DOI: 10.1111/1365-2745.14036

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

BIOLOGICAL FLORA*

Biological Flora of Britain and Ireland: *Viscum album*

No. 303

Peter A. Thomas[1] | Monika Dering[2] | Marian J. Giertych[3,4] | Grzegorz Iszkuło[3,4] | Dominik Tomaszewski[3] | Jonathan Briggs[5]

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

[2]Faculty of Forestry and Wood Technology, Poznań University of Life Sciences, Poznań, Poland

[3]Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland

[4]Institute of Biological Sciences, University of Zielona Góra, Zielona Góra, Poland

[5]Stonehouse, Gloucestershire, UK

Correspondence
Peter A. Thomas
Email: p.a.thomas@keele.ac.uk

Abstract

1. This account presents information on all aspects of the biology of *Viscum album* L. (Mistletoe) that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *Biological Flora of Britain and Ireland*: 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. *Viscum album* is a widespread obligate hemiparasite on a wide range of angiosperm and gymnosperm trees. Once thought to take just water and nutrients from its host via a haustorium, it is now suggested to also take carbon. Heavy infestations can reduce host vitality through prolific water use and carbon removal.
3. Flowers are highly reduced but are primarily pollinated by flies, ants and bees. Seeds are dispersed by birds. Removal of the epicarp is necessary for successful seedling establishment, and seeds have a sticky viscin coat, adhering it to the host bark. Vegetative spread also happens under the bark of its host resulting in densities of >700 Mistletoe plants per host.
4. *Viscum album* is a lowland species, most frequent in open human-made habitats extending into woodlands in Europe. It has been widely planted for folklore use centred around Christmas. Despite conservation concerns following removal of Mistletoe-laden old orchards, the species is thriving and needs control in some areas. Viscotoxins and lectins in leaves and shoots have been widely used in herbal medicine and now potentially in complementary cancer therapy.

KEYWORDS

climatic limitation, ecophysiology, geographical and altitudinal distribution, germination, herbivory, plant hemiparasite, reproductive biology

---

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

Mistletoe. Santalaceae (formerly Viscaceae, Loranthaceae). *Viscum album* L. is a woody, evergreen obligate hemiparasite of tree branches, divergently branching to form a spherical loose mass to 2 m diameter. It has an endophytic haustorial system of sinkers for absorbing water and dissolved nutrients from the host xylem and a green photosynthetic exophyte. Stems glabrous, up to 1 m long. Leaves opposite, without stipules, rarely whorled, green-yellowish green, 2–8 × 0.5–2.0 cm oblanceolate to narrowly obovate, rounded at apex, narrowed at base, entire, 3–7 parallel veins, glabrous, coriaceous. Dioecious. Inflorescence inconspicuous, 3–5 flowers in crowded apical cymes, bracts united to the short pedicels. Flowers more or less sessile, actinomorphic, epigynous. Perianth in two whorls; calyx rudimentary 4-toothed in females, absent in males; tepals 4, nearly free. Male flowers scented, with four anthers sessile on tepals occupying most of the inner surface of the tepal, anthers opening with pores; rudimentary ovary sometimes present. Female flowers less fragrant, with two undifferentiated ovules fused to form a placenta, stigma sessile, c. 0.5 mm long; nectaries forming a ring between the tepals and stigma; staminoides sometimes present. Fruits pale green turning white (occasionally yellow) viscid berry, globose or pyriform, 6–10 mm, 1-seeded.

A number of subspecies are recognised, treated as forms, varieties or even species by some (Mejnartowicz, 2006). Subspecies *album* L. (= var. *platyspermum* Kell.) is found in Britain and across the entire range, on dicotyledonous trees and shrubs: leaves variable, berry usually white and globose; edges of the seed entire; embryos 2–3. Other subspecies are recognised in mainland Europe, restricted to evergreen conifers, and only reliably identified by their host plants although some morphological, biochemical and genomic differences have been identified (Nagl & Stein, 1989; Schaller et al., 1998). Subspecies *abietis* (Wiesb.) Abrom. found on *Abies* spp. in central and south Europe (Idžojtić et al., 2008), leaves up to 8 cm, not more than three times as long as broad, berry usually white, pyriform. Subspecies *austriacum* (Wiesb.) Vollm. (= subsp. *laxum* Boiss. & Reut.) found on *Pinus* and more rarely *Larix* and *Picea* species in central and southern Europe and northwards to c. 54°N, leaves 2–4(−6) cm, up to six times as long as wide, berry usually yellow. Subspecies *creticum* N.Böhling, Greuter, Raus, B.Snogerup, Snogerup & Zuber endemic to Crete on *Pinus halepensis* subsp. *brutia*, leaves 1–3 cm up to four times as long as broad, berry white (Böhling et al., 2002; Mellado & Zamora, 2014a; Zuber, 2004).

Viscum album subsp. *album* is native to Britain and most of Europe except the north and east margins.

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Within Britain, *Viscum album* subsp. *album* is native and widespread (Figure 1) but is most abundant in the south-west English midlands and the adjoining southern Welsh borders (Figure 2). Elsewhere across mainland Britain, this species is either scarce or locally common, sometimes locally abundant, in extensive but isolated colonies (Briggs, 2021). As a consequence, *V. album* is found in around a third of 10-km squares in Britain (923 of 2805) and the Channel Islands (4 of 14) (Hill et al., 2004). The abundance in the south-west midlands area has been known and remarked on since the 19th century (Bull, 1864) and confirmed in two national survey projects; in the 1970s (Perring, 1973) and the 1990s (Briggs, 1999, 2021). Suggestions that this distribution is due to the presence of orchards are incorrect. The pattern is related to climate and geography, the species growing well in an area where, coincidentally, apple orchards are also common (Briggs, 2021). Many of the scattered populations outside the main area may originate from deliberate and ongoing naturalised plantings (Briggs, 2021). For example, the northern records from Brora and Pittentrail in East Sutherland are both deliberately planted on *Malus domestica* (Mick Crawley, personal communication). In Ireland, *V. album* is not native but has been widely planted and naturalised (Nelson, 2008) and Hill et al. (2004) note its presence in <1% of hectads (8 of 985).

Outside Britain, *V. album* is widely distributed in Europe, Asia and north Africa, but with a patchy and fragmented range. The distribution is due to a combination of climatic preference, host presence and seed-vector abundance (Krasylenko et al., 2020; Mellado & Zamora, 2014a, 2016). The range (Figure 3) includes western and central Europe, the Apennine peninsula, the Balkans, and Anatolia. In the north, it reaches southern Sweden, and in the east the Black Sea and the mountains south of the Caspian Sea. The overall distribution area extends from 10°W to 80°E and from about 60°N to 35°S (Boratyńska & Boratyński, 1976; Krasylenko et al., 2020; Zuber, 2004). Detailed descriptions of the distribution can be found in Tubeuf et al. (1923) and Zuber (2004). Inevitably, the distribution of *V. album* is limited by the distribution of its host species, but subsp. *album* at least can utilise such a wide range of hosts that its distribution is unlikely to be affected by host range.

Viscum album subsp. *album* is primarily a lowland species. Within the main growing area in Britain the species shows a preference for altitudes below 200 m, with the main population tracing the Wye and Usk valleys, the Cotswold escarpment and high ground in Somerset and the Forest of Dean (Figure 2), but it can occur at higher altitudes. For most of its European range *V. album* is restricted to altitudes below 1000 m but in favourable conditions (Section 2.1) it can be found at much higher altitudes, reaching 450–1550 m in the Swiss Alps (Boratyńska & Boratyński, 1976; Dobbertin et al., 2005; Krasylenko et al., 2020; Tubeuf et al., 1923; Zuber, 2004). Subspecies *austriacum* can occur even higher on warm sites exposed to the sun, reaching 2150 m at the treeline of its host *Pinus sylvestris* in the Sierra de Baza, southern Spain (Zamora & Mellado, 2019).

Beyond the native range there are established colonies of *V. album* in North America including a long-established naturalised and expanding population in Sonoma County, California introduced *c.* 1900 mostly for Christmas decorations and medicinal use (Hawksworth & Scharpf, 1986; Shaw & Lee, 2020). The population is tolerated but monitored for further dispersion, and new infestation points are removed (Shaw & Lee, 2020). A smaller established population on Vancouver Island, British Columbia was recorded in 1989 on

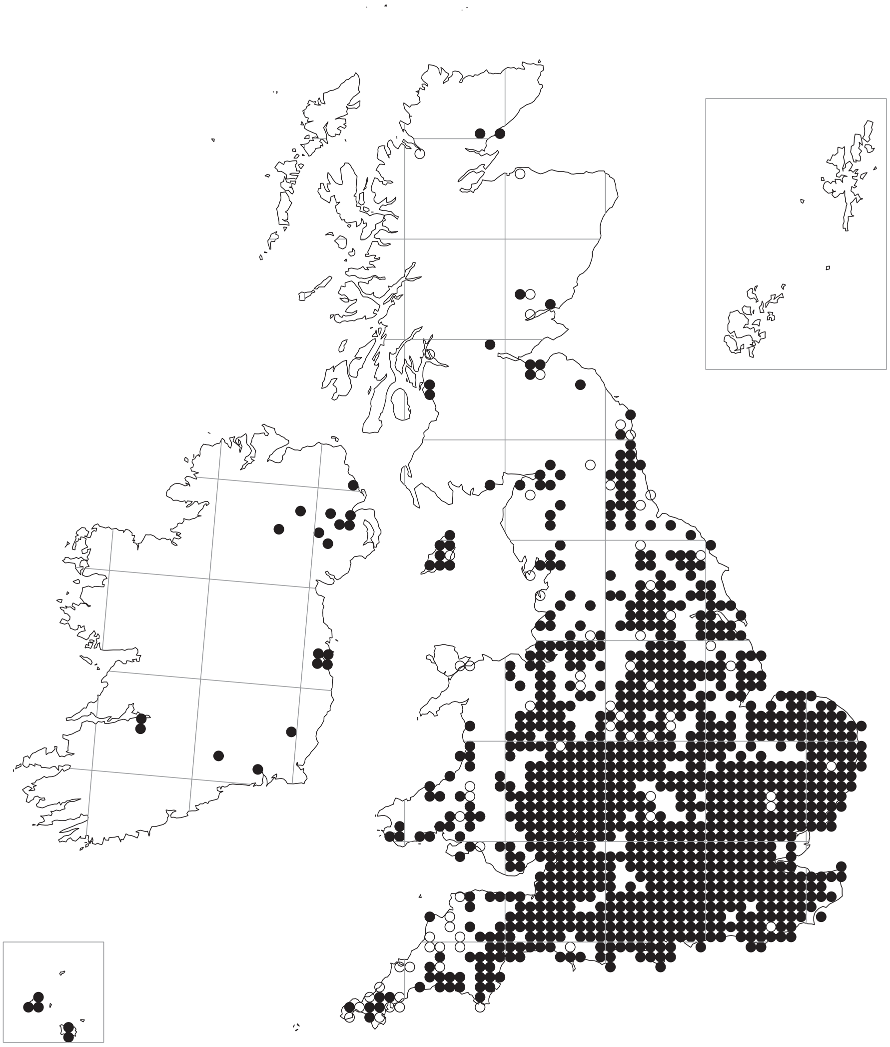

FIGURE 1 The distribution of *Viscum album* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (●) Native 1970–2019; (○) native pre-1970. Mapped by Kevin Walker, mainly from records collected by members of the Botanical Society of Britain and Ireland, using Dr A. Morton's DMAP software.

five apple trees, probably introduced in the 1950's (Dorworth, 1989) but it has been reportedly eradicated (Kope, 2020).

2 | HABITAT

2.1 | Climatic and topographical limitations

Viscum album is adapted to temperate climates, outside the extreme continental regions. In Britain, its current distribution is associated with a mean temperature of 3.8°C in January and 15.9°C in July (Hill et al., 2004). Reportedly, cooler summers can be compensated for by mild winters (Lakatos & Mirtchev, 2014) since mild winters and warm springs are suggested to reduce photoinhibition, and thus promote the expansion of the species (Sangüesa-Barreda et al., 2018). Iversen (1944) recorded that Mistletoe thrived in England with a mean July temperature of 16°C, in Scandinavian countries 17°C, and in the European part of Russia of 18°C on condition that the temperature of the coldest month lies above −5 to −6°C, with a minimum of −8°C. Confirmation of this comes from the largest Mistletoe population in Sweden at Lake Mälaren which has a mean July temperature of more than 17°C with at least 15 days with a maximum temperature above 25°C, and mean January temperature down to −3.4°C (Walldén, 1961). Such a general rule is undoubtedly over-simplistic because of the existence of outlying colonies (Briggs, 2021). For example, in Ireland, where the species was introduced, localities all lie within lower summer temperatures; plants survive but with reduced reproduction and dispersal (Nelson, 2008).

In Britain, the occurrence of subsp. *album* coincides with a comparatively low annual precipitation of 788 mm (Hill et al., 2004). At the southern edge of the range of subsp. *album* in the Pannonian Basin, Hungary, where precipitation is mostly between 570 and 650 mm, summer aridity is a major limiting factor in its distribution, compounded by high summer temperatures and the sum of high daily mean air temperature from March to November (Molnár & Végvári, 2017). It is likely that in dry environments, water availability within the host is an important limiting factor. Perhaps because of this, high relative humidity appears to be important at the edge of its range. A study in urban ecosystems in Kaliningrad on the Baltic Sea showed that the geographical distribution and infestation intensity of Mistletoe was positively affected by a high relative humidity (Skrypnik et al., 2020).

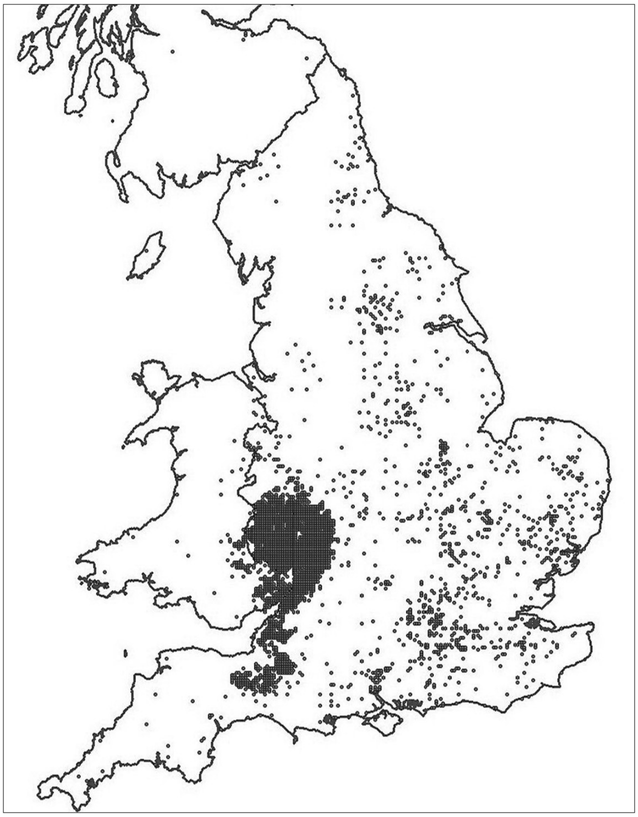

FIGURE 2 The distribution of *Viscum album* in England and Wales, derived from a survey in the 1990s and plotted on 2 km × 2 km squares of the National Grid to highlight details of the main distribution. From Briggs (2021)

As a hemiparasite on tree hosts, there are few topographical limitations. However, Mistletoe is light-demanding (Dobbertin & Rigling, 2006) with an Ellenberg value adjusted for Britain of L7—a plant of well-lit areas (Hill et al., 2004) and, as such, it thrives in full light. The need for light, and the tendency of birds dispersing the seeds to use prominent perches (Section 5.1) results in Mistletoe growing in open places such as the edge of forests, open areas or near roads (Kartoolinejad et al., 2007) and occupies mainly the upper part of the tree crown (Bilgili et al., 2020), and, for subsp. *austriacum*, the tallest trees in the stand (Dobbertin & Rigling, 2006; Pilichowski et al., 2018). Mistletoe also more easily infects young shoots, not only because they have thinner bark, but also because in general they are situated in more sun-exposed, peripheral tree crowns (Mellado & Zamora, 2014a). Moreover, the seed embryos contain chloroplasts and light is required for germination and development of the hypocotyl (Becker, 1986; Section 8.4).

2.2 | Substratum

Viscum album is a hemiparasite of tree branches with water and nutrients taken from the host and so has no direct link to substratum. For this reason, soil properties do not affect the parasite directly as its host plays the role of intermediary between the Mistletoe and the soil. Thus, Ellenberg values modified for Britain are intermediate: soils of average moisture (F5), pH 5–7 (R6) and of intermediate fertility (N5) (Hill et al., 2004). Nonetheless, if the host suffers from

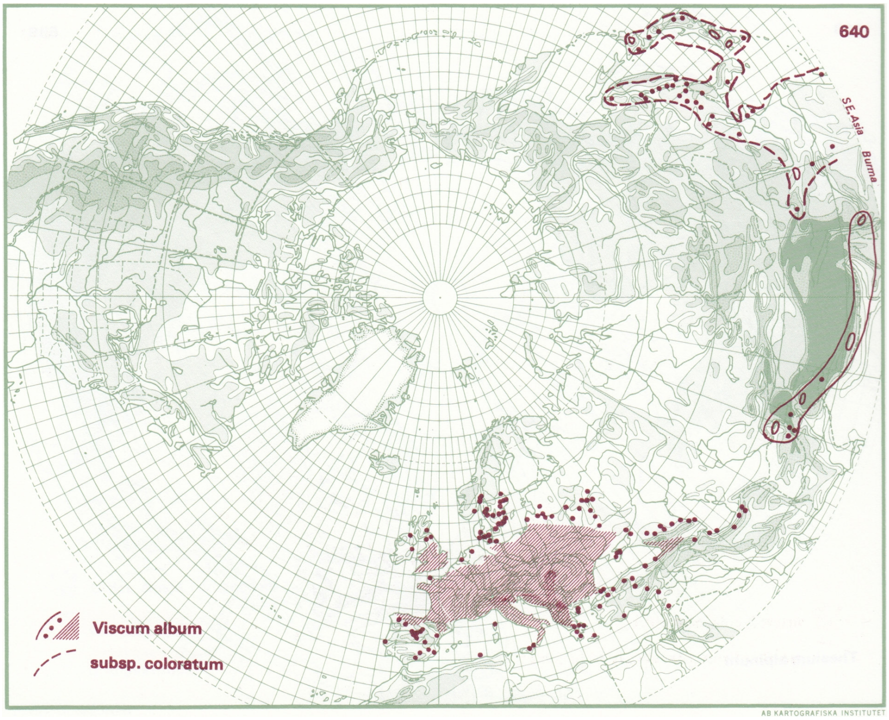

FIGURE 3 The circumpolar distribution of *Viscum album* from Hultén & Fries (1986); ● indicates isolated occurrences; hatched areas indicate regions of common or fairly common occurrence. Broken lines outline the distribution of *V. album* spp. *coloratum*, now treated as a separate species *Viscum coloratum* (Kom) Nakai.

deficiencies, it may influence the Mistletoe too, but to a minor extent (Zuber, 2004).

Although not in contact with the ground, Walldén (1961) noted that subsp. *album* in Sweden, eastern Denmark and Norway, was found only on hosts on limestone soils and calcareous clays, possibly due to Mistletoe needing the better nutrient status of these host trees at the edge of its range. A similar limitation to calcareous soils and an absence on leached sandy and clay soils is noted in the Netherlands, Belgium, Spain and Slovakia (De Graaf, 1980; Fiedler & Vyhnálek, 1977; Galiano et al., 2011; Laurent, 1900) but is not obvious elsewhere. Other subspecies, living on coniferous hosts, are mostly found on more neutral to acidic soils.

3 | COMMUNITIES

Due to its parasitic nature above-ground, *V. album* subsp. *album* is rarely considered in defining community types (it is absent from Rodwell, 1991) and is not restricted to particular communities. Its occurrence is dictated by the presence of suitable host trees across a wide range of communities (Briggs, 2021). As such, it is likely that Mistletoe is not appreciably affected by community structure or by flora below the canopy trees. Other subspecies, dependent upon conifer hosts in mainland Europe, are more restricted to specific conifer-dominated communities (Zuber, 2004).

Viscum album can affect the composition of communities. In Mediterranean pinelands of south-east Spain, light availability, soil fertility (particularly phosphate and potassium) and diversity of soil microbial communities are higher under trees parasitised by *V. album* subsp. *austriacum* with a higher seed rain of fleshy-fruited woody plants from birds attracted to feed on Mistletoe berries (Mellado et al., 2016; Mellado & Zamora, 2016, 2017). These have caused long-term changes to the plant community, including acting as centres for the establishment of woody plants such as *Berberis hispanica* over pine seedlings. The nutrient enriched soil under parasitised trees also increased the cover and diversity of herbaceous plants, which attracted rabbits, *Oryctolagus cuniculus* (L.), to the area as indicated by a five times higher amount of rabbit droppings; $0.40 \pm 0.03\,\mathrm{g/m^2}$ under parasitised trees versus $0.08 \pm 0.07\,\mathrm{g/m^2}$ under nonparasitised trees (Hódar et al., 2018), leading to further changes in community composition.

Viscum album subsp. *album* occurs on a wide range of woody hosts; a review by Barney et al. (1998) identified 452 host taxa, across 92 genera in 44 families, particularly the Rosaceae. The most common hosts in Britain are *Malus domestica* cultivars, *Tilia* × *europaea*, *Crataegus monogyna* and *Populus* × *canadensis*, and to a lesser extent species of *Salix* and *Sorbus*. In Britain it is noteworthy that many of the main hosts are of cultivated origin (Briggs, 2021). Other species are used more rarely across the Mistletoe range including *Acer campestre*, those in the genera *Corylus*, *Juglans*, *Pyrus*, *Betula* and with a longer list of very infrequent hosts (Idžojtić et al., 2006; Nienartowicz et al., 2022; Sell & Murrell, 2009), including species not native to Europe such as *Quercus palustris*, *Q. coccinea*, *Q. rubra* and *Robinia pseudoacacia* (Berthet, 2008; Box, 2000).

In Sweden, Walldén (1961) recorded that 75% of host trees were *Tilia cordata*, and further east in the Czech Republic and Poland, the most common host species were *Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *A. saccharinum*, *Crataegus monogyna*, *Robinia pseudoacacia*, *Tilia cordata*, *T. platyphyllos* and *Populus* × *canadensis* (Baltazár et al., 2013; Bulíř, 2017; Kołodziejek et al., 2013). Further east in Iran, the commonest hosts are listed as *Carpinus betulus*, *Parrotia persica*, *Populus caspica* and *Alnus glutinosa* (Daryaei & Moghadam, 2012; Kartoolinejad et al., 2007). In mainland Europe, *Betula* and *Acer* are more frequently recorded as hosts than in Britain (Briggs, 2021) although *Betula* is a poor host in northern areas such as Sweden (Walldén, 1961). In California, where Mistletoe is naturalised, the main hosts are *Acer saccharinum*, *Malus sylvestris*, *Robinia pseudoacacia*, *Alnus rubra*, *Populus fremontii* Wats., and *Salix lasiandra* Benth. (Hawksworth & Scharpf, 1986).

Genista cinerea in southern France is the only host tree recorded naturally to host two different subspecies of *Viscum*—subsp. *album* and *austriacum* (Grazi & Zemp, 1986). Barney et al. (1998) lists 22 host species for subsp. *austriacum*.

Mistletoe is possibly never found on *Fagus sylvatica* and is rare on *Pyrus communis*, *Prunus domestica*, *Sorbus aria*, species of *Alnus*, *Fraxinus* and *Ulmus* (in northern areas) and, despite urban mythology, European species of *Quercus* (Briggs, 2021; Fiedler & Vyhnálek, 1977; Walldén, 1961; Zuber, 2004). Box (2000, 2019) recorded just 11 Mistletoe-oaks in Britain, concentrated in Herefordshire, a frequency probably unchanged since the 17th century.

In Britain, subsp. *album* is most frequently found in open human-made habitats especially parkland, gardens, orchards, roadsides, cemeteries and churchyards, and less frequently in woodlands (Briggs, 2021). In mainland Europe, this subspecies is found in similar habitats, extending more into woodlands and woodland edges.

4 | RESPONSE TO BIOTIC FACTORS

Since *V. album* is an aerial hemiparasite, it does not compete with other species except for its host and occasionally dense growths of *Hedera helix* (Cadbury & Oswald, 2009). There are no data on competition with other parasitic epiphytes such as *Loranthus europaeus*.

Viscum album subsp. *album* is extremely resistant to stress related to air pollution (Patykowski & Kołodziejek, 2013). The distribution and abundance of Mistletoe in Kaliningrad (Russia) was unaffected by heavy metal contamination of soil or air polluted by nitrogen dioxide (Skrypnik et al., 2020). Other studies have, however, shown a negative impact of pollution on the abundance and distribution of subsp. *abietes* (Hofstetter, 1988).

Since *V. album* most often grows in the host crown, it is rarely browsed. However, low-growing Mistletoe or that on fallen and felled trees are eagerly and rapidly eaten by rabbits *Oryctolagus cuniculus* (L.) and roe deer *Capreolus capreolus* (L.) (Tubeuf et al., 1923).

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

Viscum album is a rare species in many places, sometimes occurring as solitary individuals, particularly when first colonising an area. Being dioecious, solitary plants of Mistletoe are unlikely to produce seeds and invade surrounding hosts. However, in areas where it is more common (Section 1) it is often locally abundant and can fill the crown of a host tree. Up to 30 *Viscum* plants have been recorded on single *Crataegus monogyna* hosts in the Netherlands (De Graaf, 1980) and more than 100 plants on *Acer saccharum* in Cambridge (Cadbury & Oswald, 2009). Subspecies *austriacum* in southeast Spain has been found to range from 6 to 87 plants on *Pinus nigra* individuals of reproductive age (>5 years old) with a mean of 22.83 ± 6.55 (SE), with 2 to 7 (4.92 ± 0.56) large-sized Mistletoes older than 31 years. By contrast, parasitic loads on *Pinus sylvestris* ranged from 6 to 79 reproductive Mistletoes per tree (mean 20.53 ± 4.57), with from 1 to 10 old Mistletoes (mean 4.73 ± 0.70) (Mellado & Zamora, 2019). In the southwestern Alps of France, plantations of *Pinus nigra* subsp. *nigra* have *V. album* subsp. *austriacum* populations of 287 ± 161 (SE) per tree with a maximum of 720 Mistletoe plants, acquired over 10–15 years, with an acquisition rate as high as 110 Mistletoe plants per year (Vallauri et al., 2002). Near Hampton Court, London, UK, a location with an established Mistletoe colony, an avenue of 199 hybrid limes, *Tilia* × *europaea* 'Koningslinde', newly planted in 1994, was rapidly colonised, with infections on 52% of new trees by 2008 (Marris, 2007, 2008).

Variation in density between hosts is partly due to differing susceptibility of individual trees such that some individuals can be heavily laden while others nearby remain unaffected (Briggs, 2021), attributed to differing biochemical composition. Seed delivery can also be highest on trees attractive to birds, particularly isolated individuals and those in clumps, in avenues and on ridges, and also dominant trees (Durand-Gillmann et al., 2014; Lorenc & Véle, 2022; Walldén, 1961). *Loranthus europaeus* in the Czech Republic is commoner on larger diameter trees, those closer together and those with less competition, defined by the basal area of other trees within a 12 m radius (Matula et al., 2015) and a similar pattern may be true in *V. album*. Clumping of individuals on a host is also increased by clonal spread below the bark, helping to spread Mistletoe vegetatively within a host (Section 6.3), and by polyembryonic seeds (Section 8.4) where up to four individuals can form a single composite plant.

Local abundance has been increased by planting the most favourable hosts as crops (such as apples and poplars) and the deliberate planting of Mistletoe in gardens and public areas. The neglect of traditional orchards and other plantations as they have become less economic has also led to increased density (Briggs, 2021; Szmidla et al., 2019; Tsopelas et al., 2004). By contrast, abundance has also been reduced locally by extensive collecting for Christmas decoration and by control of Mistletoe in susceptible orchards (Zuber, 2004).

5.2 | Performance in various habitats

Viscum album occupies a variety of habitats over its geographical range which may result in some variability in plant performance. However, the data are insufficient to allow habitat-specific patterns to be recognised and interactions between Mistletoe and its hosts are more likely to affect performance of both organisms.

It is likely that host species will influence the growth rate of *V. album* but direct published evidence is lacking. However, in the case of another mistletoe, *Phoradendron juniperinum*, growing on *Juniperus osteosperma* (a non-nitrogen-fixing tree) and *Phoradendron californicum* growing on *Acacia greggii* (a nitrogen-fixing tree) the growth rate on *Acacia greggii* was seven times higher compared to *Juniperus osteosperma*. This is most likely due to the nitrogen content in xylem sap being 3.5 times higher in the nitrogen-fixing host than in the non-nitrogen-fixing host (Schulze et al., 1984). Investigation may show a similar pattern in *V. album*.

