake, Hollingsworth, Hollingsworth, Jenkins, & Collin, 2005). *Ulmus glabra* is also distinctive since it is the only non-suckering elm, sets abundant viable seed in most years and is the most exclusively woodland elm, especially in northern Britain (Christy, 1922; Grime, Hodgson, & Hunt, 2007; Petrokas & Baliuckas, 2014; Stace, Preston, & Pearman, 2015).

Zebec, Idžojtić, Poljak, and Modrić (2015) showed that, in Croatia at least, the variation in leaf morphology was more variable within populations than between populations of *U. glabra*, even though environmental and climatic factors differ considerably between separate populations. Nevertheless, two ill-defined subspecies (or varieties) of *U. glabra* are sometimes recognised (although not in *Flora Europaea*): spp. *glabra* (ssp. *scabra* (Miller) Dostál) with broadly ovate leaves with acute lateral lobes, a short, forked trunk and low, broad crown and more southern distribution; and spp. *montana* Hyl. with narrowly obovate leaves, lacking lateral lobes and a long single trunk with a tall, narrow crown, commoner in the north and west of Europe (Bugala, Boratyński, & Iszkuło, 2015; Lindquist, 1931; Myking & Yakovlev, 2006; Stace, 2010). The distinction has been seen to be geographically most explicit in Norway based on differences in chloroplast DNA (Myking & Yakovlev, 2006). Janjic (1976) went further to divide ssp. *glabra* into forma *nitida*, *cornuta* and *elliptica*, and ssp. *montana* having a discrete forma *denudata*. *Ulmus glabra* var. *trautvetteri* Johansson, with hairy fruits, has been recognised in

the Caucasus region although this is sometimes treated as the separate species *Ulmus elliptica* Koch (Collin, Bilger, Eriksson, & Turok, 2000; Uotila, 1997). There are numerous cultivars of *U. glabra* (Fontaine, 1968) but the most widespread is almost certainly the weeping *U. glabra* 'Camperdownii,' originally discovered c. 1840 at Camperdown House near Dundee, Scotland (Bugala et al., 2015; Geerinck, 1999). Other varieties while less common can also make large trees. The Monumental Trees (2018) archive of notable trees lists *U. glabra* 'Exoniensis' (18 specimens), *U. glabra* 'Horizontalis' (3), *U. glabra* 'Camperdownii' (3), *U. glabra* f. *cornuta* (2), *U. glabra* 'Lutescens' (2), *U. glabra* var. *pendula* (1) and *U. glabra* var. *serpentina* (1). Accepted variety names and synonyms are given by Brummitt (1992).

Wych elm is primarily native to the north of Britain and at higher altitudes, and is more sporadic in the south where *U. procera* and *U. minor* are more frequent (Melville, 1944; Richens, 1976). *Ulmus glabra* is primarily a woodland tree, forming mixed or pure stands, especially on basic soils but is also found in hedges, field borders and along streamsides, and as a colonist of ungrazed grassland, rocky ground and waste ground (Preston, Pearman, & Dines, 2002; Willmot, 1980). Edlin (1956) gave a figure of 13,000 ha of elm woodland in Britain (mostly wych elm) but, although comparatively resistant to

Dutch elm disease (DED) compared to other European elms (Gibbs, 1978), most mature trees outside of Scotland and the uplands of northern England have now been killed (Stace et al., 2015).

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Ulmus glabra occurs throughout the British Isles (Figure 1) but is much commoner in the north and west, particularly in hilly areas, and is not native in some parts of the south-east and in Cornwall (Stace, 2010; Stace et al., 2015). It is the only elm native to Ireland (Savill, 2013). It is not, however, native in the Outer Hebrides, Orkney, Shetland or Channel Islands although it is a rare alien in all these. In 2015, it was estimated that *U. glabra* woodland made up around 0.1% of Scottish woodland area and the largest remaining areas in the Highlands were at Fort William and Ardnamurchan, Loch Ness, Cromarty and the Black Isle (Bowditch & Macdonald, 2016).

Ulmus glabra is a holarctic species (Figure 2) with a centre of distribution in Europe (Zajac & Zajac, 2009). It is the most northerly and has the widest range of all the European elms, occurring in 72% of European territories (Grime et al., 2007). It reaches its northern limit

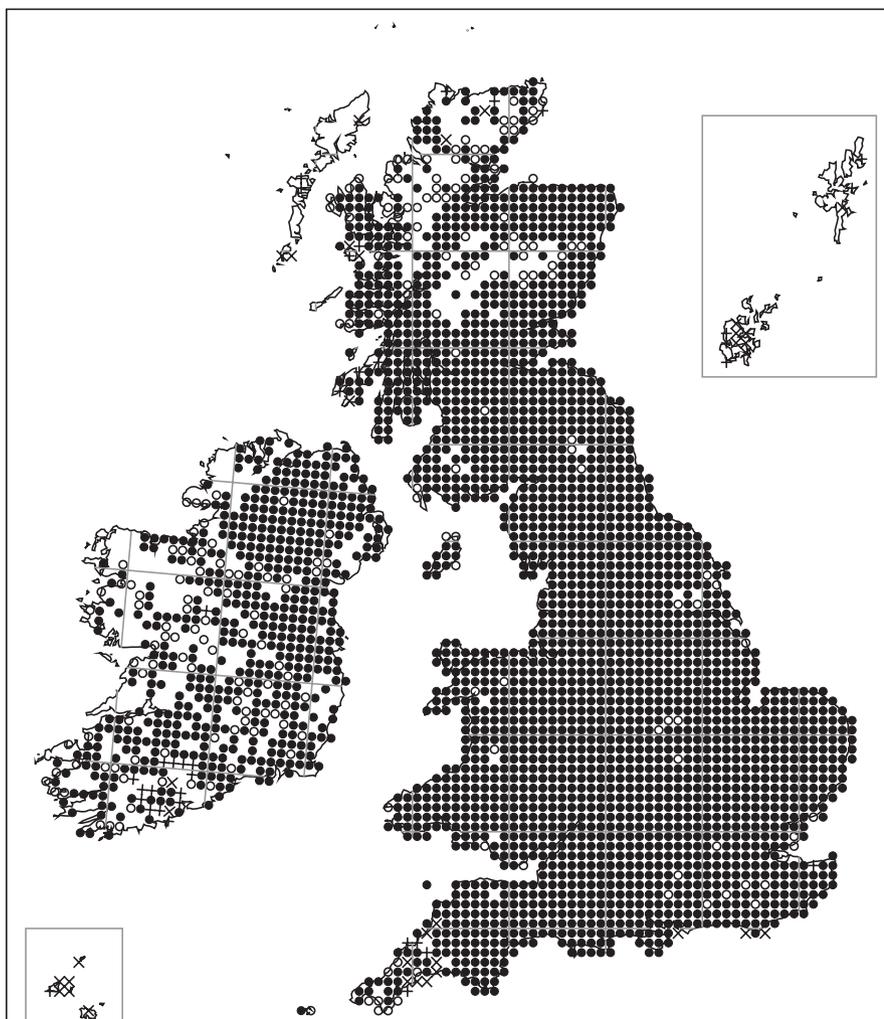


FIGURE 1 The distribution of *Ulmus glabra* in the British Isles, including ssp. *glabra* and ssp. *montana*. Each dot represents at least one record in a 10-km square of the National Grid. (●) native 1970 onwards; (○) native pre-1970; (+) non-native 1970 onwards; (x) non-native pre-1970. Mapped by Colin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

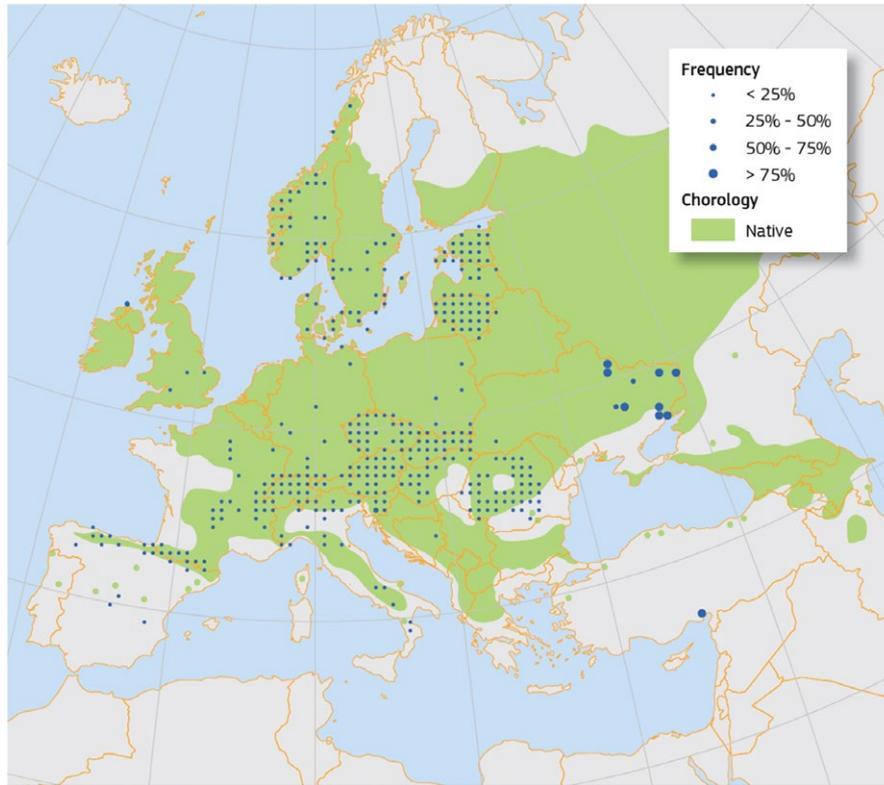


FIGURE 2 Distribution of *Ulmus glabra* across Europe. Frequency of occurrence are from field observations as reported by the National Forest Inventories. From: Caudullo and de Rigo (2016), reproduced courtesy of the European Union

above the Arctic circle at 67°N in Beiar, Norway, 65°60'N in Sweden and 65°20'N in Finland (Caudullo & de Rigo, 2016; Heybroek, 1982; Moe, 1998; Petrokas, 2008), and extends east in Russia to 60°E along the Urals. To the south, it is found on the west and north borders of the Black Sea, extending south to Bulgaria, northern Greece and central Italy (Abruzzo). *Ulmus glabra* is thought to be the only elm native to Spain (Jeffers, 1999) and it has been recently confirmed as present in Portugal (Portela-Pereira, Monteiro-Henriques, Neto, & Costa, 2008). The most southerly native European site is probably in Sicily where it has been found on Mt. Madonie (Raimondo, 1977) and Mt. Nebrodi (Maniscalco, Raimondo, & Schicchi, 2009). It is also found in north and west Asia and North Africa where it is likely to have been introduced (Grime et al., 2007). A number of cultivars of *U. glabra* have been successfully grown in New Zealand but since 1989 these have also suffered from DED (Ganley & Bulman, 2016).

In Britain, seedlings of *U. glabra* are found up to 300 m altitude but naturally occurring adults and planted individuals occur up to c. 530 m (Grime et al., 2007; Preston, Pearman, and Dines, 2002). In mainland Europe, *U. glabra* grows from near sea level in the Netherlands to the upper montane or subalpine forests further east (Mioduszewski & Korczyk, 2013) but reaches a lower altitude than *Fagus sylvatica* in the Bavarian Alps (Mellert et al., 2011). It reaches its altitudinal limits at 700–800 m in Norway (Odland & Birks, 1999), 970–990 m in subalpine forests on south-facing slopes in southern Sweden (Kullman, 2008), 1,400 m in the Alps (Gellini & Grossoni, 1973; Heybroek, 1982), 1,545 m in the western Caucasus (Akotov,

2009) and 2,000 m in north Iran along the Caspian Sea (Heshmati, 2007). In the Caucasus, Akatov (2009) found a sharp decrease in stem diameter above 1,490 m, suggesting that the limit of wych elm has shifted upwards over the past 15–20 years due to climate change. However, in Slovakia, Máliš et al. (2016) showed that between 1966–1979 and 2005–2007, the lower altitudinal limit of *U. glabra* seedlings moved upwards by some 500 m, resulting in a substantial contraction of its altitudinal range, but the authors were unsure whether this was due to a climatic shift or the effects of DED being more prevalent at lower altitudes.

2 | HABITAT

2.1 | Climatic and topographical limitations

Along with many common British broadleaved trees, *Ulmus glabra* is classified as a European temperate species adapted to cool, humid oceanic summers (Brzeziecki & Kienast, 1994; Caudullo & de Rigo, 2016; Giesecke et al., 2008; Hill, Preston, & Roy, 2004; Savill, 2013). Brzeziecki and Kienast (1994) classified the temperature requirement of *U. glabra* to be similar to *Quercus robur*, *Fraxinus excelsior*, *Alnus glutinosa*, *Malus sylvestris* and *Tilia cordata*. Wych elm is, according to Heybroek (1982), more tolerant of low temperatures than *U. minor* accounting for its more northerly distribution, although Grime et al. (2007) suggest that its more northerly and westerly distribution is due to its sensitivity to drought. Certainly, wych elm is said to be

less tolerant of low humidity than most elms (Heybroek, 1982). In central Spain, dry periods of longer than a month are seen as detrimental (Rossignoli & Génova, 2003). In Sweden, the northern range of *U. glabra* is limited by a mean temperature of the coldest month lying between -9.5°C and -15°C (Giesecke et al., 2010; Prentice & Helmisaari, 1991). An investigation of the presence of *U. glabra* and other broadleaves in two localities near their distribution limits in Sweden (Holtjärnen) and Finland (Nautajärvi), found a continuous fluctuation in abundance of *U. glabra* over the last 8,000 years and a particularly strong decline in the last 1,000 years in terms of biomass and pollen accumulation rate under several temperature scenarios (Giesecke et al., 2010). *Ulmus glabra* is considered to be the least sensitive of the elms to low temperature, capable of withstanding winter temperatures down to -50°C (Larcher, 1981). It can also withstand mean monthly temperatures of the coldest month down to -15°C , similar to *Quercus robur*, *Fraxinus excelsior* and *Corylus avellana* (Sykes, Prentice, & Cramer, 1996). However, Giesecke, Miller, Sykes, Ojala, Seppä, and Bradshaw (2010) calculated that *U. glabra* is present when the growing degree-day sum (above 5°C) is as little as 850 (compared to 1,100 in *Tilia cordata* and *Quercus robur*; Giesecke, Miller, Sykes, Ojala, Seppä, and Bradshaw, 2010). At its upper altitudinal limit in the Caucasus, the winters are mild and snowy (average January temperature -3°C) and the summers are warm and wet (average July temperature 19°C , annual precipitation $>1,200$ mm) with a frost-free period of about 160 days (Akatorov, 2009). Autoecology diagrams based on field observations for *U. glabra* vs. *U. laevis* and *U. minor* forest plots are compared in Caudullo and de Rigo (2016). The observed and potential presence of the three species in Europe are shown by plotting annual precipitation, annual average temperature, mean temperature of the coldest month and total precipitation of the driest month, showing that *U. glabra* is found in shaded habitats and those with higher, less variable precipitation.

Randin et al. (2013) compared the upper limits of 18 tree species in elevation in Switzerland and in latitude in Europe and found that *U. glabra*, along with *Populus tremula* and *Acer platanoides*, grew closer to their thermal limit at high latitudes than they did at high elevations where they are thus not filling their thermal niche. This was considered to be mostly likely due to historic limitations in post-glacial recolonisation and a possible lag behind changing climate at high elevations. Slope appears to be unimportant to adult trees although juveniles are recorded as being more frequent on south-facing slopes, especially in unshaded habitats (Grime et al., 2007).

2.2 | Substratum

The best growth of *Ulmus glabra* is seen on moist, fertile soils that are neutral to alkaline (Peterken & Mountford, 1998; Savill, 2013). Brzeziecki and Kienast (1994) classify the best soils as: soil aeration index 2 (on a scale of 1 high, 5 low), soil moisture index 4 (1 dry, 5 wet); nitrate index 5 (1 low, 5 high); and pH index 4 (1 acidic, 5 alkaline). *Ulmus glabra* seedlings planted on granitic soil at 950 m altitude in the Czech Republic showed 97% mortality after 14 years while those planted in holes to which 1 kg of dolomitic limestone

was added suffered just 32% mortality (Balcar, Kacálek, & Kuneš, 2009). Piedallu, Gégout, Lebourgeois, and Seynave (2016) analysed a database of $>46,000$ plots across France and concluded that the distribution of *U. glabra* is primarily dictated by an intolerance of summer soil water deficit (drought), and to a lesser extent by low C/N ratios and even less by an intolerance of temporary waterlogging. In Lady Park Wood, Gloucestershire, Peterken and Mountford (1998) found the highest density of *U. glabra* on alluvial soils, a colluvial fan, the rendzinas of upper slopes and on the moist plateau. Although *U. glabra* is frequent alongside streams, and prefers moist soils across Europe (Brunet, 1991; Fremstad, 1983; Hill et al., 2004; Oberdorfer, 1992; Tcherepanov, 2004), it is rarely found in waterlogged areas (Caudullo & de Rigo, 2016) although it will cope with periodic inundation or variably moist soils (Diekmann, 1996). In the wettest elm-ash forests on Öland, Sweden, *U. glabra* is partly replaced by *U. minor* (Diekmann, 1996). Soil fertility is generally high in the best sites for wych elm and requirement for N is similar to that for *Fraxinus excelsior*, *Acer platanoides* and *Tilia cordata* with an Ellenberg value for N of 6 corrected for Britain (Diekmann, 1996; Ellenberg, Weber, Düll, Wirth, & Werner, 1991; Hill et al., 2004). As such, *U. glabra* is usually excluded from oligotrophic sites by intolerance of low N availability (Prentice & Helmisaari, 1991). Where mineral elements are lower than the optimum range, or the soils are alkaline, *U. glabra* shows poor growth. However, the addition of organic matter, such as manure, or the addition of chemical fertilisers, together with suitable irrigation, improves health and growth (Rahmani, Shoraki, & Banedjschafie, 2009).

Optimum soil reaction for *U. glabra* is pH 7.1–8.0 (cf. >8.0 for *U. minor*—Ellenberg et al., 1991; Hill, Preston, and Roy, 2004; Mittempergher, 2014). *Ulmus glabra* becomes increasingly rare on moderately acid soils below pH 6.0 and is usually absent from strongly acidic soils (Grime et al., 2007; Peterken & Mountford, 1998) although Peterken (1993) records *U. glabra* on soils down to pH 4.7 in Britain.

Despite its preference for moist soils, seedlings and saplings of *U. glabra* are also found on more drought-prone soils on limestone cliffs and screes, quarry heaps and lead-mine spoil throughout Europe (Elvisto, Pensa, & Paluoja, 2016; Grime et al., 2007; Jackson & Sheldon, 1949; Magnes & Drescher, 2001; Preston, Pearman, and Dines, 2002) and even in cracks in walls and roofs, such as around the Rila Monastery in Bulgaria (Pavlova & Georgieva, 2015) and in the shallow soil of green roofs in southern Finland (Gabrych, Kotze, & Lehvävirta, 2016). Like its more usual moist woodland habitats, it is thought that the majority of these rocky sites will either hold water or have moving water near the soil surface (Heybroek, 1982).

3 | COMMUNITIES

Ulmus glabra is often seen in hedgerows, dense woodland edges (Herlin & Fry, 2000) and as an occasional roadside tree in European cities, especially in the Netherlands, and as a common park tree in mainland Europe. It is also widely planted in urban areas of North

America (Rewald, Holzer, & Göransson, 2015). However, in Britain, it is most abundant in woodlands (Savill, 2013). In scrub and hedgerows of the Midlands, it is associated with *Fraxinus excelsior*, *Ilex aquifolium*, *Quercus robur* and *Ulmus procera* (Trueman, Poulton, & Reade, 2013).

In the classification of British plant communities (Rodwell, 1991), *Ulmus glabra* is often at its most abundant in the base-rich *Fraxinus excelsior*–*Acer campestre*–*Mercurialis perennis* woodland (W8), particularly where rainfall is high in the wetter north-west, wetter regions of the south-east and to a lesser extent locally wet sites in the east. *Ulmus glabra* often co-occurs with the non-native *Acer pseudoplatanus*, which is likely to replace *U. glabra* as DED spreads through the north. In the south-east, *U. glabra* tends to be replaced by the suckering elms, *U. procera* and *U. minor*, and *U. glabra* is often most abundant in high forest or in large-coppice underwood. Since its saplings are more shade tolerant than ash (Merton, 1970) the proportion of elm in ash woodlands tends to increase over time (Grime et al., 2007). *Ulmus glabra* is most frequent and abundant in the *Geranium robertianum* subcommunity of W8, forming a mixed canopy with *Fraxinus excelsior* and *Acer pseudoplatanus*, although it is better grown and forms a co-dominant canopy in the deeper and moister soils of the *Allium ursinum* subcommunity; it is still frequent in the more species-rich *Teucrium scorodonia* subcommunity but plays a less prominent role (Rodwell, 1991).

