

Biological Flora of Britain and Ireland: *Hammarbya paludosa*

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Abstract

1. This account presents information on all aspects of the biology of *Hammarbya paludosa* (L.) Kuntze (bog orchid, bog adder's-mouth orchid) (*Malaxis paludosa* (L.) Sw., *Ophrys paludosa* L.), 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. *Hammarbya paludosa* is a small bisexual perennial forb. It occurs in open habitats in bogs, mires and heaths as well as semi-shaded open woodland and, in some areas, in shaded coniferous forest. It is found in a few locations in the southern England (the New Forest, Dorset, Devon and Cornwall), in Cumbria and Northumberland, and in western counties in Wales. It is rare in Ireland but wide spread but very local in Scotland. *H. paludosa* has a Holarctic circumboreal range. Ninety per cent of known locations are recorded in Northern Europe and the British Isles.
3. *Hammarbya paludosa* occurs in *Sphagnum*, other mosses and bare peat, overlying a variety of superficial deposits and sedimentary, metamorphic and igneous rocks. The pH of the rooting substrates ranges from acidic to neutral and slightly alkaline. Its nutrient status is oligotrophic, although occasionally mesotrophic, and very rarely eutrophic. It grows well in conditions of consistent lateral flow of water in the substratum.
4. *Hammarbya paludosa* is visited by small insects of the order Diptera. Two species of gnats are recorded as orchid pollinators: *Phronia digitata* and *Sciara thomae*. It produces a small amount of nectar but is often considered as non-rewarding. The seeds are dust-like, dispersed by wind and water and the species has a short-term seed bank. Tiny bulbils (propagules) are formed on the leaf margins. They are dispersed by water.
5. *Hammarbya paludosa* has declined in Britain since the late 19th century primarily due to drainage of its mire habitats in lowland regions of southern and eastern England and Wales. The decline slowed down by the 2000s, and new locations have been found in Scotland and Ireland.

*Nomenclature of vascular plants follows Stace (2019) and, for non-British species, Flora Europaea (1964–1980), or Cherepanov (1995) for the territory of Russia and neighbouring countries. Nomenclature of mosses follows Ignatov et al. (2006).

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KEYWORDS

climatic limitation, communities, conservation, geographical and altitudinal distribution, mycorrhiza, populations, vivipary

Bog orchid (Orchidaceae, subfamily Epidendroideae, tribe Malaxideae). *Hammarbya paludosa* (L.) Kuntze is a perennial herbaceous rhizomatous hemicryptophyte. Pseudobulb 0.2–0.7 × 0.3–1.0 cm, includes terminal internode of rhizome encapsulated by thick, fleshy, succulent sheaths of two upper leaves. Leaves 1–3 (4), 1–3 × 0.5–1 cm, pale-green or yellow-green, elliptic, glabrous, sessile, margins curved inwards. Roots 0.1–0.2 cm in diameter, 0.5–1.5 cm to 3–5 cm long, often absent. Rhizome with few to numerous hair-like trichomes 0.2–0.5 cm long. Flowering stem terminal, erect, pale yellowish green, glabrous, 3- to 5-angled, 3–10 (25) cm, 1–3 lower bracts without flowers; upper bracts, sharply triangular, narrow, pointed, 1-nerved, 0.3 cm long. Flowers small, green-yellow, 5–20 (55) in spike-like inflorescence. Two outer perianth segments ('sepals') vertically erect, 0.1 × 0.2 cm, ovate, with acuminate tip; third outer perianth segment bent downwards, ovate, obtuse, 0.12 × 0.2 cm. Two inner perianth segments ('petals') 0.06 × 0.15 cm, oval, strongly recurved backwards; labellum directed upwards, 0.12 × 0.2 cm, ovate, acuminate, entire on margins, not lobed, spur absent. Column very short, with four waxy pollinia, whole pollinia with removable viscidium, pollinium compact, anther incumbent. Pedicels 0.2–0.4 cm and ovaries 0.3 × 0.4 cm twisted by 360°.