The effect of *V. album* on its hosts is much better understood. The presence of *V. album* reduces nitrogen content and photosynthesis of host leaves, causes reduced leaf size and tree vitality, shoot die-off distal to the Mistletoe, a reduction of the quality and volume of wood produced, higher mortality, as well as reduced flowering and fruiting, and increased susceptibility to damage from insects and fungi, to a range of angiosperm hosts but especially conifers (Barbu, 2009, 2012; Catal & Carus, 2011; Daryaei & Moghadam, 2012; Hosseini et al., 2007; Ozturk et al., 2019; Raftoyannis et al., 2015; Sangüesa-Barreda et al., 2013; Szmidla et al., 2019; Tubeuf et al., 1923; Yan et al., 2016; Yang et al., 2017). As an example, *V. album* subsp. *album* on *Malus domestica* can result in significant reductions in girth, crown size and fruit crop (Preston, 1977). Trees of *Malus domestica* 'Discovery' infected as saplings showed most impact, 10 years after infection, on smaller M9, M26 and MM111 rootstocks than the larger M25 rootstock. Mistletoe plant size and berry numbers were lower on the M25 rootstock, which may be due to the experimental centrally placed infections being shaded by the more vigorous M25 trees (Preston, 1977).

Large infestations of *V. album* subsp. *austriacum* on *Pinus sylvestris* in mainland Europe have been shown to reduce radial growth by 37%–64% and basal area increment by 29% depending upon infection level (Bilgili et al., 2018; Kollas et al., 2017; Pilichowski et al., 2018). *Pinus nigra* in southwest Spain better tolerates parasitism by subsp. *austraicum*, minimising the impact on reproduction but at the expense of reduced growth. However, *P. sylvestris*, which grows at higher elevations and is only a recent host due to climate change, is showing a greater effect of parasitism, with a strong decline in reproduction with no perceptible loss of growth. Parasitised *Pinus sylvestris* produced fewer cones per tree (28.5 ± 17.48 SE on parasitised trees vs. 317.63 ± 251.64 on nonparasitised trees), smaller cones with fewer seeds (5.86 ± 0.69 vs. 13.18 ± 1.07), smaller seeds (0.07 ± 0.01 g vs. 0.15 ± 0.01 g) with lower germination (70.41 ± 2.90% vs. 90.00 ± 1.90%) and lower seedling emergence (68.31 ± 3.01% vs. 88.33 ± 2.1%) (Mellado & Zamora, 2019). In Valais, Switzerland, infected branches of *P. sylvestris* had shorter needles (21.6 mm vs. 27.0 mm) with a lower dry weight (6.2 g vs. 26.6 g) and branches held fewer generations of needles (2.9 vs. 4.2) significantly altering the crown architecture (Rigling et al., 2010). Moreover, the same subsp./host combination has been shown to make trees more susceptible to a greater reduction in growth following insect defoliation and during droughts, compared to uninfected trees (Camarero et al., 2019). Infestation rates of subsp. *album* have been shown to be higher in pure stands of *P. sylvestris* (45.1% of trees) than in mixed stands with 50% *P. pinaster* (25.4% of trees) (van Halder et al., 2019).

The negative effects of Mistletoe on hosts have been partially attributed to the profligate water loss by Mistletoe (Section 6.5), aided by Mistletoe-induced stomatal closure of the pine and consequent reduced carbon assimilation (Zweifel et al., 2012). Indeed, in Valais, Switzerland, a dry environment with 500 mm annual precipitation, *Pinus sylvestris* with more than *c*. 10%–20% of its total leaf area attributable to Mistletoe is at the threshold of keeping a positive carbon balance (Zweifel et al., 2012).

Viscum album may continue to live on dead host trees for a number of years. In Silwood Park, Berkshire, Mistletoe on *Sorbus sargentiana* lived for three full growing seasons after the host tree died. In Sunninghill Park, Berkshire, a large population of Mistletoe survived at least two full growing seasons on a dead *Populus × canadensis* including the very dry summer of September 2022 (personal communication, Mick Crawley).

5.3 | Effect of frost, drought, and so forth

In winter, leaves of *V. album* subsp. *album* were not damaged by freezing to −20°C, while in summer, −5°C caused permanent damage (Hincha et al., 1997) although no significant damage was observed in flowers and pollen in April at temperatures of −8°C near the northern range limit in Sweden (Walldén, 1961). Winter temperatures below −20°C may kill all Mistletoe leaves and shoots, however they grow back from adventitious buds on the haustoria (Tubeuf et al., 1923; Walldén, 1961). Photosynthetic efficiency of subsp. *austriacum* was noted to decrease after freezing treatment with temperatures lower than −22.3°C when hosted by *Pinus sylvestris* and −17.5°C when hosted by *P. halepensis* (Sangüesa-Barreda et al., 2018). Tikkanen et al. (2021) showed that the seeds of subsp. *album* tolerated lower temperatures at germination than seeds of subsp. *austriacum*, which may explain why the former has a more northern geographic distribution than the latter.

If in the north of its range, the spread of Mistletoe is limited by low temperature, then in the south it is limited by drought. This is especially true of the first developmental stages of Mistletoe. Research on subsp. *austriacum* in Spain has shown that seed mortality increases toward the tree periphery, because of desiccation of the fruits due to lower humidity (Mellado & Zamora, 2014a; Sangüesa-Barreda et al., 2018). In the case of adult individuals, drought tolerance of leaf cells is very high in winter and is substantially lowered in spring and summer (Lösch & Bienert unpubl. in Zuber, 2004). According to Walldén (1961) *V. album* in Sweden resprouts more easily after significant frost damage than after drought damage.

Viscum album is presumed to be intolerant of salt as it is absent from hosts on saline sites (Hill et al., 2004).

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Mistletoe is easy to recognise, with older specimens having a prominent globose silhouette up to 2 m in diameter (Figure 4; Becker, 1986). Being hemiparasites of trees and located among

FIGURE 4 Mature plants, detail and multiple growths of *Viscum album* on hosts; fruiting branches in early winter (left), multiple growths on a riverside poplar, seen in winter (centre), extensive growths on an orchard apple tree in late summer showing dieback of host and Mistletoe (right). Photographs by Jonathan Briggs.

branches sometimes high above-ground level they are often very noticeable. The spherical structure is a result of dichasial branching of internodes of similar length for each cohort of internodes and leaves. Each year one pair of internodes is usually produced from a terminal bud (Zuber, 2004). Importantly, in the first 5 years, the Mistletoe produces only dichasial leaves and long internodes. Later, one long internode with one short shoot accompanied by one pair of scale leaves and one pair of foliage leaves appear each year (Troll, 1937). As a result, normal-size foliage leaves are not decussate to the previous year's leaves, but to the scale leaves instead. Scale leaves may remain for eight or more years (Schönland, 1888). This general plan sometimes is disrupted, and many abnormalities are observed, such as shoots remaining dormant for several years, only one shoot developing, whorls of 3–6 shoots forming, or more than two leaves may be produced in the same whorl (Schönland, 1888). The spherical shape is also a consequence of growth that occurs without phototropism or geotropism in adult plants (Frochot & Sallé, 1980; Tubeuf et al., 1923).

In Mistletoe, the stems and leaves remain green over their lifespan. Leaves usually live for around 2 years (17 months–3 years) (Zuber, 2004) but can live up to 3–4 years, especially on elm and fir hosts, indicating that some traits of Mistletoe may be host-dependent (Ramm et al., 2000). In subsp. *austriacum*, leaves remain the same size once fully expanded in the first season while in subsp. *album* and subsp. *abietis*, leaf growth continues for perhaps 4 years in good growing conditions (Pfiz & Küppers, 2010).

Stems remain alive longer than leaves, and growth rate of internodes increases until 5–7 years of age and then it clearly declines (Montfort & Müller, 1951; Riyekstin'sh, 1980). Since each shoot produces just two new shoots (pseudodichotomous growth), biomass growth of Mistletoe is comparatively constant up to about 10 years of age, after which the rate declines (Durand-Gillmann et al., 2014). At the age of 10, no difference in relative growth rate was found between the three subspecies of *V. album* in a common garden experiment: subsp. *album* 0.61 g/g; subsp. *austriacum* 0.53 g/g; subsp. *abietis* 0.53 g/g per growing season. These values are similar to other broadleaved shrubs and other mistletoe species but higher in comparison with trees in central Europe (Pfiz & Küppers, 2010; Schulze et al., 1984).

The leaf area density (LAD: the total one-sided leaf area per unit volume) is very low compared to other woody species; 2.4 ± 0.5 m^2/m^2 (SE, $n = 15$) in subsp. *austriacum*, 3.6 ± 1.0 m^2/m^2 ($n = 15$) in *abietis* and 5.1 ± 0.6 m^2/m^2 ($n = 9$) in *album* (Pfiz & Küppers, 2010). The only plant communities with a comparable LAD are grasslands (4.5–18.5 m^2/m^2) (Pfiz & Küppers, 2010). Low LAD is most likely due to the Mistletoe leaf blades being tilted close to the vertical with a minimum of self-shading. Indeed, the leaf blades can be completely vertical, especially when the internodes grow close to the horizontal.

The epidermis on stems and leaves lacks cuticular ornamentation and may be covered with wax crystals, most frequently in the form of irregular platelets and rodlets, which can degenerate and disappear. No difference in wax microstructure has been observed between the adaxial and abaxial leaf sides and between male and female plants (Haas et al., 2003; Westerkamp & Demmelmeyer, 1997).

In the majority of plants with secondary growth, a periderm with high suberin content replaces the epidermal tissue being produced by phellogen when the primary growth stops. However, stems of *Viscum*, and the Viscaceae in general, have a cuticular epithelium. This was first described for stems of the European Mistletoe by Damm (1902), defined as a thick tissue produced by epidermal and subepidermal cell layers and is high in cutin. The epithelium plays a similar role as periderm, even if its origin and chemical constituents are different (Wilson & Calvin, 2003).

Another characteristic of *V. album* stems is that stomata in its stems have a transverse orientation (Butterfass, 1987). Such orientation is not widespread in angiosperms and seems to be more frequent in succulent plants. In *Viscum*, however, the epidermis may function for several years without being replaced by cuticular epithelium. In this situation, secondary stem growth results in increasing diameter and epidermal cells are stretched transversally (tangentially). Epidermal cells of young shoots are papilliform and arranged in longitudinal rows (Figure 5), and paracytic (rarely anomocytic) stomata are distributed among them (Becker, 2004; Khan et al., 2009). Stomata on the stems are frequent and, because they are transversally orientated, they may maintain their functionality when they are stretched (Figure 5). All these traits result in prolonged and higher photosynthetic production within the stems.

Viscum album has amphistomatic leaves with stomata distributed on both sides (Figure 6) with a density of between 36 and 121 stomata per mm^2 (Baillon et al., 1988; Escher et al., 2008; Mehrvarz et al., 2012; Tubeuf et al., 1923). This density is lower than in most trees and shrubs (Kelly & Beerling, 1995).

Leaf anatomy is not differentiated into mesophyll, palisade and spongy parenchyma as in most leaves (Khan et al., 2009; Ramm

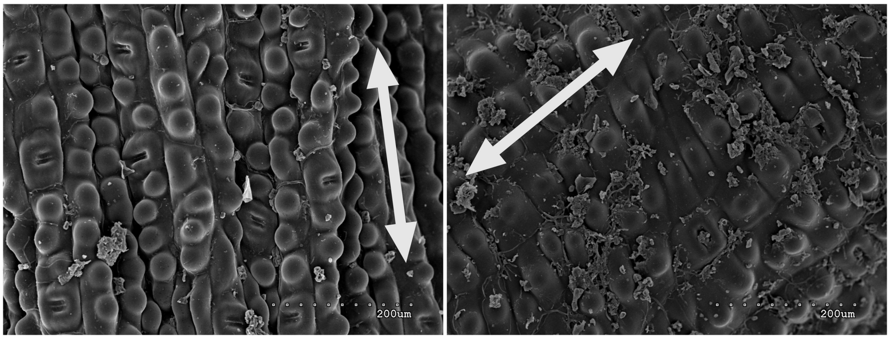

FIGURE 5 Comparison between a young (left) and 3.5-year-old stem (right) of *Viscum album*. Epidermal cells and stomata on shoots are arranged in longitudinal rows (arrows indicate the direction). They are subject to transversal stretching (right).

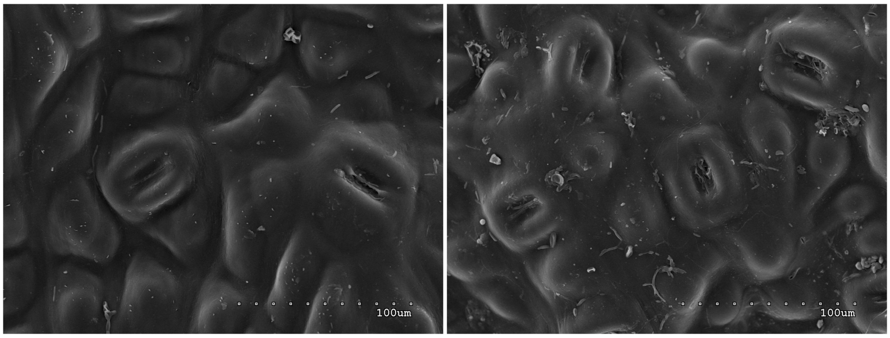

FIGURE 6 Stomata on abaxial (left) and adaxial (right) leaf surfaces of *Viscum album*.

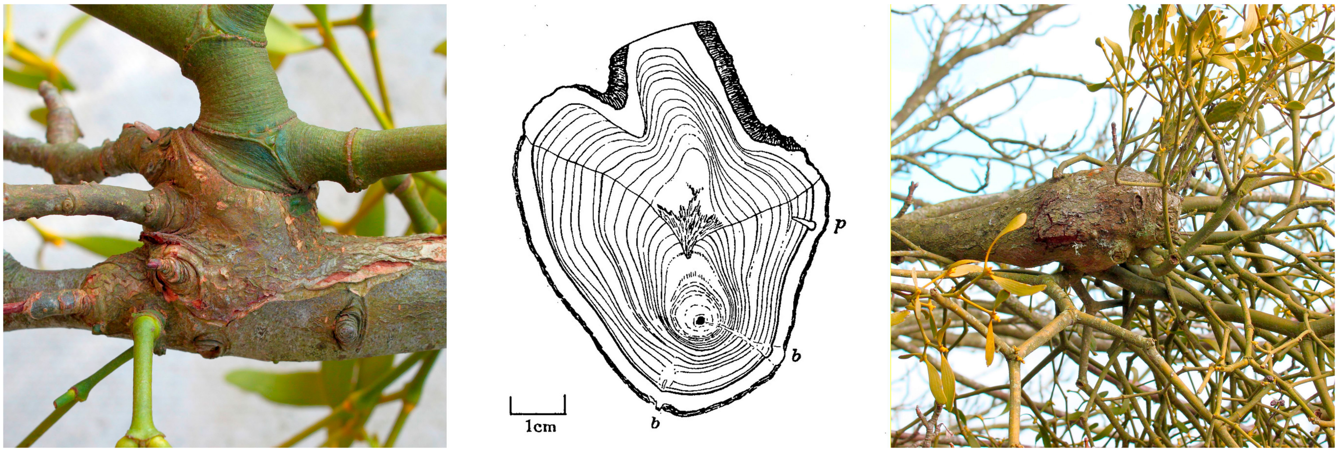

FIGURE 7 Haustoria, the host–parasite interface, of *Viscum album*: Left: A typical example on apple showing one dominant growth with reduced host branch diameter beyond the infection (left). Centre: A section of a haustorium on apple, host tissue (in TS) below, parasite tissue (in LS) above, showing synchronised annual growth rings subsequent to initial infection point (the lowest part of the parasite). p marks a cortical strand with a secondary sinker about 3 years old. b marks dormant host buds. Right: A more complex haustorium, several decades old and possibly with multiple infections. Line drawing from Thoday (1956), photographs by Jonathan Briggs.

et al., 2000). This structure may help the leaf blade maximise photosynthesis regardless of its orientation within the spheroidal shape of the shrub, especially as reorientation would be limited due to leaf thickness and the lack of a petiole. As leaves become larger, the annual increase in crown volume is extraordinarily low, which results in very high leaf area densities not found in any other woody species (Pfiz & Küppers, 2010).

6.1.1 | The haustorium and the host–parasite junction

Viscum album has an endophytic haustorial system of 'sinkers'; wedge-shaped inclusions in the host tissue that provide the plant with water and nutrients from the host's vascular system. During the first year, hypocotyls from germinating seeds penetrate the host cambial cells to establish a primary sinker. These ensure the plant has an early and sufficient water supply (Mylo et al., 2021). Early development of these sinkers is dealt with in Section 8.5.

After each sinker reaches the host cambium, a haustorial meristem is induced, and active penetration stops. The meristem then produces tissue simultaneously with the host cambium over many years. The subsequent wedge-shaped parasitic inclusion within the host wood (Figure 7) is the mature sinker. Such sinkers give the impression that the hemiparasite has actively penetrated deep into the wood whereas the two organisms have simply grown together, retaining and expanding the vascular connection. Sinkers can 'penetrate' the host by more than 5 cm within 4 years. In older plants, the principal or primary sinker is more prominent and larger than others (Thoday, 1951; Zuber, 2004).

The entire endophytic part of the Mistletoe plant expands basipetally rather than acropetally with respect to the host branch. Close to the point of infection there is often visible hypertrophy of the host tissues. Broad ridges along the host branches are associated with flattened cortical strands of the parasite (Section 6.3) elongating under the host branch surface. As they grow longitudinally along the branch, these strands produce secondary sinkers which in turn develop radially within the host. Adventitious buds are often produced on cortical strands above these sinkers, developing into secondary aerial shoots (Büssing, 2000a; Mylo et al., 2021; Sallé, 1979, 1983; Smith & Gledhill, 1983; Thoday, 1951).

Anatomical studies of the Mistletoe-host interface demonstrate a gradual lignification of the Mistletoe parenchyma in this region (Mylo et al., 2021). In the zone of primary contact between Mistletoe and its host, the resulting hypertrophy may thicken the host branch by about 50% (Figure 7). The sex of the parasite has no or little influence on the morphometry of the haustorium (Mylo et al., 2021). It was suggested by Smith and Gledhill (1983) that the increased growth of the host wood acts to strengthen the mechanical anchorage of the Mistletoe. Hypertrophy of the host tissues could provide an increased area of haustorium/host connection, aiding water transfer from the host.

6.2 | Mycorrhiza

Viscum album, being a hemiparasite on host branches and having no roots, does not enter into a direct mycorrhizal relationship. However, a parasitic *Cuscuta* species (Convolvulaceae) in Pennsylvania, USA only successfully parasitised herbaceous hosts that had a mycorrhizal association, and the *Cuscuta* plants grew faster and lived longer (Sanders et al., 1993). It is speculated that *V. album* may also be affected by the host mycorrhizas.

Some other mistletoes seem to conversely affect the mycorrhizal community of the host. An *Arceuthobium* mistletoe (Santalaceae) in a study in Yellowstone National Park reduced ectomycorrhizal fungi diversity of its host *Pinus contorta*, seemingly selecting for fungal species that imposed a lower carbon demand on the host (Cullings et al., 2005). Another mistletoe, *Phoradendron juniperinum* Engelm. (Santalaceae) reduced levels of mycorrhizal abundance by up to 38% in heavily infested host plants of *Juniperus monosperma* Engelm. in Arizona (Gehring & Whitham, 1992). Whether *V. album* has a similar interaction with the mycorrhizal associations of its hosts is, however, largely unknown and worthy of further research.

6.3 | Perennation: Reproduction

Chamaephyte (Hill et al., 2004). *Viscum album* is a dioecious species that spreads between hosts exclusively by seed. *V. album* starts flowering 3–7 years after germination (Kahle-Zuber, 2008; Walldén, 1961).

Within a host, Mistletoe can resprout with adventitious shoots following cutting or harvest (Kahle-Zuber, 2008; Walldén, 1961). This growth can be very vigorous—it was possible to collect *c.* 100 kg of Mistletoe in the next few successive seasons of harvesting from the same host tree (Walldén, 1961). Resprouting also follows damage by fire or frost. This response was noted particularly in the Cretan endemic *V. album* subsp. *creticum* that invades *Pinus halepensis* subsp. *brutia*. Böhling et al. (2002) recorded that a fire that does not kill the host removes the external part of the parasite which can resprout from surviving tissues within the host tree.

Viscum album can spread vegetatively through a host tree. Cortical strands containing vascular tissue grow from the haustorium following the host vascular cambium and phloem (Thoday, 1951). These strands can photosynthesise and have been measured as reaching 4–6 cm, growing at 0.75 cm per year (Wangerin, 1937, quoted in Zuber, 2004) before producing secondary haustoria and adventitious shoots (Sallé, 1983).

The minimum age of a plant may be estimated based on the number of internodes (Pfiz & Küppers, 2010), though some parts may be missing. Age can also be estimated by uncovering the tip of the primary sinker and referring the infection point to the particular growth ring of the host tree (Noetzli et al., 2003). The difference between this anatomical and field method of age estimation might be up to 3 years (Bilgili et al., 2013). The field method can overestimate the age of the old plants and underestimate the youngest (Noetzli et al., 2003). The field method is also limited in observing only the extant plant, without considering resprouting or vegetative spread, resulting in underestimation if the original growth has been damaged or cut.

Mistletoe may live for up to 30–40 years (Nierhaus-Wunderwalt & Lawrenz, 1997; Stypiński, 1997) in both their natural and planted range; a reported age of 37 years on apple trees was given in its exotic range in Victoria, British Columbia, Canada (Kope, 2020). However, results of direct investigations give lower estimations. Accordingly, the oldest *V. album* subsp. *creticum* was estimated to be 22 years old (Böhling et al., 2002), while maximum age of subsp. *austriacum* in Turkey was 24 years old (Bilgili et al., 2020), and the age of the oldest individual of subsp. *abietis* confirmed in a study conducted in the Rhine valley in Switzerland was 24.

6.4 | Chromosomes

$2n = 20$ (Barlow et al., 1978). Species of *Viscum* have notably large chromosomes (Wiens & Barlow, 1975), and DNA content for *V. album* is 2C = *c.* 160 pg (Schröder et al., 2022), although values between 107.0 and 205.8 pg have been reported (Nagl & Stein, 1989; Zonneveld, 2010). The genome of *V. album* is one of the largest among flowering plant species so far tested, estimated to be 88.55 Gbp (1C) with *c.* 55% of its size made up of repetitive components, and only 0.03% as genes (Novák et al., 2020). The guanine–cytosine content is similar to other flowering plants at 39% (Novák et al., 2020). Recent investigation of gene content in *V. album* yielded *c.* 39,000 open reading frames giving *c.* 32,000 proteins (Schröder et al., 2022). Proteomic fingerprinting of *V. album* is in its early stages (Vergara-Barberán et al., 2017) but is likely to prove useful in investigating its pharmaceutical uses (Section 10.5).

In the majority of *Viscum* species, a ring formation appears at meiosis involving 4–12 chromosomes (e.g. African *Viscum obscurum*, Wiens & Barlow, 1979), and the remaining chromosomes form regular bivalents. Male plants of *V. album* have been shown to have six bivalents and a ring of eight chromosomes dominates (Barlow, 1981).

Triploid individuals of *V. coloratum* have been found in Japan at a frequency of 1.73% (Barlow, 1981) and tetraploids have been reported for the African *Viscum capens* subsp. *hoolei* (Wiens & Barlow, 1979) but neither have been reported in *V. album*. In dioecious *Viscum* species, including *V. album*, a high level of sex-associated and floating chromosome translocations (i.e. not sex-specific) complexes occur (Barlow, 1981; Mechelke, 1976; Wiens & Barlow, 1979) due to reciprocal translocations of chromosome fragments. In plants, the permanent translocation heterozygosity was archived via linking translocation with sex determination systems and it is known for >50 species, including *V. album* (Holsinger & Ellstrand, 1984). In *Viscum* species, the permanent sex-specific translocation heterozygosity is noted among male individuals. The set of translocated chromosomes segregates together and thus behaves as a large Y-chromosome. In both sexes floating translocations occur and translocation homozygotes and heterozygotes are noted.

It is assumed that fixed translocation heterozygosity plays a fundamental role in the evolution and stabilising of dioecy in *Viscum* because it enabled two nonallelic sex determinants present on different chromosome to be in a genetic linkage (Holsinger & Ellstrand, 1984). It also has selective value as it enables the accumulation and maintenance of adaptive gene complexes (Wiens & Barlow, 1975). This heterozygosity seems to be important for *Viscum* species that, although being dioecious, are at some risk of biparental inbreeding leading to loss of genetic variability (Barlow, 1981; Stanton et al., 2009). Barlow (1981) argued that because most dioecious species of *Viscum* tend to form small populations which limits the mating opportunity, and have small, insect-pollinated flowers that further reduces cross-pollination due to reduced insect foraging, the sex-associated translocations (and also floating translocations) may offer the same selective advantage as in monoecious congeners.

Supernumerary chromosomes (B-chromosomes) can be found in *V. album* and other *Viscum* species in both males and female plants but at different frequencies (Barlow, 1981; Barlow et al., 1978). Three different B chromosomes were detected in individuals from populations of *V. album* from Europe and Japan but the final polymorphism is yet not known (Barlow et al., 1978). The existence of these optional genomic components was initially interpreted as boosting the diversity, while current hypotheses are related with the possible harmful consequences and antagonistic relationship with A-chromosomes (Jones & Houben, 2003).

6.5 | Physiological data

Chloroplasts in Mistletoe are elongated, 7–8 μm long, and show C_3 features (Tuquet & Sallé, 1996). The thylakoid system has numerous grains consisting of 3–20 thylakoids and steep lamellae (Hudak & Lux, 1986). The chlorophyll content of Mistletoe leaves is host dependent (Üstüner, 2019; Üstüner & Düzenli, 2017; Vicaş et al., 2010), with a mean of 7.1 mg/g of chlorophyll *a* and 1.9 mg/g of chlorophyll *b*. These values are within the ranges reported for other angiosperms. Age-related variability was also observed, with older leaves showing a higher content of chlorophyll *a*, and younger ones with more chlorophyll *b* (Lee et al., 2016).

In adult *V. album*, the photosynthetic area of stems (47%) is almost the same as that of the leaves (53%) The combination of evergreen leaves and perennial evergreen stems allow the plant to photosynthesise throughout the year (Míguez et al., 2015). *V. album* is photosynthetically active at temperatures below freezing point (Schröder et al., 2022). The impact of stems on the overall photosynthetic production is much bigger than in other woody plants (Míguez et al., 2015).

The mitochondrial genome of *Viscum* species has been subject to reductive evolution, a common feature among parasitic plants (Maclean et al., 2018; Schröder et al., 2022). The mitogenome is exceptionally variable in size (Skippington et al., 2015, 2017) with a limited but highly variable number of respiratory genes compared to other plants (Petersen, Cuenca, Møller, et al., 2015; Senkler et al., 2018). Out of nine common genes of this respiratory complex, two are missing and the remaining are pseudogenes in *V. album* (Zervas et al., 2019). Consequently, a lack of complex I genes has forced a rearrangement of the respiratory chain in this species (Busch, 2018; Petersen et al., 2022; Senkler et al., 2018). Only two transcripts encoding subunits of complex I were detected in recent studies of the gene space in *V. album* (Schröder et al., 2022). Both subunits play a secondary function in the mitochondrial proteome of *V. album*—one is engaged in fatty acid biosynthesis and the second in photorespiration. In comparison to some *Viscum* species that are missing *ccmB* and *matR* genes, *V. album* probably accrued them via horizontal gene transfer from two different hosts (Skippington et al., 2017).

Similar to the mitogenome, the plastome (chloroplast genome) of *Viscum* has also been subject to a reduction in size, structural rearrangement and gene loss (Guo et al., 2020). These changes are especially clear in photosynthetic genes, which are under relaxed selection that mirrors the shift to parasitism (Petersen, Cuenca, & Seberg, 2015). The plastome of *V. album* is intermediate in size (128,921 bp) compared to other *Viscum* species (Petersen, Cuenca, & Seberg, 2015). *V. album* has lost several genes from its plastome (e.g. *rpl33*, *ndh* genes and *infA*) and others have been pseudogenized e.g. *matK* and some *ndh* genes (Petersen, Cuenca, & Seberg, 2015).

The rate of photosynthesis in Mistletoe is lower than that of the host's assimilation organs (Pfiz & Küppers, 2010), although this rate is dependent on the season and age of the Mistletoe leaves (Míguez et al., 2015). The net CO_2 assimilation rate is relatively low and ranges from 1.8 to 10.2 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$ (Li et al., 2003; Míguez et al., 2015) with an overall mean of 4.5 ± 3.5 (assumed to be SD) $\mu mol\,CO_2\,m^{-2}\,s^{-1}$ (Escher et al., 2008). Photosynthesis rates per unit area are similar between leaves and stems (Míguez et al., 2015).