In *Fraxinus excelsior*–*Sorbus aucuparia*–*Mercurialis perennis* woodland (W9) of less base-rich soils of the north-west, *U. glabra* is less frequent (although it can be locally abundant). The dominant *F. excelsior* is still accompanied by *U. glabra* and *A. pseudoplatanus*, mixed with *Quercus petraea*, and saplings of these can be found mixed with *Betula pubescens* and *Sorbus aucuparia*. Wych elm and its co-associate trees are most abundant in the typical subcommunity, becoming much rarer in the *Crepis paludosa* subcommunity on sites inaccessible to herbivores. On the wetter soils of *Alnus glutinosa*–*Fraxinus excelsior*–*Lysimachia nemorum* woodland (W7), *U. glabra* and particularly *A. pseudoplatanus* occur as occasional trees in the *Deschampsia cespitosa* subcommunity. On the less base-rich soils of *Quercus robur*–*Pteridium aquilinum*–*Rubus fruticosus* woodland (W10), *A. pseudoplatanus*, *F. excelsior* and, to a lesser extent, *U. glabra* are a minor component of the canopy. These species are also a minor component of the more acidic beech woodland *Fagus sylvatica*–*Rubus fruticosus* (W14). On base-rich lowland soils of the north and west, *U. glabra* is also a minor component of *Crataegus monogyna*–*Hedera helix* scrub (W21) particularly the *Hedera helix*–*Urtica dioica* subcommunity and the moist, eutrophic soils of the *Mercurialis perennis* subcommunity. But as soils become moister and more eutrophic, *Ulmus procera* and *U. minor* become more prominent, particularly in the *Mercurialis perennis* and *Brachypodium sylvaticum* subcommunities.

Ulmus glabra saplings, along with other common trees, such as *Fraxinus excelsior*, *Fagus sylvatica* and *Acer pseudoplatanus*, also occur in the *Acer pseudoplatanus*–*Sambucus nigra* subcommunity of the open vegetation of the *Epilobium angustifolium* community (OV27) particularly on burnt sites such as old bonfire sites and burnt railway embankments (Rodwell, 2000).

In mainland Europe, *U. glabra* occurs as an occasional roadside tree in European cities, especially in the Netherlands, and as a common park tree. It also occurs in a wide range of mixed forests often associated with species of *Fraxinus*, *Tilia* and *Corylus avellana* (Aarrestad, 2000; Caudullo & de Rigo, 2016). On limestone escarpments and limey to siliceous substrates from Spain to eastern Europe, *U. glabra* occurs in a number of Tilio–Acerion habitat types (Campos, Garcí-Mijangos, Herrera, Loidi, & Biurrun, 2011; Imbrea, Corpade, Corpade, & Nicolin, 2016; Paal, 2009). In Estonia, it is most widespread in *Ulmus glabra*–*Acer platanooides*–*Allium ursinum* woodland (similar to W8 above) or, where the herb layer is scarce, *Ulmus glabra*–*Brachythecium rutabulum*–*Thuidium philibertii*. These two communities can also be found on talus walls but are generally replaced by the species-rich *Ulmus glabra*–*Fraxinus excelsior*–*Aegopodium podagraria*. Wetter and lower parts of talus slopes have *Ulmus glabra*–*Alnus incana*–*Matteuccia struthiopteris* (Paal, 2009). Similarly, in the Ural Mountains, wych elm occurs in the canopy of the lime woodlands *Aconito lycoctoni*–*Tilion cordatae* and *Brachypodio pinnati*–*Tilietum cordatae*, both in the broadleaved deciduous forests of the Southern Urals (Willner et al., 2016) and particularly the relatively species-poor *Acer platanooides*–*Tilia cordata*–*Ulmus glabra* woodlands (Chytrý et al., 2010). In Western Norway, *U. glabra* is found in similar associations, including the associations of Ulmo–*Tilietum* on dry talus slopes, Alno–*Ulmum* at the top of hillsides on unstable soils, and also as a scattered canopy tree in the more species-rich Alno–*Prunetum* on lower hillsides (Austad & Skogen, 1990).

Ulmus glabra is also associated with thermophilous oak forests in the Ural Mountains, forming a canopy tree in the oak-dominated alliance *Brachypodio pinnati*–*Quercetum roboris* (Willner, Solomeshch, Čarni, Bergmeier, Ermakov, and Mucina, 2016). *Ulmus glabra* is a very minor component (<1.2% of trees) of *Fagus sylvatica* forests in Ukraine, Romania and Switzerland (Borlea, 2004; Commarmot et al., 2005). At higher altitudes favouring conifers (1,000–1,600 m), *U. glabra* is an infrequent, subdominant component of the canopy in *Abieti*–*Fagetum dinaricum* forests on limestone and dolomite in Slovenia, Bosnia and Herzegovina (Boncina, 2000; Nagel, Svoboda, Rugani, & Diaci, 2010) and as a small understorey tree (5.5–28.0 cm DBH) in the *Corylo*–*Piceetum* association in north-east Poland, dominated by *Pinus sylvestris*, *Picea abies* and *Quercus robur*, wych elm making up <0.002% of the total basal area, primarily on the more fertile sites (Andrzejczyk & Brzeziecki, 1995). Wych elm is a subdominant and occasional canopy tree of poorly drained forests on river plains woodlands of *Piceetum compositae* and *Piceetum tiliosasperulesum* (Drobyshev, 2001). Wych elm is also widely planted in urban areas of North America (Rewald et al., 2015).

4 | RESPONSE TO BIOTIC FACTORS

The ecological needs of *Ulmus glabra* are similar to those of *Fraxinus excelsior*. Not surprisingly, a number of studies in Europe have shown that before the ravages of DED, the two species would vie for dominance (Kuijper et al., 2010; Leemans, 1992; Malmer, Lindgren, &

Persson, 1978). Pušpure, Laiviānš, Matisons, and Gaitnieks (2016) found in repeated surveys in 2005, 2010 and 2015 that *U. glabra* was initially the third most abundant tree, after ash and *Prunus avium*. Over 10 years, adult ash trees progressively succumbed to ash dieback. However, *U. glabra* also declined from an initial density of 1,554 trees/ha (trees >6 cm DBH) reaching 1,208 trees/ha after 10 years due to DED, while the other main species increased in density, even ash. Elm was progressively replaced by *Alnus glutinosa*, suited to the moist soils. In mainland Europe, both wych elm and ash have a preference for high pH, soil N and soil moisture. Wych elm is more demanding of the first two (Diekmann, 1996) so competition tends to be limited except under optimum conditions for elm where it will out-compete ash (Kuijper et al., 2010; Thomas, 2016). On optimal moist, calcareous clays in southern Sweden, Malmer et al. (1978) found that wych elm saplings dominated while the number of ash saplings had reduced by 40% between 1935 and 1969. There is some indication that *Acer pseudoplatanus* can out-compete both wych elm and ash when understorey density is high, increasing competition (Helliwell & Harrison, 1979; Pigott, 1969). *Ulmus glabra* is also a consistent associate of *Tilia* spp. in ancient woodlands (Abraham & Rose, 2000; Pigott, 1969) and is regarded as an Ancient Woodland Indicator in Worcestershire and Derbyshire (Kirby, 2006).

Ulmus glabra coppices well from basal stump sprouts after felling. However, Onaindia, Dominguez, Albizu, Garbisu, and Amezaga (2004) showed that in northern Spain, *U. glabra* was the third most abundant tree in old-growth forest (16% cover compared to 53% in dominant *Quercus robur* and 24% in *Fagus sylvatica*), yet it was absent from clear-cut areas felled 30 and 60 years ago. Similarly, Tavankar and Bonyad (2015) found stem density of *U. glabra* was higher in protected forest (10.8 stems/ha) than in harvested stands (3.3 stems/ha; time since harvesting was unstated) in Iran. This suggests that *U. glabra* is sensitive to clear-felling in open, warm areas, possibly due to the removal of shady, humid conditions created by surrounding trees. Closed forest conditions are known to favour *U. glabra* (Götmark, Fridman, Kempe, & Norden, 2005). Repeat surveys in southern Sweden since 1909 showed that wych elm numbers increased at the expense of the less-shade-tolerant *Quercus robur*, and the trend was only reversed after 1970 with the advent of DED opening up the stands (Brunet, Bukina, Hedwall, Holmström, & von Oheimb, 2014; Brunet, Hedwall, Holmström, & Wahlgren, 2016). However, elm was still the most abundant species in the upper shrub layer in 2011 with a mean cover of 25%.

Predation of seeds and seedlings can be very high (Bowditch & MacDonald, 2016; Grime et al., 2007)—see Section 8.3—especially by rodents (Dostál, Cvrčková, & Novotný, 2011). In Białowieża National Park, Poland, Kuijper, Jędrzejewska, Brzeziecki, Churski, Jędrzejewski, and Żybura (2010) found that *Carpinus betulus* and *U. glabra* were the most browsed species of tree. The readiness with which *U. glabra* is browsed appears to be common throughout its range. In southern Sweden, many woodland trees, particularly, *U. glabra*, *Quercus* spp. and *Fagus sylvatica*, date from the first half of the 19th century and are thought to have grown up during a period of less extensive browsing (Malmer, Lindgren, and Persson, 1978).

This led to the number of elms more than tripling between 1916 and 1970 (prior to DED). Similarly, in beech forest over limestone in central Germany, Heinrichs, Winterhoff, and Schmidt (2012) recorded that between 1955–1960 and 2009 *U. glabra* increased in cover and frequency in the shrub layer, as did a number of other broadleaved species. This was attributed to an increase in hunting over this period, doubling the number of culled roe deer (*Capreolus capreolus* L.) and a concomitant decrease in browsing. A reduction in domestic livestock produces a similar increase in elm regeneration (Navroodi, 2015). In northern Spain, Onaindia et al. (2004) noted that the cover of *U. glabra* in woodland lightly grazed primarily by cattle (c. 0.2 animal-unit months) was 5% compared to 16% in ungrazed woodland. In central Russia, *U. glabra* along with *Alnus glutinosa* and *Fraxinus excelsior* invade and then dominate developing flood-plain forest beside watercourses abandoned by beaver *Castor fiber* L. (Evstigneev & Belyakov, 1997; Logofet, Evstigneev, Aleinikov, & Morozova, 2016). Okołów (1978) noted that people walking along set “tourist” routes through Białowieża National Park, Poland were damaging above-ground roots. Damage was least in *U. glabra* (38.6% of roots damaged), compared to 47.9% in *Tilia cordata*, 71.0% in *Carpinus betulus* and 89.9% in *Picea abies*. However, of the roots that were damaged, *U. glabra* had 67.1% of roots with >25% damage to the surface area compared to 54.8% in *C. betulus* and 33.3% in *T. cordata*; damage was highest (79.8%) in *P. abies*.

4.1 | Dutch elm disease

Dutch elm disease is described in detail in Section 9.3. Regrowth of top-killed trees from basal sprouts usually reaches reproductive age before being killed back by the next wave of DED. These successive waves of DED have led to the effective loss of isolated trees in the east of Britain but in the west, with higher original populations, *U. glabra* has survived by: (1) continued survival of trees that were mature before the outbreak; (2) stump sprouts from trees whose main stem was killed by the disease; and, most importantly, (3) regeneration from seed (Peterken & Mountford, 1998). Trees that survived tended to be slow growing on dry sites and be hidden in the subcanopy creating “refuge locations where the elms are either unattractive to *Scolytus* beetles or more likely to escape notice” (Peterken & Mountford, 1998).

The effect of DED has been to reduce the contribution of wych elm to basal area and biomass of woodlands (Peterken & Jones, 1989) and reduce its prominence as a canopy tree. For example, in the spruce-fir-beech forests of the Czech Republic, the cover of wych elm reduced from 43% in 1970 before the main wave of DED to 3% cover in the 1990s (Šamonil & Vrška, 2008); in this case, *U. glabra* was replaced by *Fagus sylvatica*. However, despite these reductions, the abundance of individual trees has not declined as noticeably. In more mixed, lowland stands, elm is being replaced by *Acer pseudoplatanus*. For example, in a forest in central Germany, *U. glabra* made up 27% of stems but declined due to DED after 1992. By 1996, *A. pseudoplatanus* made up 81% of the seedlings (c. 52,000 seedlings/ha), whereas *U. glabra* contributed 3% (Hüppe &

Röhrig, 1996). In mainland Europe, however, recruitment from seed is more or less balancing mortality due to DED (H. Solheim, pers. comm., 2006, quoted in Hahn & Emborg, 2007; Myking & Skrøppa, 2007). Indeed, in *Carpinus betulus* woodland on limestone of central Germany, Becker, Spanka, Schröder, and Leuschner (2016) showed that *U. glabra* had increased in the shrub layer from almost complete absence in 1970 to 8% cover by 2011, in this case aided by conversion management from coppice into high forest and by increased atmospheric N inputs.

Repeat surveys since 1945 have shown a similar response in an unmanaged *U. glabra* population in mixed deciduous woodland at Lady Park Wood, Forest of Dean. DED arrived in Britain in 1972 (Brasier & Gibbs, 1973) and by 1985 about 65% of the canopy and subcanopy trees recorded in 1945 at Lady Park Wood had been killed (Peterken & Mountford, 1998). This was followed by vigorous regeneration by seedlings and some sprouts from stumps of infected trees, and by 1993 numbers of *U. glabra* had increased by 40% compared to 1972, although DED continues to kill vigorous, exposed individuals. Peterken and Mountford (1998) suggested that, *U. glabra* is likely to persist in two forms: (1) a large fast-turnover subpopulation of fast-growing but repeatedly infected trees, arising mainly from seed regenerating in gaps, and less vigorous sprouts from infected trees that will not reach the canopy but persist as an informal coppice cycle; and (2) a small, low-turnover subpopulation of slow-growing individuals growing in suboptimal dry or secluded sites that tend to avoid the attention of the *Scolytus* vector. However, a third form exists as single large individuals isolated from other elm trees and so out of range of the *Scolytus* vectors (Menkis, Östbrant, Wågström, & Vasaitis, 2016; Wadley & Wolfenbarger, 1944). These trees, known as escapees, are not necessarily resistant to DED and survive by avoiding infection by the disease.

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

Across its natural range, *U. glabra* tends to occur as scattered, isolated trees. For example, in the West Carpathians of central Slovakia, *U. glabra* density was <1 tree/ha out of a total tree density of 243 trees/ha (Holeksa et al., 2009), and mixed beech forests in Slovenia had 0–28 *U. glabra*/ha out of a total tree density of 338–470 trees/ha (Nagel, Firm, Rozenbergar, & Kobal, 2016). Similarly, at the edge of its range, such as in Iran, it is a scattered tree in mountain forests (Fazlollahi, Ahmadlo, & Keshtiban, 2015). This lack of gregariousness is encouraged by *U. glabra* being a non-suckering elm and by DED. For example, in eastern England, where wych elm is infrequent and never gregarious, DED has removed and continues to remove individual trees creating an even less gregarious distribution (Rackham, 2003). In Denmark, DED has resulted in a low density so that individual trees are no nearer than 400–500 m apart (Nielsen & Kjær, 2010).

Seedlings and saplings, however, can be dense and aggregated due to abundant regeneration in an area (Grime et al., 2007). In

western and central Poland, many woodlands contain a single specimen of *U. glabra* but in some sites it was found by Napierała-Filipiak, Filipiak, Łakomy, Kuźmiński, and Gubański (2016) to be locally dominant as saplings in small patches of 100–200 m². Moreover, E.W. Jones (1960 quoted by Peterken & Mountford, 1998) noted that *U. glabra* (and *Tilia cordata* and *T. platyphyllos*) were “markedly gregarious” in parts of the Wye Valley, possibly helped by selective thinning of limes during 1940–1945 that opened up the canopy. As noted in Section 4, Pigott (1975) observed that *U. glabra* seedlings were clustered in openings in the canopy in Białowieża Forest, Poland.

5.2 | Performance in various habitats

Grime et al. (2007) classify *U. glabra* as an intermediate between competitor and stress-tolerant competitor. Being wind-dispersed, *U. glabra* will readily invade open areas such as abandoned wooded meadows and pastures and respond to high light levels with rapid growth (Olsen, 1978). Nevertheless, being relatively shade tolerant, it will equally well persist into closed, mature woodland (Herlin & Fry, 2000; Pålsson, 1994; von Oheimb & Brunet, 2007). This flexibility explains why seedlings and saplings can establish in unshaded rocky habitats as described in Section 2.2.

Within woodlands, seedlings tend to germinate in open patches without herbaceous vegetation (Grime et al., 2007) but can establish in deep shade. In Białowieża Forest, Poland, Pigott (1975) observed that *U. glabra* seedlings were largely restricted to openings in the canopy associated with patches of *Urtica dioica* that cast a very deep shade that was seemingly too dense for other tree species.

Ulmus glabra is usually classified as comparatively to very shade tolerant: Brzeziecki and Kienast (1994) list it as 3 on a scale of 1 (shade intolerant) to 4 (tolerant), and the Ellenberg value for light is 4 (a half shade plant), similar to *Fraxinus excelsior* (Ellenberg, Weber, Düll, Wirth, and Werner, 1991; Hill, Preston, and Roy, 2004). However, while *F. excelsior* becomes shade intolerant as adults (Thomas, 2016), wych elm retains its shade tolerance and so in the dense shade in woodlands in Öland, Sweden, elm and *Acer platanoides* increase at the expense of *Quercus* spp. and *F. excelsior* (Diekmann, 1994). However, Pigott (1975) noted that wych elm tended to be absent below the canopy of mature elms, perhaps due to excessive shade. However, care needs to be taken in ascribing all absences to inability to cope with shade. For example, Götmark, Fridman, Kempe, and Toet (2005) found very little *U. glabra* regeneration in spruce, pine and mixed conifer woodlands in Sweden. But this was attributed to the absence of seed parents and the limited wind dispersal of elm seeds rather than the deep shade since similarly little regeneration was found in comparatively open birch woodlands. Niinemets and Valladares (2006) classified *U. glabra* and *U. minor* as having similar shade tolerance: 3.53 and 3.36, respectively, on a scale of 0 (very intolerant) to 5 (very tolerant).

Seedlings in deep shade may grow very slowly but seedlings and saplings can survive for many years, forming a seedling bank that can respond to an increase in light by rapid height and increment growth (Nisbet, 1893). Certainly in central Russia, Drobyshev

(2001) found that in small gaps (<200 m²) *U. glabra* and *Tilia cordata* saplings out-competed *Picea abies* and *Acer platanoides* by faster growth. Growth in unshaded places can be very fast. Nisbet (1893) suggested that wych elm will grow faster than *Fagus sylvatica* when well-lit. Mioduszewski and Korczyk (2013) classified young wych elm (<10 years old) as one of the fast-growing forest species. Loudon (1844) recorded a planted wych elm that reached 7.6–12.2 m height in 10–26 years, and another tree that reached 20.1 m in height and 0.6 m in diameter in 40 years. In the shade of canopy trees, growth is slower. Under ash on limestone in Derbyshire, England, Merton (1970) found wych elms 29 cm diameter after 80 years and 45 cm diameter after 140 years.

Once wych elm becomes a canopy tree, however, its maximum rate of growth declines sharply and is comparatively slow at 0.46 m/year, compared to 0.85 m/year in *Quercus robur* and *Q. petraea*, 0.75 m/year in *Fraxinus excelsior* and 0.7 m/year in *Fagus sylvatica* (Prentice & Helmisaari, 1991). In mixed woods dominated by ash in north-east Italy, Alberti et al. (2005) found a relationship between DBH and height: $\text{height} = 1.34 \times \text{DBH}^{0.92}$, $r^2 = .94$, $n = 13$, $p < .001$.

Trees normally reach maximum height at the age of 60 at which point they can be 40 m high and 150 cm DBH (Mayer, 1977). Individual trees over 200 years old have been reported on limestone in the Derbyshire Dales (Merton, 1970) and Serbia (Medarevic et al., 2011), although the maximum age is 400–700 years (Brzeziecki & Kienast, 1994; Mioduszewski & Korczyk, 2013), a 100 years or more longer than *U. minor*. A 438-year-old wych elm was recorded in 1994 in northern Poland, where most of the old elms are found in parks and along roadsides (Pacyniak, 2003). The oldest tree known in Italy, at Piazza Regina Margherita in San Lorenzo, southern Italy, has been dated at 717 ± 100 years old (Monumental Trees, 2018).