The genus *Hammarbya* L. is monospecific. *H. paludosa* is sometimes included in genus *Malaxis* Sol. ex Sw. (Pridgeon et al., 2005), which, however, was shown to be polyphyletic (Cameron, 2005). Tribe Malaxideae includes nearly 2000 species world-wide. Phylogenetic analyses suggested division of the tribe into four: two terrestrial and two epiphytic (Cameron, 2005) or two terrestrial and one epiphytic clades (Tang et al., 2015). *Hammarbya* is morphologically close to the clade of terrestrial species of *Malaxis* and *Liparis* with conduplicate leaves. However, its distinctive column structure (Szlachetko & Margońska, 2002) and extensive vivipary (the precocious and continuous growth of the offspring when still attached to the maternal parent) suggest that additional phylogenetic study is necessary to determine the genus position within Malaxideae (Cameron, 2005). The phenotype of *H. paludosa* is uniform across the species range. No variation worthy of formal taxonomic recognition has been reported.

Hammarbya paludosa is native to the British Isles, particularly in the colder and wetter regions, where it is a very localised plant of bog and mire vegetation.

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

The historic and present distribution of *Hammarbya paludosa* in the British Isles is shown in Figure 1. Its distribution in the British Isles has been summarised by K. J. Walker (personal communication), as following. The species stronghold is in Scotland where it is scattered throughout the Hebridean Islands (Jura, Islay, Colonsay, Mull, Coll,

Tiree, Muck, Eigg, Rum, Skye, Raasay, Outer Hebrides), Orkney and Shetland, and the northwest and northeastern highlands. It is uncommon in the border regions of Scotland and England but is locally common in the English Lake District and in north and mid Wales. In comparison it has virtually disappeared from lowland eastern and southeast England with only a single population surviving in Norfolk, at Roydon Common near to King's Lynn. It was last recorded in many lowland English counties during the 19th century, usually following the drying out of fens and bogs following drainage (Cambridgeshire, 1855; Huntingdonshire, 1840; Suffolk, 1889; Surrey, 1896; Lincolnshire, 1820). Its remaining English strongholds are in the New Forest, Hampshire and on the Dorset heaths where there are around 60 and 15 surviving populations respectively. It also survives on two sites on Dartmoor in south Devon and two sites on Bodmin Moor in East Cornwall. In Ireland it is very rare with a highly scattered distribution around the coast. Currently only around 30 populations are known although it is probably still overlooked in many regions.

H. paludosa has one of the largest ranges in the family Orchidaceae: holarctic and circumboreal, covering the northern parts of Europe, Asia and North America. Of an estimated 12,467 locations of the species recorded world-wide, 97% are European (GBIF, 2020). Among them, c. 17% are known from the British Isles and 60% from Scandinavia (Figure 2). The species is relatively common in north-western Russia (Bragina & Vakhrameeva, 2008; Efimov, 2011). The most northern population of *H. paludosa* in Russia is known from the Chunozero Lake (67°61'90"N, 32°49'47"E), in Murmansk Oblast (Blinova, 2003).

The species is strongly represented in Scandinavia and the Baltic region (Hultén & Fries, 1986; Jarzombkowski et al., 2014; Sotek, 2010). The number of sites is also relatively high in Denmark, the Netherlands and Belgium (GBIF, 2020). With increased continentality of climate, the number of locations of *H. paludosa* decreases substantially and the species is thinly spread across much of central Europe. Scattered populations are found in Poland (Jarzombkowski et al., 2014), Germany (Kadereit et al., 2016), France (Letellier, 2014), Czech Republic (Kaplan et al., 2018), Lithuania (Lietuvos, 2007), Western and Northern Ukraine (Carpathians, Polesye and Rastochie) (Didukh, 2009), in Belarus (Shvets & Skuratovich, 2005), and in Austria, Hungary, the North Macedonia, Slovakia and Switzerland (Maiz-Tome, 2017), as well as across the central part of European Russia (Kirilova, 2019; Volkova, 2010). The southern limit of the species range in Europe includes a few isolated locations in Romania (Bartók et al., 2019), in Italy (Prosser & Bertolli, 2016), in Bulgaria (Peev et al., 2011) and in the Southern Urals, Russia (Mamaev et al., 2004).