The monosaccharide content of Mistletoe leaves is dependent on host species (Arda et al., 2003; Krzaczek, 1976), simple sugars (glucose, fructose, sucrose, raffinose) ranging from 0.02% to 0.235% dry weight and for starch 4.5% to 20%. There is less variation in the content of the polysaccharides galactose, arabinose, xylose and rhamnose (Krzaczek, 1976). The level of carbohydrates (glucose, fructose, sucrose and sum hexose unit) in xylem sap of Mistletoe depends greatly on the season when growing on *Populus* × *euramericana* (highest in spring), but not on *Abies alba*, where the sugar content is lower (Escher, Eiblmeier, Hetzger, & Rennenberg, 2004a). However, according to Krzaczek (1976) the amount of simple sugars and starch depends upon the Mistletoe subspecies, the host plant species, and the organ used for analysis. In most cases, *V. album* subsp. *album* stems contain slightly more sugar than the leaves, while the opposite is true in subsp. *abietis* and subsp. *austriacum*.

Viscum album has traditionally been described as a hemiparasite that takes just water and nutrients from its host while providing its own fixed carbon through photosynthesis. However, there is a growing body of evidence showing that Mistletoe extracts at least some carbon from its host. Despite a low net photosynthesis rate in Mistletoe compared to their host, Mistletoe has very high relative growth rates (Section 5.2) (Pfiz & Küppers, 2010), undoubtedly due to carbon intake from the host (Richter & Popp, 1992). Based on experiments using C^{13}-labelled carbon dioxide, Wang et al. (2022) suggest complete carbon autonomy of Mistletoe. However, this assimilation was measured over a relatively short term and on only one host species, and acropetal carbon transport from more distant parts of the plants cannot be ruled out. However, Escher and Rennenberg (2006) found C^{13}-labelled glutamine in subsp. *abietis* tissues, derived from host xylem sap. Richter and Popp (1992) calculated that 22.6%–43% of the carbon may come from the host, but this carbon probably does not come from the direct products of the host's photosynthesis because the Mistletoe haustorium does not penetrate the host's phloem tissue (Khan et al., 2009; Ramm et al., 2000).

Viscum album can apparently utilise inorganic nitrogen as judged by the presence of nitrate reductase (Escher, Eiblmeier, & Rennenberg, 2004). However, many trees contain low levels of nitrate in their xylem sap, and organic nitrogen appears to be the major source of nitrogen (Escher, Eiblmeier, & Rennenberg, 2004). Influx rates into *V. album* from either *Populus × euramericana* or *Abies alba* has been measured at 0.24–0.55 μmol Nh^{-1} g^{-1} fw for organic glutamine and 0.0001–6.8 μmol Nh^{-1} g^{-1} for nitrate. There was, however, a clear preferential influx of glutamine over nitrate at the concentrations found in the xylem sap of the hosts (Escher, Eiblmeier, & Rennenberg, 2004; Urech, 1997). Indeed, xylem sap in *V. album* contains high levels of low molecular weight amino acids, particularly asparagine and glutamine, reaching highest levels in spring at 1873 ± 2225 (SD) and 2519 ± 5458 nmol N ml^{-1}, respectively, in Mistletoe on *Abies alba* (Escher, Eiblmeier, Hetzger, & Rennenberg, 2004b). Levels in Mistletoe on *Populus × euramericana* were lower for asparagine (794 ± 391 nmol N ml^{-1}) and higher for glutamine (3354 ± 5326 nmol N ml^{-1}) in spring. The authors concluded that asparagine, at higher levels than that in either host, is converted from glutamine, which is lower than in either host. This mechanism contributes not just nitrogen but the liberated carbon contributes to the carbon gain of the Mistletoe. *V. album* also accumulates reduced sulphur compounds at a higher concentration than its hosts (Escher et al., 2003).

Nitrogen content of leaves and the activity of the enzyme phosphoenolpyruvate carboxylase are dependent on the host species and the season of the year (Kim et al., 2019; Li et al., 2001). Nitrogen content in leaves of *V. album* subsp. *album* can be about 3% dry weight and, when the host is the nitrogen-binding *Robinia pseudoacacia*, it reaches up to 5% (Türe et al., 2010). During senescence of Mistletoe leaves in late summer (Section 7) only viscotoxin is selectively degraded and the sulphur and nitrogen reabsorbed into the stems. Other leaf proteins are lost when the leaf abscises (Schrader-Fischer & Apel, 1993).

Mistletoes of many different species generally consume more water per unit of carbon dioxide assimilated than their hosts (Scalon & Wright, 2015). The δC^{13} index decreases with increase of the mean annual temperature in Mistletoe, and it is at a relatively constant level in the host trees (Scalon & Wright, 2015). Transpiration rates have been measured at 2.5 ± 1.2 mmol H_2O m^{-2} h^{-1} in excised twigs, with a water use efficiency ratio of c. 0.006 (Escher et al., 2008), showing that Mistletoe is profligate in water use. Mistletoe maintains a high level of transpiration, even when the host is under severe drought stress, because the Mistletoe stomata, although low in density (Section 6.1), remain open. High transpiration rates are attributed to very low levels of ABA in *V. album* during the growing season combined with a low sensitivity to ABA (Escher et al., 2008; Ihl et al., 1987). High transpiration rates continue in deciduous hosts even after leaf shed due to the evergreen Mistletoe stems, until halted by frost (Ziegler et al., 2009). Water stress can be further increased by direct interception and evaporation or precipitation from Mistletoe plants, reducing annual rainfall beneath the host canopy by 2%–11% in central Poland (Klamerus-Iwan & Van Stan II, 2022).

The widely cited 'nitrogen-parasitism hypothesis' suggests that nitrogen is the most limiting resource for Mistletoes and that their high transpiration rate is used to acquire sufficient N from the host xylem (Schulze et al., 1984). However, data by Scalon and Wright (2015) showed that the difference in nitrogen content in Mistletoe and host leaves explains only 3% of the variation in the difference in δC^{13}. This finding suggests that nitrogen is not the limiting nutrient for Mistletoe, or at least is not the main component driving high transpiration rates.

Mistletoe can take up elements selectively from hosts, resulting in concentration differences between host and parasite tissues (Bell & Adams, 2011; Kim et al., 2019). Mistletoe usually contains more K, Mg, Ca, Fe, P, Mn, Cu, S, Zn, B, Ba and less Al, As, Ca, Mg, Cd, Cr, Cu, Mo, Ni, Sr, Pb, Ti and Fe than its hosts (Gebauer et al., 2018; Kamar et al., 2018; Lamont, 1983; Lamont & Southall, 1982; Mutlu et al., 2016; Popp et al., 1995; Türe et al., 2010). This is linked to reduced dry matter content, needle length or chlorophyll content of pine needles (Section 5.2).

6.6 | Biochemical data

Viscum album has a rich content of phenolic acids, phenylpropanoids, flavonoids, triterpenes and phytosterols (Dai et al., 2019; Fukunaga et al., 1989; Haas et al., 2003; Jäger et al., 2021; Schröder et al., 2022; Wollenweber et al., 2000), which can vary in concentration through the year (Wójciak-Kosior et al., 2017). The total content of polyphenol compounds for *V. album* (assumed subsp. *album*) was measured at 31.28 mg/g, the total content of flavonoids 25.10 mg/g, and the total content of phenolic acids 4.07 mg/g, all lower than found in other plants tested, *Cichorium intybus* and *Lamium purpureum* (Vergun et al., 2019). There is some evidence of biochemical differences between subspecies of *V. album*. For example, Orhan and Orhan (2006) using samples of leaves and stems combined, identified differences in fatty acids, with arachidic acid found only in subsp. *austriacum* and subsp. *abietis*, while unsaturated fatty acids, mainly oleic and linoleic acids were found in subsp. *album*. The extent of other biochemical differences are unknown.

The carbohydrate metabolism of Mistletoe is closely related to the metabolism of host tissues (Section 6.5). A number of polysaccharides have also been detected in Mistletoe leaves and berries, with esterified galacturonan being the dominant component in the leaves and arabinogalactan in the berries (Jordan & Wagner, 1986). The sticky viscin of Mistletoe seeds (Section 8.3) contains a complex of neutral and acid polysaccharides, in which hemicellulose and cellulose microfibrils play a dominant role (Azuma et al., 2000; Horbelt et al., 2022).

Three groups of lectins are found in *V. album* leaves, all of them are highly toxic (Majeed et al., 2021). The most characteristic are viscotoxins, low-molecular-mass antimicrobial peptides belonging to the thionine class, found in the leaves and shoots of Mistletoe (Azuma et al., 2000; Butu et al., 2013). The most toxic is viscumin, which inhibits protein synthesis in cell-free systems and can lead to cell death (Olsnes et al., 1982). Viscotoxin content shows great seasonal variability, declining most rapidly in leaves prior to abscission (Schrader-Fischer & Apel, 1993; Urech et al., 2006) and with differences between subspecies (Schaller et al., 1998). However, *V. album* contains several biologically active compounds such as lectins, viscotoxins, different peptides such as viscumamide, different amino acids, thiols, alkaloids, minerals, phytosterols, triterpene acids, amines, oligo and polysaccharides (Elluru et al., 2008; Ochocka & Piotrowski, 2002; Vicaş et al., 2011). There is a full review of these compounds by Pfüller (2000).

The saturated and unsaturated fatty acid content of leaves also varies depending on the subspecies and host species (Krzaczek, 1977). Subspecies *austriacum* living on pine has the highest proportion of polyunsaturated fatty acids, reaching 55.08% of total fat, most likely due to an extended period of assimilation of its host pines (Hansen et al., 1996). Based on the main components of the fat fraction, two groups were distinguished: subsp. *austriacum* with dominant oleic acid (over 40%) and subsps. *album* and *abietis*, where the dominant fraction is palmitic acid (29%–40%) (Krzaczek, 1977). Both the leaves, shoots and berries of Mistletoe also contain over 250 other primary and secondary metabolism compounds used in medicine (Song et al., 2021), discussed in Section 10.5.

The accumulation of heavy metals (Section 6.5) is influenced by the degree of environmental pollution. In an area polluted by a zinc smelter, Mistletoe accumulated less Cd, Ni, Pb and Zn than its host *Sorbus aucuparia* (Kolon et al., 2013). Mistletoe leaves sampled in mining areas of northern Germany showed higher concentrations of heavy metals (Cd 12, Cu 13, Ni 5, Pb 0.9, Zn 675 mg/kg) on low contamination sites compared to highly contaminated sites (Cd <0.1, Cu 10, Ni 0.4, Pb 1.1, Zn 123 mg/kg). This was suggested to indicate a threshold levels of contamination for the effective exclusion of heavy metals (Sharma et al., 2009).

Little is known about the selectivity of uptake of radioactive elements by Mistletoe. Indirect evidence comes from Chereji et al. (1996) comparing caesium ^{134}Cs and ^{137}Cs content in the tissues of several dozen medicinal plants (including *V. album*) in Romania *c*. 1000 km from Chernobyl in the 10 years after the nuclear power plant explosion. The content of both isotopes in Mistletoe was one of the lowest among the studied plants and in 1987 was collectively 167 Bq kg^{-1} while in potential host species it was many times higher. Similarly, the content of both these radioactive caesium isotopes in Mistletoe at the beginning of the 21st century in Slovakia, showed very low values of <0.9 and <1.95 Bq kg^{-1}, for ^{134}Cs and ^{137}Cs, respectively (Salamon et al., 2015).

7 | PHENOLOGY

Adult individuals of *V. album* flower and fruit each year (Ramm, 2006; Sell & Murrell, 2009; Tubeuf et al., 1923) with the flowering period being independent of the host species' phenology (Walldén, 1961). Flower buds develop from early summer to late September. Rising spring temperatures trigger bud opening usually in February to April but in warm conditions it can begin as early as January or even the end of December (Krasylenko et al., 2020; Ramm et al., 2000, 2016; Sell & Murrell, 2009; Stopp, 1961). In the south-west English midlands flowering generally begins in February, extending into March while it is generally later in mainland Europe. Observations in southern Sweden in 1949–1961 show that the flowering period took place from mid-March to the end of April (Walldén, 1961). However, climate change and fluctuating spring temperatures have an important modifying effect. The flowering period in Germany in 1891 was recorded between 16 March and 20 April but is now generally even later (Tubeuf et al., 1923). Similarly, in Ukraine flowering is usually in March–April, but in the Crimean Mountains in 2019 (an unusually warm winter) flowering was observed in early December 2019 (Krasylenko et al., 2020). Female flowers open earlier than the male flowers (Tubeuf et al., 1923).

Fruits develop slowly through the summer, ripening in November to December in Britain (Sell & Murrell, 2009) and western Europe. Some fruits remain attached until spring (Wangerin, 1937). Fruit dispersal by birds (Section 8.3) starts in late November and lasts through April or May, partly depending upon the timing of arrival of migrant birds, and tending to be latest in northern populations (Krasylenko et al., 2020; Stopp, 1961).

A cytological study in France shows that the cortical strands (Section 6.3) produce new sinkers from March to August, with a maximum during the first half of summer (Sallé, 1978). Activity of the intercalary meristem at the base of sinkers is from March to September with a maximum from April to June (Sallé, 1979). Dormancy of the meristematic tissue was observed from October to February (Sallé, 1979). Vegetative growth occurs primarily in the first half of the growing season with an increase in plant mass between February and June/July, and fruit growth in the second half (Urech & Baumgartner, 2019).

New shoots and leaves grow in May and June, and are kept through the winter. The oldest leaves are shed in late summer (often September) while green and turgid with little reabsorption of the chlorophyll (Schröder et al., 2022). Leaves and stems have been observed to become yellow in late winter. Male individuals seem to be especially affected by this colour alteration (Tubeuf et al., 1923). This colour change may be due to the changes in chlorophyll content although there are no important changes in chloroplast ultrastructure between winter and summer leaves (Hudak & Lux, 1986). Colour may also be connected with changes in nitrogen concentrations resulting from its allocation to reproductive organs during intensive flower production. During spring and summer, plants recover their predominantly green colouration. Seeds germinate between February and April but can be as late as May in northern regions (Zuber, 2004).

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Within *Viscum* species dioecy appears to be ancestral, despite monoecy currently dominating the genus, and having evolved independently eight times (Maul et al., 2019). Currently, dioecy is common among species from Africa and Madagascar, the hypothetical centre of the origin (Maul et al., 2019; Wiens & Barlow, 1979).

The female and male flowers are highly reduced (Figure 8), a trait often associated with anemophily. However, Mistletoe pollen is too heavy and sticky to be easily transported by the wind, thus anemophily has only marginal significance for Mistletoe and may occur when male and female plants are in close proximity (Hatton, 1965; Heinricher, 1919; Walldén, 1961). Therefore, the pollination of the dioecious flowers is almost obligatory by a range of insects (Table 1) that are attracted by a fruit-like smell and rewarded by nectar (Becker, 2004). Most effective are various winter-active insect species, mainly flies (Muscidae, Drosophilidae, Calliphoridae, Heleomyzidae, Milichiidae, Sepsidae, Syrphidae)—which can move pollen up to 2 km—and ants (Formicidae) (Becker, 1986; Hatton, 1965; Ramm et al., 2000, 2016; Sell & Murrell, 2009; Walldén, 1961). Honey bees (*Apis mellifera* L., Hymenoptera, Apidae) and the bumblebees *Bombus terrestris* (L.) and *B. lapidaries* (L.) are potentially effective pollinators although they have only been seen on male flowers—this however may be misleading. Observations and discussions made by Walldén (1961) support the argument that both female and male flowers produce nectar and scent which attract bee pollinators. The scent of male and female flowers is perceived as identical (comparable to apple juice, ripe apples or orange blossom), but the difference lies in their intensity. The male flowers produce more volatile sweet-scented substances and relatively small amounts of nectar, while the female flowers produce more nectar but are considered less aromatic. In lower temperatures, because of weaker aroma, female flowers may appear less attractive for insects which results in fewer visits. It therefore seems the insects are attracted mainly by the scent from the nectaries of male flowers, and by the nectar secreted around the stigmata of female flowers (Ramm et al., 2000). Pollinators were observed to visit Mistletoe only sporadically when temperature was below 10°C (Hatton, 1965).

In mainland Europe, a low ratio of male flowers to female has been reported (Noryśkiewicz & Noryśkiewicz, 2017). Of a total of 1958 Mistletoes examined in Sweden, 28.4% were male and 71.6% female (Walldén, 1961). Sex ratios observed in Britain are, however, rather more equal than this (Briggs, 2021).

8.2 | Hybrids

Natural hybridization is possible between subspecies, yet the reliable recognition of the hybrids is possible only by using molecular markers (Piotrowski et al., 2003). It is currently impossible to estimate the frequency of natural hybridization, or the leading direction of the gene transfer. It seems that hybridization occurs more often

FIGURE 8 Flowers and berries of *Viscum album*: Female flowers (left), male flowers (centre), mature berries (right). Photographs by Jonathan Briggs.

TABLE 1 Pollinators recorded from *Viscum album* in Great Britain and continental Europe

Species classification	Recorded in GB	Source
DIPTERA		
Anthomyiidae		
Lasiomma sp.	Yes	1
Calliphoridae		
Calliphora vicina Robineau-Desvoidy	Yes	2
Heleomyzidae		
Heteromyza rotundicornis (Zetterstedt)	Yes	3
Milichiidae		
Madiza glabra Fallén	Yes	3
Muscidae		
Eudasyphora cyanella (Meigen)	Yes*	3
Helina reversio (Harris)	Yes	4
Musca autumnalis De Geer	Yes	3
M. domestica L.	Yes	3
Polleniidae		
Pollenia amentaria (Scopoli)	Yes	2
P. rudis (Fabricus)	Yes	3
Scatopsidae		
Reichertella pulicaria (Loew)	Yes	2
Sepsidae		
Sepsis cynipsea (L.)	Yes	2
S. duplicata Haliday	Yes	2
S. flavimana Meigen	Yes	5
Syrphidae		
HYMENOPTERA		
Andrenidae		
Andrena fulva (Müller in Allioni)	Yes	6
A. helvola (L.)	Yes	6
Andrena rufula Schmiedeknech	No	6
Apidae		
Apis mellifera L.	Yes*	3
Bombus terrestris (L.)	Yes	1
B. lapidarius (L.)	Yes	7
Formicidae		
Formica sp.	Yes	5
Megachilidae		
Osmia cornuta (Latreille)	Yes	6

Sources: 1. Krasylenko et al. (2020), 2. Kahle-Zuber (2008), 3. Hatton (1965), 4. Ramm et al. (2016), 5. Ramm et al. (2000), 6. Teppner et al. (2016), 7. Walldén (1961). Presence in GB based on NBN Atlas (2022).

*Indicates recorded in Great Britain on *Viscum*.

in populations from the Mediterranean though it was also noted in Central Europe (Piotrowski et al., 2003; Zuber & Widmer, 2000). In the latter case, the hybridization was reported only between subsp. *album* and subsp. *abietis*. Those two taxa are genetically closer to each other than to subsp. *austriacium* which may facilitate hybridisation (Mejnartowicz, 2006; Zuber & Widmer, 2000, 2009). There are no known hybrids in Britain and Ireland.

Artificial hybridization experiments in the 19th century, crossing female subsp. *album* and male subsp. *abietis*, gave 44 viable offspring. (Heinricher, 1919). However, no information is given about viability of hybrids or how many flowers were initially pollinated which precludes any conclusions about the rate of the hybridization. Piotrowski et al. (2003) tested a bulked sample of 118 individuals representing all three taxa of different origin in Europe and reported a total of 15 hybrids.

8.3 | Seed production and dispersal

After pollination a fruit (pseudoberry) develops on the terminal shoots of female plants. Fruits are normally solitary, but may form in pairs, triplets or rarely multiple groups (Becker, 2004; Tubeuf et al., 1923). The mature ovoid fruit is usually 9 mm × 8 mm (Derbidge et al., 2016). According to Tubeuf et al. (1923) the berries of subsp. *album* are wider than long, while the berries of subspecies on conifers are longer than wide. The size of the berries may depend on the number of embryos; subsp. *austriacum* on conifers tends to have fewer embryos in comparison to subspecies from deciduous trees (Tubeuf et al., 1923). The fruit crop estimated for subsp. *austriacum* in Spain was 2000 berries/m^2 (Mellado & Zamora, 2014a). Preston (1977) gives the average number of 175 berries per kg of Mistletoe fresh mass (range 96–237), depending on the individual apple host.

Mistletoe produces berries regularly every season and the full ripening of the seed takes almost a year (Briggs, 2021; Zuber, 2004). At the beginning the fruit of subsp. *album* is green but changes to white and becomes translucent in the late autumn and winter, with no evidence of ultraviolet reflectance changing the colour perceived by birds (Burkhardt, 1982). Each berry contains a single seed that lacks a testa and is coated with viscin that gives the highly adhesive properties crucial for Mistletoe's dispersion and successful recruitment. A typical seed contains 1–2, rarely 3–5, embryos with hypocotyl and two cotyledons and haustorium that emerges from the endosperm (Becker, 2004; Briggs, 2021; Derbidge et al., 2016; Frochot & Sallé, 1980; Tubeuf et al., 1923). The average size of the embryos for subsp. *austriacum* is 5.47 × 3.98 mm, for subsp. *abietis* 6.42 × 4.20 mm and for subsp. *album* 5.20 × 4.30 mm (Tubeuf et al., 1923). The green and photosynthetically active embryo is visible inside of the fruit of subsp. *austriacum* (less so in subsp. *album*; Tubeuf et al., 1923) and requires light from the very beginning (Briggs, 2021). Studies confirmed a circadian variation in the outline of the fruit shape of subsp. *album* which does not appear to be directly linked to temperature, humidity, or light flux, nor to turgor pressure as a result of xylem sap flow. However, there was some link with the number of hours of sunshine perhaps as a result of photosynthetic activity within the fruit (Derbidge et al., 2016).

Some seeds may be dispersed simply by gravity. Seed rain of subsp. *austriacum* under various *Pinus* species in southern Spain varied with altitude from 830.27 ± 183.79 (SE) seeds/m^2 at 1300 m to 110.32 ± 49.14 seeds/m^2 at 1900 m (Zamora & Mellado, 2019). However, the effectiveness of falling below the host in recruitment success is doubted (Frochot & Sallé, 1980). Zoochory is more effective in recruitment with endozoochory being more frequent and effective in terms of recruitment success than exozoochory (Mellado & Zamora, 2014b). Birds are the primary dispersal vectors while small mammals are consumers of berries (Section 9.1).

Generalist bird dispersers predominate in Europe while a few mistletoe specialist frugivores are noted in Australia, South America and Africa (Watson & Rawsthorne, 2013). According to Mellado and Zamora (2014b) the use of generalist birds by subsp. *austriacum* and so the ability to switch between different bird species, has allowed it to spread across a diverse and wide European range. The main dispersers of *V. album* in Europe are thrushes (*Turdus viscivorus* L., *T. torquatus* L., *T. philomelos* Brehm, *T. iliacus* L., *T. merula* L., *T. pilaris* L.), Waxwing *Bombycilla garrulus* L., tits (*Periparus ater* L., *Cyanistes caeruleus* (L.), *Parus major* L.), Jay *Garrulus glandarius* (L.), Eurasian Blackcap *Sylvia atricapilla* (L.) and European Robin *Erithacus rubecula* (L.) (Mathiasen et al., 2008; Mellado & Zamora, 2014b; Tubeuf et al., 1923; Walldén, 1961). The increasing population size of the Mistle thrush (*T. viscivorus*) in Hungary has been linked to an expansion of *V. album* during recent decades (Varga et al., 2014). In Britain, the list of dispersers is more limited, including Mistle thrush, Fieldfare (*T. pilaris*) and Waxwing, and, in recent decades, Eurasian Blackcap and, possibly, the rose-ringed parakeet *Psittacula krameri* (Scopoli) (Briggs, 2021).

The birds either feed on the whole fruit (*Turdus* spp.) or peel off the exocarp and feed on the endocarp (e.g. *Parus* spp.) which determines the mode of dispersal (Mathiasen et al., 2008; Tubeuf et al., 1923). Eating the whole fruit results in endozoochory where the seed is regurgitated or defecated. Feeding on the endocarp relates to exozoochory where seeds adhere to a bird's beak, legs, or feathers and are rubbed off onto a branch of a potential host which initiates the infection. With either method, the seed is still covered with some of its viscin coat, which allows it to adhere to a potential host (Horbelt et al., 2022). Seed germination and seedling establishment is not affected by the mode of the dispersion (Mellado & Zamora, 2014b).

Mistle thrushes in Spain feed on fallen berries in addition to those actively collected in the tree canopy (Mellado & Zamora, 2014b). However, studies in Spain and Britain have shown that, although *Turdus* species are the most important consumers, they are less efficient in terms of Mistletoe recruitment (Briggs, 2021; Mellado & Zamora, 2014b). Mistle thrushes eat 6–10 berries at once, which are digested for *c*. 30 min. (Tubeuf et al., 1923), but these birds are highly territorial and tend to deposit seeds in latrines in relatively restricted areas or preferred trees which acts to reduce the distance of seed dispersal (Skórka & Wójcik, 2005). Frochot and Sallé (1980) reported that the estimated distance of seed dispersal by Mistle thrush might be *c*. 20 km considering the time of the digestion and speed of flying. However, factors such as road density or building density may change dispersal distances by birds (Rybalka, 2017) and in northeast Spain 3.5 km was more realistic for bird dispersal (Ramsauer et al., 2022). More details about the behaviour of the major dispersers in Britain are given by Briggs (2021) and in Spain by Mellado and Zamora (2014b).

8.4 | Viability of seeds: Germination

The fruits ripen in December, but the seeds need a period of winter dormancy before germination occurs. No mitotic activity or DNA synthesis in the cells of the terminal meristem is observed during dormancy (Sallé, 1976). Dormancy can last 6 months, but in warm conditions it can be shortened to 1–3 months for a proportion of the more mature seeds (Tubeuf et al., 1923). It is also possible to shorten the dormancy period using intense artificial lighting (Stopp, 1961). The normal germination period in Britain is from February to April but can be later in parts of mainland Europe.

The mature seeds comprise 1–3 chlorophyllous embryos embedded in a green endosperm, centrally placed in the translucent ripe berry. Polyembryonic seeds (Section 8.4) can develop where up to four individuals can form a single ‘plant’, growing close together or even growing on each other and effectively parasitising each other. This can result in single ‘plants’ bearing both male and female flowers.

Seeds require light for germination, and viability drops quickly in darkness; 84% after 8 days, 68% after 14 days, 36% after 21 days and zero after 5 weeks (Tubeuf et al., 1923). Light may be unnecessary for continued growth of the seedling (Stopp, 1961) but is probably still necessary for the seedling to thrive and connect to the host via negative phototropism. The epicarp is a barrier for the hypocotyl after germination (Stopp, 1961) and so germinating seeds are trapped inside fruits that remains on the trees until summer (Frochot & Sallé, 1980). This barrier is effectively removed by birds distributing seeds without the berry casing (Frochot & Sallé, 1980)—Section 8.3.

Germination occurs regardless of surface or situation. Host bark morphology seems unimportant, probably because Mistletoe establishes most effectively on thin, smooth bark of younger branches even on hosts with fissured bark. There is no recorded effect of bark pH and chemistry on establishment. Indeed, seeds will germinate on glass, stone, wood, paper or free-hanging on a thread (Frochot & Sallé, 1980; Stopp, 1961). Seed germination is also independent of host phenology (Tubeuf et al., 1923). Walldén (1961) found 97% viability for seeds in berries fallen to the ground, where successful growth would be impossible.

The minimum germination temperature according to Stopp (1961) is 8–10°C. However, in the case of Danish populations, the germination rate was 65% at 5°C. At 30°C, germination efficiency was reduced to 46% by fungal infection (Stanton et al., 2010). The optimum temperature for germination is 15–20°C (Lamont, 1983; Stanton et al., 2010). In low-temperature storage, seeds of subsps *album* and *austriacum*, underwent a colour change from green to brown, associated with a loss of viability (Tikkanen et al., 2021). The storage temperature at which 50% of seeds lost viability was −15°C in subsp. *austriacum* and between −15°C and −19°C in subsp. *album* (moisture content of the seeds was not measured). There was almost 100% failure of seed germination of subsp. *austriacum* at −26°C while 10.6% of subsp. *album* seeds still germinated at this temperature. At −30°C neither subspecies germinated (Tikkanen et al., 2021). Seeds of subsp. *album* can be smaller than those of subsp. *austriacum*, which may reduce their tolerance to low temperatures. Seedlings are resistant against frost down to −15°C (Wangerin, 1937). Humidity has no effect on germination.