Ulmus glabra produces a dense canopy and abundant litter that is short-lived (Grime et al., 2007) and of higher pH (c. 5.9) than that of other common deciduous trees such as species of *Betula*, *Quercus* and *Fagus sylvatica* (Dursun, Ineson, Frankland, & Boddy, 1993; Falkengren-Grerup, Brunet, & Diekmann, 1998). Oostra, Majdi, and Olsson (2006) compared 67-year-old monocultures of *U. glabra*, *Fraxinus excelsior*, *Fagus sylvatica*, *Carpinus betulus*, *Picea abies* and *Quercus robur* in southern Sweden. They confirmed that wych elm produced the highest pH of the O-horizon (pH 5.87) and deeper horizons (5.31–5.87) and had the highest base saturation (77.9% in the O-horizon—compared to 9.83% under *P. abies*—and 32.3%–54.5% in deeper horizons). In the O-horizon, the wych elm stand had the lowest soil organic carbon (SOC: $11.8 \pm 0.5\%$ SE, $n = 4$), total nitrogen ($0.59\% \pm 0.02\%$) and cation exchange capacity (33.5 ± 2.5 cmol_c/kg) of any of the species. But at deeper horizons (3–20 cm depth), wych elm soil had the highest levels of any species tested (SOC, 3.0%–5.0%; total nitrogen, 0.19%–0.35%; cation exchange capacity, 7.1–12.5 cmol_c/kg). Overall, wych elm had the highest total SOC after *P. abies* and was the highest of the angiosperm species. Total fine root biomass (<5 mm diameter) for wych elm was 1,490 g dry mass/m², second only to *Q. robur* (1,760 g dry mass/m²) and much higher than in *F. sylvatica* (596 g dry mass/m²). Wych elm had 22.5% of the fine roots in the O-horizon; less than the shallow-rooted *F. sylvatica*

(28.0%) and *P. abies* (48.9%) but high compared to *Q. robur* (14.0%), *F. excelsior* (5.2%) and *C. betulus* (2.4%). The greater proportion of SOC at depth under the comparatively shallowly-rooted wych elm was suggested to be due to greater earthworm activity caused by the low-acidity and nutrient-rich leaf litter. It was concluded that of the species tested, wych elm would sequester most soil carbon. The high availability of nutrients under wych elm was higher even than under ash, helping in rapid nutrient cycling.

5.3 | Effect of frost, drought, etc.

5.3.1 | Frost

As an oceanic species, Brzeziecki and Kienast (1994) classified the resistance of *U. glabra* to late-spring frosts as 2 on a scale from 1 (high resistance) to 5 (low); winter frost resistance scored 4 on the same scale, higher than *U. minor* (5). Bud break is earlier in *U. glabra* than in most trees with ring-porous wood anatomy and so could render it more vulnerable to cavitation from late-spring frosts (Grime et al., 2007). However, Jansen et al. (2004) showed that many members of the Ulmaceae, including *U. glabra*, have pit membranes with a torus between narrow vessels and vascular tracheids; a similar situation to that found in gymnosperms. The narrow tracheary elements and pit membranes will impede hydraulic conductivity but offer greater resistance to freezing-induced cavitation.

A storm with freezing rain over Slovenia and Croatia in 2014, with ice deposits up to 10 cm thick, did least damage to *Abies alba* and *Picea abies* while *U. glabra*, *Pinus sylvestris*, *Acer pseudoplatanus* and *Carpinus betulus* suffered an intermediate amount of damage. *Fagus sylvatica*, *Quercus petraea* and *Ostrya carpinifolia* suffered the highest damage. This suggests a fair ability to withstand winter storms. Commonest sized trees damaged were 20–30 cm DBH; damage was primarily by being snapped or uprooted (Nagel et al., 2016).

5.3.2 | Drought

Ulmus glabra is intermediate in ability to withstand drought and was classified at 3 (scale 1–5) by Brzeziecki and Kienast (1994) and 2.41 on a scale of 0 (very intolerant) to 5 (very tolerant) by Niinemets and Valladares (2006), and is less drought tolerant than *U. minor* (3.39). Rackham (2003) suggested that *U. glabra* is more vulnerable to drought on the drier soils of East Anglia. The drought sensitivity of *U. glabra* was underlined by Venturas, López, and Gascó (2013), working with saplings 2.1–2.4 m tall planted in central Spain, who found that *U. glabra* suffered 50% loss in hydraulic conductivity at –0.5 MPa xylem water potential, compared to –1.1 MPa in *U. minor* (Table 1). The larger vessels of *U. glabra* allow a maximum xylem specific conductivity and maximum leaf specific conductivity that is 2–3 times higher than in *U. minor* (Table 1). This demonstrates that *U. glabra* is adapted primarily for efficient water transport in moist habitats rather than drought resistance when it is at comparatively high risk of cavitation. Coultherd (1978) investigated the effect of the severe 1976 drought in Britain on established and recently

TABLE 1 Xylem anatomy and hydraulic features of *Ulmus glabra* and *U. minor* saplings, 2.1–2.4 m tall and 0.9–1.5 cm diameter, grown in central Spain. Data are from Venturas et al. (2013). Values are $M \pm SE$. Columns with the same letters are not significantly different at $p < .05$ (analyses from original publication)

Variable	Units	<i>U. glabra</i>	<i>U. minor</i>	n
Vessel frequency	vessels per mm ²	71.4 ± 2.4a	60.8 ± 4.2b	5
Average vessel area	µm ²	1,392 ± 22a	941 ± 22b	5
Vessel lumen cross-sectional area	%	10.0 ± 0.3a	5.9 ± 0.4b	5
Hydraulic diameter	µm	56.6 ± 1.0a	43.4 ± 1.7b	5
Theoretical hydraulic conductance	µm ²	20.1 ± 1.1a	7.2 ± 0.8b	5
% of grouped vessels in wood adjacent to the pith	%	91.7 ± 2.3a	98.5 ± 2.5a	5
% of grouped vessels in earlywood	%	45.8 ± 3.3a	48.3 ± 3.4a	5
% of grouped vessels in latewood	%	88.4 ± 2.2a	87.8 ± 2.5a	5
Maximum xylem-specific conductivity	kg m ⁻¹ s ⁻¹ MPa ⁻¹	2.64 ± 0.18a	1.26 ± 0.23b	10
Leaf xylem-specific conductivity	kg m ⁻¹ s ⁻¹ MPa ⁻¹ 10 ⁴	3.91 ± 0.73a	2.35 ± 0.48a	10
50% loss of conductivity threshold	MPa	-0.50 ± 0.07a	-1.13 ± 0.11b	10
80% loss of conductivity threshold	MPa	-0.91 ± 0.16a	-2.07 ± 0.57b	10

planted elm trees and found that mortality was higher in trees already suffering from DED.

5.3.3 | Flooding

Wych elm is not a wetland species but seedlings are occasionally found in topogenous and soligenous mires (Grime et al., 2007). Niinemets and Valladares (2006) classified the waterlogging tolerance of *U. glabra* as 2.03 on a scale of 0 (very intolerant) to 5 (very tolerant), comparable to many other woodland trees, despite its ability to produce adventitious roots (Frye & Grosse, 1992; Glenz, Schlaepfer, Iorgulescu, & Kienast, 2006). Frye and Grosse (1992) found that flooding 1-year-old seedlings under 10 cm of water for 120 days reduced height and diameter growth but had little effect on survival. Mellert, Fensterer, Küchenhoff, Reger, Kölling, Klemmt, and Ewald (2011) modelled the behaviour of *U. glabra* in response to waterlogging in the Bavarian Alps and showed that waterlogging did not appear to affect distribution. In mainland Europe, *U. glabra* is replaced on wet soils by *U. laevis* (Borlea, 2004).

5.3.4 | Pollution

Like *U. procera*, wych elm is tolerant of exposure to atmospheric pollution, restricted growing conditions and pollarding, all commonly found in urban areas (Rose & Webber, 2011; Savill, 2013). It is also tolerant of exposure to sea winds (Savill, 2013) and to de-icing salt (Klincsek & Torok, 1978; Rose & Webber, 2011; Suchara, 1982). *Ulmus glabra*, *Fraxinus excelsior* and *Crataegus monogyna* have a similar tolerance to soil contaminated with de-icing salt (Dobson, 2009),

while *U. glabra* is moderately tolerant of de-icing salt spray (whereas other two species were only “intermediate”; Dobson, 2009; Soldini et al., 1974). Soldini et al. (1974) classify *U. glabra* as not tolerant of saline soils but this was on central reservations of dual carriageways and the salt concentration (from additions of up to 240 g of salt/m²) was likely to be higher than in other studies.

Rewald et al. (2015) placed 8-week-old *U. glabra* seedlings in a phytotron with non-limiting water and nutrients, and with or without commercial mycorrhizal inoculant (composed of various *Glomus* spp.). Mycorrhizal seedlings were smaller (as expected due to cost of supporting the mycorrhiza) but when 50 mM NaCl was added, the biomass of non-inoculated seedlings was reduced and fine root respiration increased over the next 36 days but mycorrhizal plants were unaffected by adding salt. The salt did not produce any root necrosis or induce leaf chlorosis so the stress was considered to be mild. Similarly, trees planted close to a factory emitting sulphur dioxide were 35% lighter (dry mass) compared to those grown 17 km away. This reduction in growth was not relieved by applications of lime and fertiliser (Hadjørg, 1975).

Ulmus glabra has been found to be more sensitive to ozone when compared with *U. minor*, showing severe reddish stippling and bronzing on the upper surface of leaves, while the lower surface appears unharmed (Sanz & Calatayud, 2009). *Ulmus glabra* was found to be one of the most susceptible species to ozone injury in the Alps, both in Switzerland, where it was considered as a potential bioindicator (Skelly et al., 1999) and in the Lombardy and Valtellina regions of northern Italy where it showed clear symptoms when exposed to ozone levels up to 70–85 ppb (Cozzi, Ferretti, & Innes, 2000). *Ulmus glabra* is also less tolerant to ozone than *U. laevis* (Manning, Godzik, & Musselman, 2002) and *U. americana* and *U. thomasii* (Rhoads, Harkov,

& Brennan, 1980). Greater damage caused by ozone may be exacerbated by the higher tropospheric ozone concentration at higher elevations where *U. glabra* normally grows in mainland Europe.

5.3.5 | Fire

The bark of young trees is readily damaged by fire but the thicker bark of older trees can offer some protection. However, damaged tissue is prone to infection by fungi (Stipes & Campana, 1981). Fast-growing regeneration after fire from seedlings has been recorded in the Caucasus Mountains (Omarova & Asadulaev, 2016). Tinner et al. (2000) rates *U. glabra* from palaeobotanical data as being comparatively sensitive to medium and high fire frequency, similar to *Fraxinus excelsior* and *Tilia* spp.

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Ulmus glabra is a large forest tree, reaching 41–45 m height and 78 cm DBH in tall mixed forest (Holeksa et al., 2009), compared to <36 m in *U. laevis* and *U. minor*. It can regularly live for 400 years (see Section 5.2).

The international catalogue of monumental trees, notable for their size or prominence in the landscape (Monumental Trees, 2018), includes 110 specimens of *U. glabra* from 16 European countries (20 trees in Germany, 11 in the Netherlands, 6 in Slovakia, 5 in Italy, 4 in Poland and the others in decreasing order in Austria, Switzerland, Sweden, UK, Hungary, Czech Republic, Lithuania and Montenegro). Sixty-two trees are wider than 100 cm DBH (ranging between 100 and 248 cm DBH) with a height ranging between 18 and 44 m. Within the genus, only *U. laevis* is more abundant with 223 monumental specimens but *U. glabra* is more frequent than *U. minor* (107 individuals) and *U. x hollandica* (86 individuals).

The largest *U. glabra* recorded in Britain was a specimen near Uttoxeter, Staffordshire that was 37 m tall and 4.9 m in diameter in 1636 (The Tree Register, 2018). Two UK trees with a DBH >1 m are regarded as monumental, located at the Brahan Estate, Dingwall (230 cm DBH), and at Stevenage (160 cm DBH), both 25 m tall (Monumental Trees, 2018). However, a database of UK ancient trees (Woodland Trust, 2018) lists 450 specimens of *U. glabra*, over 210 of them with diameters between 1 and 4.77 m DBH. A number of these trees are multi-stemmed as a result of previous coppicing.

Unlike most other elms, *U. glabra* rarely suckers but sprouting from the base of the tree is common (Elwes & Henry, 1913). In Lithuania, Petrokas (2011) noted that 78% of *U. glabra* were bifurcated or trifurcated fairly low down the trunk, linked to the production of strong ascending branches. Only 6.4% were decurrent with an upright, unbranched stem. A study of a number of solitary individuals in Slovakia revealed that a tree of 50 years, 15.1 m tall, with a crown width of 10.8 m and 43.7 cm DBH, typically had a total leaf area of 353.9 m², a crown volume of 793.9 m³, with a leaf area index of 4.2 m²/m² and crown volume of 9.5 m³/m². In a typical tree, 1 m³ of canopy contained 0.4 m² of leaf area (Vreštiak, 1993).

Skre (1993) observed that in seedlings grown at various constant temperatures, the specific leaf area (SLA) varied from 18 ± 2 m²/kg at 9°C to 36 ± 3 m²/kg at 21°C. Under field conditions, Alberti et al. (2005) noted a SLA of 22.4 ± 4.5 m²/kg in *U. glabra* compared to 13.8 ± 3.7 m²/kg in *Fraxinus excelsior*. Trees that had been micro-propagated and planted out for 6 years had a significantly higher SLA (14.77 ± 3.17 m²/kg, SD) than similar grafted trees (12.74 ± 3.45 m²/kg), and had a lower dry leaf mass: 0.32 ± 0.13 g, SD micropropagated; 0.40 ± 0.24 g grafted (Đurkovič et al., 2010).

Møller (1995) (see Section 9.1) suggested that stressed leaves had a greater asymmetry in width between the two halves of a leaf and in the distance between side veins, and was reflected in greater vulnerability to insect herbivory. Stress from watering trees with saline water and from DED both resulted in more asymmetrical leaves (Møller, 1999; Møller & Van Dongen, 2003). Stomatal density ranges from 280 to 300 per mm² (Fiorin, Brodribb, & Anfodillo, 2016; Zarinkamar, 2007). Chloroplast diameter is 5.0 ± 0.2 μm (SE, n = 3), similar to other woody species examined (Harbinson & Woodward, 1984).

The wood of *U. glabra* is ring-porous in the stem, semi-ring-porous in roots near the stem, and diffuse-porous in more distal roots (Trockenbrodt, Richter, Möller-Lindenhof, & Dujesiefken, 2001). Wood density when dried to 15% moisture is in the range 592–690 kg/m³, similar to *Fagus sylvatica* and *Fraxinus excelsior* (Alberti et al., 2005; Kiaei & Samariha, 2011; Savill, 2013). Species of elm cannot usually be readily identified by wood anatomy (Schweingruber, 1990) but *U. glabra* can be distinguished from *U. carpinifolia* since in the former the rays are shorter and wider with 4–5 rays/mm, compared to 6–8 per mm in the latter (Safdari & Golchinfar, 2011). Elm wood is very durable in contact with water. Muč (1986) gives durability figures of 100 years in open air and 500 years submersed in water. Bark thickness has been calculated by Thill and Palm (1983) in Belgium to be 0.3 cm in trees 11 cm DBH and 2.5 cm in trees 94 cm DBH. The anatomy of bark during its development is discussed in detail by Trockenbrodt (1991, 1994).

6.2 | Mycorrhiza

Arbuscular mycorrhizal. *Ulmus glabra* has been found to form symbioses with several *Glomus* spp. (Harley & Harley, 1987; Rewald et al., 2015; Wang & Qiu, 2006). Section 5.3.4 includes more ecological detail. Ectotrophic mycorrhiza have not been identified.

6.3 | Perennation: Reproduction

Ulmus glabra is tolerant of coppicing and pollarding. It will readily produce sprouts from the base of the stump but regeneration is normally from seed (Savill, 2013). Mioduszewski and Korczyk (2013) suggest that grafting of elms is “difficult.” In their study using Polish material, graft survival during the first year after planting varied from 38% to 100% depending upon the clone used. Similarly, propagation success from cuttings can be low, and significantly less than in *U. laevis*. Rooting percentage can be low but so can duplication success (i.e. getting at

least one plantlet from each sampled tree), an important consideration for maintaining genetic diversity when propagating (Collin et al., 2004). Success of cuttings can be improved by grafting as a primary propagation step to bulk-up and “re-juvenate” material before creating new trees in secondary propagation using cuttings (Collin et al., 2004). Use of indole butyric acid at 8,000 ppm has been shown to improve rooting success of cuttings (Shahraji, Farokhnia, & Hatamzadeh, 2007).

Machon, LeFranc, Bilger, Mazer, and Sarr (1997) found that *U. glabra* in France was genetically diverse ($H_T = 0.373$ —slightly more than in *U. minor*, $H_T = 0.342$) and highly polymorphic but most individual trees were homozygous. Similarly, Čurn et al. (2014) found higher genetic diversity in *U. glabra* than in *U. minor* in the Czech Republic. High genetic diversity in *U. glabra* is undoubtedly a consequence of sexual reproduction in this species. The diversity in *U. glabra* was apparently similar to pre-DED populations so genetic diversity does not appear to have been reduced by smaller population sizes (Machon et al., 1997).

Ulmus glabra and hybrids have been micropropagated from leaf discs, anthers, buds, cambium and embryo tissue (Ben Jouira, Hassairi, Bigot, & Dorion, 1998; Biroščíková, Spišáková, Lipták, Pichler, & Ďurkovič, 2004; Corredoira, Vieitez, & Ballester, 2002; Dorion, Ben Jouira, & Jouanin, 2004; Grbić, Skočajić, Đukić, Đunisijević-Bojović, & Marković, 2015; Malá et al., 2013; Zabihi, Hosseininasr, Jeloudar, & Jalilvand, 2008) primarily as a method to propagate DED-resistant trees. However, in comparison to *U. minor* and *U. laevis* which grow directly from a stored bud material, micropropagation of *U. glabra* is best achieved by micrografting of the apical part of the bud axis onto *U. minor* micro-rootstock material (Harvengt, Meier-Dinkel, Dumas, & Collin, 2004). Attempts have been made to cryopreserve buds and seeds of European elms as a gene bank in liquid nitrogen (Chmielarz, 2010; Harvengt et al., 2004)—see Section 8.4.

Ďurkovič et al. (2015) found that micropropagated DED-resistant hybrid ‘Dodoens’ (*Ulmus glabra* ‘Exoniensis’ × *U. wallichiana* P39) had higher levels of cellulose and lower hemicellulose than original plants. Grafts of a ‘Dodoens’ scion onto the stem of a DED-tolerant *U. pumila* ‘Puszt’ rootstock, designed to reduce the likelihood of DED transmission through root grafts, had a higher content of lignin and hemicellulose than micropropagated plants, which may give them some mechanical advantage. The micropropagated trees had a significantly higher SLA ($147.73 \pm 31.70 \text{ cm}^2/\text{g}$, *SD*) than grafted trees (127.41 ± 34.54) 6 years after planting out, and had a lower dry leaf mass ($0.32 \pm 0.13 \text{ g}$ micropropagated; $0.40 \pm 0.24 \text{ g}$ grafted). This suggests that micropropagated trees were less mature than grafted trees (Ďurkovič et al., 2010).

Gartland et al. (2000) discussed successful genetic modification of elms, including *U. glabra*, using *Agrobacterium tumefaciens* and *A. rhizogenes* as an early stage towards creating new resistant varieties.

6.4 | Chromosomes

$2n = 28$ (Stace et al., 2015). The amount of DNA per diploid cell has been measured at $4.37 \pm 0.103 \text{ pg}$, which is not significantly

different from *U. minor* (Loureiro, Rodriguez, Gomes, & Santos, 2007). Genome size was estimated at 2,136 Mbp ($1n$ value) by Loureiro et al. (2007) with no statistically significant differences detected between individuals. This is a comparatively large genome, as is the norm in the Ulmaceae (Grime et al., 2007). Ehrenberg (1949) records the presence of triploid ($2n = 42$) and tetraploids ($2n = 56$) in Swedish material.

6.5 | Physiological data

6.5.1 | Light

Ulmus glabra is semi-shade tolerant (see Section 5.2) which is reflected in a comparatively low light compensation point of $24.93\text{--}37.23 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and a light saturation point of $586\text{--}601 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Ďurkovič et al., 2010). The maximum CO_2 assimilation rate at saturating PPFD has been measured at $0.85\text{--}1.67 \text{ mmol m}^{-2} \text{ s}^{-1}$, stomatal conductance at $51.39\text{--}98.67 \text{ mmol m}^{-2} \text{ s}^{-1}$ and dark respiration rate at $1.52\text{--}1.55 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Ďurkovič et al., 2010). This semi-shade tolerance is reflected in a limited ability of *U. glabra* to use sunflecks. Harbinson and Woodward (1984) found that *U. glabra* (along with *Corylus avellana*) did not reach light saturation even at the highest photon flux density used of $230 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in simulated sunflecks 3 min long, whereas *Fraxinus excelsior* saturated at $120 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and *Fagus sylvatica* at $27 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Chlorophyll induction time for *U. glabra* (2.05 s) was similar to *F. excelsior* but much faster than for *F. sylvatica* (7.3 s). However, quantum efficiency was low in *U. glabra* ($1.31 \pm 0.06 \text{ g CO}_2/\mu\text{mol} \times 10^6$) and less than half that of *F. sylvatica* and *F. excelsior*, probably a reflection of low efficiency of electron transfer from the site of photon capture to the reaction centre (Harbinson & Woodward, 1984). Electron transfer rates (of PSII) have been measured at $c. 70 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (estimated from a figure in Samsone, Anderson, & Levinsh, 2012). Harbinson and Woodward (1984) concluded that *U. glabra* could use sunflecks but needed the brightest sunflecks to reach maximal photosynthesis.