In the Russian Far East, *Hammarbya paludosa* has been recorded in the north of Primorye Territory (Vakhrameeva et al., 2008), on Sakhalin and Kuril Islands and the Pacific shores of Kamchatka Peninsula

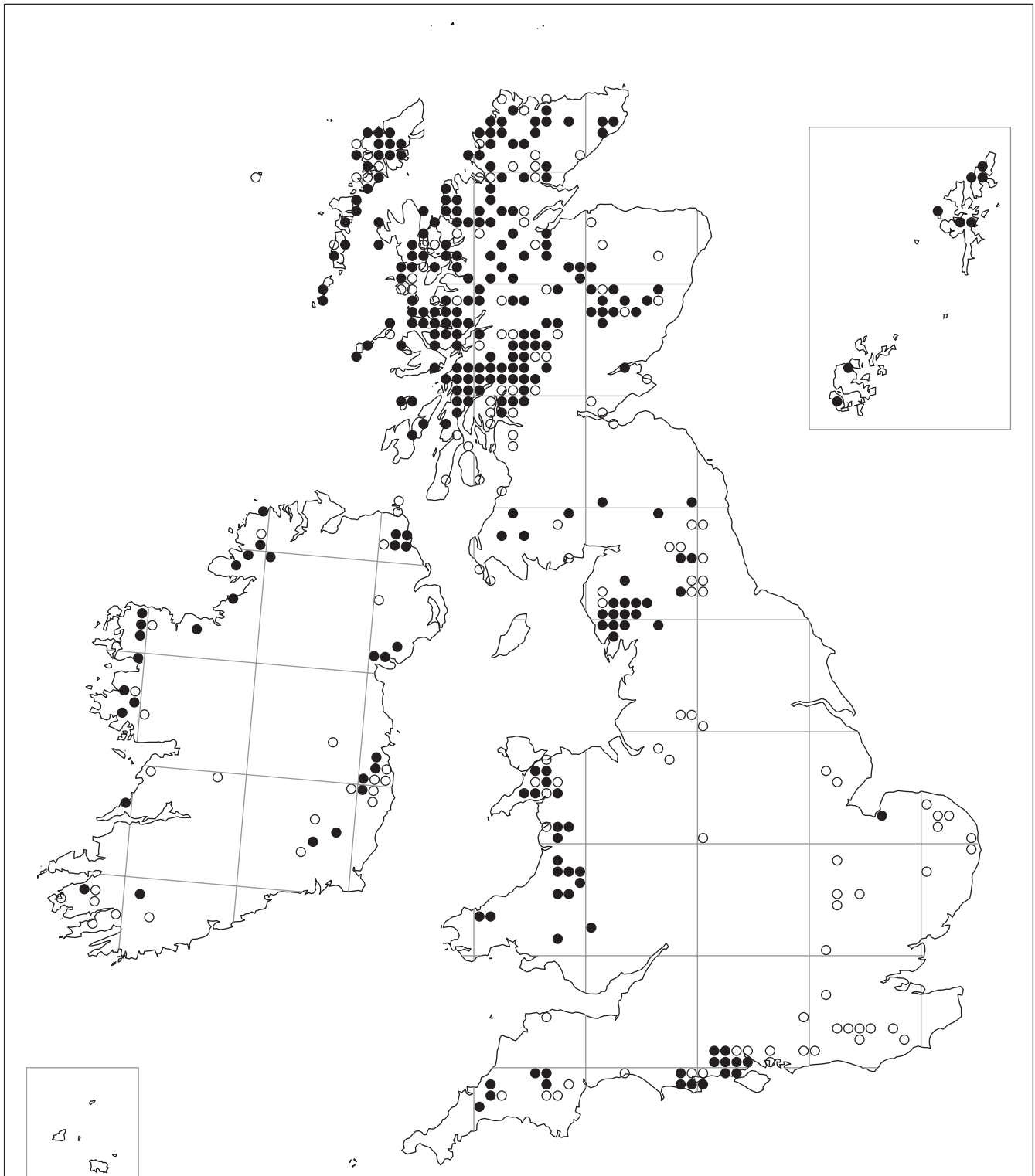


FIGURE 1 The distribution of *Hammarbya paludosa* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (●) native 1970 onwards; (○) native pre-1970. Mapped by Colin Harrower, Biological Records Centre, UK Centre for Ecology and Hydrology, mainly from records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

(Barkalov & Taran, 2019; Buri & Chernyagina, 2018). Ten locations are known from Japan (GBIF, 2020). In North America, 38 records of the species are listed from the Alaska Range, Cook Inlet Lowlands,

Agulupak River, Tanana Lowlands, Yukon River valley and scattered locations around the Gulf of Alaska and in southeast Alaska (Carlson et al., 2013). The species is also known from Yukon (Cody et al., 2001)