8.5 | Seedling morphology

At germination, 1–3 green hypocotyls (Figure 9) emerge from the seed, depending on the number of embryos present. The hypocotyls elongate through intense mitotic activity of the terminal meristematic zone and elongation of the underlying cells (Frochot & Sallé, 1980). The hypocotyls are negatively phototropic and bend toward the adjoining host bark surface (Sallé, 1983). Physical contact of the hypocotyl against the host induces flattening to form a slightly oval disc or holdfast (Frochot & Sallé, 1980; Thoday, 1951) the epithelium produces lipidic glue, which sticks the hypocotyl to the host. The holdfast widens to about 1.8 mm diameter (Figure 9) with high meristematic activity concentrated in the central part. The host periderm is lifted and the meristem penetrates the periderm and cortical parenchyma forming a primary sinker (Frochot & Sallé, 1980). In addition to mechanical forces, enzymatic processes may also help to open up the host tissues (Sallé, 1983). Studies of *V. album* subsp. *coloratum* in Korea (now regarded as *V. coloratum*) suggest that xyloglucan endotransglycosylases (XETs), glucanase, expansins and other cell wall hydrolases have a role during this stage (Ko et al., 2014).

Each sinker consists of parenchymatous cells and isodiametric vessels. The outermost vessels of the sinkers are in direct contact with those of the host xylem assuring the Mistletoe plant an early and sufficient water supply (Mylo et al., 2021). The primary sinker is the start of the haustorial structure, establishing direct connection between the hemiparasite and host xylem vessels. The seedling is not parasitic until this link is made. During this stage, while the endophytic system is establishing, the external appearance of the seedling varies very little for a year, sometimes longer. Once connection is established, the endosperm usually becomes

FIGURE 9 Germinating seeds and young seedlings *Viscum album*. (a, b) Germination in vitro, showing emergence of multiple hypocotyls from within the endosperm. (c, d) Germination on host bark, showing establishing holdfasts under which host penetration occurs. (e, f) Established seedlings 3–4 years old. Photographs by Jonathan Briggs.

detached and the hypocotyl becomes more erect, with the seedling now formed only by the remaining hypocotyl and sucker-like disc (Frochot & Sallé, 1980). The endosperm may, in some cases, remain attached for over a year, possibly continuing to support the seedling (Büssing, 2000a).

The first leaves usually appear in the year following germination, but may be delayed until the second year in some cases (Frochot & Sallé, 1980; Ramm et al., 2016). Subsequent development of the haustorium is described in Section 6.1.1.

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

Comparatively few insects and mites have been recorded on all the European subspecies of Mistletoe (Table 2). Of these, 52 species occur in Britain, 34 of them recorded on Mistletoe. Most are herbivorous insects, some feeding on dead tissue, but there are also predators. Most are Hemiptera (34) or Coleoptera (27), the rest being mainly Diptera (5), Hymenoptera (8) and Lepidoptera (7). This list does not include taxa involved in pollination (Section 8.1).

There are eight monophagous species, five of which occur in Britain (Table 2): *Cacopsylla visci* (Hemiptera, Psyllidae), *Pinalitus viscicola* (Hemiptera, Miridae) *Hypseloecus visci* (Miridae), *Ixapion variegatum* (Coleoptera, Apionidae) and *Celypha woodiana* (Lepidoptera, Tortricidae). There are also secondary *Viscum* specialists in Britain. *Anthocoris visci* (Hemiptera, Anthocoridae) is a predatory bug restricted to *Viscum*. Thompson and Blunt (2018) record a parasitoid wasp (*Triaspis* sp.; Hymenoptera, Braconidae) that may be a specialist of *Ixapion variegatum*. Haarder and Mąkol (2022) record the generalist parasitic mite *Trombidium holosericeum* (Acari, Trombidiidae) on *Pinalitus viscicola*.

British records for the specialist species are sparse, which may be due to under-recording as they are usually found when looked for (Briggs, 2011a; Thompson & Blunt, 2018). Two, *Ixapion variegatum* and *Hypseloecus visci*, were recorded as new to Britain fairly recently but they may not be recent colonists (Briggs, 2011a). The leaf-mining monophagous moth *Celypha woodiana* and *Anthocoris visci* are of conservation interest (Section 11).

A study of invertebrates in Mistletoe-laden orchards in Shropshire identified a distinct Mistletoe community (Thompson & Blunt, 2018). This community included six specialist Mistletoe species plus 26 other nonspecialist taxa made up of a wide mixture of species, of which over 30% were predatory, suggesting that many were opportunistic in occurring on *Viscum*. The presence of six species of Psocoptera was notable, and confirms personal observations by Briggs (e.g. Briggs, 2012) that these barkflies are numerous in the berry clusters, feeding on algae and fungi. Thompson and Blunt (2018) suggest these may be feeding on *Sphaeropsis visci* (Ascomycota, Botryosphaeriales) and that it may be their presence that attracts predators.

Arthropod communities on *V. album* subsp. *austriacum* growing on *Pinus nigra* and *P. sylvestris* in southeast Spain were found to be similar across hosts, and different and more diverse than communities on their hosts (Lázaro-González et al., 2017). The higher diversity was attributed to Mistletoe having extremely low concentrations of defence compounds (including a complete lack of terpenes) and high nitrogen concentrations in leaves (Lázaro-González et al., 2019b) compared to their host. The main determinant of the diversity was the size of Mistletoe plants—bigger plants were richer—while elevation made no significant difference (Lázaro-González et al., 2020). The main differences between host and Mistletoe communities were the presence on Mistletoe of the herbivores *Cacopsylla visci* and *Pinalitus viscicola* and the predator *Anthocoris visci*, noted above, and all common across Europe on a range of *Viscum* subspecies and hosts (Briggs, 2011b; Hansen & Hodkinson, 2006; Struwe et al., 2009; Varga, Keresztes, & Poczai, 2012; Zuber, 2004). These three species are especially common in southern Europe, and in southeast Spain were found to made up 19%, 5% and 15%, respectively, of the mass of arthropods on Mistletoe, representing 19.45 ± 3.84, 5.21 ± 1.60 and 15.66 ± 2.90 individuals/kg (SE), respectively, on Mistletoe compared to 0.0 ± 0.0, 0.07 ± 0.07 and 0.29 ± 0.25 individuals/kg on pine trees, both species merged (Lázaro-González et al., 2017).

It is surprising that there are few reports of mites (Acari) on Mistletoe, which may indicate that this group is still under-recorded. It is likely that harvested material or samples following tree felling will have lost many of the invertebrates living on the outer parts of the plant.

Insects found on Mistletoe are rarely seen in quantity and appear to have little impact on the plant. However some cause damage, including the monophagous weevil *Ixapion variegatum* which affects stems below flower buds and could, if numerous, reduce flowering success (Briggs, 2011a). Krasylenko et al. (2020) speculate that *Agrilus* spp. (Coleoptera, Buprestidae), if occurring in quantity, could cause mortality of Mistletoe and thus be of use in biological control.

Birds taking the berries are described in Section 8.3. In addition to these, many other birds will consume and therefore destroy the naked seeds (after removal from the berry). These are primarily Coal Tit *Periparus ater* L., Blue Tit *Cyanistes caeruleus* L., Marsh Tit *Poecile palustris* L. and Eurasian Nuthatch *Sitta europaea* L. Coal tits and blue tits also eat germinating Mistletoe plants (Baltazár et al., 2013).

Nonflying vertebrates do not often consume Mistletoe as it simply occurs too high above-ground, but when the foliage is reachable or on the ground, it is eagerly eaten by deer and rabbits (Section 4). Moreover, several mammal species, including carnivores, are suspected to eat the berries, including European Pine Marten *Martes martes* L., Beech Marten *M. foina* (Erxleb.), Fox *Vulpes vulpes* (L.), Badger *Meles meles* L. and Red Squirrel *Sciurus vulgaris* L. (Frochot & Sallé, 1980; Herrera, 1989; Tubeuf et al., 1923). This could have implications for dispersal, as these mammals may defecate a significant distance from the food source, but successful establishment would be unexpected as they are highly unlikely to defecate on tree branches. Mistletoe has also been used as animal feed (Section 10.4).

TABLE 2 Arthropods recorded from *Viscum album* in Great Britain and continental Europe

Species classification	Recorded in GB	Ecological notes	Source
INSECTA			
COLEOPTERA			
Anobiinae			
Gastrallus knizeki Zahradnik	No	Larvae feed in older stem tissues, monophagous	8
G. laevigatus (Olivier)	Yes	Larvae feed within stem, polyphagous	16
Hedobia imperialis (L.)	Yes	Larvae feed within dead stem tissue, polyphagous	5
H. pubescens (Olivier)	No	Larvae feed within older stem tissue, polyphagous	8
Anthribidae			
Noxius curtirostris (Mulsant & Rey)	No	Larvae feed within dead stem tissue, polyphagous	8
Rhaphitropis marchica (Herbst)	No	Larvae feed within dead stem tissue, polyphagous	17
Apionidae			
Ixapion variegatum (Wencker) (=*Apion variegatum* Sainte Claire-Deville)	Yes*	Larvae feed within the stems, monophagous	1a, 2, 7, 19
Buprestidae			
Agrilus jacetanus Sánchez & Tolosa	No	Larvae feed within stem, polyphagous	4
A. kutahyanus Królik	No	Larvae feed within stem, polyphagous	4
A. roscidus Kiesenwetter	No	Larvae feed within stem, polyphagous	10
A. viscivorus Bilý	No	Larvae feed within stem, polyphagous	8
Cantharidae			
Malthodes marginatus (Latreille)	Yes*	Larvae feed on saproxylic fauna	19
Cerambycidae			
Aegomorphus clavipes (Schrank)	No	Imago feeds on young bark and leaves, larvae feed within dead stem tissue, polyphagous	8
Clytus arietis (L.)	Yes	Imago feeds on pollen and nectar, larvae feed within dead stem tissue, polyphagous	8
Mesosa curculionoides (L.)	No	Larvae feed within stem, polyphagous	8
Oplosia cinerea (Mulsant)	No	Larvae feed within moist dead stem tissue, polyphagous	18
Pogonocherus hispidus (L.)	Yes	Larvae feed within stem, polyphagous	3, 14
Stenostola ferrea (Schrank)	No	Imago feeds on young bark and leaves, larvae feed within dead stem tissue, polyphagous	8
Corylophidae			
Arthrolips nana (Mulsant & Rey)	No	Lives in dead tissue, mould-feeders, polyphagous	6
Sericoderus lateralis (Gyllenhal)	Yes	Lives in dead tissue, mould-feeders, polyphagous	16
Curculionidae			
Xylosandrus germanus (Blandford)	Yes	Lives in dead tissue, mould-feeders, polyphagous	13
Laemophloeidae			
Cryptolestes corticinus (Erichson)	No	Lives in dead tissue larvae probably mould-feeders, polyphagous	8
Leptophloeus hypobori (Perris)	No	Predatory, polyphagous	16
Lathropus sepicola (Müller)	No	Lives in dead stem tissue, polyphagous	6
Melyridae			
Dasytes cyaneus (Fabr.) (=*Dasytes caeruleus* (Degeer))	Yes	Predatory larvae	8
D. plumbeus (Müller)	Yes	Predatory larvae	8
Scolytidae			
Liparthrum bartschi Mühl	No	Lives in dead tissue, monophagous	14

(Continues)

TABLE 2 (Continued)

Species classification	Recorded in GB	Ecological notes	Source
DERMAPTERA			
Forficula auricularia L.	Yes*	Omnivorous	19
DIPTERA			
Cecidomyiidae			
Asynapta viscicola (Skuhravá)	No	Stem gall inducer, monophagous	8
Drosophilidae			
Drosophila suzukii (Matsumura)	Yes	Larvae in berries; invasive pest	1
Sciaridae			
Sciaridae sp.	Yes	Saprophagic and mycophagic larvae, polyphagous	16
Stratiomyidae			
Beris vallata (Forster)	Yes*	Detritivore, polyphagous	19
Tephritidae			
Anomoia purmunda (Harris)	Yes*	Possible feeding on pollen and nectar, Polyphagous	19
HEMIPTERA			
Anthocoridae			
Anthocoris nemoralis (Fabricius)	Yes*	Predatory	16, 19
A. simulans Reuter	Yes*	Predatory	19
A. nemorum (L.)	Yes	Predatory	8
A. visci Douglas	Yes*	Predator, restricted to *Viscum*	1a, 2, 11, 19
Orius vicinus (Ribaut)	Yes*	Predatory	19
Aphididae			
Aphis fabae Scopoli—sensu stricto	Yes	Leaves, sap-sucker, polyphagous	16
Cinara pini (L.)	Yes	Sap-sucker; widespread on *Pinus*	11, 12
Tuberaphis coreana (R. Takahashi)	No	Leaves, stems sap-sucker, polyphagous	10
T. viscisucta (Zhang)	No	Causes the leaf edges to curl downward, polyphagous	10
Aphrophoridae			
Aphrophora alni (Fallén)	Yes*	Leaves sap-sucker, polyphagous	19
Coccidae			
Coccus hesperidum L. (=*Lecanium hesperidium* (L.))	Yes	Leaves, stems sap-sucker, polyphagous	8
Filippia follicularis (Targioni Tozzetti)	No	Leaves, stems sap-sucker, polyphagous	15
Gossyparia spuria (Modeer) (=*Eriococcus spurius* (Modeer), *Gossyparia ulmi* L.)	No	Leaves, stems sap-sucker, polyphagous	15
Lepidosaphes ulmi (L.)	Yes	Stems sap-sucker, polyphagous	8
Pulvinaria vitis (L.) (=P. *betulae*)	Yes	Leaves, stem sap-sucker, polyphagous	16
Saissetia oleae (Olivier)	Yes	Stems sap-sucker; polyphagous	3
Delphacidae			
Javesella pellucida (Fabricius)	Yes*	Leaves, stem sap-sucker, polyphagous	19
Diaspididae			
Carulaspis juniperi (Bouché)	Yes	Leaves, stem sap-sucker, polyphagous	3
C. visci (Schrank)	No	Leaf gall inducer, polyphagous	16
Chionaspis salicis (L.)	Yes	Stems sap-sucker, polyphagous	8
Lygaeidae			
Spilostethus pandurus subsp. *militaris* (Fabricius)	No	Larvae stem sap-sucker, polyphagous	11
Miridae			
Atractotomus mali (Meyer-Dür)	Yes*	Larvae leaf and fruit sap-sucker, imago predatory, polyphagous	19

TABLE 2 (Continued)

Species classification	Recorded in GB	Ecological notes	Source
Blepharidopterus angulatus (Fallén)	Yes*	Predatory	19
Campyloneura virgula (Herrich-Schäffer)	Yes*	Predatory	16, 19
Deraeocoris flavilinea (Costa)	Yes*	Leaves, stem sap-sucker, predatory polyphagous	19
Grypocoris stysi (Wagner)	Yes*	Imago and larva feeds on flower and small invertebrates, polyphagous	19
Hypseloecus visci (Puton)	Yes*	Leaves, sap-sucker, monophagous	1a, 2, 19
Neolygus contaminatus (Fallén)	Yes*	Leaves, stem sap-sucker, polyphagous	19
Pinalitus viscicola (Puton) (=*Orthops viscicola* (Puton))	Yes*	Leaves, sap-sucker, monophagous	1a, 2, 3, 11, 19
Nabidae			
Himacerus apterus (Fabricius)	Yes*	Predatory	19
Pentatomidae			
Pentatoma rufipes (L.)	Yes*	Leaves, stems sap-sucker, polyphagous	16, 19
Psyllidae			
Cacopsylla melanoneura Förster	Yes*	Sap-sucker, polyphagous	19
Cacopsylla visci (Curtis) (=*Psylla visci* Curtis)	Yes*	Leaves, sap-sucker, monophagous	1a, 2, 3, 11, 19
Rhyparochromidae			
Scolopostethus affinis (Schilling)	Yes*	Sap-sucker, predatory polyphagous	19
HYMENOPTERA			
Braconidae			
Ecphylus sp.	Yes	Parasitoid wasp	16
Heterospilus sp.	Yes	Parasitoid wasp	16
Triaspis sp. c.f. *T. podlussanyi* Papp	Yes*	Parasitoid wasp, parasitising *Ixapion variegatum*	19
Eupelmidae			
Eupelmidae sp.	Yes	Parasitoid wasp	16
Formicidae			
Colobopsis truncata (Spinola)	No	Feeds on honeydew and predatory, polyphagous, occupies empty corridors carved by the larvae of other insects.	8
Crematogaster scutellaris (Olivier)	No	Occupies empty corridors carved by the larvae of other insects.	8
Lasius brunneus (Latreille)	Yes	Feeds on honeydew, polyphagous	16
Temnothorax affinis (Mayr)	No	Occupies empty corridors carved by the larvae of other insects.	8
LEPIDOPTERA			
Cossidae			
Zeuzera pyrina (L.)	Yes	Larvae feed within the stem, polyphagous.	8
Erebidae			
Euproctis similis (Fuessly) (=Sphrageidus similis (Füssli))	Yes*	Larvae feed on the leaves, polyphagous	19
Notodontidae			
Thaumetopoea pityocampa (Denis & Schiffermüller)	Yes	Larvae feed on the leaves, polyphagous	12
Sesiidae			
Synanthedon loranthi (Králícek)	No	Imago feed on nectar, larvae feed directly under the stem bark, monophagous	16
Tortricidae			
Celypha woodiana (Barrett)	Yes*	Leaves, leaf-miner, monophagous	1a, 2, 3
Ditula angustiorana (Haworth)	Yes	Larvae feed on leaves and fruits, polyphagous.	3, 10

(Continues)

TABLE 2 (Continued)

Species classification	Recorded in GB	Ecological notes	Source
Epiphyas postvittana (Walker)	Yes*	Larvae feed on the leaves, polyphagous	21
PSOCOPTERA			
Caeciliusidae			
Valenzuela burmeisteri (Brauer)	Yes	Larvae feed on the leaves, polyphagous	19
V. flavidus (Stephens)	Yes	Larvae feed on lichens, moulds, fungi, leaves and stem, polyphagous	19
Ectopsocidae			
Ectopsocus briggsi McLachlan	Yes	Feed on the fungal spores and various microflora on the surface of the leaves, polyphagous	19, 20
E. petersi Smithers	Yes	Feed on the fungal spores and various microflora on the surface of the leaves, polyphagous	19
Elipsocidae			
Elipsocus hyalinus (Stephens)	Yes	Feed on berries and leaves, polyphagous	19
Stenopsocidae			
Graphopsocus cruciatus (L.)	Yes	Larvae feed on lichens, moulds, fungi, polyphagous	19
ACARI			
TROMBIDIFORMES			
Tenuipalpidae			
Cenopalpus lanceolatisetae (Attiah)	Yes	Phytophagous mite, polyphagous	9
Trombidiidae			
Trombidium holosericeum (L.)	Yes	Parasitic mite, generalist. Recorded on *Pinalitus viscicola*	22

Sources: 1. Briem et al. (2016); 1a. Briggs (2011a); 2. Briggs (2011b); 3. DBIF (2022); 4. Digirolomo et al. (2019); 5. Grzywocz (2015); 6. Grzywocz et al. (2017); 7. Harrison (2014); 8. Hellrigl (2006); 9. Khanjani et al. (2013); 10. Krasylenko et al. (2020); 11. Lázaro-González et al. (2017); 12. Lázaro-González et al. (2019a); 13. Mokrzycki et al. (2011); 14. Tubeuf et al. (1923); 15. Ulgenturk et al. (2003); 16. Varga et al. (2012b); 17. Wanat et al. (2011); 18. Zieliński and Graczyk (2003); 19 Thompson & Blunt (2018), 20 Briggs (2012), 21. Briggs (personal observation), 22. Haarder and Mąkol (2022). Presence in GB based on NBN Atlas (2022).

*Indicates recorded in Great Britain on *Viscum*.

9.2 | Plant parasites

There are no reports of plant parasites on *V. album* other than epiparasitism by other *V. album* plants (Section 8.4). This auto-parasitism, though difficult to spot from ground level, is frequently seen when examining plants in detail. The phenomenon helps reduce the disadvantages of dioecy as one sex can grow on the other. Similar parasitism is not uncommon in other mistletoe species (Krasylenko et al., 2021).

The only epiphytic species found on *V. album* are algae and lichens, frequently observed in Britain but with no formal records. The only published report is of two species, *Xanthoria parietina* (L.) Th. Fr. (Ascomycota, Teloschistales) and *Physcia tenella* (Scop.) DC. (Ascomycota, Caliciales), found in Ukraine (Krasylenko et al., 2020).

9.3 | Plant diseases

A wide variety of fungi have been recorded on *V. album* (Table 3). Most of them, especially in the phyla Basidiomycota and Zygomycota, have been found only through molecular studies (Peršoh, 2013; Peršoh et al., 2010). A total of 48 fungal isolates and 193 bacterial strains were identified from *V. album* (presumed to be subsp. *austriacum*) in Turkey (Kotan et al., 2013). The majority of fungi found on Mistletoe are endophytes, 20 of which are pathogenic and 13 are saprobic. Fifty-three of the fungi species associated with *Viscum* have records in Britain, based on the NBN Atlas (2022). Of these, four Ascomycota are Mistletoe-specific and have been recorded, albeit infrequently, on *V. album* in Britain: *Botryosphaeria visci* (Botryosphaeriales), *Plenodomus visci* (Botryosphaeriales), *Septocyta visci-britannica* (Capnodiales) and *Rhabdospora visci* (Capnodiales) (Doğan et al., 2022). *Septocyta visci-britannica* was discovered as a new species in Surrey in 2000, described by Punithalingam and Spooner (2002).

Some researchers argue that these pathogenic fungi might have use in biological control of Mistletoe (Karadžić et al., 2004; Kotan et al., 2013; Varga, Taller, et al., 2012). However, the biology of these fungal pathogens, the factors determining their occurrence and the possibility of their use as regulating factors for infections caused by Mistletoe are very poorly understood (Karadžić & Lazarev, 2005; Kotan et al., 2013).

Endophytic assemblages of *V. album* plants may vary considerably even when in close proximity. Individuals of Mistletoe on *Abies alba* separated by less than 1 cm were found to share just 15% of endophytes (Petrini et al., 1992).

TABLE 3 Fungi (by phylum and order) associated with *Viscum album*

Species classification	In GB	Ecological notes
ASCOMYCOTA		
Botryosphaeriales		
Botryosphaeria dothidea (Moug.) Ces. & De Not.	Yes	Pathogenic, endophyte, wood and bark
B. visci (Kalchbr.) Arx & E. Müll. (= *Sphaeropsis visci* (Alb. & Schwein.) Sacc.)	Yes*	Pathogenic, leaf, stem, species specific
Plenodomus visci (Moesz) Gruyter, Aveskamp & Verkley (= *Phoma visci* Sacc.)	Yes*	Pathogenic, leaf, stem, species specific
Capnodiales		
Capnobotryella renispora Sugiy.	No	Endophyte
Cladosporium cladosporioides (Fresen.) G.A. de Vries	Yes	Saprobic, species specific
C. herbarum (Pers.) Link	Yes	Saprobic, pathogenic,
Phaeotheca fissurella Sigler, Tsuneda & J.W. Carmich.	No	Endophyte
Rhabdospora visci (Bres.) Died (= *Septocyta visci* (Bres.) Punith. & Spooner)	Yes*	Pathogenic, leaf, stem, species specific
Septocyta visci-britannica Punith. & Spooner	Yes*	Pathogenic, leaf, stem, species specific
Teratosphaeria microspora Joanne E. Taylor & Crous	No	Endophyte
Chaetothyriales		
Exophiala eucalyptorum Crous	No	Endophyte
Dothideales		
Aureobasidium harposporum (Bres. & Sacc.) Herm.-Nijh.	No	Endophyte, pathogenic
A. pullulans (de Bary & Löwenthal) G. Arnaud	Yes	Endophyte, epiphyte, saprobic
Sydowia polyspora (Bref. & Tavel) E. Müll.	Yes	Pathogenic
Eurotiales		
Aspergillus flavus Link	Yes	Endophyte
A. niger Tiegh.	Yes	Endophyte
Glomerellales		
Colletotrichum gloeosporioides (Penz.) Penz. & Sacc.	Yes	Endophyte, pathogenic
Hypocreales		
Clonostachys phyllophila Schroers	No	Saprobic
Cylindrocarpon orthosporum (Sacc.) Wollenw.	No	Endophyte, pathogenic
Fusarium fujikuroi Nirenberg	No	Endophyte
F. oxysporum Schltdl.	Yes	Endophyte
F. roseum Link	Yes	Saprobic
Leptobacillium leptobactrum (W. Gams) Zare & W. Gams	No	Endophyte
Nectria cinnabarina (Tode) Fr.	Yes	Endophyte, pathogenic
Sarocladium kiliense (Grütz) Summerb.	No	Endophyte, pathogenic, saprobic
Trichoderma viride Pers.	Yes	Saprobic
Trichothecium roseum (Pers.) Link	Yes	Saprobic, pathogenic
Melanosporales		
Gonatobotrys flavus Bonord.	Yes	Endophyte
Microthyriales		
Microthyrium visci Richon	No	Saprobic
Phaeomoniellales		
Neophaeomoniella zymoides (Hyang B. Lee, J.Y. Park, Summerb. & H.S. Jung) Crous	No	Endophyte
Pleosporales		
Alternaria alternata (Fr.) Keissl.	Yes	Endophyte, saprobic, pathogenic
Epicoccum nigrum Link	Yes	Endophyte, saprobic, pathogenic.
Leptosphaeria proteicola Crous	No	Endophyte

(Continues)

TABLE 3 (Continued)

Species classification	In GB	Ecological notes
Lophiostoma corticola (Fuckel) E.C.Y. Liew, Aptroot & K.D. Hyde	No	Endophyte
Pleospora loculata (Crié) Sacc.	No	Endophyte, pathogenic
Ulocladium chartarum (Preuss) E.G. Simmons	Yes	Endophyte, pathogenic
Sordariales		
Fimetariella rabenhorstii (Niessl) N. Lundq.	No	Endophyte
Sordaria fimicola (Roberge ex Desm.) Ces. & De not.	Yes	Saprobic
Trapeliales		
Candida tropicalis (Castell.) Berkhout	No	Endophyte
Kodamaea ohmeri (Etchells & T.A. Bell) Y. Yamada, Tom. Suzuki, M. Matsuda & Mikata	No	Endophyte
Sarea difformis (Fr.) Fr.	Yes	Endophyte
Trichosphaeriales		
Hormococcus heterosporus Preuss	No	Saprobic
Nigrospora oryzae (Berk. & Broome) Petch	Yes	Endophyte
Xylariales		
Biscogniauxia nummularia (Bull.) Kuntze	Yes	Endophyte, pathogenic
Daldinia concentrica (Bolton) Ces. & De not.	Yes	Endophyte
Hypoxylon fragiforme (Pers.) J. Kickx f.	Yes	Endophyte
H. fuscum (Pers.) Fr.	Yes	Endophyte
H. howeanum Peck	Yes	Endophyte
H. rubiginosum (Pers.) Fr.	Yes	Endophyte
Jackrogersella cohaerens (Pers.) L. Wendt, Kuhnert & M. Stadler	Yes	Endophyte
J. multiformis (Fr.) L. Wendt, Kuhnert & M. Stadler	Yes	Endophyte
Nemania serpens (Pers.) Gray	Yes	Endophyte
Xylaria longipes Nitschke	Yes	Endophyte
BASIDIOMYCOTA		
Agaricales		
Cuphophyllus borealis (Peck) Bon ex Courtec.	Yes	Endophyte
Hygrocybe coccinea (Schaeff.) P. Kumm.	Yes	Endophyte
Tylospora fibrillosa (Burt) Donk	Yes	Endophyte
Boletales		
Imleria badia (Fr.) Vizzini	Yes	Endophyte
Buckleyzymales		
Buckleyzyma aurantiaca (Saito) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout	No	Endophyte
Cantharellales		
Craterellus tubaeformis (Fr.) Quél.	Yes	Endophyte
Erythrobasidiales		
Erythrobasidium hasegawae (Y. Yamada & Komag.) Hamam., Sugiy. & Komag.	No	Endophyte
Hymenochaetales		
Resinicium bicolor (Alb. & Schwein.) Parmasto	Yes	Endophyte
Malasseziales		
Malassezia restricta E. Guého, J. Guillot & Midgley	No	Endophyte
Russulales		
Lactarius rufus (Scop.) Fr.	Yes	Endophyte
Russula puellaris Fr.	Yes	Endophyte
Thelephorales		

TABLE 3 (Continued)

Species classification	In GB	Ecological notes
Tomentella stuposa (Link) Stalpers	Yes	Endophyte
Incertae sedis		
Yunzhangia auriculariae (Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout	No	Endophyte
ZYGOMYCOTA		
Mortierellales		
Mortierella macrocystis W. Gams	No	Endophyte
M. parvispora Linnem.	Yes	Endophyte
M. pulchella Linnem.	Yes	Endophyte
CHROMISTA Oomycota		
Leptomitales		
Leptomitus lacteus (Roth) C. Agardh	Yes	Fruit submerged in water
Peronosporales		
Pythium inflatum V.D. Matthews	No	Aquatic; fruit submerged in water
Pythiogeton utriforme Minden	Yes	Aquatic
Rhipidiales		
Rhipidium americanum Thaxt.	Yes	Aquatic, decaying submerged fruit
Saprolegniales		
Achlya colorata Pringsh.	Yes	Aquatic; fruit submerged in water
A. glomerata Coker	Yes	Aquatic; fruit submerged in water
A. papillosa Humphrey	No	Aquatic; fruit submerged in water
Saprolegnia diclina Humphrey	Yes	Aquatic; fruit submerged in water
S. ferax (Gruith.) Kütz.	Yes	Aquatic; fruit submerged in water
S. glomerata (Tiesenh.) A. Lund	No	Aquatic; fruit submerged in water

*Indicates recorded in Great Britain on *Viscum*.Sources: Data taken from Czeczuga et al. (2010) and Krasylenko et al. (2020).