Total chlorophyll *a* and *b* in *U. glabra* has been measured at $405\text{--}504 \text{ mg/m}^2$ (D'Ambrosio, Szabo, & Lichtenthaler, 1992; Harbinson & Woodward, 1984). This is high compared to 334 and 396 mg/m^2 in *Fagus sylvatica* and *Fraxinus excelsior*, respectively, but the low SLA of *U. glabra* ($34.2 \text{ mm}^2/\text{mg}$), compared to 41.8 and $50.3 \text{ mm}^2/\text{mg}$ in *F. sylvatica* and *F. excelsior*, respectively, results in similar total chlorophyll per leaf mass in all three species (17.2 mg/g in *U. glabra*; Harbinson & Woodward, 1984). Similarly, the ratio of chlorophyll *a* to *b* was similar in these species (3.72 in *U. glabra*; Harbinson & Woodward, 1984). Heavy infestation with galls produced by the aphids *Eriosoma ulmi* and *Tetraneura ulmi* (see Section 9.1), affected the amount of carotenoids (to 76% and 112% of control leaves, respectively, for the two aphids) and reduced chlorophyll *a* (81% and 79%, respectively) and *b* (83% and 66%, respectively) in leaves. This resulted in altered photochemical performance as a result of increases in activity of polyphenol oxidase with no apparent changes in peroxidase activity (Gailite, Anderson, & Levinsh, 2005). A doubling of ethylene production was also found in leaves with galls caused by *Eriosoma*

ulmi ($0.224 \pm 0.040 \text{ nmol g}^{-1} \text{ h}^{-1}$; SE, $n = 5$) and *Tetraneura ulmi* ($0.195 \pm 0.026 \text{ nmol g}^{-1} \text{ h}^{-1}$) compared to control leaves (Samsone et al., 2012). This increased to six times the control levels in the galled parts of the leaves from *E. ulmi* ($0.721 \pm 0.065 \text{ nmol g}^{-1} \text{ h}^{-1}$). Extra ethylene is seen as a direct cause of downregulation of photosynthesis (Samsone et al., 2012).

6.5.2 | Temperature

The ability of *U. glabra* to resist low temperatures is discussed in Section 2.1. Skre (1993) observed that in seedlings grown at various constant temperatures, the SLA varied from $18 \pm 2 \text{ m}^2/\text{kg}$ at 9°C to $36 \pm 3 \text{ m}^2/\text{kg}$ at 21°C . Under field conditions, Alberti et al. (2005) noted a SLA of $22.4 \pm 4.5 \text{ m}^2/\text{kg}$ in *U. glabra* compared to $13.8 \pm 3.7 \text{ m}^2/\text{kg}$ in *Fraxinus excelsior*. Trees that had been micropropagated and planted out for 6 years had a significantly higher SLA ($14.77 \pm 3.17 \text{ m}^2/\text{kg}$, SD) than similar grafted trees ($12.74 \pm 3.45 \text{ m}^2/\text{kg}$), and had a lower dry leaf mass: $0.32 \pm 0.13 \text{ g}$, SD micropropagated; $0.40 \pm 0.24 \text{ g}$ grafted (Đurkovič et al., 2010).

6.5.3 | Water

Transpiration rate of shoots of *U. glabra* has been measured at $0.34 \pm 0.11 \text{ mmol m}^{-2} \text{ s}^{-1}$ (SE, $n = 127$) at night and $0.60 \pm 0.13 \text{ mmol m}^{-2} \text{ s}^{-1}$ in the day (Rohula, Kupper, Räm, Sellin, & Söber, 2014). This was lower than in *U. minor* (0.49 ± 0.05 and $0.85 \pm 0.11 \text{ mmol m}^{-2} \text{ s}^{-1}$, respectively) but was overall very similar to the other 14 temperate deciduous trees tested (range 0.19–0.60 night-time, 0.48–1.25 $\text{mmol m}^{-2} \text{ s}^{-1}$ daytime). Stomatal resistance varied from $<2,000 \text{ s/m}$ at low irradiance (c. $20 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) to almost zero at higher irradiance ($240 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$). Water-use efficiency ranged from 100 to 200 g/g, depending upon irradiance (Harbinson & Woodward, 1984).

Appleby and Davies (1983) found that transpiration increased in well-watered *U. glabra* seedlings up to a maximum vapour pressure difference (VPD) of around 1.6 kPa but declined almost to zero by c. 2.2 kPa. Other species tested maintained high conductance at this VPD. In *U. glabra* (and also *Quercus robur*), part of the guard cell walls were cuticle-free and were thus permeable to water. Loss of water from the guard cells at high VPD allowed the guard cells to close while the plant was still relatively turgid, different from normal stomatal closure in response to increased water loss from inside leaf. A suggested mechanism for transpiration in *U. glabra*, other than by the tension-cohesion theory is put forward by Laschimke, Burger, and Vallen (2006).

6.5.4 | Nutrients

Leaf nitrogen content was found to be higher in *U. glabra* than in its deciduous competitors. It reached $1,530 \text{ mg/m}^2$ in *U. glabra* compared to 631 and 593 mg/m^2 in *Fagus sylvatica* and *Fraxinus excelsior*, respectively (Harbinson & Woodward, 1984). Leaf nitrogen was only higher in the thick evergreen leaves of *Ilex aquifolium* ($2,544 \text{ mg/m}^2$)

and *Hedera helix* ($2,095 \text{ mg/m}^2$). As would be expected, however, nitrogen per unit mass of leaf was highest in *U. glabra* (52.35 mg/g), almost double that of the other species tested (Harbinson & Woodward, 1984). The nitrate reductase activity of *U. glabra* leaves has also been found to be high: $>2.8 \text{ } \mu\text{mol NO}_2^- \text{ g}^{-1} \text{ dw h}^{-1}$ compared to around or below $1.0 \text{ } \mu\text{mol NO}_2^- \text{ g}^{-1} \text{ dw h}^{-1}$ in the leaves of the other tree species tested—*Quercus robur*, *F. sylvatica*, *Carpinus betulus* and *Acer pseudoplatanus* (Olsson & Falkengren-Grerup, 2003). This suggests that *U. glabra* litter helps prevent the loss of nitrate by leaching as it is rapidly converted to nitrite and ammonia in spring and taken up by plants. Bollard (1957) found low concentrations of total N in xylem sap of *U. glabra* at $30 \text{ } \mu\text{g/ml}$ (time of year is not stated), primarily as asparagine, glutamine with a small amount of nitrate.

Measurements of foliar nutrient concentrations of urban trees in the Netherlands have led to quantification of nutrient deficiency in deciduous trees, including *U. glabra*: foliar N $< 18 \text{ mg/g}$ dry matter is “too low” (“normal”: 23–27 mg/g); P $< 1.0 \text{ mg/g}$ (1.6–1.9); K $< 6.5 \text{ mg/g}$ (12.5–18) and Mg $< 0.9 \text{ mg/g}$ (1.7–2.7). These limits appear to be very similar in most commonly planted deciduous trees (Kopinga & van den Burg, 1995). Concentrations of nutrients (mg/g; SE, n not stated) in winter twigs and leaves of *U. glabra*, collected as winter fodder, are given by Hejcman, Hejcmanová, Stejskalová, and Pavlů (2014) and Hejcmanová, Stejskalová, and Hejcman (2014), respectively: N 14.6 ± 0.6 twigs (34.3 ± 3.3 leaves), P 1.5 ± 0.05 (2.7 ± 0.1), K 5.9 ± 0.3 (19.9 ± 2.7), Ca 14.7 ± 0.3 (14.2 ± 1.9) and Mg 1.4 ± 0.1 (2.7 ± 0.3). Other analyses included: neutral detergent fibre 456 ± 6 twigs (397 ± 41.2 leaves), acid detergent fibre 408 ± 6 (243 ± 12.0), acid detergent lignin 213 ± 6 (99 ± 13.4), residual ash 37.3 ± 0.3 (51.8 ± 4.6), N/P ratio 9.7 ± 0.1 (12.7 ± 0.7) and Ca/P ratio 9.8 ± 0.6 (5.2 ± 0.5). Values were very similar between *U. glabra* and *Tilia cordata* and *Salix caprea* but differences between all deciduous species tested were minor. Nutritional value of leaves but especially twigs was much poorer than meadow hay which Hejcman et al. (2014) and Hejcmanová et al. (2014) suggested reinforces the idea that post-glacial elm decline (Section 10.1) was unlikely to be due to cutting winter fodder alone. Ataşoğlu, Canbolat, Şahin, and Baytekin (2010) gave similar figures for *U. glabra* leaves in Turkey with an estimate of crude protein content of 125 mg/g dm . This, with the comparatively low neutral detergent fibre, points to *U. glabra* foliage providing adequate nutrition for goats and sheep that would not need supplementing. Dobson, Grierson, Bennett, de Howard, and Wong (2013) gave chemical analyses of a *U. glabra* leaf pressed inside a 1540 Bible from Ely and carbon dated to around that age. The analyses suggest that the elm was growing in the wet areas then surrounding the cathedral.

Boron has been known to be transported through the phloem of species that also translocate polyols. Indeed, Lehto, Räsänen, Lavola, Julkunen-Tiitto, and Aphalo (2004) found high B mobility in trees with high sorbitol content, such as *Sorbus aucuparia* ($45.10 \text{ mg sorbitol/g}$ leaf dry weight) and *Prunus padus* (28.93 mg/g), and in *Fraxinus excelsior* with high mannitol content (22.10 mg/g) but *U. glabra* had only trace amounts of sorbitol (0.16 mg/g) and undetectable

levels of mannitol. The authors concluded that B mobility was not as closely related to the presence of polyols as previously thought.

6.5.5 | Heavy metals

Heavy metal content of *U. glabra* can be high. Near the Avonmouth smelters, *U. glabra* leaves contained up to 6,246 ppm of Zn, 1,170 ppm Pb and 12.5 ppm of Cd (all dry mass): all considered to be “abnormally high” (Little, 1993; Little & Martin, 1972) but still generally lower than that found in *Quercus* sp. (6,800, 7,000 and 50 ppm, respectively). Little (1993) found that washing leaves in deionised water removed 67% of the Zn, 87% of Pb and 62% of Cd, but this increased to 96%–98% of these metals when washed with 1%–5% HNO₃ suggesting some binding to leaf surface. Little (1993) suggested that the majority of heavy metal pollution is held on the leaf surface as soluble or insoluble particles rather than being taken up by the roots and incorporated into the leaf tissue. This helps explain why the leaves were not showing any sign of toxicity as would be expected at these levels. Fluoride uptake by *U. glabra* is also high. Near aluminium smelter plants in Norway, F levels were the second highest of 25 trees and shrubs tested after *Sorbus aucuparia* (Hornvedt, 1997).

6.6 | Biochemical data

Scherl et al. (2016) identified a number of non-fluorescent chlorophyll catabolites in *U. glabra* leaves entering autumn senescence. The bark of *U. glabra* contains large amounts of solitary calcium oxalate crystals in thin-walled axial cells in the secondary phloem (Trockenbrodt, 1995) and the phloem contains mucilage-containing sacs. Hot water extracts of the phloem contain polysaccharides including galactose, galacturonic acid, galactose, rhamnose, methylgalactose, glucuronic acid and acetyl (Barsett & Smestad Paulsen, 1992; Barsett, Smestad Paulsen, & Habte, 1992). A number of chemicals is known to either attract or repel elm bark beetles (see Martín-Benito, García-Vallejo, Pajares, & López, 2005 for a review). In particular, Martín-Benito et al. (2005) found three sterols and 10 triterpenes in European elms; no bark triterpenes were unique to any one elm species and most were found in all European elms tested including *U. glabra* and *U. minor*. They found that high total triterpene and sterol content of the bark made it less preferred by bark beetles. *Ulmus glabra* had the highest total content of triterpenes (2,973.94 µg/g—more than half of it being friedelin, 1,643.29 µg/g), compared to *U. minor* that had the lowest average content of triterpenes (437.66 µg/g), with lupeol as the most abundant. Particularly effective was β-amyrin since it is in high concentration in elm species (including *U. laevis* and *U. glabra*) that are less preferred by bark beetles, and is absent or in only low concentrations in *U. minor* and *U. pumila* that are preferred by bark beetles. Inoculation of *U. glabra* with the DED fungus *Ophiostoma ulmi* (Buisman) Nannf. (Ascomycota, Ophiostomatales) induced the accumulation of a series of antifungal cadalene derivatives such as hydroxycalamenene and hydroxycadalene (Burden & Kemp, 1984), which may act as phytoalexins or allelopathic agents (Elakovich, 1987).

Ulmus glabra wood contains both syringyl-rich and guaiacyl-rich lignin; the latter appears to be involved in defence against *Ophiostoma novo-ulmi*, along with vanillin and vanillic acid, since they are found in higher quantities in cultivars resistant to DED and in infected non-resistant cultivars (Đurkovič, Kačík, Olčák, Kučerová, & Krajňáková, 2014; Elakovich, 1987). Other phytoalexins found in higher concentrations in response to fungal infection (including *Ophiostoma ulmi*, *Chondrostereum purpureum* (Pers.) Pouzar and *Coriulus versicolor* (L.) Quél.: Basidiomycota, Polyporales) are sesquiterpenoids, such as cadalene derivatives and lacinilene, and phenolic glycosides such as 7-hydroxycalamenene, 7-hydroxycadalene and a number of naphthaldehydes (including hydroxy-8-isopropyl-S-methyl-2-naphthaldehyde and its 7-methoxy and 5,6,7,8-tetrahydro derivatives), phytosterols such as sitosterol, and a number of triglycerides and fatty alcohols (Burden & Kemp, 1984; Elakovich, 1987; Lindgren & Svahn, 1968; Rowe, Seikel, Roy, & Jorgensen, 1972). These compounds were isolated from a narrow band between infected and healthy tissue in the sapwood (Burden & Kemp, 1984).

Polysaccharides, differing from those in the bark, have been found in the seeds including polygalacturonides such as arabinose, galactose and rhamnose (Barsett, Haraldstad, & Smestad Paulsen, 1991; Barsett et al., 1992). Embryos of *U. glabra* accumulate fatty acid triacylglycerols rich in capric acid (Ståhl, Banas, & Stymne, 1995) the production of which is controlled by the enzyme phosphatide 2-acylhydrolase (Ståhl, Ek, & Stymne, 1998).

7 | PHENOLOGY

Flowers open mid-January to early April, before the leaves appear (Grime et al., 2007). Flowers open from the top of tree downwards as was demonstrated by Christy (1922) who used a shotgun to remove branches to check for anther dehiscence around the tree. Seeds mature within c. 3 weeks of flowering (Wilkinson, 1978) and are shed April to July and so sometimes before the leaves appear (Hulme & Hunt, 1999). Seed and fruit growth is partially supported by photosynthesis in the leafy seed wings.

Leaves begin appearing from late April and are fully expanded by early June at the latest (Møller, 1995, 2008) although new leaves continue to develop throughout the summer. Myking and Skrøppa (2007) found in Norway that on 13 April 2005, 42% of trees were showing budburst inland at Luster (c. 100 km from the coast) while only 15% were showing budburst at Bergen on the coast. The north-south influence on budburst was much less pronounced than the coastal-inland climatic gradient. Gibberellins are known to be present in xylem sap in spring, presumably *en route* to the shoot tissue (Lang, 1970). Flower buds are initiated at the end of June into early July. Wareing (1956) quotes the work of Scheglova & Leisle which shows that long-day conditions are necessary for the formation of flower buds in *U. glabra*.

As with many European trees, cessation of growth in late summer is determined at least in part by photoperiod (Myking & Skrøppa, 2007). *Ulmus glabra* seedlings originating from the northern end of

the species' natural range show the strongest response to the latitudinal cline in critical day length (Håbjørg, 1978). Leaf fall occurs in September to November depending on the start of night frosts (Møller, 1995).

Compared to other European elms, *U. glabra* buds have low dormancy and a short chilling requirement (Ghelardini, Falusi, & Santini, 2006; Ghelardini & Santini, 2009; Santini, Ghelardini, et al., 2004). Analyses of phenological data found chilling to have little or no effect in explaining the observed variation in bud burst date in European elm species in general (Chuine, Cour, & Rousseau, 1999; Sparks & Carey, 1995) but Ghelardini, Santini, Black-Samuelsson, Myking, and Falusi (2010) found that increased winter chilling of *U. glabra* led to a decrease in the thermal time (day-degrees $>0^{\circ}\text{C}$) to bud burst. They also noted that the number of chill days (days with mean temperature $\leq 5^{\circ}\text{C}$ received from 1 October 2002) increased in Asiatic elms from <20 in *U. pumila* to <35 in *U. macrocarpa* Hance and *U. parvifolia* Jacq. to 72 in *U. villosa* Brand. ex Gamb., compared to >100 chill days in *U. glabra*. The chilling requirement was higher still in *U. minor* but was unquantified. Although the chilling requirement is fairly short in *U. glabra* compared to many European trees, it does mean that *U. glabra* from northern Italy would not have their chilling requirement met when planted in the mild winters of the Mediterranean region (Ghelardini et al., 2006). Bud break is not influenced by photoperiod (Ghelardini et al., 2010). Analysing six Lithuanian *U. glabra* populations over 7 years in a progeny field trial, Petrokas (2009) found that the selection of the trees for resistance to dieback should be based on right-angled branching of stems.

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Ulmus glabra is anemophilous but flowers are visited by insects, especially honeybees (Grime et al., 2007; Richens, 1976) as flower buds have an external filament nectary (Daumann, 1975). Pollen grains are 4–5(–7) porate, 26–36 \times 30–48 μm and have a surface with winding, wide (c. 1.5 μm), coarse ridges, giving the appearance of a reticulum in places. Ridges coalesce around the pore to form an annulus (Stafford, 1995). The whole surface is covered by very small (c. 0.1 μm) verrucae (Pilcher, 1968). *Ulmus glabra* pollen can usually be distinguished from that of *U. procera*—see Section 6.1.

Nielsen and Kjær (2010) estimated that in Danish populations average pollen dispersal was 104 m in woodlands. Since trees in the open were up to c. 500 m apart and still showed a lack of inbreeding, pollen must travel further in the open. Reductions in population size and increasing isolation of individuals after DED do not seem to have reduced genetic diversity or increased inbreeding, as similar populations changes have in other deciduous trees such as *Fagus sylvatica*, although the decline in wych elm may be too recent for its full effects to be yet apparent.

Elms are normally considered to be self-incompatible (Johnson, 1946; Richens, 1983; Townsend, 1975). However, Went (1954) recorded that some wych elm trees set self-pollinated seeds, and Hans

(1981) found self-pollination was possible in artificially pollinated flowers; fruit were produced in 75% of selfed and 60% of crossed flowers, and seed was set in 65% of selfed and 60% of crossed flowers.

Samara dry mass has been measured between 8 and 21 mg (mean 10.3 mg; Royal Botanic Gardens, Kew, 2018), and dry seed mass at 3.5 mg (Brzeziecki & Kienast, 1994; Grime et al., 2007; Hulme & Hunt, 1999; Miller, Heim, & Lundholm, 2014; Sämel & Kowarik, 2013). Samaras are normally up to 20.6 \times 12.0 mm, and seeds 5.0 \times 3.5 mm (Grime et al., 2007). Mast-year seed production is rare in *U. glabra* and certainly less common than in *U. minor* (Hulme & Borelli, 1999) and particularly in *U. laevis* (Perea, Venturas, & Gil, 2013; Venturas, Nanos, & Gil, 2014), which in central Spain can produce 24 times more seed than during a non-mast year (Venturas et al., 2015).

8.2 | Hybrids

There appear to be few breeding barriers between any of the northern European elm species, and so hybrids regularly occur, identified primarily by their intermediate morphology (Melville, 1955, 1978; Richens, 1980). See Stace (1975) and Stace et al. (2015) for diagnostic identification features of these hybrids.

Based on controlled diallelic hybridisation of *U. glabra* with Euroasiatic species, high hybridisation has been found with other elm species in the following decreasing order: *U. pumila*, *U. elliptica*, *U. japonica*, *U. minor*, *U. wilsoniana*, *U. chenmoui* and *U. parvifolia* (Mittempergher & La Porta, 1991, 1993). Successful hybridisation (Figure 3) ranged from 2.6% to 73.7% viable seed production but with evident differences when *U. glabra* was used as the male or female: *U. pumila* (73.7% vs. 0%), *U. elliptica* (60.8% vs. 18.1%), *U. wilsoniana* (39.8% vs. 18.6%), *U. chenmoui* (0% vs. 27.1%). Hybridisation with *U. minor* used as female reached 43.5% which is very high considering that self-pollination was only 2.6% (Figure 3b). Seed germination of these crosses varied considerably. For example, using *U. glabra* as the female, germination ranged from 31.6% in a hybrid with *U. japonica* to 2.8% in a hybrid with *U. villosa* (Santini, La Porta, Ghelardini, & Mittempergher, 2008).