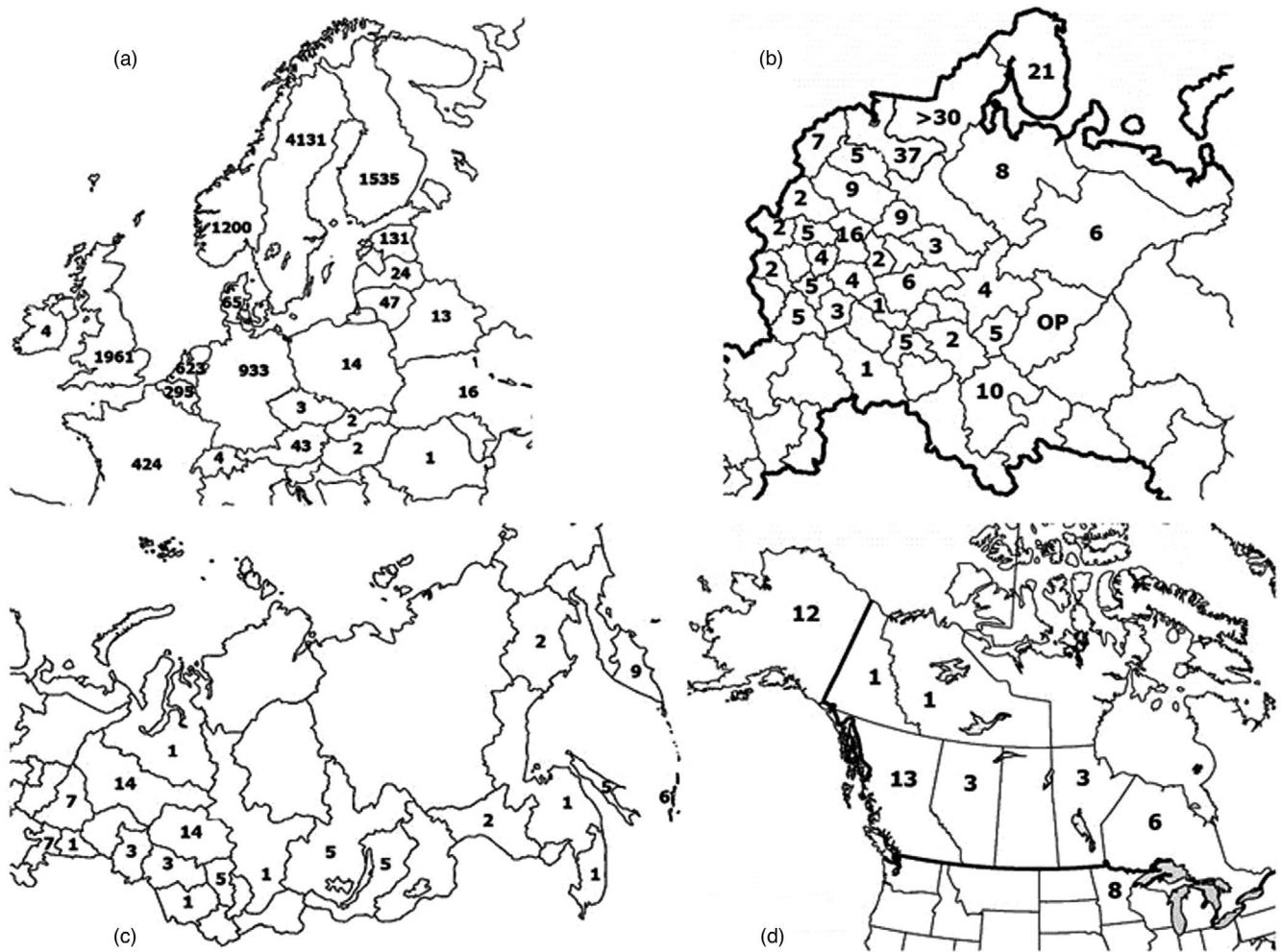


FIGURE 2 Numbers of locations of *Hammarbya paludosa* in European countries (a) based on data from GBIF (2020), administrative regions of Russia (b, c), and in the United States and Canada (d) Compiled from 97 regional floras, regional Red Data Books and publications about regional findings of the species

and several other Canadian provinces (Figure 2). Recent locations have been found in Minnesota (Whitfeld et al., 2015).