10 | HISTORY

10.1 | Prehistory

The earliest palaeobotanical record of *Viscum* sp. in Europe refers to two fossil species. *Viscum miquelii* (Geyler & Knkelin) Czeczott was found in Oligocene-Miocene deposits dated at 28.4–23.0 Ma (Mai, 2001) and in Miocene–Pliocene deposits in Central Europe (Kvaček et al., 2020; Worobiec & Lesiak, 1998). *Viscum morlotti* (Unger) Erw.Knobloch & Kvaček was more widespread in the flora of the Middle-Late Miocene in Central Europe (Holý et al., 2012), south-west France (Kvaček et al., 2011) and Styria in southern Austria (Kovar-Eder & Hably, 2006). It is not clear how these species relate to the modern *V. album*. Fossil pollen grains of *Viscum* sp. have also been detected in Miocene (4.2–4.0 Ma) sediments exposed in Northern Iceland (Denk et al., 2011).

The presence of *V. album* pollen in Pleistocene and Holocene deposits is considered an indicator of warm climate conditions and so aids paleoclimatic reconstruction (Iversen, 1944). *V. album* is inefficient at pollen dispersal, and is usually in low frequencies in deposits, implying that even small numbers of pollen grains in fossil pollen records may indicate good local populations (Noryśkiewicz & Noryśkiewicz, 2017).

In Britain, *Viscum* pollen found in the Middle-Lower Pleistocene deposits of the Cromer Forest Bed in Norfolk should probably be referred to *V. album* (Wilson, 1973). In Ireland a single pollen record from freshwater mud in Co. Waterford (Watts, 1959) suggests that the species was present during the Hoxnian interglacial of the Middle Pleistocene (Nelson, 2008; Watts, 1959). There are no fossil records of *Viscum* from postglacial deposits in Ireland. Pleistocene records of *V. album* from the Eemian interglacial have been found in Finland (Robertsson, 2000), Germany (Hrynowiecka et al., 2021) and Poland (Bober et al., 2018; Granoszewski, 2003).

The current Holocene (Subatlantic) range of all *V. album* subspecies is due in part to the postglacial migration of host tree species from refugia. For example, the effective refugial areas for *Abies alba*, and so for subsp. *abietis*, were in the northern Apennine Peninsula and the Balkans, while noneffective refugia for *Abies alba*, from which migration did not happen, were located in the Pyrenees of Italy (Cheddadi et al., 2014). The Holocene range expansion of Mistletoe, based on isopollen maps, shows that it started in the Early Boreal in the Apennines, reaching southern Scandinavia in the Late Boreal (8600–8000 years BP) and Norway at 60° N in the Atlantic period (Zagwijn, 1994). In Britain there are Boreal records (8600–8000 years BP) of Mistletoe in Cumbria (Zagwijn, 1994).

The Atlantic period of the Holocene was the optimum for the species (Iversen, 1944) and range reductions occurred in Scandinavia and Poland after this (Granoszewski, 2003; Noryśkiewicz & Noryśkiewicz, 2017; Zagwijn, 1994). There may have been a similar retreat from northern Britain. The most recent preserved northern British pollen records are currently the four Mistletoe pollen grains found in the stomach of Lindow Man, the prehistoric bog body found in 1984 dated to 2 BC–119 AD (Joy, 2009), but the origin of those grains is not known. The contemporary disappearance of *Viscum* in Denmark may reflect forest decline, mostly due to human exploitation, and in particular felling *Tilia*, more than a cooling climate (Aaby, 1983; Gandil, 1950).

10.2 | Phylogenetics

Genetic studies of *V. album* across Europe have helped demonstrate the haplotypic diversity and historic differentiation of the different subspecies. Few of these studies include British populations, with just one population included in an otherwise wide-ranging study by Zuber and Widmer (2009). Since many British Mistletoe populations are thought to have a planted origin and may be derived from imported plants (Briggs, 2021) that sample may not be representative of British populations.

Phylogeographic studies indicate that the highest haplotypic diversity in *V. album* subsp. *abietis* is located in south-east Europe (Zuber & Widmer, 2009). The most common haplotype, out of eight detected, was widespread in all refugial areas of the host and its current range demonstrates that subsp. *abietis* survived in all the refugia of its *Abies* hosts. The presence of this haplotype in the Pyrenees, which is the part of the *Abies alba* range isolated from the remaining domains, at least from the last glacial period, suggests an ancestral state of this haplotype. Additionally, it may indicate a low genetic diversity of subsp. *abietis* populations in that part of the range (Litkowiec et al., 2021; Sancho-Knapik et al., 2014) but since only one Pyrenees population was investigated this requires further investigation. Genetically very distant haplotypes were discovered in Mistletoe growing on Turkish firs (*Abies cilicica* and *A. bornmuelleriana*). The pattern of genetic divergence between *Viscum* populations from Europe and the Asia Minor Peninsula found for subsp. *abietis* were also found in two other subspecies, reflecting long-term genetic isolation between gene pools from those geographic regions.

For subsp. *austriacum*, 10 different haplotypes have been identified with the greatest diversity noted in southern populations of *Pinus sylvestris* while in northern stands, a single haplotype dominated (Zuber & Widmer, 2009). This phylogeographic structure is common in many species and mirrors the northward direction of postglacial colonisation starting at the southern refugia and any bottleneck effect that was involved during range expansions (Hewitt, 2004). In the Iberian refugium subsp. *austriacum* could also survive on *P. nigra* and *P. pinaster*. There were significant differences among subsp. *austriacum* populations as those seen in subsp. *abietis*. Subspecies *creticum* possessed private haplotypes; interestingly they were more closely related with haplotypes detected in subsp. *abietis* than to haplotypes of subsp. *austriacum*.

Thirteen haplotypes were reported across 45 studied populations of subsp. *album*. Distribution of the two dominant haplotypes, H1 and H3, showed a clear geographic pattern, dividing the gene pool into western European and central European, respectively. In the UK, haplotype H1 was detected in a single population. Genetic differentiation among Mistletoe populations growing on deciduous trees was much lower ($G_{ST} = 0.521$) than in conifer hosts ($G_{ST} = 0.867$ and $G_{ST} = 0.791$ in subsp. *austriacium* and subsp. *abietis*, respectively) (Zuber & Widmer, 2009). Similar results were obtained in studies employing isozyme markers (Mejnartowicz, 2006). Higher genetic diversity in subsp. *album* can be attributed to a much wider range of hosts and in consequence, a wider distribution of Mistletoe. The result is higher intrapopulation diversity of Mistletoe populations on broadleaf species, because most of the conifer Mistletoe populations were fixed for a single haplotype that may also point to limitations in among-population gene flow (Zuber & Widmer, 2009). Population genetic studies in subsp. *album* in Belgium based on AFLP markers, indicated restricted among-population gene flow, especially in fragmented landscapes (Stanton et al., 2009). Significant distance between populations and abundance of Mistletoe on a single host may discourage pollinators and feeding birds from long-distance movement. Additionally, since the single host tree may support several Mistletoe individuals, the probability of bi-parental inbreeding increases resulting in a relatively high inbreeding level reported for highly fragmented populations (Stanton et al., 2009).

The most detailed phylogenetic survey of the *Viscum* genus by Maul et al. (2019) was based on concatenated nuclear (ITS1, ITS2 and 5.8 S rDNA regions) and plastid (*rbc L and trnF-L*) regions. This strongly supports the monophyletic origin of the genus that was earlier suggested (Mathiasen et al., 2008; Vidal-Russell & Nickrent, 2008). The former family Viscaceae appears to have diverged in the late Lower Cretaceous, *c.* 124 mya with the Australasian ancestral distribution (Maul et al., 2019). The crown group of *Viscum* genus appeared in the early Eocene and diverged from Phoradendrae *c.* 73 mya. The phylogenetic tree showed 10 well supported genetic clades (A–J), with *V. album* located in clade B that, together with clade A, are the oldest ones in the *Viscum* genus. The ancestor of the A/B clade separated from the remaining *Viscum* species *c.* 51 mya. *V. album* shares the clade with Sub-Saharan, Northern Africa, Southern Europe, temperate continental Asia and the Near East species that indicates a complex and not fully resolved evolutionary history. Phylogeographic studies of *V. album* on chloroplast DNA that included host specificity showed significant genetic discontinuity among gene pools of Mistletoes growing on different host tree species (Zuber & Widmer, 2009). These results therefore justified the taxonomic distinction of three subspecies within *V. album* with each taxon characterised by its own set of haplotypes. The likely mechanism of this intra-species divergence is evolution by way of host-race formation (Zuber & Widmer, 2009), suggested earlier for North American *Arceuthobium americanum* (Jerome & Ford, 2002). However, more studies are needed to understand to what extend the present genetic divergence within *V. album* is driven by adaptation to particular host species and to what extent it is govern by other factors, for example niche specificity, that was recently described for a Mexican Mistletoe species complex, *Psittacanthus schiedeanus* (Ramírez-Barahona et al., 2017).

10.3 | Mistletoe in ancient rituals, customs and superstitions

Viscum album is steeped in folklore; its growth habit, parasitic nature, the fact that it 'never touches the ground' and unusual white berries against evergreen foliage all contribute to its status as a special plant. In Britain and Ireland, it is best known as a plant for kissing under at Christmas, a notorious custom that by itself makes Mistletoe one of the best-known nonedible plants. This custom is, however, a recent development, popularised in the 19th century and promoted throughout Britain and the then British Empire (Briggs, 2021). The origins of the custom are unclear, but seem likely to be related to the plant's unusual properties and appearance, and to traditions relating to protection and fertility, with echoes of midwinter fertility traditions and also perhaps the myth of the Norse God Baldur, whose death by Mistletoe was followed by a promise that the plant would symbolise love and friendship in future (Lindow, 2002). The British kissing tradition has become widely adopted worldwide, often using local Mistletoe species other than *V. album*. Other winter uses in Europe, possibly now obscured by the kissing tradition, include the gifting of Mistletoe as a New Year good luck gift.

There are many other Mistletoe traditions in Britain, including carrying it when wishing to conceive, and sleeping with it to dream about a future husband. It is also seen as a symbol of good luck and protection, kept in the house all year (renewed each midwinter) to guard against witchcraft, lightning or other misfortunes (Mabey, 1996; Vickery, 1995).

Similar traditions are found across Europe. Twigs of Mistletoe were put to beehives to ensure good honey crops in the following year (Kowalski, 2007). Mistletoe was widely associated with fertility, both in humans and other animals. Berries were given to women with wine to enhance fertility, and in Austria, a twig of Mistletoe was put into the bed to encourage conception (Paine & Harrison, 1992). In Poland, twigs of Mistletoe were put into a child's bed to protect against nightmares (Kowalski, 1998). These traditions should be viewed against the wider folklore and customs of *Viscum* species for Indo-European people, reviewed in James Frazer's *The Golden Bough* (1920) on ancient religions and customs. The book takes its name from traditions celebrating Mistletoe's tendency to be yellowish both in life and when dried.

A number of traditions celebrate the plant's location, suspended between the Earth and the heavens, enhanced by it being evergreen, representing permanence and, on a deciduous host, ongoing life throughout the year (Madeja et al., 2009). The winter-ripening berries add to this significance. It is commonly held that Mistletoe was a divine plant for the Celts during the winter months, based on Pliny's famous account of Druids harvesting Mistletoe from oaks at the winter solstice. Despite doubts about the veracity of Pliny's account it is the basis of many later Mistletoe myths. Stories of oak, Mistletoe and the Druids were popularised in Britain from the 18th century (Briggs, 2021; Sell & Murrell, 2009). In the druidic custom, according to Pliny's account (and later extrapolations), oak was venerated because it rarely holds Mistletoe (Box, 2019; Frazer, 1920). Mistletoe from oak helped ensure the return of spring (Paine & Harrison, 1992), and was made into a drink that was a cure-all for humans and enhanced the fertility of domestic animals (Aldhouse-Green, 2010; Frazer, 1920). The druidic concept continues to attract speculation. The pollen grains found in the stomach of Lindow Man (Section 10.1) led to conjecture about druidic ritual and sacrifice (Aldhouse-Green, 2010; Gowlett et al., 1989). However this pollen may simply be the result of accidental ingestion (Joy, 2009). Many traditions, including the druid account, involve harvesting of plant without it touching the ground, as ground contact would remove its sacred properties (Aldhouse-Green, 2010; Frazer, 1920; Madeja et al., 2009). This tradition continues today with the hanging of Mistletoe above the floor as part of the kissing custom.

10.4 | Uses

There is a long history, going back into the mid-19th century, of harvest and substantial trade to meet the Christmas demand (Section 10.3). Most of the British harvest has been from the main Mistletoe area of the south-west midlands, where it is easily cropped from traditional apple orchards. Domestic supply has been supplemented by imports from mainland Europe, particularly from the apple orchards of northern France. It is possible that many of the isolated Mistletoe colonies in Britain owe their existence to this trade, either planted to create a local supply and/or from abandoned berries from Christmas (Briggs, 2021).

Viscum album has been used as a winter fodder crop. Across Europe it has been used for fodder since prehistoric times (Akbulut et al., 2019; Troels-Smith, 1960; Tubeuf et al., 1923). It was probably only used as a supplemental winter feed, not a primary food source (Ahmad et al., 2018; Gębczyńska, 1980), perhaps in early spring after previous crop failure (Stypiński, 1997). Some of the earliest evidence is from Neolithic cattle coprolites in Switzerland (Akeret & Rentzel, 2001) and there are many archaeobotanical records of leaves and berries being used as fodder in Mesolithic–Neolithic cultures in areas of Belgium (Deforce et al., 2013), Sweden (Göransson, 2002), Denmark (Robinson, 2007) and France (Delhon et al., 2008). Hejcman et al. (2014) suggest that Mistletoe, having higher nutritional value than bare twigs of deciduous species in winter, may have been preferentially fed to privileged livestock such as lactating cows in prehistoric times.

Most British farmers now strive to exclude it from animals because of worries about its toxicity (Section 10.5). Sheep and cattle will, however, readily consume the plant when they can access it

(Briggs, 2021). There is still some use of *V. album* as winter fodder in Kashmir (Ahmad et al., 2018) and as forage and silage in arid areas such as parts of Turkey (Öztürk et al., 2022). Recent studies in Turkey have shown that though low in protein and moderate in fibre, it is high in minerals and ascorbic acid (0.85%) and is a useful complementary feed for ruminants (Umucalılar et al., 2007).

Consumption by humans is rare, other than drunk as a tisane. Tubeuf et al. (1923) state that during periods of food shortages, poor villagers in Germany would dry shoots of *Viscum* before grinding them to supplement rye flour.

Other potential usage includes as catalysts in partial hydrogenation reactions of biodiesel (Erenturk & Korkut, 2018), nanocellulose-based material (Horbelt et al., 2019) and inducing resistance to downy mildew disease in pearl millet *Pennisetum glaucum* (L.) R. Br. (Chandrashekhara et al., 2010).

10.5 | Pharmaceutical use

Viscum album is often considered to be a poisonous plant (Pfüller, 2000; Stein, 2000) as it contains several biologically active compounds such as lectins, viscotoxins, different peptides such as viscumamide, different amino acids, thiols, alkaloids, minerals, phytosterols, triterpene acids, amines, oligo- and polysaccharides (Elluru et al., 2008; Ochocka & Piotrowski, 2002; Vicaş et al., 2011; Yousefvand et al., 2022)—Section 6.6. Their biological properties are reviewed by Büssing (2000b) and toxicology by Stein (2000).

Pharmaceutical properties have long been known among people and cultures spanning the natural range of the species. Herbal uses were documented by ancient scholars, including in Dioscorides' *De Materia Medica* (50–70 AD), and were repeated in numerous herbals throughout the Middle Ages. Purported benefits included general healing, fertility treatments, as a calming agent, for purulent wounds, curing coughs and even mental issues (Goode et al., 2022). In Britain, Mistletoe was described as a cure for convulsions by Colbatch (1719).

In continental Europe, Mistletoe tisane is popular today as a calming drink and is a key ingredient of herbal veterinary medicines for calming pets (e.g. Dorwest, 2022). It is also an ingredient of some cosmetics. In traditional Turkish medicine, subsp. *austriacum* is used for blood pressure regulation, as a vasodilator drug, and other uses includes diabetes, arthrosis and cancer treatment (Akbulut et al., 2019; Bulut et al., 2017). The infusion made of Mistletoe in India serves as a laxative, while ash from burning dry plants is used for healing wounds (Ahmad et al., 2018). Other applications of *Viscum*-based preparations include as an astringent, diuretic, haemostatic, anaesthetic, analgesic, anti-inflammatory, antisclerotic, immune-stimulating, sedative, hepatoprotective, antioxidant, antidiabetic activities, and in treating epilepsy, migraine, ulcers, eczema, rheumatism and joint pains, and pain relief including labour pain (Ahmad et al., 2018; Büssing, 2000b; Hussain et al., 2011; Nazaruk & Orlikowski, 2016; Önay-Uçar et al., 2006; Shah et al., 2017; Ullah et al., 2022; Vicaş et al., 2011).

Extracts from dried *V. album* leaves and stems have antimicrobial properties against a range of bacteria and fungi, including *Candida albicans* (Ascomycota, Saccharomycetales) (Ertürk et al., 2003; Hussain et al., 2011). However, use of extracts of *V. album* against *Mycobacterium tuberculosis* have proved inconclusive (Deliorman et al., 2001).

Anticancer activity of *V. album* extracts is ascribed to lectins and viscotoxins that have cytotoxic and immunomodulatory properties (Amer et al., 2012; Twardziok et al., 2016) and commercial preparations are available (e.g. Iscador and AbnobaVISCUM). Use of Mistletoe in cancer therapy was proposed in 1919 but its effectiveness is not always clear (Kleijnen & Knipschild, 1994). A potential use of *Viscum* preparations in neuroblastoma supportive treatment has been identified (Menke et al., 2019). *Viscum*-based preparations have been shown to positively affect the quality of life of palliative patients and those under conventional cancer treatments (Gaafar et al., 2014; Kienle & Kiene, 2010; Thronicke et al., 2018) reducing side-effects from chemotherapy used to treat ovary, cervical and breast cancers (Hwang et al., 2019; Reynel et al., 2018; Semiglazov et al., 2006). High dosages, however, may be harmful with strong side-effects (Kienle et al., 2011).

Anti-tumour activity of *Viscum* preparations is not yet fully understood but immunostimulatory properties are certainly involved and *Viscum* extracts positively affect the dendritic cells of the immune system (Elluru et al., 2008). In vitro investigations on cervical cancer cells indicated that lectins of subsp. *abietis* are involved in inducing apoptosis (Mavrikou et al., 2020). Moreover, extracts from *V. coloratum* induce antiproliferation and antimigratory properties on osteosarcoma cells by decreasing DNA synthesis and interfering with the cell cycle and slowing metastasis (Ge et al., 2016).

11 | CONSERVATION AND MANAGEMENT

The status of *V. album* in Britain is Least Concern (Cheffings et al., 2005), a view confirmed by a national survey in the 1990's (Briggs, 1999). Concerns that orchard loss might threaten Mistletoe seem unfounded (Briggs, 2021). However, because Mistletoe is scarce in many areas, it is often included in local conservation plans, particularly local biodiversity plans. Examples include the Greater London Biodiversity Plan where it was included on the basis of local rarity, cultural value and ease of monitoring. Conservation plans often include local planting projects (Briggs, 2021). Some of the monophagous insects whose UK status is scarce, have conservation status. The leaf-mining monophagous moth *Celypha woodiana* (Lepidoptera, Tortricidae) is a Priority Species in the UK Biodiversity Action Plan and *Anthocoris visci* (Hemiptera, Anthocoridae) is considered a Nationally Notable B species.

Mistletoe has been a popular garden and parkland plant for centuries and is still actively sought-after and planted. Commercial kits are now available (Briggs, 2021) that make such plantings more frequent. Once established it can, over several decades, spread into surrounding areas. It seems unlikely that the species will become scarcer in current conditions.

Mistletoe is also a problem in many circumstances, especially areas where it is abundant and where there are multiple growths per host (Section 5.2). Since most seeds are spread locally, within the original host or to adjoining trees, such multiple infections are frequently seen, though they may have taken decades to develop in new sites. In Britain the problem is particularly acute in neglected traditional orchards in the south-west English midlands. A sustainable balance, keeping some Mistletoe, is possible with the level of management depending on the desired outcome (Briggs, 2021) ranging from simple control to ensuring some harvest for seasonal use. Simple pruning is effective in an orchard or garden situation, not killing the Mistletoe but reducing its mass. The balance of male and female plants is an important factor; controlling female plants will limit seed production and reduce further infections, a good strategy for long-term simple control. However, it is these female growths that are needed for Christmas harvesting; the berryless male being valueless except for pollination. Strategic management for such harvest will retain a proportion of female plants but will cut (and discard) much of the male growth to reduce long-term impact of those on the host.

This mix of conservation and control is similar across Europe. Mistletoe is protected in a few countries, though usually only at the border of its range. For example, it is protected in Sweden but the landowner can harvest plants to care for the host tree if it does not affect survival of the population (Swedish Environmental Protection Agency, 2016). In Norway, Mistletoe has been protected since 1956 and host trees have been protected since 1976 due to its rarity (Osthagen, 1984). De Graaf (1980) noted a severe decline of half the subsp. *album* populations since 1917–1939 in the Netherlands attributed to decline in orchards of the major host, *Malus domestica*. However, since 2017, due to the expansion of its range, Mistletoe has ceased to be protected (Anon, 2022).

Subspecies that grow on conifers are often considered as pests in commercial plantings as it has a negative impact on reproduction (Jasiczek et al., 2017). Mistletoe can be controlled by removal of host species, cultivars or genotypes sensitive to this hemiparasite (Hariri et al., 1991; Sallé et al., 1994), and by avoiding monocultures and even-aged stands (Thapa, 2013). For example, the level of Mistletoe infestation in mixed stands is lower than in monoculture *Pinus sylvestris* stands (van Halder et al., 2019). Thinning of stands should also be avoided to limit the amount of light in tree crowns and thus Mistletoe establishment (Iszkuło et al., 2020). Wrapping infected branches with sturdy black plastic to exclude light can work but may also result in rot in the host due to moisture accumulation (Bhat et al., 2022). However, the most effective and often the only method of controlling Mistletoe is pruning away infected branches and removing trees (Noetzli et al., 2003). Removing just the Mistletoe shoots does not solve the problem as the plant resprouts from the haustorium (Bhat et al., 2022; Tubeuf et al., 1923). It has been shown that the removal of branches infected by Mistletoe has a positive effect on the growth and development of *Pinus sylvestris* (Yan et al., 2016).

Removing trees may be useful when single trees are infected. However, Mistletoe infection becomes of concern only once significant numbers of plants have accumulated, and generally the most valuable, dominant hosts are the most infested (Durand-Gillmann et al., 2014; Pilichowski et al., 2018; Sangüesa-Barreda et al., 2012) and control may be difficult. Therefore, early detection can be crucial for controlling Mistletoe. Ančić et al. (2014) developed a technique for mapping the distribution and intensity of infection of subsp. *abietis* on *Abies alba* in Croatia using aerial hyperspectral scanning.

Systemic herbicides, such as glyphosate or ethefon, applied directly can be used to control Mistletoe (Baillon et al., 1988; Bhat et al., 2022). Safe herbicide doses for the host and other organisms usually do not destroy the endophytic system of the hemiparasite, allowing it to quickly resprout (Bhat et al., 2022). Simultaneous mechanical removal and chemical treatment with 5%–10% ethephon or glyphosate in a *Juglans regia* plantation in Kashmir Valley, India was very effective in controlling subsp. *album* (Bhat et al., 2022).

Changes in infestation levels and distribution range, attributable to climate change, have been reported across Britain and mainland Europe (Briggs, 2021; Laiviņš, 2003; Vallauri et al., 2002; Varga et al., 2014; Walldén, 1961; Zuber, 2004). Examples of range expansion include heavier infestations and a three-fold increase in range in Hungary (Varga et al., 2014), an expansion in both natural and urban areas in Ukraine (Krasylenko et al., 2020), eastward expansion in Poland (Lech et al., 2020), and increasing density of Mistletoe populations in Bosnia and Herzegovina (Mujezinović et al., 2017). Altitudinal increases of 150–200 m over the past 90 years have been reported in the Swiss Alps (Dobbertin et al., 2005) and 200–300 m increase in southern Spain (Zamora & Mellado, 2019).

Predictions of geographical range change as a result of climate change differ according to the predictive model used. Jeffree and Jeffree (1996) found that a predicted increase in continentality of Europe's climate (2°C decrease in coldest month and 2°C increase in the warmest month) would lead to the current range of *V. album* moving to the north-west with a retraction in its south-east range by 1200 km. This change would result in the potential loss of Mistletoe from Italy, the former Yugoslavia, Romania, Greece and Bulgaria. However, an increase in the oceanity of Europe's climate (2°C increase in coldest month and 2°C decrease in warmest month) would displace the current range by 1000 km to the south-east, potentially extending its range into Turkey and the Caucasus. The established British and Mediterranean ranges may, however, be at risk with continuing rises in winter temperatures and may possibly cause its complete loss (Jeffree & Jeffree, 1996; Zuber, 2004). However, response to climate change appears to be different for each of the three main subspecies. Subspecies *album* is predicted to spread in all directions, depending upon specific temperature changes, but subsps *austriacum* and *abietis* are likely to move north and east with a slight decrease in occurrence in southern and western Europe (Walas et al., 2022). In the case of subsps *austriacum* and *abietis*, reliant on a limited range of host species, changes of the host range is also crucial. The range of *Pinus sylvestris* and *Abies alba* is predicted to be reduced (Dyderski et al., 2018), with significant effects on the range of these two Mistletoe subspecies.

AUTHOR CONTRIBUTIONS

Jonathan Briggs, Grzegorz Iszkuło, Marian J. Giertych and Peter A. Thomas conceived the idea for this account; Peter A. Thomas, Monika Dering, Marian J. Giertych, Grzegorz Iszkuło, Dominik Tomaszewski and Jonathan Briggs each wrote sections; Peter A. Thomas compiled the first draft. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

Dr A.G. Irwin is thanked for his detailed checking of the lists of insects. Peter Thomas is grateful to Harvard Forest, Harvard University, USA for access to their libraries; Jonathan Briggs is grateful to the Open University for library access and innumerable colleagues for Mistletoe discussions over many years. In Poland, Jerzy Zieliński, Adam Boratyński and Łukasz Walas are thanked for their unstinting sharing of information.

CONFLICT OF INTEREST

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

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.14036.

DATA AVAILABILITY STATEMENT

This study does not include data.

ORCID

Peter A. Thomas https://orcid.org/0000-0003-3115-3301
Monika Dering https://orcid.org/0000-0001-7017-5541
Marian J. Giertych https://orcid.org/0000-0001-5578-9545
Grzegorz Iszkuło https://orcid.org/0000-0003-2067-729X
Dominik Tomaszewski https://orcid.org/0000-0001-7768-5747
Jonathan Briggs https://orcid.org/0000-0001-7650-1555

REFERENCES

Aaby, B. (1983). Forest development, soil genesis and human activity illustrated by pollen and hypha analysis of two neighbouring podzols in Draved Forest, Denmark. *Danmarks Geologiske Undersøgelse II. Række*, *114*, 1–114. https://doi.org/10.34194/raekke2.v114.6905

Ahmad, S., Mir, N. H., & Sultan, S. M. (2018). White-berry mistletoe (*Viscum album* L.): A hemiparasitic plant: Occurrence and ethno-botanical use in Kashmir. *Journal of Pharmacognosy and Phytochemistry*, *7*, 1831–1833.

Akbulut, S., Karakose, M., & Özkan, Z. C. (2019). Traditional uses of some wild plants in kale and Acıpayam provinces in Denizli. *Kastamonu University Journal of Forestry Faculty*, *19*, 72–81.