A critical point controlling artificial hybridisation is pollen viability and germinability. *Ulmus glabra* produces flowers comparatively late in the spring compared to other elms, so for it to be used as the male parent, pollen needs to be stored for almost a year until the next flowering period of other elms. The exceptions are *U. laevis*, which flowers later than *U. glabra* in spring, and *U. parvifolia* that flowers in the autumn (Mittempergher & La Porta, 1991). Pollen storage is difficult and Figure 4 shows that even when *U. glabra* pollen is stored in cool, dry conditions, the viability drops from c. 40% to 20% within 20 days. Assessing pollen viability quickly and cheaply has also posed challenges since pollen germination trials have worked only using an extract of the stigmatic surfaces as a substrate. Chemical tests using tetrazolium chloride and iodine potassium iodide have produced variable results in other woody plants (e.g. Sulusoglu & Cavusoglu, 2014). However, it is now possible to

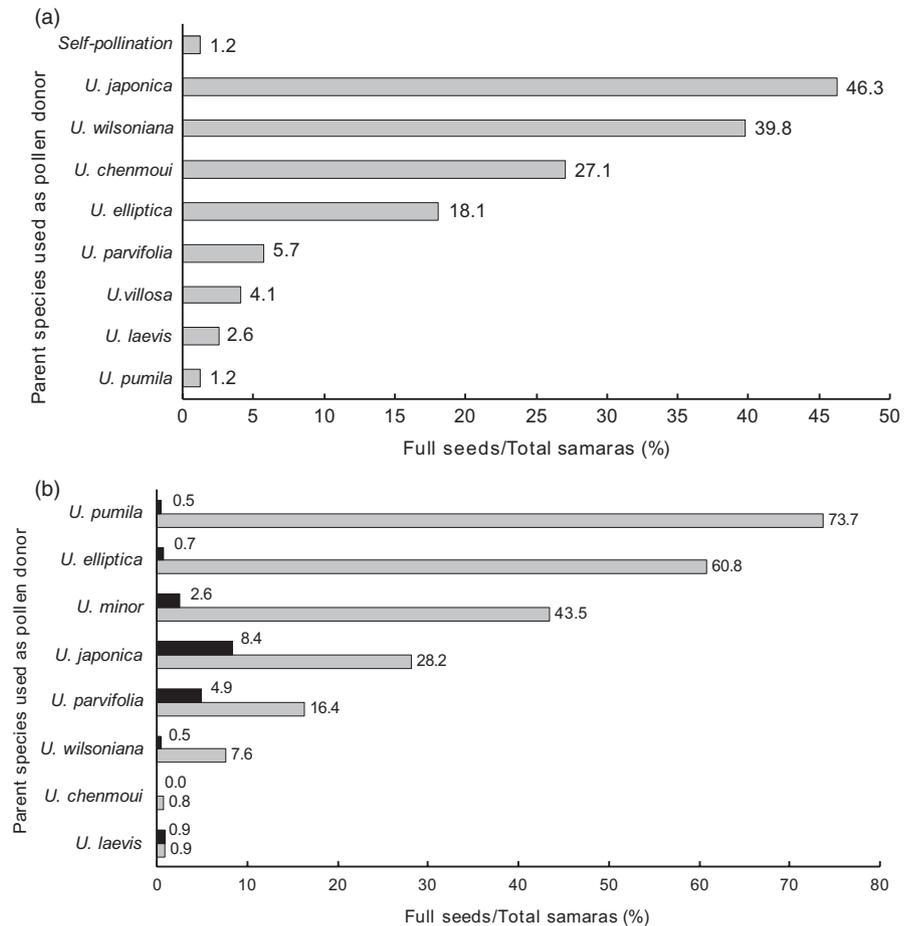


FIGURE 3 Hybridisation between *Ulmus glabra* and other *Ulmus* species. In (a) *U. glabra* is used as the female, and in (b) *U. glabra* is used as the pollen donor. The black bars represent the self-pollination values where bags were used to prevent the introduction of pollen from other flowers. The other bars represent permitted cross-pollination. The percentages are calculated as the number of full seeds compared to the total number of seeds produced by the plant branches used in the controlled crosses. Part (a) is from Mitterpergher and La Porta (1991), reproduced with permission

estimate pollen viability of *U. glabra* by its fluorochromatic reaction as a proxy (La Porta & Roselli, 1991)—see Figure 4.

8.2.1 | *U. glabra* × *U. procera*

Although both species were formerly common and overlapped in distribution over much of England and Wales, hybrids between the two are rare and restricted to south-east England. Stace et al. (2015) reported this hybrid in only 0.5% (8) of 1,583 hectads in the British Isles in which both parents occur. It is likely that hybrids are comparatively rare due to *U. procera* usually flowering earlier than *U. glabra* and many seeds produced by *U. procera* being sterile. It is also possible that hybrids have gone unrecognised and thus under-recorded. Seedling hybrids between *U. glabra* and non-*glabra* elms may be suckering or not (Brewis, Bowman, & Rose, 1996; Stace et al., 2015).

8.2.2 | *U. glabra* × *U. minor*

The hybrid between *U. glabra* and *U. minor* is relatively common in some regions despite *U. minor* flowering earlier than *U. glabra* (Mitterpergher, 2014). It is particularly common in southern England and commoner than *U. glabra* in some areas, including the Channel Islands. Stace et al. (2015) reported the hybrid in 368 hectads (50%) where both parents occur, 160 (9%) with just *U. glabra*, 7 (58%) with just *U. minor* and 4 (1%) with neither parent. This hybrid

is also widespread in western and north-eastern Europe, particularly the Netherlands where F1 hybrids have been frequently planted (Cox et al., 2014; Petrokas & Baliuckas, 2012; Richens, 1976). Jeffers and Richens (1970) considered this hybrid to be common enough to be counted as the fourth principal constituent of the English elm flora. Jeffers (1999) suggests that British populations of *U. glabra* × *U. minor* were introduced from northern France via the Netherlands in the 17th century.

Humans have likely increased this hybridisation by introduction and translocation of the parents (Cox et al., 2014). But the hybrid does occur as a range of intermediates between the two species or as backcrosses, mostly with *U. glabra*, to form a hybrid swarm (Machon et al., 1997; Richens, 1967, 1983) which may explain why in eastern England Rackham (2003) recorded suckering in just 15 (2.5%) of 604 clones. Some populations of this hybrid are coppiced and non-suckering but have still formed large apparently clonal stands (Cox et al., 2014), such as the clone in Lineage Wood, West Suffolk covering some 40 ha (Rackham, 2003). Richens (1976) records that the hybrids tend to have the smooth upper leaf surface and relatively long petiole of *U. minor* but the larger leaf size and often the tree-shape of *U. glabra* at least in first generation hybrids.

The Dutch elm (*Ulmus* × *hollandica* Mill.) and the Huntingdon elm (*U. x vegeta* (Loudon) Ley) are best considered “distinctive horticultural clones belonging to this hybrid complex” (Cox et al., 2014). Preston et al. (2002) recorded *U. x hollandica* as including *U. plotii*

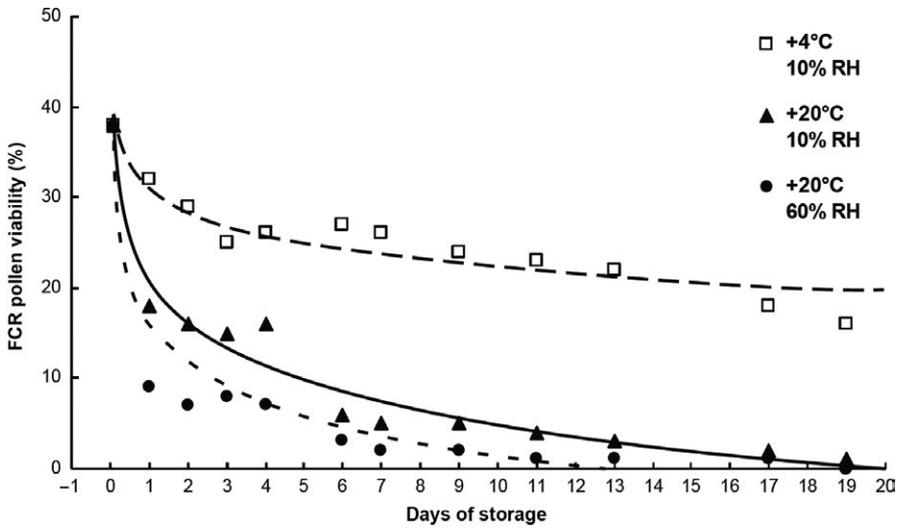


FIGURE 4 Pollen vitality of *Ulmus glabra* measured by fluorochromatic reaction (FCR) across the first 20 days after pollen collection. After collection the pollen was stored in three different temperature/humidity combinations: +4°C and 10% Relative Humidity; +20°C and 10% RH; +20°C and 60% RH. From: Mittempergher and La Porta (1991), reproduced with permission

(see below) but this conclusion is now less widely accepted. In its cultivated form, *U. x hollandica* is strongly suckering and invasive, and may have been introduced to Britain from the Netherlands by William of Orange in 1689, becoming particularly popular in the early 18th century in south-west England and the Channel Islands (Richens, 1961b, 1983, 1984; Stace et al., 2015). The natural hybrid has been reported from southern Sweden which, unlike the cultivated form, was sterile (Nilsson, 1980). *Ulmus x vegeta* is non-suckering and was raised from seeds collected at Hinchingsbrooke Park, Huntingdonshire, in the 18th century and widely planted in urban and rural areas (Richens, 1961a, 1983). Both these cultivated forms can produce abundant seeds (Brewis et al., 1996).

8.2.3 | *Ulmus glabra* × *U. minor* × *U. plotii* (?= *U. x diversifolia* Melville)

The East Anglian elm most likely arose through secondary hybridisation between *U. glabra* and the other two species (Stace et al., 2015). It is a difficult hybrid to reliably identify due in part to the wide variation inherent in *U. glabra* × *U. minor* and also in part because the “influence of *U. plotii* can be very subtle” (Stace et al., 2015) leading to a very variable leaf shape. Melville (1939) considered the East Anglian elm to be just one recognisable node in this hybrid complex. Some of this variability is undoubtedly due to the multiple backcrosses within the hybrid swarm. The hybrid is commonest in east England where two or three of the parents are found, mostly in open habitats such as hedges, stream banks, and also likely planted in churchyards and gardens (Stace et al., 2015).

8.2.4 | *Ulmus glabra* × *U. plotii* (?= *U. x elegantissima* Horw.)

This is similar to the East Anglian elm above but without any evidence of the influence of *U. minor*. A proportion of the hybrids retain the suckering habit of *U. plotii*. The hybrid produces abundant fertile seed. It is most common in central England within the range of

U. plotii (Preston et al., 2002), mostly as hedgerow, roadside and river bank trees before DED but rarely in woodlands. It was also identified in France and Belgium by Melville (1940) even though *U. plotii* is considered to be endemic to Britain. Melville (1940, 1944) considered it likely that suckering individuals of the hybrid may have outlasted *U. plotii* individuals and so be more common within the range of *U. plotii* but maps in Preston et al. (2002) do not confirm this.

8.2.5 | Dutch elm disease resistant hybrids

A number of DED-resistant elms have been bred. Resistant Asian elm species have generally been crossed with native elms to produce familiar looking trees with some of the resistance (Santini, Fagnani, et al., 2004; Santini, Pecori, Pepori, Ferrini, & Ghelardini, 2010; Smalley & Guries, 2000). In trials at the Arnold Arboretum, USA, Hans (1981) found that *U. glabra* was incompatible with the American *U. laevis* and with Asiatic *U. japonica* and *U. pumila*, and so did not hybridise with them, but was compatible with the American *U. rubra*. *Ulmus glabra* and *U. rubra* are both protogynous while the others are protandrous. However, successful crosses have been found to be dependent upon which species was used as the female; *U. glabra* × *U. japonica* (= *U. davidiana* var. *japonica* from north-east Asia) yielded hybrids but the reverse did not (Santini et al., 2010). Success also depends on which resistant clones of a species are used as the male and female parent (Townsend, 1979). Successful hybrids include (female listed first) *U. glabra* × *U. rubra* (from eastern N. American), *U. glabra* × *U. pumila* (central Asia) and *U. parviflora* (east Asia) × *U. glabra*. Santini, Fagnani, Ferrini, Ghelardini, and Mittempergher (2005) showed that hybrids between *U. minor* and *U. pumila* were more resistant to DED than *U. glabra* × *U. pumila*. Successful DED-resistant hybrids include a number based on *U. glabra* including FL 033 (*U. glabra* × *U. minor*) × *U. pumila*, FL506 and FL 509 (*U. glabra* × *U. minor*) × *U. chenmoui* and FL568, FL588, FL 589 *U. pumila* × [(*U. glabra* ‘Exoniensis’ × *U. wallichiana*) × *U. minor*] (Santini et al., 2010; Solla et al., 2005). These authors also discuss the growth rates of different hybrids as affected by location and

environmental conditions. A history of elm breeding in Europe for DED resistance is given by Mittempergher and Santini (2004). Practical and theoretical considerations in elm breeding for resistance to pathogens and parasites are outlined by Mittempergher and La Porta (1993). A number of cultivars and clones of *U. glabra* have been found to have some inherent resistance—see Section 9.3.

8.3 | Seed production and dispersal

Seed production starts at a young age. Nisbet (1893) records wych elm in Britain fruiting abundantly from around 13 years old, while Nielsen and Kjær (2010) found that 28% of small trees (<10 cm DBH; perhaps <25 years old) in eastern Denmark produced fruits and a very few trees 4–5 cm DBH produced small amounts of fruit. Under greenhouse conditions, Tyystjarvi and Pirttila (1984) observed that seed production reached the maximum seen in the study after 5 years in *U. glabra*, *U. laevis*, *Tilia cordata* and *Quercus robur*, although it was earlier in *Betula pendula*. In the more continental climate of central and eastern Europe, abundant fruiting starts later at around 30–40 years in the open and 50 years old within woodlands (Brzeziecki & Kienast, 1994; Karczmarszuk, 2002). This young age of seed production, compared to other woodland trees such as *Fraxinus excelsior* and *Fagus sylvatica* (Packham, Thomas, Atkinson, & Degen, 2012; Thomas, 2016), is an important factor in allowing *U. glabra* to survive DED since it is mostly older trees that are infected, allowing younger trees to produce seed and maintain populations and genetic diversity. *Ulmus glabra* is not usually considered to be a masting species but somewhat better seed crops occur every 1–2 years (Brzeziecki & Kienast, 1994). Seed production is least at the extremities of its range. In northern Norway populations this is probably due to fewer flowers and fewer maturing seeds with low summer temperatures (Myking & Skrøppa, 2007).

Fruits are primarily wind-dispersed, capable of invading at least 30 m and occasionally >100 m from forest edges, approximately the same distance as *Acer platanoides*, *Fraxinus excelsior* and *Tilia cordata* but less than *Pinus sylvestris* and *Betula* spp. (Evstigneev, Murashev, & Korotkov, 2017; Karlsson, 2001). But dispersal is also possible by water. Säumel and Kowarik (2013) released fruits into two lowland rivers in Germany and found that 30%–35% of fruits were washed 1,200 m downstream, similar proportions and similar journey times to those seen in other primarily wind-dispersed trees tested including *Fraxinus excelsior* and the invasive *Ailanthus altissima*, despite *U. glabra* fruits being so small and light compared to the others tested.

Hulme and Hunt (1999) looked at post-dispersal predation in semi-natural woodland in Co. Durham and identified small mammals, particularly *Apodemus sylvaticus* (L.), as the main predators. Small mammals showed a preference for *U. glabra* over *Taxus baccata* and *Fraxinus excelsior* (Hulme & Borelli, 1999; Jensen, 1985) even when wych elm was rare. Hulme and Hunt (1999) found a fourfold higher preference for elm compared to *F. excelsior* fruits which have a high phenolic content. It was concluded that wych elm seeds could be consumed almost completely and so cause local extinction of elm

seed populations. The result was a low ratio of number of seedlings to adult density for *U. glabra* (4.89–9.06 on different sites) compared to >8,000 on some sites for *F. excelsior*. But seed removal was related to seed size and burial. Removal fell by almost two-thirds in *U. glabra* when seeds were buried 3–4 cm deep, whereas larger seeds of *T. baccata* received little benefit from burial (Hulme & Borelli, 1999). Significant numbers of seeds were also seen to be taken by vertebrates, probably birds, rabbits and/or squirrels (Hulme & Hunt, 1999).

8.4 | Viability of seeds: germination

Germination is epigeal. Seeds are orthodox so germination is best if seeds are sown immediately as they readily lose viability in situ ($t_{50} = 7$ days; Richens, 1983). There is, therefore, no apparent dormancy and planting does not require pre-sowing treatment (Royal Botanic Gardens, Kew, 2018). Consequently, there is no persistent seed bank (Thompson, Bakker, & Bekker, 1997). Seeds stored ex situ will survive for a year if kept at low moisture at 0–10°C (Grime et al., 1981), and will survive –3 to –4°C at 10% moisture for 1–2 years (Shiranpour, Tabari, Hossini, & Naseri, 2012; Tylkowski, 1999) and even in liquid nitrogen at 3%–21% moisture for 2 years (Chmielarz, 2010). Intact, full seeds at 8.7% moisture content stored for 2 years in sealed containers at 4°C showed 79%–87% germination (Çiçek & Tilki, 2006). Załęski, Aniśko, and Kantorowicz (2009) provide data that suggests that *U. glabra* seeds are slightly more resistant to water loss when exposed to low humidity than *U. minor*.

A high proportion of seeds, particularly those shed early, may not be viable and germination of unsorted seed is usually <50% (Savill, 2013). The removal of obviously empty fruits increases germination to 82%–94% (Çiçek & Tilki, 2006, 2007; Royal Botanic Gardens, Kew, 2018; Tylkowski, 1999). Germination is higher at 30/20°C day/night temperatures than at a constant 20°C (Çiçek & Tilki, 2006; Shiranpour et al., 2012). Seeds germinate more rapidly at low light fluxes (Grime et al., 2007). Light was found to not be essential in the Turkish study but germination of fresh seeds kept at 30/20°C increased from 83% in the dark to 90% in constant illuminance of 1,000 lux, c. 10% full sunlight (Çiçek & Tilki, 2006). However, after 1 year of storage, the seed's light demand increased (Çiçek & Tilki, 2006; Shiranpour et al., 2012). Increased light made no difference to germination when kept at a constant 20 or 25°C. Tylkowski (1999) found that leaving the samara around the seed, and covering the samara with soil, both delayed germination. Seedlings are not drought tolerant but can withstand flooding for up to 4 months (Prentice & Helmisaari, 1991).

The type of vegetation that the seeds fall into affects establishment. Miller et al. (2014) found that 50%–53% of *U. glabra* seeds reached the soil under dense graminoids being grown as green roofs in Nova Scotia compared to 73% under creeping shrubs and 87% under erect forbs. However, germination was higher under turf-forming graminoids (2%) compared to erect forbs (<1%), attributed to a more constant moisture supply.

Despite the low germination of unsorted seeds, viable seeds germinate readily so seedlings are found in a wider range of habitats

than the adult tree (Grime et al., 2007), although followed by high seedling mortality in less optimal habitats. Persistent seedlings are generally found in the shade of larger trees, particularly where ground vegetation is discontinuous. Seedlings do not generally need exposure of mineral soil for successful establishment (Prentice & Helmisaari, 1991). However, Šebková, Šamonil, Valtera, Adam, and Janík (2012) found that *U. glabra*, along with *Sorbus aucuparia* and *Acer pseudoplatanus*, were all rare as seedlings but were most common on pit-mounds from uprooted trees in beech forests in the Czech Republic. This may be a facet of reducing competition rather than improving the supply of water or nutrients. Kuijper et al. (2010) found no correlation between *U. glabra* recruitment and any aspect of temperature or precipitation variation between repeat surveys along permanent transects between 1936 and 2002 in Białowieża Forest, Poland.

8.5 | Seedling morphology

Following extension of the radicle, the hypocotyl elongates rapidly, bringing the cotyledons above the ground and usually leaving the seed coat in the ground. Seedling development is shown in Figure 5. The first true leaves appear as two decussate pairs forming a cross. Most seedlings then produce opposite pairs of leaves. In 32 seedlings looked at by Charlton (1993b), after the first two pairs of leaves, 5 seedlings produced a third pair of leaves, 12 produced a single leaf and 15 produced a small scale leaf. Young seedlings can also carry scale leaves which usually fall after a few weeks, although in some seedlings they act as bud scales when extension growth briefly ceases and are then shed when growth resumes a few weeks later. In some vigorous seedlings, the lower axillary buds grew out in the first year as distichous shoots. In most seedlings, extension growth was stopped by the shoot-tip aborting (as happens in adult shoots) so the second-year growth was sympodial. Some seedlings, however, developed a terminal bud in early July and these retained monopodial growth for a second year (Charlton, 1993b). Leaves approach adult asymmetry during the second growing season. The morphology of developing *U. glabra* seedlings is discussed further by Charlton (1993a, 1993b).

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

Wych elm is readily browsed by large mammals (see Section 4), including roe deer and other ungulates (Heinrichs et al., 2012; Šuleková & Kodrík, 2011), sheep and goats (Ataşoğlu et al., 2010). Small mammals readily eat wych elm seedlings (Commarmot, 1981) but once the seedlings gain a woody bark they are more resistant. For example, bank voles (*Clethrionomys glareolus* Schreber) have a low preference for *U. glabra*; the bark is rarely damaged, although shoots can occasionally be bitten through (Pigott, 1985).