In the British Isles, approximately 30% of records are from below 50 m a.s.l., and only around 10% are from above 350 m a.s.l. according to the Database of the Botanical Society of the British Isles (BSBI, 2021). Very few locations are recorded above 500 m a.s.l., as at c. 500 m a.s.l. at Llyn Anafon in Abergwyngregyn in Wales (Stroh, 2015) and 560 m a.s.l. in Creag Bhocan, Beinn Dubhchraig (McIntosh, 2006). In Scotland, *H. paludosa* occurs from below 20 m a.s.l. (S. Longrigg, personal observation) up to 600 m a.s.l. at Ben Gulabin, near Spittal of Glenshee, which is also the highest confirmed altitude for this species in the United Kingdom (BSBI, 2021).

World-wide, altitudinal range of the species is bigger than in the United Kingdom. A population in a coastal location at sea level was monitored in Primorye Territory, Russia (Vakhrameeva et al., 2008). In Romania, the species was reported from open habitat of north-east aspect and at an altitude of 530 m a.s.l. in the Gutâi Mts, Maramureş County (Bartók et al., 2019). In southern Europe, isolated locations in the mountains occur at 1400–1500 m a.s.l. (Dusak & Prat, 2010; Käsermann & Moser, 1999; Peev et al., 2011; Prosser

& Bertolli, 2016), so the species is considered as Boreal-Montane (Carey & Dines, 2002). Records from Alaska came from 329 m a.s.l. in Cascade Creek and 766 m a.s.l. at lower Buckskin Glacier (Carlson et al., 2013).

2 | HABITAT

2.1 | Climatic and topographical limitations

Hammarbya paludosa occurs in ten of the 13 European climate zones identified by Metzger et al. (2005), excluding only the Anatolian, and two non-mountainous Mediterranean zones. The species is mainly associated with the Atlantic North zone in the British Isles, and with the Alpine North zone in Scandinavia (Metzger et al., 2005). The species is tightly linked to the boreal biome, with only two locations found to the south of the boreal climate in America (Whitfeld et al., 2015) and two in Eurasia, where *H. paludosa* reaches the forest-steppe biome in the Urals (Mamaev et al., 2004) and in Ukraine (Didukh, 2009).

In the British Isles, mean temperatures in the hectads ($10 \times 10 \text{ km}^2$) occupied by *Hammarbya paludosa* vary from 2.9°C in January to 13.3°C in July (Hill et al., 2004). Mean temperature range between January and July is much wider at the northern edge of the species' distribution, in Murmansk Oblast, Russia, from -11 to 12.5°C, and even wider in the continental climate of Buryatia, from -24 to 19°C (Climate Data Worldwide, 2020). In Scandinavia, the species grows in areas where the vegetation period is shorter than 140 days (Sotek, 2010).

Average annual precipitation in hectads occupied by *H. paludosa* in the British Isles is 1615 mm (Hill et al., 2004). Average annual precipitation is also high in its Norwegian range, for example, 1812 mm in Ålesund, and up to 2251 mm in Bergen. Annual precipitation in the habitats of *H. paludosa* declines with increasing climate continentality, to as low as 264 mm in Buryatia (Climate Data Worldwide, 2020). Precipitation is the most powerful climatic factor which control distribution of *Hammarbya paludosa*, explaining high numbers of the species populations in the areas with oceanic climate.

H. paludosa is typically a species of open habitats (Maiz-Tome, 2017; Skogen, 1973; Vakhrameeva et al., 2008; Zhmylev et al., 2013). Accordingly, its Ellenberg indicator score for light is very high ($L = 9$; Hill et al., 2004). Thus, it occurs in a variety of open habitats, such as *Sphagnum* bogs (Harrap & Harrap, 2009), *Sphagnum* pool mires and wet heath mosaic (Green & MacDonald, 2007), and wet grassy areas along streams and in peatlands (S. Longrigg, personal observations). It grows on minerotrophic aapa bogs, with open centres laying lower than forested edges, in the north of Russia (Kravchenko, 2007). In America the species found in muskeg (a range of wetlands with a thick layer of peat), on *Trichophorum-Sphagnum* fen in valley bottoms, and in alpine-sedge wet meadow in Alaska and British Columbia (Carlson et al., 2013). *H. paludosa* is not known from woodlands in the British Isles, although in other parts of its range plants have been found in shaded woodland, not far from the edge (e.g. Moscow Oblast, Russia; Zhmylev et al., 2013). In Montana, USA, it occurs in shaded conifer swamps dominated by *Picea mariana* (Whitfeld et al., 2015). In Sakhalin, the species occurs in open, pine, larch and birch woodlands, where crown density is low (Barkalov & Taran, 2019). In the southern part of its the North American range, *H. paludosa* occurs in shaded habitats within coniferous forest (Reeves & Reeves, 1985). Experimental studies with direct shading of the plants are required to understand its effect on *H. paludosa*.