Akeret, Ö., & Rentzel, P. (2001). Micromorphology and plant macrofossil analysis of cattle dung from the Neolithic lake shore settlement of Arbon Bleiche 3. *Geoarchaeology*, *16*, 687–700.

Aldhouse-Green, M. (2010). CHAPTER 1: The moon and the mistletoe in search of ancient druids. In *Caesar's druids: Story of an ancient priesthood* (pp. 1–19). Yale University Press. https://doi.org/10.12987/9780300165883-004

Amer, B., Juvik, O. J., Dupont, F., Francis, G. W., & Fossen, T. (2012). Novel aminoalkaloids from European mistletoe (*Viscum album* L.). *Phytochemistry Letters*, *5*, 677–681.

Ančić, M., Pernar, R., Bajić, M., Seletković, A., & Kolić, J. (2014). Detecting mistletoe infestation on silver fir using hyperspectral images. *iForest*, *7*, 85–91.

Anon. (2022). *Nature conservation act*. The Netherlands Government. https://wetten.overheid.nl/BWBR0037552/2017-03-01#Bijlage

Arda, N., Onay-Uçar, E., Koz, Ö., & Kırmızıgül, S. (2003). Monosaccharides and polyols from mistletoes (*Viscum album* L.) growing on two different host species. *Biologia*, *58*, 1037–1041.

Azuma, J.-I., Kim, N., Heux, L., Vuong, R., & Chanzy, H. (2000). The cellulose system in viscin from mistletoe berries. *Cellulose*, *7*, 3–19.

Baillon, F., Chamel, A., Fer, A., Frochot, H., Gambonnet, B., & Manzato, M. C. (1988). Lutte chimique contre le gui (*Viscum album* L.). Pénétration, transport, efficacité de deux herbicides phloème-mobiles (2,4-DB et glyphosate). *Annales des Sciences Forestières*, *45*, 1–16.

Baltazár, T., Pejchal, M., & Varga, I. (2013). Evaluation of European mistletoe (*Viscum album* L.) infection in the Castle Park in Lednice. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis*, *61*, 1565–1574.

Barbu, C. (2009). Impact of mistletoe attack (*Viscum album* ssp. *abietis*) on the radial growth of silver fir. A case study in the north of eastern Carpathians. *Annals of Forest Research*, *52*, 89–96.

Barbu, C. (2012). Impact of white mistletoe (*Viscum album* ssp. *abietis*) infection on needles and crown morphology of silver fir (*Abies alba* mill.). *Notulae Botanicae Horti Agrobotanici*, *40*, 152–158.

Barlow, B. A. (1981). *Viscum album* in Japan: Chromosomal translocations, maintenance of heterozygosity and the evolution of dioecy. *The Botanical Magazine Tokyo*, *94*, 21–34.

Barlow, B. A., Wiens, D., Wiens, C., Busby, W. H., & Brighton, C. (1978). Permanent translocation heterozygosity in *Viscum album* and *V. cruciatum*: Sex association, balanced lethals, sex ratios. *Heredity*, *40*, 33–38.

Barney, C. W., Hawksworth, F. G., & Geils, B. W. (1998). Hosts of *Viscum album*. *European Journal of Forest Pathology*, *28*, 187–208.

Becker, H. (1986). Botany of European mistletoe (*Viscum album* L.). *Oncology*, *43*(Suppl. 1), 2–7.

Becker, H. (2004). European mistletoe: Taxonomy, host trees, parts used, physiology. In A. Büssing (Ed.), *Mistletoe: The genus Viscum* (pp. 31–43). Harwood Academic. http://www.crcnetbase.com/isbn/9789058230928

Bell, T. L., & Adams, M. A. (2011). Attack on all fronts: Functional relationships between aerial and root parasitic plants and their woody hosts and consequences for ecosystems. *Tree Physiology*, *31*, 3–15.

Berthet, P. (2008). Présence du gui (*Viscum album* L.) sur chêne d'Amérique (*Quercus palustris* Münch). *Bulletin Mensuel de la Société Linnéenne de Lyon*, *77*, 155. https://doi.org/10.3406/linly.2008.13690

Bhat, K. A., Akhtar, S., Dar, N. A., Bhat, M. I., Bhat, F. A., Rizwan, R., Horielov, O., & Krasylenko, Y. (2022). Mistletoe eradicator—A novel tool for simultaneous mechanical and chemical control of mistletoe. *Journal of Visualized Experiments*, *181*, e63455.

Bilgili, E., Coskuner, K. A., Baysal, I., Ozturk, M., Usta, Y., Eroglu, M., & Norton, D. (2020). The distribution of pine mistletoe (*Viscum album* ssp. *austriacum*) in scots pine (*Pinus sylvestris*) forests: From stand to tree level. *Scandinavian Journal of Forest Research*, *35*, 20–28.

Bilgili, E., Ozturk, M., Coskuner, K. A., Baysal, I., Serdar, B., Yavuz, H., Eroglu, M., & Usta, Y. (2018). Quantifying the effect of pine mistletoe on the growth of scots pine. *Forest Pathology*, *48*, e12435.

Bilgili, E., Serdar, B., Eroglu, M., Alperen Coskuner, K., & Baysal, I. (2013). Determination of age of mistletoe (*Viscum album* ssp. *austriacum* (Wiesb.) Vollman) on scots pine (*Pinus sylvestris* L.). International Caucasian forestry symposium, October, 24–26, Artvin, Turkey, pp. 142–146.

Bober, A., Pidek, I. A., & Żarski, M. (2018). Late Saalian and Eemian interglacial at the Struga site (Garwolin plain, Central Poland). *Acta Palaeobotanica*, *58*(2), 219–229. https://doi.org/10.2478/acpa-2018-0007

Böhling, N., Greuter, W., Raus, T., Snogerup, B., Snogerup, S., & Zuber, D. (2002). Notes on the Cretan mistletoe, *Viscum album* subsp. *creticum* subsp. nova (Loranthaceae/Viscaceae). *Israel Journal of Plant Sciences*, *50*, 77–84.

Boratyńska, K., & Boratyński, A. (1976). *Viscum album* L.—Jemioła pospolita. In K. Browicz (Ed.), *Atlas rozmieszczenia drzew I krzewów w Polsce [Atlas of distribution of trees and shrubs in Poland]* (Vol. *19*, pp. 9–12). Państwowe Wydawnictwo Naukowe.

Box, J. (2019). Oaks (*Quercus* spp.) parasitised by mistletoe *Viscum album* (Santalaceae) in Britain. *British & Irish Botany*, *1*(1), 39–49. https://doi.org/10.33928/bib.2019.01.039

Box, J. D. (2000). Mistletoe *Viscum album* L. (Loranthaceae) on oaks in Britain. *Watsonia*, *23*, 237–256.

Briem, F., Eben, A., Gross, J., & Vogt, H. (2016). An invader supported by a parasite: Mistletoe berries as a host for food and reproduction of spotted wing drosophila in early spring. *Journal of Pest Science*, *89*, 749–759.

Briggs, J. (1999). *Kissing goodbye to mistletoe?* Report published by Plantlife and the Botanical Society of Britain & Ireland.

Briggs, J. (2011a). Mistletoe (*Viscum album*); a brief review of its local status with recent observations on its insect associations and conservation problems. *Proceedings of the Cotteswold Naturalists' Field Club*, *45*, 181–193.

Briggs, J. (2011b). Mistletoe—A review of its distribution, conservation and insect associates. *British Wildlife*, *23*, 23–31.

Briggs, J. (2012). *Briggs' Outer Barklouse found on Mistletoe!* [online blog]. https://Mistletoediary.com/2012/04/

Briggs, J. (2021). Mistletoe, *Viscum album* (Santalaceae), in Britain and Ireland; a discussion and review of current status and trends. *British & Irish Botany*, *3*(4), 419–454.

Bulíř, P. (2017). Extent of infection by *Viscum album* L. and changes in its occurrence on ornamental woody species in the locality of Lednice (Czech Republic). *Folia Horticulturae*, *29*, 123–134.

Bull, H. G. (1864). The mistletoe in Herefordshire. *Transactions of the Woolhope Naturalists Field Club*, *5*, 59–108.

Bulut, G., Haznedaroğlu, M. Z., Doğan, A., Koyu, H., & Tuzlacı, E. (2017). An ethnobotanical study of medicinal plants in Acipayam (Denizli-Turkey). *Journal of Herbal Medicine*, *10*, 64–81.

Burkhardt, D. (1982). Birds, berries and UV. A note on some consequences of UV vision in birds. *Die Naturwissenschaften*, *69*, 153–157.

Busch, K. B. (2018). Respiration: Life without complex I. *Current Biology*, *28*(10), R616–R618. https://doi.org/10.1016/j.cub.2018.04.030

Büssing, A. (2000a). Cultivation and development of *Viscum album* L. In A. Büssing (Ed.), *Mistletoe, the genus Viscum* (pp. 75–94). Harwood Academic Publishers.

Büssing, A. (2000b). Biological and pharmacological properties of *Viscum album* L. In A. Büssing (Ed.), *Mistletoe, the genus Viscum* (pp. 123–182). Harwood Academic Publishers.

Butterfass, T. (1987). The transverse orientation of stomata. *The Botanical Review*, *53*(4), 415–441. https://doi.org/10.1007/BF02858323

Butu, A., Rodino, S., Ferdes, M., & Butu, M. (2013). Molecular dynamics simulation for seven structures of viscotoxin. *Digest Journal of Nanomaterials and Biostructures*, *8*, 1–10.

Cadbury, C. J., & Oswald, P. H. (2009). Mistletoe undergoes an explosive increase in Cambridge. *Nature in Cambridgeshire*, *51*, 50–60.

Camarero, J. J., de Andrés, E. G., Sangüesa-Barreda, G., Rita, A., & Colangelo, M. (2019). Long- and short-term impacts of a defoliating moth plus mistletoe on tree growth, wood anatomy and water-use efficiency. *Dendrochronologia*, *56*, 125598.

Catal, Y., & Carus, S. (2011). Effect of pine mistletoe on radial growth of Crimean pine (*Pinus nigra*) in Turkey. *Journal of Environmental Biology*, *32*, 263–270.

Chandrashekhara, S., Niranjan, R., Manjunath, G., Deepak, S., & Shetty, S. H. (2010). Seed treatment with aqueous extract of *Viscum album* induces resistance to pearl millet downy mildew pathogen. *Journal of Plant Interactions*, *5*, 283–291. https://doi.org/10.1080/17429140903556539

Cheddadi, R., Birks, H. J. B., Tarroso, P., Liepelt, S., Gömöry, D., Dullinger, S., Meier, E. S., Hülber, K., Maiorano, L., & Laborde, H. (2014). Revisiting tree-migration rates: *Abies alba* (Mill.), a case study. *Vegetation History and Archaeobotany*, *23*(2), 113–122. https://doi.org/10.1007/s00334-013-0404-4

Cheffings, C. M., Farrell, L., Dines, T. D., Jones, R. A., Leach, S. J., McKean, D. R., Pearman, D. A., Preston, C. D., Rumsey, F. J., & Taylor, I. (2005). *The vascular plant red data list for Great Britain*. Species Status 7. Joint Nature Conservation Committee.

Chereji, I., Daraban, L., Dreve, S., Boscaneanu, S., Cosma, C., & Vari, E. (1996). Chernobyl-derived radiocesium in some pharmaceutical plants. *Journal of Radioanalytical and Nuclear Chemistry*, *212*, 85–92.

Colbatch, J. (1719). *A dissertation concerning mistletoe: Most wonderful specifick remedy for the cure of convulsive distempers*. Privately Published.

Cullings, K., Raleigh, C., & Vogler, D. R. (2005). Effects of severe dwarf mistletoe infection on the ectomycorrhizal community of a *Pinus contorta* stand in Yellowstone Park. *Canadian Journal of Botany*, *83*, 1174–1180.

Czeczuga, B., Godlewska, A., Mazalska, B., & Muszyńska, E. (2010). Diversity of aquatic fungi and fungus-like organisms on fruits. *Nova Hedwigia*, *90*, 123–151.

Dai, J.-K., Cao, D., Li, C.-H., Gao, J., Li, M.-Q., Fan, N., Wei, Y.-H., Sun, Z.-L., & Hou, M.-Y. (2019). Three new bioactive flavonoid glycosides from *Viscum album*. *Chinese Journal of Natural Medicines*, *17*, 545–550.

Damm, O. (1902). Über den Bau, die Entwicklungsgeschichte und die mechanischen Eigenschaften mehrjähriger Epidermen. *Beihefte Zum Botanischen Centralblatt*, *11*, 219–260.

Daryaei, M. G., & Moghadam, E. S. (2012). Effects of mistletoe (*Viscum album* L.) on leaves and nutrients content of some host trees in Hyrcanian forests (Iran). *International Journal of Agriculture: Research and Review*, *2*, 85–90.

DBIF. (2022). *Database of insects and their food plants*. http://www.brc.ac.uk/dbif/homepage.aspx

De Graaf, D. T. (1980). On the occurrence of *Viscum album* L. subsp. *album* (Loranthaceae) in The Netherlands. *Acta Botanica Neerlandica*, *29*, 377–383.

Deforce, K., Bastiaens, J., Van Neer, W., Ervynck, A., Lentacker, A., Sergant, J., & Crombé, P. (2013). Wood charcoal and seeds as indicators for animal husbandry in a wetland site during the lateuropeanc–early neolithic transition period (Swifterbant culture, ca. 4600–4000 B.C.) in NW Belgium. *Vegetation History and Archaeobotany*, *22*(1), 51–60. https://doi.org/10.1007/s00334-012-0354-2

Delhon, C., Martin, L., Argant, J., & Thiébault, S. (2008). Shepherds and plants in the Alps: Multi-proxy archaeobotanical analysis of neolithic dung from 'La Grande Rivoire' (Isère, France). *Journal of Archaeological Science*, *35*(11), 2937–2952. https://doi.org/10.1016/j.jas.2008.06.007

Deliorman, D., Ergun, F., Sener, B., & Palittapongarnpim, P. (2001). Evaluation of antimycobacterial activity of *Viscum album* subspecies. *Pharmaceutical Biology*, *39*, 381–383.

Denk, T., Grímsson, F., Zetter, R., & Símonarson, L. A. (2011). Pliocene terrestrial and marine biota of the *Tjörnes peninsula*: Warm climates and biogeographic re-arrangements. In T. Denk, F.

Grimsson, R. Zetter, & L. A. Símonarson (Eds.), *Late Cainozoic floras of Iceland: 15 million years of vegetation and climate History in the northern North Atlantic* (pp. 491–554). Springer. https://doi.org/10.1007/978-94-007-0372-8_10

Derbidge, R., Baumgartner, S., & Heusser, P. (2016). Mistletoe berry outline mapping with a path curve function and recording the circadian rhythm of their phenotypic shape change. *Frontiers in Plant Science*, *7*, 1749.

Digirolomo, F. M., Jendek, E., Grebennikov, V. V., & Nakládal, O. (2019). First north American record of an unnamed west Palaearctic *Agrilus* (Coleoptera: Buprestidae) infesting European beech (*Fagus sylvatica*) in new York City, USA. *European Journal of Entomology*, *116*, 244–252.

Dobbertin, M., Hilker, N., Rebetez, M., Zimmermann, N. E., Wohlgemuth, T., & Rigling, A. (2005). The upward shift in altitude of pine mistletoe (*Viscum album* ssp *austriacum*) in Switzerland—The result of climate warming? *International Journal of Biometeorology*, *50*, 40–47. https://doi.org/10.1007/s00484-005-0263-5

Dobbertin, M., & Rigling, A. (2006). Pine mistletoe (*Viscum album* ssp *austriacum*) contributes to scots pine (*Pinus sylvestris*) mortality in the Rhone valley of Switzerland. *Forest Pathology*, *36*, 309–322.

Doğan, G., Erdoğdu, M., Aytaç, Z., Karayel, A. I., Suludere, Z., & Ertuğrul, T. (2022). Five new foliicolous micromycete records from Turkey. *Mycotaxon*, *136*, 841–852.

Dorwest. (2022). *Valerian compound for dogs and cats*. [online retail description]. https://www.dorwest.com/product/valerian-compound-for-dogs-and-cats/

Dorworth, C. E. (1989). European mistletoe (*Viscum album* subsp *album*) in Canada. *Plant Disease*, *73*(5), 444.

Durand-Gillmann, M., Cailleret, M., Boivin, T., Nageleisen, L.-M., & Davi, H. (2014). Individual vulnerability factors of silver fir (*Abies alba* mill.) to parasitism by two contrasting biotic agents: Mistletoe (*Viscum album* L. ssp. *abietis*) and bark beetles (Coleoptera: Curculionidae: Scolytinae) during a decline process. *Annals of Forest Science*, *71*, 659–673.

Dyderski, M. K., Paź, S., Frelich, L. E., & Jagodziński, A. M. (2018). How much does climate change threaten European forest tree species distributions? *Global Change Biology*, *24*(3), 1150–1163. https://doi.org/10.1111/gcb.13925

Elluru, S. R., van Huyen, J.-P. D., Delignat, S., Kazatchkine, M. D., Friboulet, A., Kaveri, S. V., & Bayry, J. (2008). Induction of maturation and activation of human dendritic cells: A mechanism underlying the beneficial effect of *Viscum album* as complementary therapy in cancer. *BMC Cancer*, *8*(1), 161. https://doi.org/10.1186/1471-2407-8-161

Erenturk, S., & Korkut, Ö. (2018). Effectiveness of activated mistalea (*Viscum album* L.) as a heterogeneous catalyst for biodiesel partial hydrogenation. *Renewable Energy*, *117*, 374–379.

Ertürk, Ö., Kati, H., Yayli, N., & Demirbağ, Z. (2003). Antimicrobial activity of *Viscum album* L. subsp. *abietis* (Wiesb). *Turkish Journal of Biology*, *27*, 255–258.

Escher, P., Eiblmeier, M., Hetzger, I., & Rennenberg, H. (2003). Seasonal and spatial variation of reduced Sulphur compounds in mistletoes (*Viscum album*) and the xylem sap of its hosts (*Populus euramericana* and *Abies alba*). *Physiologia Plantarum*, *117*, 72–78.

Escher, P., Eiblmeier, M., Hetzger, I., & Rennenberg, H. (2004a). Seasonal and spatial variation of carbohydrates in mistletoes (*Viscum album*) and the xylem sap of its hosts (*Populus × euamericana* and *Abies alba*). *Physiologia Plantarum*, *120*, 212–219.

Escher, P., Eiblmeier, M., Hetzger, I., & Rennenberg, H. (2004b). Spatial and seasonal variation in amino compounds in the xylem sap of a mistletoe (*Viscum album*) and its hosts (*Populus* spp. and *Abies alba*). *Tree Physiology*, *24*, 639–650.

Escher, P., Eiblmeier, M., & Rennenberg, H. (2004). Differences in the influx of glutamine and nitrate into *Viscum album* from the xylem sap of its hosts. *Plant Physiology and Biochemistry*, *42*, 739–744.

Escher, P., Peuke, A. D., Bannister, P., Fink, S., Hartung, W., Jiang, F., & Rennenberg, H. (2008). Transpiration, CO_2 assimilation, WUE, and stomatal aperture in leaves of *Viscum album* (L.): Effect of abscisic acid (ABA) in the xylem sap of its host (*Populus × euamericana*). *Plant Physiology and Biochemistry*, *46*, 64–70. https://doi.org/10.1016/j.plaphy.2007.07.018

Escher, P., & Rennenberg, H. (2006). Influx of double labelled glutamine into mistletoes (*Viscum album*) from the xylem sap of its host (*Abies alba*). *Plant Physiology and Biochemistry*, *44*, 880–884.

Fiedler, J., & Vyhnálek, V. (1977). Neobvyklý nález *Viscum album*. *Floristické Správy, Biológia*, *32*, 549–550.

Frazer, J. G. (1920). The golden bough. In *The magic art and the evolution of kings* (Vol. *1*, 3rd ed.). Macmillan.

Frochot, H., & Sallé, G. (1980). Modalités deuropeaneann et d'implantation du gui. *Revue Forestière Française*, *6*, 505–519. https://doi.org/10.4267/2042/21437

Fukunaga, T., Kajikawa, I., Nishiya, K., Takeya, K., & Itokawa, H. (1989). Studies on the constituents of the Japanese mistletoe, *Viscum album* L. var. *coloratum* Ohwi grown on different host trees. *Chemical and Pharmaceutical Bulletin*, *37*, 1300–1303.

Gaafar, R., Abdel Rahman, A. R. M., Aboulkasem, F., & El Bastawisy, A. (2014). Mistletoe preparation (Viscum Fraxini-2) as palliative treatment for malignant pleural effusion: A feasibility study with comparison to bleomycin. *Ecancermedicalscience*, *8*, 424. https://doi.org/10.3332/ecancer.2014.424

Galiano, L., Martínez-Vilalta, J., & Lloret, F. (2011). Carbon reserves and canopy defoliation determine the recovery of scots pine 4 yr after a drought episode. *New Phytologist*, *190*, 750–759.

Gandil, C. (1950). Misteltonen, *Viscum album* L. *Dansk Dendrologisk Arsskrift*, *1*, 39–75.

Ge, Y., Wang, Y., Pang, L., Zhang, L., Zhai, Y., & Zhou, H. (2016). Proliferation, apoptosis, and invasion effects of mistletoe alkali on human osteosarcoma U20S *in vitro*. *Orthopaedic Surgery*, *101*, 282–290.

Gebauer, R., Volařík, D., & Urban, J. (2018). Seasonal variations of sulphur, phosphorus and magnesium in the leaves and current-year twigs of hemiparasitic mistletoe *Loranthus europaeus* Jacq. and its host *Quercus pubescens* Willd. *Journal of Forest Science*, *64*, 66–73.

Gębczyńska, Z. (1980). Food of the roe deer and red deer in the Białowieża primeval Forest. *Acta Theriologica*, *25*, 487–500. https://doi.org/10.4098/AT.arch.80-44

Gehring, C. A., & Whitham, T. G. (1992). Reduced mycorrhizae on *Juniperus monosperma* with mistletoe: The influence of environmental stress and tree gender on a plant parasite and a plant-fungal mutualism. *Oecologia*, *89*, 298–303.

Goode, E. C., Van Duser, S. E., Rogers, R. R., Williams, T. D., & Ballmann, C. G. (2022). Effects of acute mistletoe (*Viscum album* L.) ingestion on aerobic exercise performance. *Nutraceuticals*, *2*, 162–169.

Göransson, H. (2002). Alvastra pile dwelling—A 5000 year-old byre? In V. Karin (Ed.), *Nordic archaeobotany-NAG 2000 in Umeå, Miljöarkeologiska laboratoriet* (pp. 67–84). Institutionen för arkeologi och samiska studier.

Gowlett, J. A. J., Hedges, R. E. M., & Law, I. A. (1989). Radiocarbon accelerator (AMS) dating of Lindow man. *Antiquity*, *63*(238), 71–79. https://doi.org/10.1017/S0003598X00075591

Granoszewski, W. (2003). Late Pleistocene vegetation history and climatic changes at Horoszki Duże, eastern Poland: A palaeobotanical study. *Acta Palaeobotanica*, *4*, 3–95.

Grazi, G., & Zemp, M. (1986). *Genista cinerea* DC., ein natürlicher Sammelwirt für *Viscum album* L. ssp. *album* und *Viscum album* ssp. *austriacum* (Wiesb.) Vollmann. *Berichte der Deutschen Botanischen Gesellschaft*, *99*, 99–103.

Grzywocz, J. (2015). *Gastrallus laevigatus* (Olivier, 1790) (Coleoptera: Ptinidae) in upper Silesia. *Acta Entomologica Silesiana*, *23*, 1.

Grzywocz, J., Królik, R., & Szołtys, H. (2017). *Gastrallus knizeki* Zahradnik, 1996—New for the polish entomofauna deathwatch beetle (Coleoptera: Ptinidae). *Acta Entomologica Silesiana*, *25*, 1–2.

Guo, X., Liu, C., Zhang, G., Su, W., Landis, J. B., Zhang, X., Wang, H., & Ji, Y. (2020). The complete plastomes of five hemiparasitic plants (*Osyris wightiana*, *Pyrularia edulis*, *Santalum album*, *Viscum liquidambaricolum*, and *V. ovalifolium*): Comparative and evolutionary analyses within Santalales. *Frontiers in Genetics*, *11*, 597. https://doi.org/10.3389/fgene.2020.00597

Haarder, S., & Mąkol, J. (2022). Terrestrial Parasitengona mites (Trombidiformes) of Denmark—New data on parasite-host associations and new country records. *Acarologia*, *62*(2), 508–520. https://doi.org/10.24349/yglc-mnck

Haas, K., Bauer, M., & Wollenweber, E. (2003). Cuticular waxes and flavonol aglycones of mistletoes. *Zeitschrift Für Naturforschung C*, *58*(7–8), 464–470. https://doi.org/10.1515/znc-2003-7-803

Hansen, J., Vogg, G., & Beck, E. (1996). Assimilation, allocation and utilization of carbon by 3-year-old scots pine (*Pinus sylvestris* L) trees during winter and early spring. *Trees-Structure and Function*, *11*, 83–90.

Hansen, L. O., & Hodkinson, I. D. (2006). The mistletoe associated psyllid *Cacopsylla visci* (Curtis, 1835) (Homoptera, Psyllidae) in Norway. *Norwegian Journal of Entomology*, *53*, 89–91.

Hariri, E. B., Sallé, G., & Andary, C. (1991). Involvement of flavonoids in the resistance of two poplar cultivars to mistletoe (*Viscum album* L.). *Protoplasma*, *162*, 20–26.

Harrison, T. (2014). *Ixapion variegatum* (Wencker) (Apionidae) in Berkshire. *The Coleopterist*, *23*, 129.

Hatton, R. H. S. (1965). Pollination of mistletoe (*Viscum alba* L.). *Proceedings of the Linnean Society of London*, *176*(1), 67–76. https://doi.org/10.1111/j.1095-8312.1965.tb00936.x

Hawksworth, F. G., & Scharpf, R. F. (1986). Spread of European mistletoe (*Viscum album*) in California, U.S.A. *European Journal of Plant Pathology*, *16*, 1–5.

Heinricher, E. (1919). Ein Versuch Samen, allenfalls Pflanzen, aus der Kreuzung einer Laubholzmistel mit der Tannenmistel zu gewinnen. *Berichte der Deutschen Botanischen Gesellschaft*, *37*, 392–398.

Hejcman, M., Hejcmanová, P., Stejskalová, M., & Pavlů, V. (2014). Nutritive value of winter-collected annual twigs of main European woody species, mistletoe and ivy and its possible consequences for winter foddering of livestock in prehistory. *The Holocene*, *24*(6), 659–667. https://doi.org/10.1177/0959683614526904

Hellrigl, K. (2006). Untersuchungen über Insekten der Misteln in Südtirol (*Viscum album*: Loranthaceae). *Forest Observer*, *2*(3), 43–68.

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

Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the quaternary. *Philosophical Transactions of the Royal Society of London, Series B*, *359*, 183–195. https://doi.org/10.1098/rstb.2003.1388

Hill, M. O., Preston, C. D., & Roy, D. B. (2004). *PLANTATT. Attributes of British and Irish plants: Status, size, life history, geography and habitats*. Centre for Ecology and Hydrology.

Hincha, D. K., Pfüller, U., & Schmitt, J. M. (1997). The concentration of cryoprotective lectins in mistletoe (*Viscum album* L.) leaves is correlated with leaf frost hardiness. *Planta*, *203*(2), 140–144. https://doi.org/10.1007/s004250050175

Hódar, J. A., Lázaro-González, A., & Zamora, R. (2018). Beneath the mistletoe: Parasitized trees host a more diverse herbaceous vegetation and are more visited by rabbits. *Annals of Forest Science*, *75*, e77.

Hofstetter, M. (1988). [Spreading of the Mistletoe in Switzerland]. [German]. *Schweizerische Zeitschrift fuer Forstwesen. Journal Forestier Suisse*, *139*, 97–127.

Holsinger, K. E., & Ellstrand, N. C. (1984). The evolution and ecology of permanent translocation heterozygotes. *The American Naturalist*, *124*(1), 48–71. https://doi.org/10.1086/284251

Holý, F., Kvaček, Z., & Teodoris, V. (2012). A review of the early Miocene mastixioid flora of the Kristina mine at Hrádek nad Nisou in North Bohemia (The Czech Republic). *Acta Musei Nationalis Pragae Series B—Historia Naturalis*, *68*(3–4), 53–118.

Horbelt, N., Eder, M., Bertinetti, L., Fratzl, P., & Harrington, M. J. (2019). Unravelling the rapid assembly process of stiff cellulosic fibers from mistletoe berries. *Biomacromolecules*, *20*, 3094–3103.

Horbelt, N., Fratzl, P., & Harrington, M. J. (2022). Mistletoe viscin: A hygro- and mechano-responsive cellulose-based adhesive for diverse material applications. *PNAS Nexus*, *1*, 1–11.