Seeds form a valuable source of food in spring and are readily eaten high in the crown by a number of bird species, particularly finches including greenfinch *Chloris chloris* L., bullfinch *Pyrrhula*

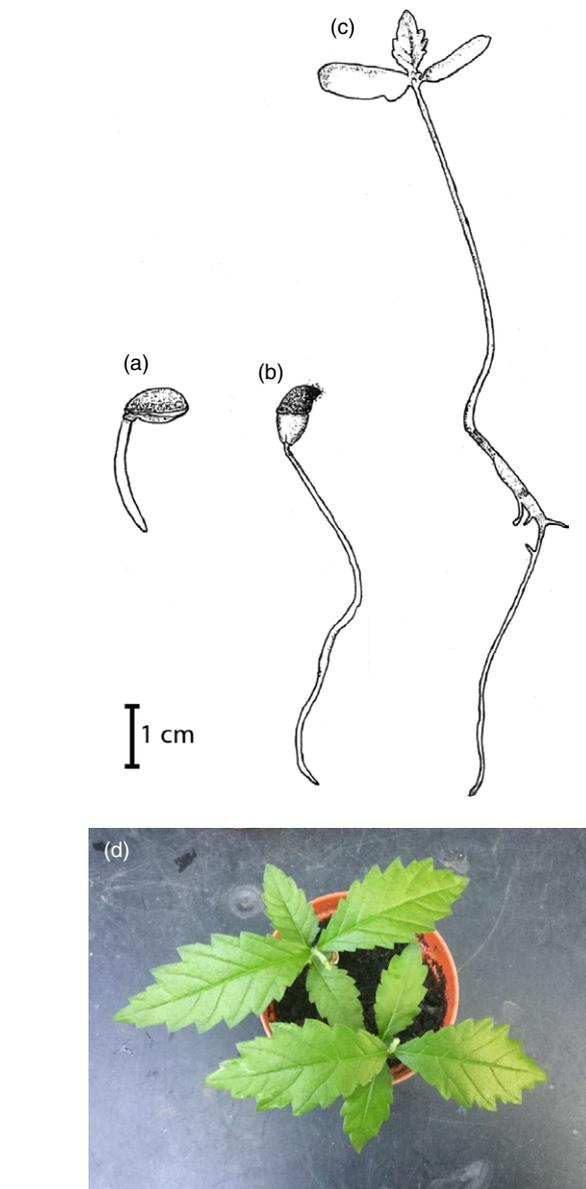


FIGURE 5 Seedlings of *Ulmus glabra* at (a) 1 day, (b) 2 weeks, (c) 4 weeks and (d) 6 weeks after germination. Seedlings in (d) show the first and second pairs of true leaves. Drawings by David Furness [Colour figure can be viewed at wileyonlinelibrary.com]

pyrrhula (L.), goldfinch *Carduelis carduelis* (L.), linnet *C. cannabina* (L.), siskin *C. spinus* (L.), chaffinch *Fringilla coelebs* L. and hawfinch *Coccothraustes coccothraustes* (L.) (Bryant, 2011; Mountfort, 1956; Newton, 1967), often visiting in mixed groups. The finches only eat seeds from unripe fruits with pale seeds and green samaras (Bryant, 2011). In Denmark, tree sparrows *Passer montanus* (L.) have also been seen to eat elm seeds that have fallen to the ground (Erritzoe, 2010). Birds have been seen to remove all the samaras from trees in Essex (Christy, 1922), in this case probably sparrows (*Passer* spp.) and greenfinches. Birds eat the seed, allowing the opened samaras to drop to the ground. Grey squirrels *Sciurus carolinensis* Gmelin, have also been recorded feeding on wych elm fruits in Scotland (Bryant, 2011).

Three mites have been recorded on *U. glabra* in Britain (Table 2). Phytoseiid mites (Acari, Phytoseiidae) have been found to be comparatively common on *U. glabra* in Finland, comparable in numbers to those found on *Fraxinus excelsior* and *Malus domestica* (Tuovinen & Rokx, 1991).

Southwood (1961) recorded 82 species of insect on elms in Britain, and Kennedy and Southwood (1984) recorded 124 species of phytophagous insects and mites on “two species” of *Ulmus* (presumably *U. glabra* and *U. procera*). In both cases, the number of species was comparatively low and comparable to *Corylus avellana* and much lower than found on *Quercus* spp., implying that the leaves are relatively unpalatable (Grime et al., 2007) or *U. glabra* has not been in Britain long enough to acquire more phytophagous insects. Table 2 lists 70 insect species associated with wych elm in Britain; somewhat fewer than the almost 100 species found on *Fraxinus excelsior* (Thomas, 2016). However, the fissured nature of the bark provides a diverse habitat for a range of fauna. In Germany this was found to consist of Araneae, Psocoptera, Rhynchota, Diptera and Coleoptera; Nicolai (1986) gives detailed species lists.

Almost half of the species of insects recorded on *U. glabra* in Table 2 are Hemiptera. Of these, two leaf galling species (Hemiptera, Homoptera, Pemphigidae) are particularly common on elms (Samsone et al., 2012). The elm-currant aphid *Eriosoma ulmi* L. produces rolled leaf galls, and alternates with secondary hosts of *Ribes* spp. Damage has been reported by this aphid on between 61% and 82% of leaves in the Czech Republic and Poland (Kmieć & Kot, 2010; Urban, 2003b). Second, the elm sack gall aphid *Tetraneura ulmi* L. produces brown, bean-shaped galls on elm leaves, with grasses as the secondary hosts. In a study in the Czech Republic, *T. ulmi* was more abundant on *U. minor* than *U. glabra*, although numbers were not given (Urban, 2003a). Bayram (2008) lists species of Neuroptera that prey on galling insects in Turkey. The leafhopper *Ribautiana ulmi* (L.) (Hemiptera, Homoptera, Cicadellidae) is often found on elms but can occur on other woody plants. Claridge (1986) looked at where it occurred on trees of *U. glabra* ‘Camperdownii’ and found largest numbers: in parts of the canopy receiving most light; on basal leaves (compared to more distal leaves) and; on the parts of a leaf exposed to light. The leaves in all these areas were thicker, had higher tannin content, higher leaf toughness and lower water content. But they also have higher carbohydrate and soluble protein levels which was presumed to favour this leafhopper that feeds on mesophyll cells.

Of the many Lepidoptera found on wych elm (Table 2), the white-letter hairstreak butterfly *Satyrrium w-album* (Knoch) is possibly the insect most strongly associated with *U. glabra*. The larvae feed on flowers and leaves, normally at the top of trees. It is predominantly in England and Wales but since 2018 has been found breeding in Scotland (Butterfly Conservation, 2018). It has, however, declined significantly with DED. Of the moths, the dusky-lemon sawfly *Xanthia gilvago* (Denis & Schiffermuller) (Lepidoptera, Noctuidae) and the clouded magpie *Abraxas sylvata* (Scopoli) are particularly associated with wych elm. Found locally throughout Britain, it feeds

mainly on buds and ripening seeds. The orange sawfly *X. citrigo* (L.) feeds mainly on *Tilia* spp. but can be common on wych elm throughout Britain (David Emley, personal communication). The comma butterfly *Polygona c-album* L., has expanded its range due to climate change and has altered its host plant from *Humulus lupulus* to include other hosts, particularly *U. glabra* and *Urtica dioica* (Braschler & Hill, 2007; Nylén & Janz, 1996). The rare micro-moth *Stigmella ulmiphaga* (Preissecker) (Lepidoptera, Nepticulidae) is a leafminer of *U. glabra* in mainland Europe (Møller, 1995). The wood-borer *Chilecomadia valdiviana* (Philippi) (Lepidoptera, Cossidae) has been reported in Chile associated with *U. glabra* (Angulo & Olivares, 1991). Larvae of *Agrochola circellaris* (Hufnagel) (Lepidoptera, Noctuidae) can infest seeds of *U. glabra* but Skrzypczynska (2006) found <1.1% of seeds were affected in southern Poland.

Table 2 lists beetles found on wych elm in Britain. A number of other beetles are found on wych elm in mainland Europe. The elm leaf beetle *Pyrrhalta luteola* Müller (= *Xanthogaleruca luteola* Müller) (Coleoptera, Chrysomelidae) is associated with *U. glabra* and *U. minor* but especially with *U. procera* (Mahani, Hatami, & Seyedoleslami, 2003; Miller, 2000). It is one of the most serious pests of *U. glabra* in the United States, skeletonising leaves (Bosu, Miller, & Wagner, 2007; Costello, Scott, Peterson, & Adams, 1990). *Rhynchaenus rufus* Schrk (Coleoptera, Curculionidae) is a common leafminer on *U. glabra* in mainland Europe (Møller, 1995) and a serious introduced pest in Australia (Lefoe, Dominiak, Worsley, & Davies, 2014). Møller (1995) claimed that infestations of *R. rufus* were higher in leaves that were stressed, determined by greater variation in widths between the two halves of a leaf and in the distance between side veins.

Several *Scolytus* bark beetles are native to Britain (Table 2). All can be vectors of DED but most notable is the large elm bark beetle *Scolytus scolytus* (F.) (Coleoptera, Curculionidae). *Hylurgopinus rufipes* Eichhoff native to North America is a minor pest of *U. glabra* (EPPO, 2013), and if introduced to Britain would probably be a very effective vector of DED (Flø, Krokene, & Økland, 2014).

Dutch elm disease is having a mixed impact on beetles. The rare longhorn beetle *Rosalia alpina* (L.) (Coleoptera, Cerambycidae), normally found in *Fagus sylvatica*, has been found in dead *U. glabra* in Poland and Germany as populations expand into dying stands of elm (Bartnik, Michalcewicz, & Ciach, 2015; Bussler, Schmidl, & Blaschke, 2016; Michalcewicz, Ciach, & Bodziarczyk, 2011). Conversely threatened species such as *Quedius truncicola* F. & L. (Coleoptera, Staphylinidae), whose larva primarily feeds on dipterous larvae in very rotten wood, and the red click beetle *Elater ferrugineus* L. (Coleoptera: Elateridae), are undoubtedly declining in mainland Europe with increased removal of old diseased trees (Musa et al., 2013; Sörensson, 1996). Faccoli and Favaro (2016) using field and laboratory trials in north-east Italy showed that *U. glabra* is very susceptible to the Asian long-horned beetle *Anoplophora glabripennis* (Motschulsky) (Coleoptera, Cerambycidae), along with *Acer pseudoplatanus*, *Betula pendula* and *Salix alba*. The four species together made up 97.5% of the 1,140 infected trees. Kletečka (1996) lists beetles found on living and dying elms in the Czech Republic.

TABLE 2 Mites and insects recorded from *Ulmus glabra* in Britain. Nomenclature follows that of the Database of Insects and their Food Plants (DBIF, 2018)

Species/classification	Ecological notes	Source
Acari		
Eriophyidae		
<i>Aculus brevipunctatus</i> (Nalepa)	Larvae and adults; galling; <i>Ulmus</i> spp.	2
<i>Eriophyes filiformis</i> (Nalepa)	Larvae and adults; galling; <i>Ulmus</i> spp.; rare	2
Rhyncaphytopidae		
<i>Rhyncaphytoptus ulmivagrans</i> Keifer	Larvae and adults; leaves; <i>Ulmus</i> spp.	2
Hemiptera		
Callaphididae		
<i>Tinocallis nevskyi</i> Remaudière, Quednau & Heie	Adults and larvae on underside of leaves. Native to Asia	7
<i>Tinocallis platani</i> (Kaltenbach)	Aphid on leaves; <i>Ulmus</i> spp.	2
Cicadellidae		
<i>Alebra wahlbergi</i> (Boheman)	Larvae and adults; leaves; wide range of tree	2
<i>Allygus commutatus</i> Fieber	On shrubs and trees	2
<i>Alnetoidia alneti</i> (Dahlbom)	Larvae and adults; leaves; wide range of tree	2
<i>Edwardsiana hippocastani</i> (Edwards, J.)	Larvae and adults; leaves; range of tree	2
<i>E. plebeja</i> (Edwards, J.)	Larvae and adults; leaves; range of tree	2
<i>Fagocyba cruenta</i> (Herrich-Schaeffer)	Larvae and adults; leaves; wide range of tree	2
<i>Ribautiana ulmi</i> (L.)	Larvae and adults; leaves, wide range of woody	2
<i>Zonocyba bifasciata</i> (Boheman)	Larvae and adults; leaves; <i>Ulmus</i> and <i>Carpinus</i> spp.	2
<i>Zygina schneideri</i> (Gunthart)	<i>Ulmus</i> and woody Rosaceae; rare	2
Coccidae		
<i>Pulvinaria regalis</i> (Canard)	Larvae and adults; scale; wide range of tree	2
Diaspididae		
<i>Lepidosaphes conchyformis</i> (Gmelin in L.)	Scale; wide range of tree; introduced	2
Eriococcidae		
<i>Eriococcus spurius</i> (Modeer)	Scale; <i>Ulmus</i> and <i>Carpinus</i> spp.	2
Miridae		
<i>Asciodema fieberi</i> (Douglas & Scott in Fieber)	Larvae and adults; leaves; <i>Ulmus glabra</i> only	2
<i>Orthotylus viridinervis</i> (Kirschbaum)	Leaves; <i>Ulmus glabra</i> only	2
Pemphigidae		
<i>Colopha compressa</i> (Koch, C.L.) I	Galling aphid on leaves; <i>Ulmus</i> spp.	2
<i>Eriosoma lanigerum</i> (Hausmann) I	<i>Ulmus</i> spp.	2
<i>E. ulmi</i> L.	Common leaf-rolling galler	2
<i>Kaltenbachiella pallida</i> (Haliday) I	Galling aphid on leaves; <i>Ulmus</i> spp.	2
<i>Schizoneura grossulariae</i> (Schule) I	Larvae and adults; galling; <i>Ulmus</i> spp.	2
<i>S. lanuginosa</i> Hartig, T. I	Galling aphid on leaves; <i>Ulmus</i> spp.	2
<i>S. patchae</i> Börner, C. & Blunck I	Galling and rolling on leaves; <i>Ulmus</i> spp.	2
<i>S. ulmi</i> (L.) I	Larvae and adults; galling and rolling on leaves; <i>Ulmus</i> and <i>Ribes</i> spp.	2
<i>Tetraneura ulmi</i> (L.) I	Galling aphid on leaves; <i>Ulmus</i> spp.	2
Psyllidae		

(Continues)

TABLE 2 (Continued)

Species/classification	Ecological notes	Source
<i>Psylla ulmi</i> Forster	Louse; introduced and rare; <i>Ulmus</i> spp.	2
Hymenoptera		
Tenthredinidae		
<i>Kaliofenusa pusilla</i> (Serville)	Leaf-mining sawfly on <i>Ulmus glabra</i> in Ireland	8
Lepidoptera (butterflies)		
Lycaenidae		
<i>Satyrrium w-album</i> (Knoch)	Larvae; buds, flowers and leaves; <i>Ulmus</i> spp. especially <i>U. glabra</i>	2
<i>Strymonidia w-album</i> (Knoch)	Larvae; buds, flowers and leaves; <i>Ulmus</i> , <i>Fraxinus</i> , <i>Ligustrum</i> and <i>Rubus</i> spp.	2, 5
Nymphalidae		
<i>Nymphalis polychloros</i> (L.)	Larvae; gregarious and webbing on leaves; migrant; wide range of woody plants	2
<i>Polygonia c-album</i> (L.)	Larvae; leaves; mostly on <i>Ribes</i> and <i>Humulus lupulus</i> and increasingly <i>U. glabra</i>	2
Lepidoptera (macro-moths)		
Geometridae		
<i>Abraxas sylvata</i> (Scopoli)	Larvae; leaves; <i>Ulmus</i> , <i>Corylus</i> and <i>Fagus</i> spp., especially <i>U. glabra</i>	2, 3, 5
<i>Discoloxia blomeri</i> (Curtis)	Larvae; leaves; on <i>Ulmus glabra</i>	2
<i>Epirrita autumnata</i> (Borkhausen)	Larvae; leaves; wide range of shrubs and trees	2
<i>E. christyi</i> (Allen)	Larvae; leaves; wide range of trees	2
<i>Lomographa temerata</i> (Denis & Schiffermuller)	Larvae; wide range of trees	2
Noctuidae		
<i>Agrochola circellaris</i> (Hufnagel)	Larvae; buds, flowers, fruits, seeds, leaves; wide range of trees	2, 5
<i>Conistra vaccinii</i> (L.)	Larvae; leaves; wide range of woody and non-woody plants	2
<i>Cosmia affinis</i> (L.)	Larvae; <i>Ulmus glabra</i> and <i>U. procera</i>	2, 5, 11
<i>C. diffinis</i> (L.)	Larvae; <i>Ulmus glabra</i> and <i>U. procera</i>	2, 5, 10
<i>C. pyralina</i> (Denis & Schiffermuller)	Larvae; wide range of trees	2
<i>Eupsilia transversa</i> (Hufnagel)	Larvae; wide range of woody and non-woody plants	2
<i>Xanthia citrigo</i> (L.)	Larvae; webbing; <i>Tilia</i> , <i>Ulmus</i> and <i>Rubus</i> spp.	2
<i>X. gilvago</i> (Denis & Schiffermuller)	Larvae; buds, flowers, fruits, seeds, leaves; <i>Ulmus</i> , <i>Rubus</i> and <i>Hedera</i> spp. <i>U. glabra</i> mainly, occasionally <i>U. procera</i>	2, 5
Sesiidae		
<i>Synanthedon vespiformis</i> (L.)	Larvae; bark, stumps; wide range of trees	2
Lepidoptera (micro-moths)		
Coleophoridae		
<i>Coleophora serratella</i> (L.)	<i>Ulmus</i> , <i>Alnus</i> , <i>Betula</i> and <i>Corylus</i> spp.	2, 4
<i>C. limosipennella</i> (Duponchel)	<i>Ulmus</i> spp.	2, 4
<i>C. badiipennella</i> (Duponchel)	<i>Ulmus</i> spp.	2, 4
<i>C. violacea</i> (Ström)	<i>Ulmus</i> spp.	2, 4
Gelechiidae		
<i>Carpatolechia fugitivella</i> (Zeller)	Larvae; webbing; <i>Ulmus glabra</i>	2
Gracillariidae		
<i>Phyllonorycter tristrigella</i> (Haworth)	Larvae; mining; <i>Ulmus</i> spp.	2, 4
Nepticulidae		
<i>Stigmella lemniscella</i> (Zeller)	Larvae; mining; <i>Ulmus</i> spp.	2, 4
<i>S. ulmivora</i> (Fologne)	Larvae; mining; <i>Ulmus</i> spp.	2, 4
<i>S. viscerella</i> (Stainton)	Larvae; mining; <i>Ulmus</i> spp.	2, 4

(Continues)

TABLE 2 (Continued)

Species/classification	Ecological notes	Source
Pyrilidae		
<i>Pleuroptya ruralis</i> (Scopoli)	Larvae; leaf rolling	6
Tortricidae		
<i>Phtheochroa schreibersiana</i> (Frölich)	<i>Ulmus</i> spp. and a range of other trees	4
<i>Pandemis cerasana</i> (Hübner)	Range of woody plants	4
<i>Archips crataegana</i> (Hübner)	Range of woody plants	4
Yponomeutidae		
<i>Atemelia torquatella</i> (Lienig & Zeller)	<i>Ulmus</i> and <i>Betula</i> spp.	4
<i>Ypsolopha vittella</i> (L.)	<i>Ulmus</i> and <i>Fagus sylvatica</i>	4
Coleoptera		
Curculionidae		
<i>Acrantus vittatus</i> (F.)	Larvae and adults; bark; <i>Ulmus</i> and <i>Fraxinus</i> spp.	2
<i>Anthonomus ulmi</i> (Degeer)	Larvae; feeding on flower buds; <i>Ulmus</i> , <i>Crataegus</i> and <i>Prunus spinosa</i>	2
<i>Rhynchaenus alni</i> (L.)	Larvae; mining; <i>Ulmus</i> and <i>Alnus</i> spp.	2
<i>Scolytus laevis</i> (Chapuis)	Larvae and adults; bark, wood; commonest in lowlands; <i>Ulmus</i> spp.	1, 2
<i>S. multistriatus</i> (Marsham)	Larvae and adults; bark and dead branches; range of trees	2
<i>S. scolytus</i> (F.)	Larvae and adults; stems; range of trees	2
Oedemeridae		
<i>Ischnomera sanguinicollis</i> (F.)	Larvae; wide range of trees	2
Scolytidae		
<i>Ernoporus caucasicus</i> Lindemann	Larvae and adults; bark; <i>Tilia</i> , <i>Ulmus glabra</i> ; rare	2
Diptera		
Tachinidae		
<i>Senometopia excisa</i> (Fallén)	Parasitic on <i>Abraxas sylvata</i> feeding on <i>Ulmus glabra</i>	3
Cecidomyiidae		
<i>Janetiella lemeei</i> (Kieffer)	Larvae; galling of stems and leaves; <i>Ulmus</i> spp.	2
<i>Physemocelis ulmi</i> (Kieffer)	Larvae; galling on leaves; <i>Ulmus</i> spp.	2
Syrphidae		
<i>Platycheirus splendidus</i> Rotheray	Isolated from <i>Schizoneura ulmi</i> galls on <i>Ulmus glabra</i> in Scotland	9
Thysanoptera		
Phlaeothripidae		
<i>Liothrips setinodis</i> (Reuter)	Larvae and adults; leaves; range of trees	2
Thripidae		
<i>Oxythrips ulmiflorum</i> (Haliday)	Larvae and adults; bark; Ulmaceae; rare	2

1. Atkins, O'Callaghan, and Kirby (1981); 2. DBIF (2018); 3. Collins (1999); 4. Emmet (1979); 5. Emmet and Heath (1991); 6. Henwood (1999); 7. Hopkins (1997); 8. Knight (2004); 9. Rotheray (1988); 10. Waring (2005); 11. Waring and Hopkins (2008).