2.2 | Substratum

The name 'bog orchid' reflects a widespread connection with different types of wetlands, most commonly bogs and mires (Preston et al., 2002). In the British Isles the species is usually found growing directly on *Sphagnum* (Figure 3a), on the edges of islands within or along the edge of bog pools or runnels among wet heath, blanket bog or in valley mires (e.g. on the islands of Rum and Colonsay and in Dorset and Hampshire; K. J. Walker,

personal communication; on the Isle of Soay and near Tyndrum; S. Longrigg, personal observations). It has also been seen in a raised gully in Glen Falloch, on Beinn Challum, on a steep bank above a small stream south-west of Crianlarich, by a very small inflow stream to a lochan on the Isle of Eigg, and overlooking a small rocky stream in Glen Vorlich W (S. Longrigg, personal observations). In the New Forest, Hampshire, it also occurs along peaty runnels on the very gentle slopes of valley mires (e.g. Denny Bog; K. J. Walker, personal communication). Very occasionally, plants are found on dry ground (e.g. near Loch Doire an Lochan on Soay; S. Longrigg, personal observation).

Sphagnum is the most common substratum for the species in the other parts of its range. This includes floating mats and rafts of *Sphagnum* species at the shores of lakes (Bootsma et al., 2002; Sadokov & Philippov, 2017). In Sweden, such floating rafts were 0.6–0.8 m thick. *H. paludosa* also occurs on *Hypnum* spp. and some other mosses, both on the moss cushions and in between them, sometimes on bare peat (Figure 3f; Reeves & Reeves, 1985; McIntosh, 2006; Whitfeld et al., 2015). *H. paludosa* can also grow on rocks with moss cover (Kravchenko, 2007), wet sand (Barkalov, 2009; Lütt et al., 2004; van Dijk et al., 2015), wet slacks in volcanic ashes (Barkalov, 2009) and disturbed peat works (Becker, 2005; Golovko et al., 2009; Kravchenko, 2007; Shvedchikova et al., 2012).

H. paludosa is described as a hydrophyte (Philippov, 2015). Consistent and constant saturation of the substratum is considered as a key condition for successful growth. Accordingly, the Ellenberg value for soil moisture is very high ($F = 9$; Hill et al., 2004). The species cannot tolerate any substantial drying of the substratum (Harrap & Harrap, 2009; Skogen, 1973). At the same time, stagnant saturation of the soil with standing water does not favour growth (Harrap & Harrap, 2009). In the British Isles, plants of *H. paludosa* are associated with moving water such as small streams and runnels, or ditches (Figure 3d), in or beside sloping wet flushes, and on seepage-fed bogs (Figure 3b). In other parts of the range, the species is also found in areas of bogs with lateral flow of water and near small streams (Blinova, 2016; Bragina & Vakhrameeva, 2008; Lieurade & Thomassin, 2011; Philippov, 2015). Some habitats are spring-fed (Philippov, 2015), or in the Netherlands, seepage-fed (van Dijk et al., 2015). The lateral flow of water seems to be a defining ecological factor for *H. paludosa* habitats (Harrap & Harrap, 2009; Stroh, 2015).