Hosseini, S. M., Kartoolinejad, D., Mirnia, S. K., Tabibzadeh, Z., Akbarinia, M., & Shayanmehr, F. (2007). The effects of *Viscum album* L. on foliar weight and nutrients content of host trees in Caspian forests (Iran). *Polish Journal of Ecology*, *55*, 579–583.

Hrynowiecka, A., Stachowicz-Rybka, R., Niska, M., Moskal-del Hoyo, M., Börner, A., & Rother, H. (2021). Eemian (MIS 5 e) climate oscillations based on palaeobotanical analysis from the Beckentin profile (NE Germany). *Quaternary International*, *605–606*, 38–54. https://doi.org/10.1016/j.quaint.2021.01.025

Hudak, J., & Lux, A. (1986). Chloroplast ultrastructure of semiparasitic *Viscum album* L. *Photosynthetica*, *20*(2), 223–224.

Hultén, E., & Fries, M. (1986). *Atlas of north European vascular plants: North of the tropic of cancer I–III*. Koeltz Scientific Books.

Hussain, M. A., Khan, M. Q., Hussain, N., & Habib, T. (2011). Antibacterial and antifungal potential of leaves and twigs of *Viscum album* L. *Journal of Medicinal Plant Research*, *5*, 5545–5549.

Hwang, W. Y., Kang, M. H., Lee, S. K., Yeom, J. S., & Jung, M. H. (2019). Prolonged stabilization of platinum-refractory ovarian cancer in a single patient undergoing long-term mistletoe extract treatment: Case report. *Medicine*, *98*(8), e14536. https://doi.org/10.1097/MD.0000000000014536

Idžojtić, M., Kogelnik, M., Franjić, J., & Škvorc, Ž. (2006). Hosts and distribution of *Viscum album* L. ssp. *album* in Croatia and Slovenia. *Plant Biosystems*, *140*, 50–55.

Idžojtić, M., Pernar, R., Glavaš, M., Zebec, M., & Diminić, D. (2008). The incidence of mistletoe (*Viscum album* ssp. *abietis*) on silver fir (*Abies alba*) in Croatia. *Biologia*, *63*, 81–85.

Ihl, B., Jacob, F., Meyer, A., & Sembdner, G. (1987). Investigations on the endogenous levels of abscisic acid in a range of parasitic phanerogams. *Journal of Plant Growth Regulation*, *5*, 191–205.

Iszkuło, G., Armatys, L., Dering, M., Ksepko, M., Tomaszewski, D., Ważna, A., & Giertych, M. J. (2020). Jemioła jako zagrożenie dla zdrowotności drzewostanów iglastych. *Sylwan*, *164*(3), 226–236. https://doi.org/10.26202/SYLWAN.2019121

Iversen, J. (1944). Viscum, Hedera and Ilex as climate indicators: A contribution to the study of the post-glacial temperature climate. *Geologiska Föreningen i Stockholm Förhandlingar*, *66*(3), 463–483. https://doi.org/10.1080/11035894409445689

Jäger, T., Holandino, C., Melo, M. N. d. O., Peñaloza, E. M. C., Oliveira, A. P., Garrett, R., Glauser, G., Grazi, M., Ramm, H., Urech, K., & Baumgartner, S. (2021). Metabolomics by UHPLC-Q-TOF reveals host tree-dependent phytochemical variation in *Viscum album* L. *Plants*, *10*, e1726.

Jasiczek, N., Giertych, M. J., & Suszka, J. (2017). Influence of mistletoe (*Viscum album*) on the quality of scots pine (*Pinus sylvestris*) seeds. *Sylwan*, *161*(7), 558–564 [In polish with English abstract]. https://doi.org/10.26202/sylwan.2017055

Jeffree, C. E., & Jeffree, E. P. (1996). Redistribution of the potential geographical ranges of mistletoe and Colorado beetle in Europe in response to the temperature component of climate change. *Functional Ecology*, *10*, 562–577.

Jerome, C. A., & Ford, B. A. (2002). The discovery of three genetic races of the dwarf mistletoe *Arceuthobiumuropeanm* (Viscaceae) provides insight into the evolution of parasitic angiosperms. *Molecular Ecology*, *11*(3), 387–405. https://doi.org/10.1046/j.0962-1083.2002.01463.x

Jones, N., & Houben, A. (2003). B chromosomes in plants: Escapees from the A chromosome genome? *Trends in Plant Science*, *8*(9), 417–423. https://doi.org/10.1016/S1360-1385(03)00187-0

Jordan, E., & Wagner, H. (1986). Structure and properties of polysaccharides from *Viscum album* (L.). *Oncology*, *43*(suppl 1), 8–15.

Joy, J. (2009). *Lindow man*. British Museum Press.

Kahle-Zuber, D. (2008). *Biology and evolution of the European mistletoe (Viscum album)* (PhD dissertation). ETH Zurich.

Kamar, V., Dagalp, R., & Tastekin, M. (2018). Determination of heavy metals in almonds and mistletoe as a parasite growing on the almond tree using ICP-OES or ICP-MS. *Biological Trace Element Research*, *185*, 226–235.

Karadžić, D., & Lazarev, V. (2005). The most significant parasite and saprophyte fungi on mistletoe (*Viscum album* L.) and possibilities of their usage in bio-control. *Glasnik Šumarskog Fakulteta Univerziteta u Banjoj Luci*, *3*, 34–46.

Karadžić, D., Lazarev, V., & Milenković, M. (2004). The most significant parasitic and saprophytic fungi on common mistletoe (*Viscum album* L.) and their potential application in biocontrol. *Glasnik Šumarskog Fakulteta*, *89*, 115–126.

Kartoolinejad, D., Hosseini, S. M., Mirnia, S. K., Akbarinia, M., & Shayanmehr, F. (2007). The relationship among infection intensity of *Viscum album* with some ecological parameters of host trees. *International Journal of Environmental Research*, *1*, 143–149.

Kelly, C. K., & Beerling, D. J. (1995). Plant life form, stomatal density and taxonomic relatedness: A reanalysis of Salisbury (1927). *Functional Ecology*, *9*, 422–431.

Khan, M. A., Sharif, T., Ahmad, M., Zafar, M., & Tareen, R. B. (2009). Anatomical characterization of parasitic plants of Pakistan. *Pakistan Journal of Botany*, *41*(6), 2661–2669.

Khanjani, M., Farzan, S., Asadi, M., & Khanjani, M. (2013). Checklist of the flat mites (Acari: Trombidiformes: Tenuipalpidae) of Iran. *Persian Journal of Acarology*, *2*, 235–251.

Kienle, G. S., Grugel, R., & Kiene, H. (2011). Safety of higher dosages of Viscum album L. in animals and humans—Systematic review of immune changes and safety parameters. *BMC Complementary and Alternative Medicine*, *11*, article 72.

Kienle, G. S., & Kiene, H. (2010). Review article: Influence of *Viscum album* L. (European mistletoe) extracts on quality of life in cancer patients: A systematic review of controlled clinical studies. *Integrative Cancer Therapies*, *9*(2), 142–157. https://doi.org/10.1177/1534735410369673

Kim, C.-W., An, C.-H., Lee, H.-S., Yi, J.-S., Cheong, E. J., Lim, S.-H., & Kim, H.-Y. (2019). Proximate and mineral components of *Viscum album* var. *coloratum* grown on eight different host tree species. *Journal of Forestry Research*, *30*, 1245–1253.

Klamerus-Iwan, A., & Van Stan, J. T., II. (2022). Rainfall interception by common mistletoe (*Viscum album* L. ssp. *album*): An additional water loss from infected forests. *Ecohydrology*, *2022*, e2485.

Kleijnen, J., & Knipschild, P. (1994). Mistletoe treatment for cancer review of controlled trials in humans. *Phytomedicine*, *1*(3), 255–260. https://doi.org/10.1016/S0944-7113(11)80073-5

Ko, S. M., Kwon, Y. K., Kim, J. H., Song, I.-J., Lee, H.-Y., Choi, D.-W., Liu, J. R., & Kim, S. W. (2014). Transcriptome analysis of mistletoe (*Viscum album*) haustorium development. *Horticulture, Environment, and Biotechnology*, *55*, 352–361.

Kollas, C., Gutsch, M., Hommel, R., Lasch-Born, P., & Suckow, F. (2017). Mistletoe-induced growth reductions at the forest stand scale. *Tree Physiology*, *38*, 735–744.

Kołodziejek, J., Patykowski, J., & Kołodziejek, R. (2013). Distribution, frequency and host patterns of European mistletoe (*Viscum album* subsp. *album*) in the major city of Lodz, Poland. *Biologia*, *68*, 55–64.

Kolon, K., Samecka-Cymerman, A., Klink, A., & Kempers, A. J. (2013). *Viscum album* versus host (*Sorbus aucuparia*) as bioindicators of urban areas with various levels of pollution. *Journal of Environmental Science and Health Part A—Toxic/Hazardous Substances & Environmental Engineering*, *48*, 205–210.

Kope, H. H. (2020). European mistletoe (*Viscum album* subsp. *album*) in Victoria, British Columbia, Canada: An eradication follow-up. *Canadian Plant Disease Survey*, *100*, 158–161.

Kotan, R., Okutucu, A., Görmez, A. A., Karagoz, K., Dadasoglu, F., Karaman, İ., Hasanekoglu, İ., & Kordali, Ş. (2013). Parasitic bacteria and fungi on common mistletoe (*Viscum album* L.) and their potential application in biocontrol. *Journal of Phytopathology*, *161*, 165–171.

Kovar-Eder, J., & Hably, L. (2006). The flora of Mataschen—A unique plant assemblage from the late Miocene of eastern Styria (Austria). *Acta Palaeobotanica*, *46*(2), 157–233.

Kowalski, P. (1998). *Leksykon—Znaki świata: Omen, przesąd, znaczenie [lexicon—signs of the world: Omen, superstition, meaning. In polish]*. Wydawnictwo Naukowe PWN.

Kowalski, P. (2007). *Kultura magiczna. Omen, przesąd, znaczenie*. Wydawnictwo Naukowe PWN.

Krasylenko, Y., Sosnovsky, E., Atamas, N., Popov, G., Leonenko, V., Janošíková, K., Sytschak, N., Rydlo, K., & Sytnyk, D. (2020). The European mistletoe (*Viscum album* L.): Distribution, host range, biotic interactions and management worldwide with special emphasis on Ukraine. *Botany*, *98*(9), 499–516. https://doi.org/10.1139/cjb-2020-0037

Krasylenko, Y., Těšitel, J., Ceccantini, G., Oliveira-da-Silva, M., Dvořák, V., Steele, D., Sosnovsky, Y., Piwowarczyk, R., Watson, D. M., & Teixeira-Costa, L. (2021). Parasites on parasites: Hyper-, epi-, and autoparasitism among flowering plants. *American Journal of Botany*, *108*(1), 8–21. https://doi.org/10.1002/ajb2.1590

Krzaczek, T. (1976). Pharmacobotanical research on the sub-species *Viscum album* L. II. Saccharides. *Annales Universitatis Mariae curie-Sklodowska—Sectio D. Medicina*, *31*, 281–290.

Krzaczek, T. (1977). Pharmacobotanical research of the sub-species *Viscum album* L. IV. Acids and amines. *Annales Universitatis Mariae curie-Sklodowska—Sectio D. Medicina*, *32*, 281–291.

Kvaček, Z., Teodoridis, V., & Denk, T. (2020). The Pliocene flora of Frankfurt am Main, Germany: Taxonomy, palaeoenvironments and biogeographic affinities. *Palaeobiodiversity and Palaeoenvironments*, *100*(3), 647–703. https://doi.org/10.1007/s12549-019-00391-6

Kvaček, Z., Teodoridis, V., & Roiron, P. (2011). A forgotten Miocene mastixioid flora of Arjuzanx (Landes, SW France). *Palaeontographica Abteilung B*, *285*(1–3), 3–111. https://doi.org/10.1127/palb/285/2011/3

Laiviņš, M. (2003). Baltais āmulis *Viscum album* L. Kurzemē [distribution and migration of white mistletoes *Viscum album* L. in Kurzeme (south–west Latvia)]. *Folia Geographica*, *11*, 52–58.

Lakatos, F., & Mirtchev, S. (2014). *Handbook of the major forest pests in south East Europe: GCP/KOS/005/FIN*. FAO. https://www.fao.org/publications/card/en/c/b91199f2-08c7-41d7-95d9-5b522fdc9a51/

Lamont, B. (1983). Mineral nutrition of mistletoes. In M. Calder & P. Bernhardt (Eds.), *The biology of mistletoes* (pp. 185–204). Academic Press.

Lamont, B. B., & Southall, K. J. (1982). Distribution of mineral nutrients between the mistletoe, *Amyema preissii*, and its host, *Acacia acuminat*. *Annals of Botany*, *49*, 721–725.

Laurent, E. (1900). De l'influence du sol sur la dispersion du Gui et de la Cuscute en Belgique. *Bulletin de l'Agriculture*, *16*, 457–510.

Lázaro-González, A., Hódar, J. A., & Zamora, R. (2017). Do the arthropod communities on a parasitic plant and its hosts differ? *European Journal of Entomology*, *114*, 215–221.

Lázaro-González, A., Hódar, J. A., & Zamora, R. (2019a). Mistletoe generates non-trophic and trait-mediated indirect interactions through a shared host of herbivore consumers. *Ecosphere*, *10*, e02564.

Lázaro-González, A., Hódar, J. A., & Zamora, R. (2019b). Mistletoe versus host pine: Does increased parasite load alter the host chemical profile? *Journal of Chemical Ecology*, *45*, 95–105.

Lázaro-González, A., Hódar, J. A., & Zamora, R. (2020). Ecological assembly rules on arthropod community inhabiting mistletoes. *Ecological Entomology*, *45*, 1088–1098.

Lech, P., Żółciak, A., & Hildebrand, R. (2020). Occurrence of European mistletoe (*Viscum album* L.) on forest trees in Poland and its dynamics of spread in the period 2008–2018. *Forests*, *11*(1), 83. https://doi.org/10.3390/f11010083

Lee, B., Salitxay, T., Phouyhaxay, P., Sung, I., & Park, C. (2016). Chlorophyll contents, total polyphenols, and the antioxidant activity in mistletoe (*Viscum album*) artificially cultivated on *Prunus mume*. *Journal of the Korean Society of International Agriculture*, *28*, 420–425.

Li, X. M., Pfiz, M., Kuppers, M., Einig, W., Rennenberg, H., & Hampp, R. (2003). Sucrose phosphate synthase in leaves of mistletoe: Its regulation in relation to host (*Abies alba*) and season. *Trees-Structure and Function*, *17*, 221–227.

Li, X. M., Wanek, W., Nehls, U., Popp, M., Hampp, R., Rennenberg, H., & Einig, W. (2001). Phosphoenolpyruvate carboxylase in mistletoe leaves: Regulation of gene expression, protein content, and covalent modification. *Physiologia Plantarum*, *112*, 343–352.

Lindow, J. (2002). The tears of the gods: A note on the death of Baldr in Scandinavian mythology. *The Journal of English and Germanic Philology*, *101*, 155–169.

Litkowiec, M., Sękiewicz, K., Romo, A., Ok, T., Bou Dagher-Kharrat, M., Jasińska, A. K., Sobierajska, K., Boratyńska, K., & Boratyński, A. (2021). Biogeography and relationships of the *Abies* taxa from the mediterranean and central Europe regions as revealed by nuclear DNA markers and needle structural characters. *Forest Ecology and Management*, *479*, 118606. https://doi.org/10.1016/j.foreco.2020.118606

Lorenc, F., & Véle, A. (2022). Characteristics of *Pinus sylvestris* stands infected by *Viscum album* subsp. *austriacum*. *Austrian Journal of Forest Science*, *1*, 31–50.

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

Maclean, A. E., Hertle, A. P., Ligas, J., Bock, R., Balk, J., & Meyer, E. H. (2018). Absence of complex I is associated with diminished respiratory chain function in European mistletoe. *Current Biology*, *28*, 1614–1619.

Madeja, J., Harmata, K., Kołaczek, H., Karpińska-Kołaczek, M., Piątek, K., & Naks, P. (2009). Bracken (*Pteridium aquilinum* (L.) Kuhn), mistletoe (*Viscum album* (L.)) and bladder-nut (*Staphylea pinnata* (L.))—Mysterious plants with unusual applications. Cultural and ethnobotanical studies. In J.-P. Morel & A. M. Mercuri (Eds.), *Plants and culture: Seeds of the cultural heritage of Europe* (pp. 207–215). Edipuglia.

Mai, H. D. (2001). Die mittelmiozänen und obermiozänen Floren aus der Meuroer und Raunoer Folge in der Lausitz. Teil II: Dicotyledonen. [The middle and upper Miocene floras of the Meuro and Rauno sequences in the Lusatica region: Part II: Dicotyledones]. *Palaeontographica Abteilung B*, *257*, 35–174.

Majeed, M., Hakeem, K. R., & Rehman, R. U. (2021). Mistletoe lectins: From interconnecting proteins to potential tumour inhibiting agents. *Phytomedicine Plus*, *1*, 100039.

Marris, T. (2007). Survey of mistletoe *Viscum album platyspermum* at Hampton Court Palace. *The London Naturalist*, *86*, 35–46.

Marris, T. (2008). A further survey of mistletoe *Viscum album platyspermum* at Hampton Court Palace. *The London Naturalist*, *87*, 53–56.

Mathiasen, R. L., Nickrent, D. L., Shaw, D. C., & Watson, D. M. (2008). Mistletoes: Pathology, systematics, ecology, and management. *Plant Disease*, *92*, 988–1006.

Matula, R., Svátek, M., Pálkov, M., Volařík, D., & Vrška, T. (2015). Mistletoe infection in an oak forest is influenced by competition and host size. *PLoS ONE*, *10*, e0127055.

Maul, K., Krug, M., Nickrent, D. L., Müller, K. F., Quandt, D., & Wicke, S. (2019). Morphology, geographic distribution, and host preferences are poor predictors of phylogenetic relatedness in the mistletoe genus *Viscum* L. *Molecular Phylogenetics and Evolution*, *131*, 106–115. https://doi.org/10.1016/j.ympev.2018.10.041

Mavrikou, S., Tsekouras, V., Karageorgou, M.-A., Moschopoulou, G., & Kintzios, S. (2020). Anticancer and biochemical effects of *Viscum album* L. protein extracts on HeLa cells. *Plant Cell, Tissue and Organ Culture*, *140*, 369–378.

Mechelke, F. (1976). Sex-correlated complex heterozygosity in *Viscum album* L. *Die Naturwissenschaften*, *63*(8), 390. https://doi.org/10.1007/BF00607945

Mehrvarz, S. S., Shavvon, R. S., & Golmohammadi, N. (2012). Notes on the genus *Viscum* (Viscaceae) in Iran: A new combination based on morphological evidence. *African Journal of Agricultural Research*, *7*(11), 1694–1702. https://doi.org/10.5897/AJAR11.1382

Mejnartowicz, L. (2006). Relationship and genetic diversity of mistletoe (*Viscum album* L.) subspecies. *Acta Societatis Botanicorum Poloniae*, *75*(1), 39–49. https://doi.org/10.5586/asbp.2006.007

Mellado, A., Morillas, L., Gallardo, A., & Zamora, R. (2016). Temporal dynamic of parasite-mediated linkages between the forest canopy and soil processes and the microbial community. *New Phytologist*, *211*, 1382–1392.

Mellado, A., & Zamora, R. (2014a). Linking safe sites for recruitment with host-canopy heterogeneity: The case of a parasitic plant, *Viscum album* subsp. *austriacum* (Viscaceae). *American Journal of Botany*, *101*, 957–964.

Mellado, A., & Zamora, R. (2014b). Generalist birds govern the seed dispersal of a parasitic plant with strong recruitment constraints. *Oecologia*, *176*, 139–147. https://doi.org/10.1007/s00442-014-3013-8

Mellado, A., & Zamora, R. (2016). Spatial heterogeneity of a parasitic plant drives the seed-dispersal pattern of a zoochorous plant community in a generalist dispersal system. *Functional Ecology*, *30*, 459–467.

Mellado, A., & Zamora, R. (2017). Parasites structuring ecological communities: The mistletoe footprint in Mediterranean pine forests. *Functional Ecology*, *31*, 2167–2176.

Mellado, A., & Zamora, R. (2019). Ecological consequences of parasite host shifts under changing environments: More than a change of partner. *Journal of Ecology*, *108*, 788–796.

Menke, K., Schwermer, M., Schramm, A., & Zuzak, T. J. (2019). Preclinical evaluation of antitumoral and cytotoxic properties of *Viscum album* fraxini extract on pediatric tumor cells. *Planta Medica*, *85*(14/15), 1150–1159. https://doi.org/10.1055/a-1013-0382

Míguez, F., Fernández-Marín, B., Hernández, A., Becerril, J. M., & García-Plazaola, J. I. (2015). Does age matter under winter photoinhibitory conditions? A case study in stems and leaves of European mistletoe (*Viscum album*). *Functional Plant Biology*, *42*(2), 175–185. https://doi.org/10.1071/FP14083

Mokrzycki, T., Hilszczański, J., Borowski, J., Cieślak, R., Mazur, A., Miłkowski, M., & Szołtys, H. (2011). Faunistic review of Polish Platypodinae and Scolytinae (Coleoptera: Curculionidae). *Polish Journal of Entomology*, *80*, 343–364.

Molnár, A., & Végvári, Z. (2017). Bioclimatic constraints of European mistletoe *Viscum album* at its southern distribution limit at past and present temporal scales, Pannonian Basin, Hungary. *Climate Research*, *71*(3), 237–248.

Montfort, C., & Müller, L. (1951). Grundsätzliches zur Lebensrhythmik der Mistel (*Viscum album* L). Im jährlichen Längenzuwachs und in der Blattgestaltung. *Berichte der Deutschen Botanischen Gesellschaft*, *64*(4), 297–303. https://doi.org/10.1111/j.1438-8677.1951.tb02139.x

Mujezinović, O., Dautbašić, M., Mujčinović, A., & Zahirović, K. (2017). Značajke borove imele (*Viscum album* subsp. *austriacum* (Wiesb.) Vollmann (1914)) na crnom boru u Bosni i Hercegovini. [Characteristics of mistletoe shrubs (*Viscum album* subsp. *austriacum* (Wiesb.) Vollmann (1914)) on black pine in Bosnia and Herzegovina.]. *Šumarski List*, *9–10*, 477–483.

Mutlu, S., Osma, E., Ilhan, V., Turkoglu, H. I., & Atici, O. (2016). Mistletoe (*Viscum album*) reduces the growth of the scots pine by accumulating essential nutrient elements in its structure as a trap. *Trees-Structure and Function*, *30*, 815–824.

Mylo, M. D., Hofmann, M., Delp, A., Scholz, R., Walther, F., Speck, T., & Speck, O. (2021). Advances on the visualization of the internal structures of the European mistletoe: 3D reconstruction using microtomography. *Frontiers in Plant Science*, *12*, 715711. https://doi.org/10.3389/fpls.2021.715711

Nagl, W., & Stein, B. (1989). DNA characterization in host-specific *Viscum album* subspecies (Viscaceae). *Plant Systematics and Evolution*, *166*, 243–248.

Nazaruk, J., & Orlikowski, P. (2016). Phytochemical profile and therapeutic potential of *Viscum album* L. *Natural Product Research*, *30*, 373–385.

NBN Atlas. (2022). https://nbnatlas.org/

Nelson, E. C. (2008). Mistletoe (*Viscum album* L.) in Ireland: A review of records and status. *The Irish Naturalists' Journal*, *29*, 87–94.

Nienartowicz, A., Rutkowski, L., Kamiński, D., & Kunz, M. (2022). Occurrence of *Viscum album* subsp. *album* L. on *Laburnum anagyroides* Medik. in Toruń, Poland. *Ecological Questions*, *33*, 33–37.

Nierhaus-Wunderwalt, D., & Lawrenz, P. (1997). Zur Biologie der Mistel. *Merkblatt für die Praxis*, *28*, 1–8.

Noetzli, K. P., Müller, B., & Sieber, T. N. (2003). Impact of population dynamics of white mistletoe (*Viscum album* ssp. *abietis*) on European silver fir (*Abies alba*). *Annals of Forest Science*, *60*, 773–779.

Noryśkiewicz, A. M., & Noryśkiewicz, B. (2017). Remarks on pollen representation of mistletoe (*Viscum album* L.). *Ecological Questions*, *26*, 19–26. https://doi.org/10.12775/EQ.2017.011

Novák, P., Guignard, M. S., Neumann, P., Kelly, L. J., Mlinarec, J., Koblížkov, A., Dodsworth, S., Kovař, A., Pellicer, J., Wang, W., Macas, J., Leitch, I. J., & Leitch, A. R. (2020). Repeat-sequence turnover shifts fundamentally in species with large genomes. *Nature Plants*, *6*, 1325–1329.

Ochocka, J. R., & Piotrowski, A. (2002). Biologically active compounds from European mistletoe (*Viscum album* L.). *Canadian Journal of Plant Pathology*, *24*, 21–28.

Olsnes, S., Stirpe, F., Sandvig, K., & Pihl, A. (1982). Isolation and characterization of viscumin, a toxic lectin from *Viscum album* L. (mistletoe). *Journal of Biological Chemistry*, *257*, 13263–13270.

Önay-Uçar, E., Karagöz, A., & Arda, N. (2006). Antioxidant activity of *Viscum album* ssp. *album*. *Fitoterapia*, *77*, 556–560.

Orhan, D. D., & Orhan, I. (2006). Fatty acid composition of *Viscum album* subspecies from Turkey. *Chemistry of Natural Compounds*, *42*, 641–644.

Osthagen, H. (1984). Fredede planter i Norge. *Blyttia*, *42*, 157–162.

Ozturk, M., Coskuner, K. A., Usta, Y., Serdar, B., & Bilgili, E. (2019). The effect of mistletoe (*Viscum album*) on branch wood and needle anatomy of scots pine (*Pinus sylvestris*). *IAWA Journal*, *40*, 352–365.

Öztürk, Y. E., Gülümser, E., Mut, H., Başaran, U., & Çopur Doğrusöz, M. (2022). A preliminary study on change of mistletoe (*Viscum album* L.) silage quality according to collection time and host tree species. *Turkish Journal of Agriculture and Forestry*, *46*, 104–112.

Paine, L. K., & Harrison, H. C. (1992). Mistletoe: Its role in horticulture and human life. *HortTechnology*, *2*(3), 324–330. https://doi.org/10.21273/HORTTECH.2.3.324

Patykowski, J., & Kołodziejek, J. (2013). Comparative analysis of antioxidant activity in leaves of different hosts infected by mistletoe (*Viscum album* L. subsp. *album*). *Archives of Biological Sciences*, *65*, 851–861.

Perring, F. (1973). Mistletoe. In P. S. Green (Ed.), *Plants: Wild and cultivated* (pp. 139–145). Botanical Society of the British Isles, E.W. Classey, Middlesex.

Peršoh, D. (2013). Factors shaping community structure of endophytic fungi—evidence from the *Pinus–Viscum*-system. *Fungal Diversity*, *60*, 55–69. https://doi.org/10.1007/s13225-013-0225-x

Peršoh, D., Melcher, M., Flessa, F., & Rambold, G. (2010). First fungal community analyses of endophytic ascomycetes associated with *Viscum album* ssp. *austriacum* and its host *Pinus sylvestris*. *Fungal Biology*, *114*, 585–596.

Petersen, G., Cuenca, A., Møller, I. M., & Seberg, O. (2015a). Massive gene loss in Mistletoe (*Viscum*, Viscaceae) mitochondria. *Scientific Reports*, *5*, 17588.

Petersen, G., Cuenca, A., & Seberg, O. (2015b). Plastome evolution in hemiparasitic mistletoes. *Genome Biology and Evolution*, *7*(9), 2520–2532. https://doi.org/10.1093/gbe/evv165

Petersen, G., Rao, R. S. P., Anderson, B., Zervas, A., Seberg, O., Rasmusson, A. G., & Møller, I. M. (2022). Genes from oxidative phosphorylation complexes II–V and two dual-function subunits of complex I are transcribed in *Viscum album* despite absence of the entire mitochondrial holo-complex I. *Mitochondrion*, *62*, 1–12.

Petrini, O., Sieber, T. N., Toti, L., & Viret, O. (1992). Ecology, metabolite production, and substrate utilization in endophytic fungi. *Natural Toxins*, *1*, 185–196.

Pfiz, M., & Küppers, M. (2010). Dense crowns of the hemiparasitic mistletoe *Viscum album* L. exhibit shrub-like growth and high dry matter turnover. *Flora*, *205*(12), 787–796. https://doi.org/10.1016/j.flora.2010.04.016

Pfüller, U. (2000). Chemical constituents of European mistletoe *Viscum album* L. In A. Büssing (Ed.), *Mistletoe, the genus Viscum* (pp. 101–122). Harwood Academic Publishers.