In mainland Europe, the elm leafminer *Fenusa ulmi* (Hymenoptera, Tenthredinidae) has a higher preference for *U. glabra* than *U. minor* and *U. procera* (Mahani et al., 2003; Miller, 2000). The East Asian sawfly *Aproceros leucopoda* Takeuchi (Hymenoptera, Argidae) is an invasive pest of elms has been recorded in mainland Europe on *U. glabra* but more so on *U. minor* (Blank et al., 2010, 2014; Glavendekić, Petrović, & Petaković, 2013; Zandigiacomo, Cargnus, & Villani, 2011).

A variety of nematodes has been found on wych elm. *Bursaphelenchus ulmophilus* sp. n. (Nematoda, Parasitaphelenchinae)

has been found in *U. glabra* suffering from DED, carried by the *Scolytus* spp. elm beetles (Ryss, Polyaniina, Popovichev, & Subbotin, 2015). Many *Bursaphelenchus* species are known to be associated with the wood of various trees, particularly conifers, and in some are notable pests. *Panagrellus ulmi* sp. n. (Nematoda, Panagrolaimidae) has been found in Iran within wetwood cankers of *U. glabra* caused by *Lelliottia nimipressuralis* (Carter) (Enterobacteriaceae) (Abolafia, Alizadeh, & Khakvar, 2016) and *Meloidogyne ulmi* sp. n. is known to cause root galls of elms, including *U. glabra*, in Tuscany (Palmisano &

Ambrogioni, 2000). Earthworms can be very common beneath elms since the leaf litter, being low in phenols, is readily eaten by them (Satchell & Lowe, 1967). In experimental trials, soils supplied with elm leaves and earthworms had larger amounts of bacteria, protozoa and nematodes (Winding, Rønn, & Hendriksen, 1997).

9.2 | Plant parasites and epiphytes

A number of parasitic/saprobic fungi are associated with *U. glabra*. *Rigidoporus ulmarius* (Sowerby) Imazeki (Basidiomycota, Polyporales) is a bracket fungus that is very common on elm although it can occasionally be found on *Salix* and *Aesculus* spp. (British Mycological Society, 2018). The elm oyster *Hypsizygus ulmarius* (Bull.) Redhead (Basidiomycota, Agaricales) is also common on dying and dead elm wood, standing and fallen, and *Macrodiplodia ulmi* Sacc. (Ascomycota, Incertae sedis) occurs on dead attached branches (British Mycological Society, 2018). Fenwick (1998) noted that while *Auricularia auricula-judae* (Bull.: St Am.) Berk (Basidiomycota, Auriculariales) was normally found on *Sambucus nigra* (62% of observations) and *Acer pseudoplatanus* (20%), it was also occasionally found on *U. glabra* (9%) in north-east England. A number of other species are associated with wych elm in mainland Europe, notably the rare *Hypochnicium vellereum* (Ellis & Crag.) Parm. (Basidiomycota, Aphyllophorales), found on decorticated *U. glabra* wood in Finland (Kotiranta & Saarenoksa, 1993). *Ulmus glabra* wood is moderately resistant to decay (3 on 1–5 scale; Brzeziecki & Kienast, 1994). Slime moulds associated with *U. glabra* are given in Table 3.

Kowalski (2004) investigated endophytes of *U. glabra* leaves. On leaves with no necrosis, endophytes were rare, 18 taxa found on just 22% of leaf fragments. In necrotic areas associated with galls, 25 species were detected; some were unique but many species were found in both necrotic and non-necrotic areas. Bugała et al. (2015) list fungi found on *U. glabra* in Poland.

Ulmus glabra has a high bark pH (4.5–7.1) similar to *Fraxinus excelsior*, *Tilia cordata* and *Acer* spp. and all three species carry a rich bryophyte and lichen community, especially in polluted areas (Douglass, Rotehro, & Holden, 2010; Hallingbäck, 1992; Löbel & Rydin, 2009; Mežaka, Brūmelis, & Piterāns, 2012; Nordbakken & Austad, 2010; Weibull, 2001). In Estonia, wych elm carried 39 species of lichen, compared to 46 on *F. excelsior* and 38 spp. on *Acer platanoides* (Jüriado, Liira, & Paal, 2009) and in Latvia it carried the highest number of “woodland key habitat” epiphyte species of any broadleaved tree (Gerra-Inohosa, Pušpure, & Bambi, 2015). Since the litter of wych elm is rich in nutrients and decomposes comparatively quickly (Shilenkova & Tiunov, 2013), the bryophyte flora below *U. glabra* is rich, similar to that below *F. excelsior* and *Acer platanoides* and much higher than under *Betula pendula* and *Quercus robur* in Sweden (Weibull & Rydin, 2005). Mežaka, Brūmelis, and Piterāns (2008) give an extensive list of the epiphytes found on *U. glabra* in Latvia. A number of lichens is highly dependent on elm species, including nationally scarce species that are priority species under the UK Biodiversity Action Plan, including *Anaptychia ciliaris*, *Bacidia incompta*, *Caloplaca luteoalba*, *Collema fragrans* and *Cryptolechia carneolutea* (Edwards, 2005).

9.3 | Plant diseases

9.3.1 | Dutch elm disease

The first modern epidemic of DED, caused by the vascular wilt fungus *Ophiostroma ulmi* (= *Ceratostomella ulmi* Buis, *Ceratocystis ulmi* (Buis.) C. Moreau), entered Britain on imported logs and killed c. 30% of elms between 1920 and 1940 (Napierała-Filipiak et al., 2016). Similar losses were reported across Europe with even heavier losses in North America. The second epidemic in the 1970s was caused by

TABLE 3 Slime moulds (Amoebozoa, Myxomycetes) associated with *Ulmus glabra*. Nomenclature follows the Fungal Records Database of Britain and Ireland (British Mycological Society, 2018)

<i>Arcyria denudata</i> (L.) Wettst.	Fallen trunk
<i>Badhamia affinis</i> Rostaf.	Live bark
<i>B. panicea</i> (Fr.) Rostaf.	Dead wood
<i>Brefeldia maxima</i> (Fr.) Rostaf.	Rotting wood
<i>Calomyxa metallica</i> (Berk.) Nieuwl.	Live bark
<i>Comatricha nigra</i> (Pers.) J. Schröt.	Fallen branch
<i>Cribraria persoonii</i> Nann.-Bremek.	Rotting wood
<i>C. violacea</i> Rex	Live bark
<i>Echinostelium minutum</i> de Bary	Live bark
<i>Fuligo septica</i> var. <i>flava</i> (Pers.) Morgan	Dead wood
<i>Hemitrichia minor</i> G. Lister	Live bark
<i>H. pardina</i> (Minakata) Ing	Live bark
<i>Licea belmontiana</i> Nann.-Bremek.	Live bark
<i>L. bryophila</i> Nann.-Bremek.	Live bark
<i>L. denudescens</i> H.W. Keller & T.E. Brooks	Live bark
<i>L. inconspicua</i> T.E. Brooks & H.W. Keller	Live bark
<i>L. marginata</i> Nann.-Bremek.	Live bark
<i>L. parasitica</i> (Zukal) G.W. Martin	Live bark
<i>L. pedicellata</i> (H.C. Gilbert) H.C. Gilbert	Bark
<i>L. synsporos</i> Nann.-Bremek.	Live bark
<i>Lycogala epidendrum</i> (J.C. Buxb. ex L.) Fr.	Dead wood
<i>L. flavofuscum</i> (Ehrenb.) Rostaf.	Base of trunk
<i>L. terrestre</i> Fr.	Fallen trunk
<i>Macbrideola cornea</i> (G. Lister & Cran) Alexop.	Live bark
<i>Metatrachia floriformis</i> (Schwein.) Nann.-Bremek.	Fallen trunk
<i>Perichaena chrysosperma</i> (Curr.) Lister	Live bark
<i>Physarum album</i> (Bull.) Chevall.	Dead wood
<i>P. decipiens</i> M.A. Curtis	Live bark
<i>Reticularia lycoperdon</i> Bull.	Dead trunk
<i>Stemonitopsis typhina</i> (F.H. Wigg.) Nann.-Bremek.	Fallen branch, trunk
<i>Symphytocarpus flaccidus</i> (Lister) Ing & Nann.-Bremek.	Bark
<i>Trichia affinis</i> de Bary	Dead wood
<i>T. scabra</i> Rostaf.	Dead wood
<i>T. varia</i> (Pers. ex J.F. Gmel.) Pers.	Dead wood

Ophiostoma novo-ulmi, now the dominant species of *Ophiostoma* in Europe, where two races met—Eurasian (EAN) and North American (NAN) (Brasier, 1991). It entered Europe on Canadian elm logs (Brasier, 2008) and by 1980 killed an estimated 28 million mature elms (Gibbs, Brasier, & Webber, 1994) and caused the subsequent death of around 20 million young elms, removing 90% of mature *U. minor*. For example, the elm population of Paris has decreased from 30,000 (half of them in the Bois de Vincennes) in 1970 to around 1,000 (Pinon, Husson, & Collin, 2005). Resistant hybrids were developed and planted in millions after the first epidemic wave (e.g. 'Commelin,' 'Groeneveld,' 'Plantyn,' 'Doedens' and 'Clusius') which contained *U. glabra* as parents, and which, unfortunately, showed partial or complete susceptibility to *O. novo-ulmi* (Dunn, 2000). *Ulmus glabra* has been less affected than suckering elms (Cogolludo-Agustín, Agúndez, & Gil, 2000) and is now the most numerous elm in central and eastern Europe. But *U. glabra* is by no means immune and indeed is more susceptible to the DED fungus than *U. minor* or *U. laevis* (Napierała-Filipiak et al., 2016; Pinon et al., 2005). In 4-year-old (3–4 m high) *U. glabra* in the Czech Republic inoculated with *O. novo-ulmi*, sap flow was reduced 10 days after inoculation and total occlusion of xylem stopped sap flow after 11–16 days (Urban & Dvořák, 2013, 2014). This is faster than reported in *U. americana* where it took 8–17 days for sap flow to begin to decline and 6 weeks to eventual death (MacHardy & Beckman, 1972; Roberts, 1966). Pinon et al. (2005) used 2-year-old plants inoculated with fungus and found mortality was *U. glabra* 40%, *U. laevis* 35%, *U. minor* 6% but there was great variation in susceptibility between the 200 clones they tested. However, no clone of a native elm species reached the level of resistance of the best cultivars (see Section 8.2), such as 'Sapporo Autumn Gold,' 'Lutece Nanguen' and 'Dehesa de Amanuel' (Buiteveld, Van Der Werf, & Hiemstra, 2015; Heybroek, 1993b; Martín et al., 2015; Smalley & Lester, 1973; Townsend, 1979).

The spread of DED into northern Britain and mainland Europe has been slower than further south; it was found in Scotland in 1938 (Peace, 1960; Redfern, 1977) and in the west part of the Central Lowlands by 1947. This has been ascribed to temperature conditions being less suitable for the main beetle vectors, *Scolytus multistriatus* and especially *S. scolytus* (see Section 11). *Ulmus glabra* and *U. laevis* are less attractive to the beetle vectors than *U. minor* (Webber, 2000), but *U. glabra* is still a preferred host. In two-choice tests, *S. multistriatus* preferred *U. glabra* 100% of times in combination with *Salix* sp., *Fagus sylvatica*, *Quercus* sp. and *Alnus* sp. (Anderbrant, Yuvaraj, Martin, Gil, & Witzell, 2016). At the height of the main epidemic, *U. glabra* appeared to be more resistant than *U. procera*, which was attributed to its comparative rarity, and its growing in woodland rather than exposed in agricultural land, so escaping the notice of the beetle (Savill, 2013). In arid and windy areas, the beetles prefer to feed on branches of smaller understorey trees, and so smaller trees may become infected while larger, more exposed trees do not (Petrokas, 2008). The fungus can spread through root grafts. It is suggested that *Diaporthe eres* Nitschke (= *Phomopsis oblonga* (Desm.) Traverso) (Diaporthales, Ascomycota) may compete with the beetle for habitat within the wood (Webber, 1981).

The disease is still prevalent, causing successive waves of death across the UK and mainland Europe at 15–25 year intervals (Harwood, Tomlinson, Potter, & Knight, 2011; Łakomy et al., 2016). Once new stems arising from basal sprouts reach 5–9 m and around 10 cm DBH they are susceptible to the *Scolytus* beetles (Bowditch & Macdonald, 2016; Savill, 2013) creating cycles of re-infection (Harwood et al., 2011). The optimum bark thickness for beetle development is 5–8 mm (Manojlović & Sivčev, 1995). However, by this time, they have started producing viable seed and so are contributing to the long-term survival of *U. glabra* populations. Moreover, Nielsen and Kjær (2010) observed that *U. glabra* individuals isolated from others by at least 300 m still received pollen from a minimum of three other trees. They suggest that this maintains a genetic interconnectedness among the remaining trees of *U. glabra* over distances further than *Scolytus* beetles normally move. However, the maintenance of genetic variation in isolated, older trees may increase the resistance of populations to the disease (Sengonca & Leisse, 1984; Solla et al., 2005).

Isolated mature elms have survived throughout Britain presumably due to some innate resistance. Other mature elms (such as in and around Brighton) have been kept alive by active management including sanitation zones by felling infected trees and the use of insecticides and fungicides. Various vaccines that stimulate the elm to produce antifungal compounds have been developed, including Dutch Trig[®], although these need to be applied each year (Bowditch & MacDonald, 2016). A review of the effectiveness of control policy during the two epidemics is given by Tomlinson and Potter (2010).

9.3.2 | Other fungi

Ulmus glabra is susceptible to *Armillaria mellea* and is host to a number of *Armillaria* spp. (Table 4). A number of ascomycetes, notably *Taphrina ulmi* and *Asteromella ulmi* (Table 4) are pathogens causing leaf spot on *U. glabra*, and *Plectophomella concentrica* causes canker and dieback in *U. glabra* in Britain (British Mycological Society, 2018; Redfern & Sutton, 1981). *Stegophora ulmea* (Fries) Sydow & Sydow (Ascomycota, Diaporthales) is native to North America and has been identified in horticultural plants in the UK although is probably not at large. It causes black spots on leaves of a number of elm species (McGranahan & Smalley, 1981) and can cause significant defoliation and twig dieback in nurseries. It is an especial problem for hybrid cultivars resistant to DED as their parents are particularly susceptible to *S. ulmea*. It is a minor problem for mature elms and is rarely fatal and even severely blighted parts can recover in dry conditions (EPPO, 2005). Powdery mildew fungi, *Erysiphe clandestina* var. *clandestina* and *Phyllactinia guttata* (Wallr.) Lév. (Ascomycota, Erysiphales) have been described on *U. glabra* in mainland Europe (Tavanaei, Aadel, & Khodaparast, 2009).

9.3.3 | Bacteria

Bacterial elm yellows has been found on *U. glabra* in Croatia, France and Germany belonging to *Candidatus Phytoplasma solani* (16SrXII-A

TABLE 4 Fungi (by Order) directly associated with *Ulmus glabra* not including those found on soil or litter below the trees, or those found solely on dead wood. Details of these can be found in the Fungal Records Database of Britain and Ireland (British Mycological Society, 2018). Nomenclature follows this database. Fungi that can be lichenised were identified from the British Isles List of Lichens and Lichenicolous Fungi (Natural History Museum, 2018)

Species/classification	Ecological notes
Zygomycota	
Mortierellales	
<i>Mortierella gamsii</i> Milko	Bark
Ascomycota	
Botryosphaerales	
<i>Phyllosticta ulmi</i> Westend.	Dying leaves causing dead spots
Capnodiales	
<i>Mycosphaerella ulmi</i> Kleb.	Living leaves
<i>Phloeospora</i> sp. Wallr.	Underside of leaves
Diaporthales	
<i>Diaporthe eres</i> Nitschke	Living buds
<i>Stegophora ulmea</i> (Fries) Sydow & Sydow	Elm black spot on many <i>Ulmus</i> spp.
Erysiphales	
<i>Erysiphe clandestina</i> Biv.	Leaves
<i>E. ulmi</i> Castagne	On stump sprouts
Helotiales	
<i>Calycella lenticularis</i> (Bull.) Boud.	Bark, wood
<i>Encoelia furfuracea</i> (Roth) P. Karst.	Twigs
Incertae sedis	
<i>Asteromella ulmi</i> Boerema	Dead leaves
<i>Plectophomella concentrica</i> Redfern & B. Sutton	Canker and dieback in <i>U. glabra</i>
<i>Sclerococcum sphaerale</i> (Ach. ex Ficin. & C. Schub.) Fr.	Lichen
Lecanorales	
<i>Cladonia coniocraea</i> (Flörke) Spreng.	Lichen
<i>Cliostomum griffithii</i> (Sm.) Coppins	Lichen
<i>Geosmithia putterillii</i> (Thom) Pitt	Bark
<i>Neonectria coccinea</i> (Pers.) Rossman & Samuels	Bark
Ophiostomatales	
<i>Ophiostoma novo-ulmi</i> Brasier	Causal agent of Dutch elm disease
<i>O. ulmi</i> (Buisman) Nannf.	Original causal agent of Dutch elm disease
Orbiliales	
<i>Orbilina auricolor</i> (A. Bloxam) Sacc.	Bark, wood
<i>O. comma</i> Graddon	Bark, dead wood
Ostropales	
<i>Stictis radiata</i> (L.) Pers.	Inner surface of loose bark

(Continues)

TABLE 4 (Continued)

Species/classification	Ecological notes
Peltigerales	
<i>Collema fragrans</i> (Sm.) Ach.	Lichen
Pleosporales	
<i>Aposphaeria ulmicola</i> (Berk.) Sacc.	Bark
<i>Didymosphaeria celata</i> (Curr.) Sacc.	Bark
<i>Dothidella ulmi</i> (C.-J. Duval) G. Winter	Live leaves
<i>Phaeosphaeria microscopica</i> (P. Karst.) O.E. Erikss.	Leaves
Taphrinales	
<i>Taphrina ulmi</i> (Fuckel) Johanson	Causes leaf elm spot
Xylariales	
<i>Kretzschmaria deusta</i> (Hoffm.) P.M.D. Martin	Living and dead trunks
Basidiomycota	
Agaricales	
<i>Aphanobasidium rubi</i> (Grosse-Brauckm.) Boidin & Gilles	Bark of living trunk
<i>Armillaria gallica</i> Marxm. & Romagn.	Stump, roots of dead tree
<i>A. mellea</i> (Vahl) P. Kumm.	Dead trunk
<i>A. ostoyae</i> (Romagn.) Herink	Dead wood
<i>Mycena clavicularis</i> (Fr.) Gillet	Bark
<i>M. hiemalis</i> (Osbeck) Qué.	Living trunk
<i>M. pseudocorticola</i> Kühner	Living trunk
<i>M. tenerrima</i> (Berk.) Qué.	Bark of living tree
<i>Pleurotus cornucopiae</i> (Paulet) Rolland	Live and dead wood
Atheliales	
<i>Athelopsis lembospora</i> (Bourdot) Oberw.	Living bark
Botryosphaerales	
<i>Botryosphaeria quercuum</i> (Schwein.) Sacc.	Parasitic on twigs
Corticiales	
<i>Dendrothele citrisporella</i> Boidin & Duhem	Live bark
Diaporthales	
<i>Cytospora populina</i> (Pers.) Rabenh.	Bark
Polyporales	
<i>Rigidoporus ulmarius</i> (Sowerby) Imazeki	Bracket fungus
Tremellales	
<i>Tremella mesenterica</i> Retz.	Bark

subgroup) (Boudon-Padieu et al., 2004; Katanić, Krstin, Ježić, Zebec, & Ćurković-Perica, 2016; Mäurer, Seemüller, & Sinclair, 1993), and hybrids of *U. glabra* in North America (Sinclair, Townsend, Griffiths, & Whitlow, 2000). It causes witches brooms and yellowing of leaves (Mittengergher, 2000). *Xylella fastidiosa* (Gammaproteobacteria) is known as a pest of ornamental and economic trees the USA and Taiwan (Sherald & Kostka, 1992), moved by sap-sucking insects.

Since 2013 several subspecies have become serious economic pests of *Olea europaea* and citrus trees in Europe (Azevedo, Araujo, & Lacava, 2016; White, Bullock, Hooftman, & Chapman, 2017), plus infecting species of *Quercus*, *Platanus* and *Ulmus*, including *U. glabra* where it causes bacterial leaf scorch (Sherald & Kostka, 1992). *Ulmus* species are affected by the subspecies 'multiplex' of *X. fastidiosa* (Baldi & La Porta, 2017). Pockets of bacterial wetwood rot in *U. glabra* were recorded by Lindeman (2008).