Pilichowski, S., Filip, R., Koscielska, A., Zaroffe, G., Zyzniewska, A., & Iszkulo, G. (2018). Influence of *Viscum album* ssp *austriacum* (Wiesb.) Vollm. n tree radial growth of *Pinus sylvestris* L. *Sylwan*, *162*, 452–459.

Piotrowski, A., Ochocka, J. R., Stefanowicz, J., & Łuczkiewicz, M. (2003). Molecular genetic survey of European mistletoe (*Viscum album*) subspecies with allele-specific and dCAPS type markers specific for chloroplast and nuclear DNA sequences. *Planta Medica*, *69*, 939–944.

Popp, M., Mensen, R., Richter, A., Buschmann, H., & Vonwillert, J. D. (1995). Solutes and succulence in southern African mistletoes. *Trees-Structure and Function*, *9*, 303–310.

Preston, A. P. (1977). Effects of mistletoe (*Viscum album*) on young apple trees. *Horticulture Research*, *17*, 33–38.

Punithalingam, E., & Spooner, B. M. (2002). New taxa and new records of Coelomycetes for the UK. *Kew Bulletin*, *57*, 533–563.

Raftoyannis, Y., Radoglou, K., & Bredemeier, M. (2015). Effects of mistletoe infestation on the decline and mortality of *Abies cephalonica* in Greece. *Annals of Forest Research*, *58*, 55–65.

Ramírez-Barahona, S., González, C., González-Rodríguez, A., & Ornelas, J. F. (2017). The influence of climatic niche preferences on the population genetic structure of a mistletoe species complex. *New Phytologist*, *214*(4), 1751–1761. https://doi.org/10.1111/nph.14471

Ramm, H. (2006). *Einfluß bodenchemischer Standortfaktoren auf Wachstum und pharmazeutische Qualität von Eichenmisteln* (Viscum album auf Quercus robur und petraea). Landbauforschung Völkenrode, Bundesforschungsanstalt für Landwirtschaft.

Ramm, H., Rispens, J., & Urech, K. (2016). Weißbeerige Mistel (*Viscum album* L.). In U. Meyer & P. A. Pedersen (Eds.), *Anthroposophische Pharmazie. Grundlagen, Herstellungsprozesse, Arzneimittel* (pp. 239–261). Salumed Verlag.

Ramm, H., Urech, K., Scheibler, M., & Grazi, G. (2000). Cultivation and development of *Viscum album* L. In A. Büssing (Ed.), *Mistletoe. The genus Viscum* (pp. 75–94). Harwood Academic Publishers.

Ramsauer, J., Brotons, L., Herrando, S., & Morán-Ordóñez, A. (2022). A multi-scale landscape approach to understand dispersal of the mistletoe by birds in Mediterranean pine forests. *Landscape Ecology*, *37*, 511–528.

Reynel, M., Villegas, Y., Kiene, H., Werthmann, P. G., & Kienle, G. S. (2018). Intralesional and subcutaneous application of *Viscum album*

L. (European mistletoe) extract in cervical carcinoma in situ: A CARE compliant case report. *Medicine*, *97*(48), e13420. https://doi.org/10.1097/MD.0000000000013420

Richter, A., & Popp, M. (1992). The physiological importance of accumulation of cyclitols in *Viscum album* L. *New Phytologist*, *121*, 431–438.

Rigling, A., Eilmann, B., Koechli, R., & Dobbertin, M. (2010). Mistletoe-induced crown degradation in Scots pine in a xeric environment. *Tree Physiology*, *30*, 845–852.

Riyekstin'sh, I. (1980). Vliyaniye rasteniya khozyaina na prirost i dolgovechnost' omely beloy (*Viscum album* L.) v Latviyskoy SSR. *Botanicheskiye Sady Pribaltiki. Ekologicheskiye Issledovaniya*, *1*, 18–22.

Robertsson, A.-M. (2000). The Eemian interglacial in Sweden, and comparison with Finland. *Netherlands Journal of Geosciences*, *79*(2–3), 325–333. https://doi.org/10.1017/S0016774600021806

Robinson, D. E. (2007). Exploitation of plant resources in the Mesolithic and Neolithic of southern Scandinavia: From gathering to harvesting. In S. Colledge & J. Conolly (Eds.), *The origins and spread of domestic plants in Southwest Asia and Europe* (pp. 359–374). Left Coast Press.

Rodwell, J. S. (1991). British plant communities. In *Woodlands and scrub* (Vol. *I*). Cambridge University Press.

Rybalka, I. A. (2017). Relationship between density of the white mistletoe (*Viscum album* L.) and some landscape and environmental characteristics of urban areas in the case of Kharkiv. *Ekologicheskiy Vestnik*, *1*(39), 87–97.

Salamon, I., Labun, P., & Petruska, P. (2015). *Occurrence of heavy metals, radioactivity, and pesticide residues in raw materials of elderberry and other herbs and fruits in Slovak Republic*. International Society for Horticultural Science (ISHS).

Sallé, G. (1976). Étude cytologique et cytochimique de l'extrémité des cordons corticaux du *Viscum album*. Mise enuropeane d'uneuropeann mucilagineuse. *Protoplasma*, *90*, 283–295.

Sallé, G. (1978). Origin and early growth of the sinkers of *Viscum album* L. *Protoplasma*, *96*, 267–273. https://doi.org/10.1007/BF01287687

Sallé, G. (1979). Le système endophytique du *Viscum album*: Anatomie et fonctionnement des suçoirs secondaires. *Canadian Journal of Botany*, *57*(4), 435–449. https://doi.org/10.1139/b79-056

Sallé, G. (1983). Germination and establishment of *Viscum album* L. In D. M. Calder & P. Bernhardt (Eds.), *The biology of mistletoes* (pp. 145–159). Academic Press.

Sallé, G. C., Hariri, E. B., & Andary, C. (1994). Polyphenols and resistance of poplar (*Populus* spp.) to mistletoe (*Viscum album* L.). *Acta Horticulturae*, *381*, 756–762. https://doi.org/10.17660/ActaHortic.1994.381.109

Sancho-Knapik, D., Peguero-Pina, J. J., Cremer, E., Camarero, J. J., Fernández-Cancio, Á., Ibarra, N., Konnert, M., & Gil-Pelegrín, E. (2014). Genetic and environmental characterization of *Abies alba* Mill. populations at its western rear edge. *Pirineos*, *169*, e007. https://doi.org/10.3989/Pirineos.2014.169007

Sanders, I. R., Koide, R. T., & Shumway, D. L. (1993). Mycorrhizal stimulation of plant parasitism. *Canadian Journal of Botany*, *71*, 1143–1146.

Sangüesa-Barreda, G., Camarero, J. J., Pironon, S., Gazol, A., Peguero-Pina, J. J., & Gil-Pelegrín, E. (2018). Delineating limits: Confronting predicted climatic suitability to field performance in mistletoe populations. *Journal of Ecology*, *106*, 2218–2229. https://doi.org/10.1111/1365-2745.12968

Sangüesa-Barreda, G., Linares, J. C., & Camarero, J. J. (2012). Mistletoe effects on scots pine decline following drought events: Insights from within-tree spatial patterns, growth and carbohydrates. *Tree Physiology*, *32*(5), 585–598. https://doi.org/10.1093/treephys/tps031

Sangüesa-Barreda, G., Linares, J. C., & Camarero, J. J. (2013). Drought and mistletoe reduce growth and water-use efficiency of Scots pine. *Forest Ecology and Management*, *296*, 64–73.

Scalon, M. C., & Wright, I. J. (2015). A global analysis of water and nitrogen relationships between mistletoes and their hosts: Broad-scale tests of old and enduring hypotheses. *Functional Ecology*, *29*, 1114–1124.

Schaller, G., Urech, K., Grazi, G., & Giannattasio, M. (1998). Viscotoxin composition of the three European subspecies of *Viscum album*. *Planta Medica*, *64*, 587–682.

Schönland, S. (1888). Contributions to the morphology of the mistletoe (*Viscum album*, L.). *Annals of Botany*, *2*(7), 283–291.

Schrader-Fischer, G., & Apel, K. (1993). The anticyclic timing of leaf senescence in the parasitic plant *Viscum album* is closely correlated with the selective degradation of sulfur-rich viscotoxins. *Plant Physiology*, *101*, 745–749. https://doi.org/10.1104/pp.101.3.745

Schröder, L., Hohnjec, N., Senkler, M., Senkler, J., Küster, H., & Braun, H.-P. (2022). The gene space of European mistletoe (*Viscum album*). *The Plant Journal*, *109*, 278–294.

Schulze, E.-D., Turner, N. C., & Glatzel, G. (1984). Carbon, water and nutrient relations of two mistletoes and their hosts: A hypothesis. *Plant, Cell & Environment*, *7*, 293–299.

Sell, P., & Murrell, G. (2009). *Flora of Great Britain and Ireland, Vol. 3. Mimosaceae—Lentibulariaceae*. Cambridge University Press.

Semiglazov, V. F., Stepula, V. V., Dudov, A., Schnitker, J., & Mengs, U. (2006). Quality of life is improved in breast cancer patients by standardised mistletoe extract PS76A2 during chemotherapy and follow-up: A randomised, placebo-controlled, double-blind, multicentre clinical trial. *Anticancer Research*, *26*(2B), 1519–1529.

Senkler, J., Rugen, N., Eubel, H., Hegermann, I., & Braun, H.-P. (2018). Absence of complex I implicates rearrangement of the respiratory chain in European mistletoe. *Current Biology*, *28*, 1606–1613.

Shah, S. S., Rehman, Y. U., Iqbal, A., Rahman, Z. U., Zhou, B., Peng, M., & Li, Z. (2017). Phytochemical screening and antimicrobial activities of stem, leaves and fruit extracts of *Viscum album* L. *Journal of Pure and Applied Microbiology*, *11*, 1337–1349.

Sharma, P., Steckel, H., Koschinsky, A., & Schnug, E. (2009). Potential correlation of heavy metals in surface soils with infestation of *Viscum album* in poplar trees. *Landbauforschung Voelkenrode*, *59*, 11–18.

Shaw, D. C., & Lee, C. A. (2020). Expansion of the invasive European mistletoe in California, USA. *Botany*, *98*, 517–524.

Skippington, E., Barkman, T. J., Rice, D. W., & Palmer, J. D. (2015). Miniaturized mitogenome of the parasitic plant *Viscum scurruloideum* is extremely divergent and dynamic and has lost all nad genes. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(27), E3515–E3524. https://doi.org/10.1073/pnas.1504491112

Skippington, E., Barkman, T. J., Rice, D. W., & Palmer, J. D. (2017). Comparative mitogenomics indicates respiratory competence in parasitic *Viscum* despite loss of complex I and extreme sequence divergence, and reveals horizontal gene transfer and remarkable variation in genome size. *BMC Plant Biology*, *17*(1), 49. https://doi.org/10.1186/s12870-017-0992-8

Skórka, P., & Wójcik, J. D. (2005). Population dynamics and social behavior of the Mistle thrush *Turdus viscivorus* during winter. *Acta Ornithologica*, *40*, 35–42.

Skrypnik, L., Maslennikov, P., Feduraev, P., Pungin, A., & Belov, N. (2020). Ecological and landscape factors affecting the spread of European mistletoe (*Viscum album* L.) in urban areas (a case study of the Kaliningrad City, Russia). *Plants*, *9*(3), 394. https://doi.org/10.3390/plants9030394

Smith, P. L., & Gledhill, D. (1983). Anatomy of the endophyte of *Viscum album* L. (Loranthaceae). *Botanical Journal of the Linnean Society*, *87*(1), 29–53. https://doi.org/10.1111/j.1095-8339.1983.tb00982.x

Song, C., Wei, X.-Y., Qiu, Z.-D., Gong, L., Chen, Z.-Y., Ma, Y., Shen, Y., Zhao, Y.-J., Wang, W.-H., Lai, C.-J.-S., & Yang, B. (2021). Exploring the resources of the genus *Viscum* for potential therapeutic applications. *Journal of Ethnopharmacology*, *277*, 114233.

Stace, C. A. (2019). *New flora of the British Isles* (4th ed.). C & M Floristics.

Stanton, S., Honnay, O., Jacquemyn, H., & Roldán-Ruiz, I. (2009). A comparison of the population genetic structure of parasitic *Viscum* *album* from two landscapes differing in degree of fragmentation. *Plant Systematics and Evolution*, *281*, 161–169.

Stanton, S., Torrado, S. B., & Honnay, O. (2010). Seed germination tests of the parasitic perennial *Viscum album* (Viscaceae) from fragmented habitats at the northern edge of its range. *Plant Ecology and Evolution*, *143*(2), 113–118.

Stein, G. E. (2000). Toxicology of mistletoe extracts and their compounds. In A. Büssing (Ed.), *Mistletoe, the genus Viscum* (pp. 183–194). Harwood Academic Publishers.

Stopp, F. (1961). *Unsere Misteln*. Ziemsen Verlag.

Struwe, I., Gertsson, C.-A., & Coulianos, C.-C. (2009). Två insekter monofaga på mistel nyupptäckta i Sverige: Bladloppan *Cacopsylla visci* (Curtis, 1835) (Hemiptera, Psyllidae) och skinnbaggen *Pinalitus viscicola* (Puton, 1888) (Hemiptera, Miridae). [Insects monophagous on mistletoe (*Viscum album* L.) newly discovered in Sweden: *Cacopsylla visci* (Curtis, 1835) (Hemiptera, Psyllidae) and *Pinalitus viscicola* (Puton, 1888) (Hemiptera, Miridae).]. *Entomologisk Tidskrift*, *130*, 155–160.

Stypiński, P. (1997). Biologia i ekologia jemioły pospolitej (*Viscum album*, Viscaceae) w Polsce. *Fragmenta Floristica et Geobotanica Series Polonica, Supplementum*, *1*, 1–117.

Swedish Environmental Protection Agency. (2016). *Protected species*. https://www.naturvardsverket.se/en/topics/species-protection/protected-species/

Szmidla, H., Tkaczyk, M., Plewa, R., Tarwacki, G., & Sierota, Z. (2019). Impact of common mistletoe (*Viscum album* L.) on Scots pine forests—A call for action. *Forests*, *10*, e847.

Teppner, H., Ebmer, A. W., Gusenleitner, F. Z., & Schwarz, M. (2016). The bees (Apidae, Hymenoptera) of the botanic garden in Graz, an annotated list. *Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark*, *146*, 19–68.

Thapa, D. A. K. (2013). *Detection and mapping of incidence of Viscum album in Pinus sylvestris forest of southern French Alpe using satellite and airborne optical imagery* (thesis). University of Twente. https://itc.academia.edu/SunilThapa

Thoday, D. (1951). The haustorial system of *Viscum album*. *Journal of Experimental Botany*, *2*, 1–19.

Thoday, D. (1956). Modes of union and interaction between parasite and host in the Loranthaceae. I. Viscoideae, not including Phoradendreae. *Proceedings of the Royal Society of London. Series B*, *145*, 531–548.

Thompson, I., & Blunt, G. (2018). Invertebrate communities of old traditional orchards in South Shropshire. *Field Studies*, *14*, 6.

Thronicke, A., Oei, S. L., Merkle, A., Matthes, H., & Schad, F. (2018). Clinical safety of combined targeted and *Viscum album* L. therapy in oncological patients. *Medicine*, *5*(3), 100. https://doi.org/10.3390/medicines5030100

Tikkanen, O.-P., Kilpeläinen, J., Mellado, A., Hämäläinen, A., Hódar, J. A., Jaroszewicz, B., Luoto, M., Repo, T., Rigling, A., Wang, A., Li, M.-H., & Lehto, T. (2021). Freezing tolerance of seeds can explain differences in the distribution of two widespread mistletoe subspecies in Europe. *Forest Ecology and Management*, *482*, 118806. https://doi.org/10.1016/j.foreco.2020.118806

Troels-Smith, J. (1960). Ivy, mistletoe and elm climate indicators—Fodder plants. A contribution to the interpretation of the pollen zone border VII–VIII. *Geologiske Undersøgelse IV. Række*, *4*(4), 1–32. https://doi.org/10.34194/raekke4.v4.7000

Troll, W. (1937). *Vergleichende Morphologie der höheren Pflanzen* (Vol. 1). Borntraeger.

Tsopelas, P., Angelopoulos, A., Economou, A., & Soulioti, N. (2004). Mistletoe (*Viscum album*) in the fir forest of mount Parnis, Greece. *Forest Ecology and Management*, *202*, 59–65.

Tubeuf, K., Neckel, G., & Marzell, H. (1923). *Monographie der mistel*. R. Oldenbourg.

Tuquet, C., & Sallé, G. (1996). Characteristics of chloroplasts isolated from two mistletoes originating from temperate (*Viscum album*) and tropical (*Tapinanthus dodoneifolius*) areas. *Plant Physiology and Biochemistry*, *34*, 283–292.

Türe, C., Böcük, H., & Aşan, Z. (2010). Nutritional relationships between hemi-parasitic mistletoe and some of its deciduous hosts in different habitats. *Biologia*, *65*, 859–867.

Twardziok, M., Kleinsimon, S., Rolff, J., Jäger, S., Eggert, A., Seifert, G., & Delebinski, C. I. (2016). Multiple active compounds from *Viscum album* L. synergistically converge to promote apoptosis in Ewing sarcoma. *PLoS ONE*, *11*(9), e0159749. https://doi.org/10.1371/journal.pone.0159749

Ulgenturk, S., Kaydan, M. B., Toros, S., & Gurkan, M. O. (2003). A survey of the eriococcidae (Hemiptera: Coccoidea) of Ankara Province, Turkey. *Phytoparasitica*, *31*, 442–445.

Ullah, M., Mehmood, S., Ali Khan, R., Ali, M., Fozia, F., Waqas, M., Ullah, R., Alotaibi, A., & Sultan, M. A. (2022). Assessment of antidiabetic potential and phytochemical profiling of *Viscum album*, a traditional antidiabetic plant. *Journal of Food Quality*, *2022*, 5691379.

Umucalılar, H. D., Gülşen, N., Coşkun, B., Hayirli, A., & Dural, H. (2007). Nutrient composition of mistletoe (*Viscum album*) and its nutritive value for ruminant animals. *Agroforestry Systems*, *71*, 77–87.

Urech, K. (1997). Accumulation of arginine in *Viscum album* L: Seasonal variations and host dependency. *Journal of Plant Physiology*, *151*, 1–5.

Urech, K., & Baumgartner, S. (2019). Annual dynamic of mass production of *Viscum album* L. on *Malus domestica* L. *Phytomedicine*, *61*, 153080.

Urech, K., Schaller, G., & Jaggy, C. (2006). Viscotoxins, mistletoe lectins and their isoforms in mistletoe (*Viscum album* L.) extracts Iscador—Analytical results on pharmaceutical processing of mistletoe. *Arzneimittel-Forschung/Drug Research*, *56*, 428–434.

Üstüner, T. (2019). The effects of mistletoe (*Viscum album* L.) on the physiological properties of some drupe trees in Turkey. *Turkish Journal of Agriculture and Forestry*, *43*, 485–491.

Üstüner, T., & Düzenli, S. (2017). Determination of the chemical compositions of *Viscum album* ssp. album and soft core hosts. *Journal of Chemical Metrology*, *11*, 68–77.

Vallauri, D. R., Aronson, J., & Barbero, M. (2002). An analysis of forest restoration 120 years after reforestation on badlands in the southwestern Alps. *Restoration Ecology*, *10*, 16–26. https://doi.org/10.1046/j.1526-100X.2002.10102.x

van Halder, I., Castagneyrol, B., Ordóñez, C., Bravo, P., Perrot, M. d.' R. L., & Jactel, H. (2019). Tree diversity reduces pine infestation by mistletoe. *Forest Ecology and Management*, *449*, e117470.

Varga, I., Poczai, P., Tiborcz, V., Aranyi, N. R., Baltazár, T., Bartha, D., Pejchal, M., & Hyvönen, J. (2014). Changes in the distribution of European mistletoe (*Viscum album*) in Hungary during the last hundred years. *Folia Geobotanica*, *49*(4), 559–577. https://doi.org/10.1007/s12224-014-9193-5

Varga, I., Taller, J., Baltazár, T., Hyvönen, J., & Poczai, P. (2012b). Leaf-spot disease on European mistletoe (*Viscum album*) caused by *Phaeobotryosphaeria visci*: A potential candidate for biological control. *Biotechnology Letters*, *34*, 1059–1065.

Varga, I. P., Keresztes, B., & Poczai, P. (2012a). Data to the Hungarian insect fauna of European mistletoe (*Viscum album*). *Növényvédelem*, *48*, 153–164.

Vergara-Barberán, M., Lerma-García, M. J., Nicoletti, M., Simó-Alfonso, E. F., Herrero-Martínez, J. M., Fasoli, E., & Righetti, P. G. (2017). Proteomic fingerprinting of mistletoe (*Viscum album* L.) via combinatorial peptide ligand libraries and mass spectrometry analysis. *Journal of Proteomics*, *164*, 52–58.

Vergun, O. M., Grygorieva, O. V., Brindza, J., Shymanska, O. V., Rakhmetov, D. B., Horčinová-Sedlačková, V., Korablova, O. A., Fishchenko, V. V., & Ivanišová, E. (2019). Content of phenolic compounds in plant raw of *Cichorium intybus* L., *Lamium purpureum* L. and *Viscum album* L. *Інтродукція Рослин*, *83*, 87–96.

Vicaş, S., Vasile, L., Stelian, P., & Bandici, G. (2010). Chlorophyll and carotenoids pigments from mistletoe (*Viscum album*) leaves using different solvents. *Analele Universitatii din Oradea, Fascicula Biologie*, *17*, 213–218.

Vicaş, S. I., Rugină, D., Leopold, L., Pintea, A., & Socaciu, C. (2011). HPLC fingerprint of bioactive compounds and antioxidant activities of *Viscum album* from different host trees. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, *39*, 48–57.

Vickery, R. (1995). *A dictionary of plant-lore*. Oxford University Press.

Vidal-Russell, R., & Nickrent, D. L. (2008). The first mistletoes: Origins of aerial parasitism in Santalales. *Molecular Phylogenetics and Evolution*, *47*(2), 523–537. https://doi.org/10.1016/j.ympev.2008.01.016

Walas, Ł., Kędziora, W., Ksepko, M., Rabska, M., Tomaszewski, D., Thomas, P. A., Wójcik, R., & Iszkuło, G. (2022). The future of *Viscum album* L. in Europe will be shaped by temperature and host availability. *Scientific Reports*, *12*(1), 17072. https://doi.org/10.1038/s41598-022-21532-6

Walldén, B. (1961). Misteln vid dess Nordgräns. *Svensk Botanisk Tidskrift*, *55*, 427–549.

Wanat, M., Jałoszyński, P., Miłkowski, M., Ruta, R., & Sawoniewicz, J. (2011). New records of occurrence of fungus weevils (Coleoptera: Anthribidae) in Poland. *Wiadomości Entomologiczne*, *30*, 69–83.

Wang, A., Lehmann, M. M., Rigling, A., Gessler, A., Saurer, M., Du, Z., & Li, M.-H. (2022). There is no carbon transfer between Scots pine and pine mistletoe but the assimilation capacity of the hemiparasite is constrained by host water use under dry conditions. *Frontiers in Plant Science*, *13*, 902705.

Wangerin, W. (1937). Loranthaceae. In O. van Kirchner, E. Loew, & C. Schroeter (Eds.), *Lebensgeschichte der Blütenpflanzen Mitteleuropas* (Vol. *II/1*, pp. 953–1146). Ulmer.

Watson, D. M., & Rawsthorne, J. (2013). Mistletoe specialist frugivores: Latter day 'Johnny Appleseeds' or self-serving market gardeners? *Oecologia*, *172*, 925–932.

Watts, W. A. (1959). Interglacial deposits at Kilbeg and Newtown, Co. Waterford. *Proceedings of the Royal Irish Academy*, *60B*, 79–134.

Westerkamp, C., & Demmelmeyer, H. (1997). *Blattoberflächen mitteleuropäischer Laubgehölze: Atlas und Bestimmungsschlüssel [Leaf surfaces of central European woody plants: Atlas and keys]*. Gebrüder Borntraeger.

Wiens, D., & Barlow, B. A. (1975). Permanent translocation heterozygosity and sex determination in east African mistletoes. *Science*, *187*(4182), 1208–1209.

Wiens, D., & Barlow, B. A. (1979). Translocation heterozygosity and the origin of dioecy in *Viscum*. *Heredity*, *42*(2), 201–222. https://doi.org/10.1038/hdy.1979.23

Wilson, C. A., & Calvin, C. L. (2003). Development, taxonomic significance and ecological role of the cuticular epithelium in the Santalales. *IAWA Journal*, *24*(2), 129–138. https://doi.org/10.1163/22941932-90000326

Wilson, D. G. (1973). Notable plant records from the Cromer Forest bed series. *New Phytologist*, *72*(5), 1207–1234. https://doi.org/10.1111/j.1469-8137.1973.tb02097.x

Wójciak-Kosior, M., Sowa, I., Pucek, K., Szymczak, G., Kocjan, R., & Luchowski, P. (2017). Evaluation of seasonal changes of triterpenic acid contents in *Viscum album* from different host trees. *Pharmaceutical Biology*, *55*, 1–4.

Wollenweber, E., Wieland, A., & Haas, K. (2000). Epicuticular waxes and flavonol aglycones of theuropeann mistletoe, *Viscum album* L. *Zeitschrift für Naturforschung*, *55c*, 314–317.

Worobiec, G., & Lesiak, M. A. (1998). Plant megafossils from the Neogene deposits of Stawek-1A (Bełchatów, Middle Poland). *Review of Palaeobotany and Palynology*, *101*(1), 179–208. https://doi.org/10.1016/S0034-6667(97)00075-4

Yan, C. F., Gessler, A., Rigling, A., Dobbertin, M., Han, X. G., & Li, M. H. (2016). Effects of mistletoe removal on growth, N and C reserves, and carbon and oxygen isotope composition in scots pine hosts. *Tree Physiology*, *36*, 562–575.

Yang, D., Goldstein, G., Wang, M., Zhang, W. W., Wang, A. Y., Liu, Y. Y., & Hao, G. Y. (2017). Microenvironment in the canopy rivals the host tree water status in controlling sap flow of a mistletoe species. *Tree Physiology*, *37*, 501–510.

Yousefvand, S., Fattahi, F., Hosseini, S. M., Urech, K., & Schaller, G. (2022). Viscotoxin and lectin content in foliage and fruit of *Viscum album* L. on the main host trees of Hyrcanian forests. *Scientific Reports*, *12*, 10383.

Zagwijn, W. H. (1994). Reconstruction of climate change during the Holocene in western and Central Europe based on pollen records of indicator species. *Vegetation History and Archaeobtany*, *3*, 65–88. https://doi.org/10.1007/BF00189928

Zamora, R., & Mellado, A. (2019). Identifying the abiotic and biotic drivers behind the elevational distribution shift of a parasitic plant. *Plant Biology*, *21*, 307–317.

Zervas, A., Petersen, G., & Seberg, O. (2019). Mitochondrial genome evolution in parasitic plants. *BMC Evolutionary Biology*, *19*(1), 87. https://doi.org/10.1186/s12862-019-1401-8

Ziegler, H., Weber, J., & Lüttge, U. E. (2009). Thermal dissipation probe measurements of sap flow in the xylem of trees documenting dynamic relations to variable transpiration given by instantaneous weather changes and the activities of a mistletoe xylem parasite. *Trees*, *23*, 441–450.

Zieliński, S., & Graczyk, D. (2003). The mistletoe *Viscum album* L.—A new host plant for larvae *Oplosia fennica* (Payk.) (Coleoptera: Cerambycidae). *Przegląd Przyrodniczy*, *14*, 174–175.

Zonneveld, B. J. M. (2010). New record holders for maximum genome size in eudicots and monocots. *Journal of Botany*, *2010*, 527357.

Zuber, D. (2004). Biological flora of Central Europe: *Viscum album* L. *Flora*, *199*, 181–203. https://doi.org/10.1078/0367-2530-00147

Zuber, D., & Widmer, A. (2000). Genetic evidence for host specificity in the hemi-parasitic *Viscum album* L. (Viscaceae). *Molecular Ecology*, *9*, 1069–1073.

Zuber, D., & Widmer, A. (2009). Phylogeography and host race differentiation in the European mistletoe (*Viscum album* L.). *Molecular Ecology*, *18*, 1946–1962.

Zweifel, R., Bangerter, S., Rigling, A., & Sterck, F. J. (2012). Pine and mistletoes: How to live with a leak in the water flow and storage system? *Journal of Experimental Botany*, *63*, 2565–2578.

How to cite this article: Thomas, P. A., Dering, M., Giertych, M. J., Iszkuło, G., Tomaszewski, D., & Briggs, J. (2022). Biological Flora of Britain and Ireland: *Viscum album*. *Journal of Ecology*, *00*, 1–39. https://doi.org/10.1111/1365-2745.14036