9.3.4 | Viruses

Elm mottle virus causes foliar mottling, ringspots and line pattern leaf symptoms in *U. glabra* in western and Central Europe, and is common in Scotland (Jones & Mayo, 1973; Schmelzer, Schmidt, & Schmidt, 1966). The virus is seed-borne in wych elm and no vectors are known (Nienhaus & Castello, 1989).

10 | HISTORY

Elm pollen production is relatively high (Newsome & Adams-Groom, 2017), although along with *Fraxinus*, *Salix* and *Tilia*, modern-day trees are poorer producers of pollen than other woodland species (Broström et al., 2008). Nevertheless, *Ulmus* pollen is readily found in peat analyses and 2% of total pollen is taken as indicative of local presence (Huntley & Birks, 1983). Pollen grains of *U. glabra*, *U. laevis* and *U. minor* are virtually identical (Stafford, 1995); however, Stockmarr (1970) showed that pollen from *Ulmus* can be statistically distinguished to species level. Scanning electron microscopy has shown *U. procera* to be readily distinguishable from other elm species. *Ulmus minor* pollen grains are, however, still very difficult to distinguish from *U. glabra*, which have similar sculpturing and almost the same number of pores (Stockmarr, 1974). Macrofossils of *Ulmus* are seldom preserved other than as wood or charcoal (Godwin, 1975), although Kullman (1998) reported an *U. glabra* leaf dating to c. 9500 BP in Sweden.

Pollen grains of Ulmoideae have been found in chalk deposits c. 80 million years old and that of *Ulmus* species from Palaeozoic sediments 66–58 million years old (Bugala et al., 2015). Speciation of our current European elms occurred between the Lower Oligocene, about 35 million years ago, and the Miocene, 24–25 million years ago (Mai, 1995).

Like many angiosperm trees, *Ulmus* species likely survived in the Upper Pleistocene in refugia in the Iberian Peninsula, Italy and Greece and into Eastern Europe and Russia (Bennett, Tzedakis, & Willis, 1991; Carrión et al., 2008; Chytrý et al., 2010; Stewart & Lister, 2001; Svenning, Normand, & Kageyama, 2008). However, unlike *U. minor*, the absence of lineage-C haplotypes in Spanish *U. glabra* suggests a limited refugium of *U. glabra* in Iberia, whereas its presence in both elms (*U. glabra* and *U. minor*) in Italy indicates that this was likely their major refugium (Gil, Fuentes-Utrilla, Soto, Cervera, & Collada, 2004). The migration rate of *U. glabra* in the Boreal period 9500–8000 BP was estimated in Myking (2002) at 100–1,000 m/year, similar to other large deciduous trees, adding credence to the

presence of northern refugia. Certainly, thermophilous trees such as *Ulmus glabra*, *Quercus robur*, *Corylus avellana*, *Tilia cordata* and *Alnus glutinosa* arrived in south-east Norway and the Scandes Mountains of Sweden before 8000 BP (Kullman, 1998; Myking & Yakovlev, 2006; Sørensen, Høeg, & Pedersen, 2015; Stewart & Lister, 2001) reaching a maximum at 7200–6400 BP (Giesecke, 2005). During the Atlantic period, *U. laevis* was the first elm to arrive in northern Europe (Tolonen, 1980) forming woodland with *Carpinus betulus*, *Fagus sylvatica* and *T. cordata* in the lowlands, followed by *Abies alba* and *U. glabra* in the uplands (Kalis, Merkt, & Wunderlich, 2003). Similarly, further east in the Rila Mountains of Bulgaria, *Ulmus*, along with *Quercus*, *Tilia* and *Corylus* appeared in the early Holocene from 11800 until c. 6700 BP when it was replaced with mixed *Pinus/Abies* forest (Bozilova & Tonkov, 2000). By 5000 BP, *U. glabra*, *Q. robur* and *A. glutinosa* had penetrated onto the northern parts of the Kazakhstan Foothills (Kremenetski, Tarasov, & Cherkinsky, 1997), after which they declined due to drier and more continental conditions.

Ulmus glabra was the first elm to arrive in the British Isles in the Holocene (Godwin, 1975) and probably was the only elm to reach the north and west (Birks, 1989). In East Anglia, *U. glabra* was undoubtedly mixed with smaller amounts of *U. minor* since the early Holocene (Bennett, 1983a, 1983b). According to Huntley and Birks (1983) and Birks (1989), *U. glabra* was present in southern England c. 9500 BP and spread rapidly (500–600 m/year) through central England and into Wales. It reached eastern Ireland by 9000 BP and north-west Ireland by 7700 BP. Its spread into Scotland slowed after 8500 BP to less than 100 m/year most likely due to an unfavourable climate, high light exposure and possibly acidic soils. It reached north-west Scotland by 6200 BP, although it remained a minor component of the scrub and small woodlands of Caithness (Peglar, 1993). A detailed study of Roudsea Wood National Nature Reserve, Cumbria, revealed that the mid-Flandrian woodland (6680–5150 BP) was composed of *Quercus* and *Corylus avellana* (both 10%–30%) with *Tilia cordata* (5%–25%), *Fraxinus excelsior* (5%–15%), *Alnus glutinosa* (15%–20%), *Betula* (5%–15%) and *Ulmus* cf. *U. glabra* (2%–15%; Birks, 1982).

The natural distribution of elms has been extensively altered by human introductions. Jeffers (1999) used leaf morphology to suggest introductions in the Bronze Age of *U. procera* from Spain and East Anglian and East Midlands population of *U. minor* from Central Europe. *Ulmus minor* growing along the coast of Essex and Kent likely came from northern France in the Iron Age; Cornish *U. minor* from Brittany in first millennium AD; and *U. glabra* × *U. minor* from northern France via the Netherlands in the 17th century. Philip II of Spain imported many plants from England to his park near Madrid in 1555 (Heybroek, 1962). Also, the botanist Dodonee in the 17th century wrote that elms were common in the Argonne (Huberty, 1904). Henry IV of France had planted thousands of elms on the occasion of the birth of the child Louis XIII of France in 1601.

10.1 | Elm decline

Ulmus glabra was at its maximum in the British Isles by 6000 to 5500 BP as a regular component of a complex woodland mosaic (Parker,

Goudie, Anderson, Robinson, & Bonsalle, 2002) but was followed by a widespread and rapid decline between 5400 and 4800 BP (Garbett, 1981; Peglar, 1993; Peglar & Birks, 1993; Sturludottir & Turner, 1985). In any one area, the decline was remarkably rapid over a handful of years. For example, at Diss Mere, Norfolk, *Ulmus* pollen fell by 73% in just 6 years (Peglar, 1993; Peglar & Birks, 1993). This did not necessarily lead to a significant contraction in the range of elm across Britain but pollen records dropped from up to 20%–30% of total tree pollen to rarely accounting for >5% afterwards. The declines were largest in south-west and central-southern England, and smaller in the north and west of Britain, reflecting the proportion of elm in these areas (Parker et al., 2002). Patterns of subsequent elm recovery varied: in Ireland, elm recovered on fertile soils by 4500 BP (O'Connell, 1980) while in south-east England it did not thereafter recover to pre-decline levels (Godwin, 1940; Peglar & Birks, 1993). This is partly attributable to continued human intervention; for example, between 2600 and 1110 BP in Denmark, woodland development was altered by intensive anthropogenic disturbance maintaining a comparatively open canopy, allowing *U. glabra* and *Quercus robur* to persist in woodlands dominated by *Fagus sylvatica* and *Fraxinus excelsior* (Hannon, Bradshaw, & Emborg, 2000).

Elm decline has been variously attributed to a cooling climate or to the arrival of agriculture and loss of forests (associated with an increase in grass and weed pollen) tied to the use of the trees for fodder, perhaps by “shredding” (removing all side branches), reducing the amount of flowering (Garbett, 1981; Heybroek, 1963, 1993a; Troels-Smith, 1960). Certainly, modern elm pollards in western Norway appear to produce few seeds (as judged by the lack of juvenile trees), which is reversed when pollarding is stopped (Austad & Skogen, 1990) suggesting that repeated cutting of branches reduced flowering and pollen production. But the decline appeared to be synchronous across northern Europe, and in Britain and Ireland it started synchronously over a period of 3–4 decades (Parker et al., 2002). The conclusion is that the decline was caused by DED or similar disease aided by climatic and human factors (Perry & Moore, 1987). Fossil remains of the elm bark beetle *Scolytus scolytus* have been found in elm decline deposits (Girling & Greig, 1985) although the beetles appear lower in the stratigraphy than the decline in elm pollen (Parker et al., 2002). However, the abruptness and synchronicity of the elm decline does point to DED being likely the primary cause.

10.2 | Uses

Elm has been used as firewood since Neolithic times at least, but the small quantities of charcoal remains found, compared to its likely availability, suggests that it was not a favoured species (Out, 2010). Small quantities of *U. glabra* charcoal have also been identified from Bronze Age funeral pyres in Ireland (O'Donnell, 2016). It has also been used extensively for construction across Europe (Nordhagen, 1954; Out & Dörfler, 2015) into northern Iran (Madhoushi, 2016) but poor dimensional stability and durability have limited its use (Ayтин & Korkut, 2016). However, it is very durable when kept wet and so

has been used in boat building and as paddles in canal locks (Mućk, 1986). Wych elm has also been used in Britain to make practice longbows, and bow staves of *U. glabra* have been found in Holmegaard, Denmark dating back 8,000 years (Bergman, 1993). Wych elm splits more easily than other elms (Wilkinson, 1978) but the interlocking grain has made it useful for wheel hubs, chair seats and coffins (Ayтин & Korkut, 2016) and also as a decorative veneer (Mućk, 1986). A recent survey of sawmills in Scotland gave the perceived use of elm timber as 36% for furniture, 22% for wood turning and carving, 17% for wood fuel, and 9% for coffins and various other small uses (Bowditch & MacDonald, 2016).

In the Mediterranean Basin and areas of western Europe, elms including *U. glabra*, but probably more *U. minor* (Caudullo & de Rigo, 2016; Gil et al., 2004), were planted from Roman times up to the mid-20th century, as living supports for grapevines (Heybroek, 2015; Richens, 1983). In Italy, until 70 years ago, there were specific clones of *U. minor* that were used as live supports for grapes (Fregoni, 1991), propagated by grafting. They were easily manually defoliated during the summer to feed cattle with protein-rich fodder (richer than alfalfa) in a season where green fodder was scarce. This also allowed the grapes to get more sun, and young pruned twigs could be used as ties for the grapes. The commonest clones were ‘Sementino’ and ‘Curzol’ and were readily moved around the countryside as farmers started new vineyards using twigs of these clones (Gambi, 1980). This elm-grape co-cultivation was called “Grape married to elm” (Ovid, *Metamorphoses*, XIV, 663–666) and was common in all central–north Italy since Roman and Etruscan times (Aversano et al., 2017; Richens, 1983). The use of clonal elm cultivation was a critical element for the easy and fast DED spread in the 20th Century.

The leaves have been used as fodder for cattle and sheep (Brockmann-Jerosh, 1918; Evelyn, 1664; Forster & Heffner, 1954; Fuentes-Utrilla, López-Rodríguez, & Gil, 2004) and in west Norway, old pollarded *U. glabra* are still used to provide animal fodder (Nordbakken & Austad, 2010). Green samaras have been eaten by humans as green salad (Carter, 2016). Young leaves of Wych elm are also edible and can be eaten raw or cooked, although tough and they have a mucilaginous texture. The fibrous bark has been used for making ropes; “wych” is linked to words meaning bending, binding, weaving (Friedrich, 1970) and with the Anglo Saxon meaning “with pliant branches”; *glabra* probably refers to the bark being smoother than in *U. minor* (Petrokas, 2008).

Ulmus glabra is first mentioned culturally in the *Hypnerotomachia Poliphili* of 1499 (Rhizopoulou, 2016). The botanist Matthioli (1544) commented on the medical benefits of elm bark and use of twigs to close wounds, remove scabies, make hair stronger, make skin beautiful and purge the intestines. Based on the teaching of the Greek botanist Theophrastus (3rd century BC), he recognised two species *Campestris* elm (“Ptelea,” *U. minor*) and Mountain elm (“Oroptelea,” *U. glabra*) and describe them in detail. In the Middle Ages, wych elm was regarded as an unlucky tree associated with fertility, death and melancholy (Milner, 2011). However, Elwes and Henry (1913) quote various superstitions surrounding wych elm. In Herefordshire a

spray of wych elm was a potent safeguard against witchcraft and a powerful wand in the hand of a witch. It was also formerly used as a riding switch to ensure good luck on a journey. Churns made in the Midlands were left with a hole in which a piece of wych elm wood could be inserted to help butter form quickly.

Powdered inner bark of elm has been used as a wheat flour substitute, used to thicken soups and stews, and added to flour to make bread (Anon, 2011). The mucilage in the inner bark has been used for its healing and astringent properties, particularly for ulcers, burns and inflammation (Barsett & Smestad Paulsen, 1985), as a useful remedy for diarrhoea, as a mild diuretic, and as a remedy for rheumatism, used internally as a tisane or externally on the affected area (Anon, 2011). Leaves have also been used as a herbal remedy to treat cardiac disorders and arrhythmias (Delfan et al., 2014). Extracts of "plant material" of *U. glabra* have shown high antimicrobial activity against the tuberculosis bacterium *Mycobacterium tuberculosis* (Tosun, Akyüz Kızılay, Şener, Vural, & Palittapongarnpim, 2004). Galls growing on *U. glabra* leaves has been used in traditional medicine according to the 17th century English herbalist Nicholas Culpeper (Anon, 2011).

11 | CONSERVATION

As a result of population decline due to DED, *Ulmus glabra* has been classified as threatened, near-threatened or rare in Norway (Kålås, Viken, & Bakken, 2006; Myking & Skrøppa, 2001), Sweden (Pihlgren et al., 2010) and Serbia (Glavendekić et al., 2013). Reviews of the management decisions made during and after the pandemic in the 1970s and lessons to be learned are given in Harwood et al. (2011) and Potter, Harwood, Knight, and Tomlinson (2011).

Ulmus glabra is a species with substantial conservation interest beyond the inherent value of any species. It directly supports a wide range of species of lichens, fungi, insects and its decline is having a negative effect on many epiphytes and fungal specialists on elm (Coleman, 2009; Edwards, 2005; Sundberg et al., 2015). *Ulmus glabra* is also a key large, long-lived structural component of woodland habitats across Europe (e.g. Coleman, 2009; Watson, Hawksworth, & Rose, 1988; Weibull & Rydin, 2005). It is a minor component of several forest types, but is more significant in upland, northern and ravine areas, and is protected in the EU-wide Natura system within several woodland types, especially Tilio–Acerion forests of slopes, screes and ravines Special Areas of Conservation (JNCC, 2017), as well as through national conservation designations.

In northern parts of Europe, *U. glabra* can currently grow beyond the reach of DED, because the ranges of the main vectors, *Scolytus* species, are more limited by temperature. Solheim, Eriksen, and Hietala (2011) indicate a northern limit of *Scolytus* in 2011 at about 63° latitude, with approximately a third of the Norwegian coastal range of *U. glabra* thus out of reach of DED. As noted in Section 11.1, it is reasonable to expect the range of *U. glabra* to expand as the climate warms. That same warming will however also allow the *Scolytus* vector to pursue *U. glabra* up through the latitudes, and thus the

disease may well keep pace with the range expansion of *U. glabra*, or even outpace it.

Away from the dynamic and possibly transient temperature-based refuge populations in higher latitudes, the conservation interest of *U. glabra* is dominated by the impacts of DED and the consequences for associated species. The declining status of *U. glabra* in Sweden (Pihlgren et al., 2010) is, for example, leading to a negative effect on many epiphytes and fungi (Sundberg et al., 2015). The vulnerability of *U. glabra* to the pathogen means that naturalistic or low intervention conservation management fails to protect the species or its functions within woodland. Given this, there have been perhaps three types of conservation response:

Acceptance of loss. This is the default action, simply accepting that *U. glabra* disappears as a large tree and exists only as a shrubby form, repeatedly coppiced by further DED attacks. The ability of *U. glabra* to maintain itself through regrowing basal shoots is probably less than other elm species, and can be limited by herbivory on the vulnerable shoots, so the persistence of the species is not guaranteed under this approach, despite some replacement by seedlings, and its functions as a large tree are largely lost. The additional damage caused by a loss of the genetic diversity has been addressed through genetic conservation programmes such as EUFORGEN or the UK's National Tree Seed Project (Royal Botanic Gardens, Kew, 2017).

Refuges. There has been interest over the years in maintaining *U. glabra* where it might be defended by topography and the temperature limitations of the vector. This approach does not have a good record, with seemingly plausible candidates like offshore islands (e.g. Isle of Man) or areas where the disease vector has been temperature-limited (Scottish Highlands, Scandinavia) proving ultimately vulnerable (e.g. Bowditch & MacDonald, 2016). These authors also proposed this approach for the remaining uninfected populations in Scotland such as the Isle of Mull—but with a minimum separation from the mainland of 1,500 m of sea, it is unclear how robust this refuge could be. Elsewhere, keeping *U. glabra* as low hedges is likely to allow its vegetative persistence (Eriksson, 2001) and the maintenance of a number of geographically separated populations will aid the maintenance of genetic diversity. Indeed, in Norway, more than 100 conservation plots have been established for *U. glabra* (Myking & Skrøppa, 2001).

Resistance. Virulent pathogen outbreaks like DED remove the susceptible majority of individuals and may leave behind resistant individuals. The standard approach is to use individuals demonstrating resistance as the basis for tree breeding and hybridisation programmes, which are discussed below (Ingwell & Preisser, 2011; Stoyanov, 2004). An example of a simpler, popular approach with elm has been the "Great British Elm Experiment" (Conservation Foundation, 2017) which simply propagated apparently resistant elms and distributed the trees to schools, community groups, local authorities and private landowners for planting. Given that inoculation trials have shown that genuine DED resistance is extremely rare (Coleman, 2009) this field-resistance based approach seems unlikely to be successful.

Traditionally, conservation has valued the nativeness and naturalness of species and ecosystems extremely highly. For example,

Heller and Hobbs (2014) noted that “Nativeness serves as a proxy for naturalness.” The same authors, however, drive home the point that

Management rhetoric seems paradoxically to ask that managers allow for change so that ecosystems can adapt but also that they not permit change so that systems can remain intact.

This is then a description of the conservation difficulties for *U. glabra*. Given the limitations of approaches to maintain the species, there may be no alternative to losing the characteristics and functions of *U. glabra* (at least as a large, long-lived tree)—except to step outside the exclusivity of nativeness as the limiting criterion for conservation. There are approaches which aim to fill as much as possible of the niche and functions left vacant by the demise of *U. glabra* through the use of species and genotypes that are not native. For example, the British charity Butterfly Conservation has operated a long-running trial on the Isle of Wight, UK, to test the suitability of DED-resistant species and hybrids, driven by the aim of supporting the elm-feeding white-letter hairstreak butterfly, *Satyrrium w-album* (Knoch) (Brookes, 2016). This trial suggests the need for planting a range of non-native elm trees to maintain a “native” ecological function. An analogous approach is the creation of a hybrid chestnut to, in the words of the American Chestnut Foundation, “re-establish the American chestnut’s function in its native range” (American Chestnut Foundation, 2017). Whether conservation managers and foresters are prepared to consider the replacement of *U. glabra* with non-native elms may depend on the level of redundancy for the functions of *U. glabra* that exists with the forests. In Scotland, for example, the key large long-lived tree species in many upland ash woods and protected Tilio–Acerion woods are *U. glabra* and *Fraxinus excelsior*. Given the immediate threats of DED and ash dieback to these tree species (Thomas, 2016), if we exclude alternative non-native approaches, the disruption to the ecosystem is likely to be large. In summary, the future conservation of *U. glabra* seems—paradoxically—likely to be based on its absence, and in some places its replacement with alternative non-native species and hybrids.

11.1 | Climate change

Modelling of *U. glabra* distribution by Sykes and Prentice (1995) showed that the southern boundary will not move north significantly. However, due to vulnerability to stress-induced cavitation, Venturas et al. (2013) suggest that aridification of the Iberian Peninsula may jeopardise long-term survival and cause a retreat from southern extremes. The northern boundary is likely to move north to cover most of Scandinavia, exceeding 70°N, and move east into Siberia (Sykes & Prentice, 1995). Indeed, saplings of *U. glabra*, and other trees of the subalpine forest belt in northern Sweden, have already moved 50–300 km northwards and 500–800 m in elevation, reaching elevations where they grew in the warmest part of the Holocene 9,500–8,000 years ago (Kullman, 2003, 2008). As noted above, climate change will facilitate a range extension of the

beetle vector of DED. Moreover, increased stomatal closure in response to drier and warmer conditions will, according to Sutherland, Pearson, and Brasier (1997), allow more rapid spread of the DED fungus through the xylem once in the tree. However, high summer temperatures may reduce spore formation in the pupal chambers (Faccoli & Battisti, 1997).

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