H. paludosa is commonly regarded as an obligate acidophile (Bragina & Vakhrameeva, 2008; Maiz-Tome, 2017; Stroh, 2015). Its Ellenberg soil reaction value is very low, indicating that it occurs in acid conditions ($R = 2$; Hill et al., 2004). Actual pH measurements in different parts of the species' range describe habitats from acid to neutral or even slightly alkaline (Table 1). In the British Isles it is occasionally found in base-rich flushes (Pearman et al., 2008). Base-rich karst mires are the only habitats in isolated locations of the species in Tula oblast (Volkova, 2010) and Bashkortostan (Muldashev, 2011) in Russia. In the Netherlands, *H. paludosa* is identified as an indicator of a rare pH condition, marginal between acid and alkaline, which is



FIGURE 3 *Hammarbya paludosa* at locations in England: (a) and (b) The New Forest, Hampshire (50°47'48.3"N, 1°38'51.5"W); and in Scotland: (c) Tom Soilleir (56°7'12"N, 4°33'57"W), (d) Ben Venue (56°12'35"N, 4°29'19"W), (e) Near Tyndrum (56°26'44"N, 4°42'37"W), (f) The Isle of Soay (57°9'16"N, 6°11'24"W). Red dots mark individual plants. Photos: (a), (b), Mike Dodd; (c)–(f), Sarah Longrigg

TABLE 1 Soil pH in the habitats of *Hammarbya paludosa* in different parts of its European range

Location	Soil pH	Reference
Norway	4.6–5.9	Skogen (1973)
Leningrad Oblast, Russia	5.57–6.75	Bragina (2001a)
Murmansk Oblast, Russia	6.5–6.8	Blinova (2016)
Vologda Oblast, Russia	6.29	Sadokov and Philippov (2017)
Poland	5.1–7.5	Pawlikowski and Jarzombkowski (2009)
Poland	4.5–6.5	Jarzombkowski et al. (2014)
Ukraine	4.5–5.5	Golovko et al. (2009)
Romania	6.4	Bartók et al. (2019)

very sensitive to acidification (van Dijk et al., 2015). Further investigation into this 'marginal' pH condition would answer the question about actual pH requirements of this orchid species and its mycorrhizal symbionts, which could be also sensitive to soil reaction.

The low Ellenberg value for soil fertility, suggests a preference for very low nutrient conditions (N = 2; Hill et al., 2004). Few actual measurements of nutrient concentrations in the habitats of the species have been carried out (Golovko et al., 2009; van Dijk et al., 2015). Most estimates rely on a type of habitat: meso-oligotrophic (Danylyk et al., 2018; Mamaev et al., 2004) and mesotrophic mires (Blinova, 2003; Golovko et al., 2009; Skogen, 1973), oligotrophic bogs (Lieurade & Thomassin, 2011; Puchnina et al., 2015; Stroh, 2015), rich eutrophic bogs (Gunnarsson et al., 2002; Kozhin, 2015; Pawlikowski & Jarzombkowski, 2009; Philippov, 2015) and eutrophic woodlands (Whitfeld et al., 2015). Concentrations of exchangeable calcium in the habitats of *H. paludosa* vary from very low (Golovko et al., 2009; Mamaev et al., 2004) to as high as 29.2–58.7 mg Ca²⁺/dm³ (Pawlikowski & Jarzombkowski, 2009). Measurements of chemical compositions in 12 locations for *H. paludosa* in the Netherlands (van Dijk et al., 2015) revealed substantial variation for bicarbonate, calcium, nitrogen (ammonium) and phosphorus (Table 2). Effects of particular nutrients on *Hammarbya paludosa* are still not well understood. A review of the species' habitats in Russia concluded that nutrient concentrations in the substrata have no direct effect on its performance in those habitats (Vakhrameeva et al., 2008). However, more focused, experimental studies are required for evaluation of *H. paludosa* response to nutrient variability.

TABLE 2 Water pH (0.2 M NaCl extraction) and concentrations of total carbon (bicarbonate), ammonium (analysed with hydrazine sulphate), exchangeable calcium and extractable phosphate (Olsen-P test) ions ($\mu\text{mol/L}$) at 10 cm depth, at 12 locations of *Hammarbya paludosa* populations in the Netherlands investigated by van Dijk et al. (2014, 2015)

Location	pH	HCO_3^-	Ca	NH_4^+	PO_4^{3-}
1	5.0	75	174	15	9.4
2	5.4	50	541	4	0.4
3	5.7	478	232	13	0.9
4	4.7	23	427	22	4.4
5	5.4	87	185	5	0.5
6	4.9	10	169	15	0.3
7	5.4	128	192	6	1.6
8	5.3	22	291	5	26.4
9	5.4	153	74	6	11.4
10	6.5	90	104	11	0.0
11	5.5	297	184	13	4.3
12	6.5	2850	1115	28	1.9

3 | COMMUNITIES

In Britain, *Hammarbya paludosa* is often associated with National Vegetation Classification (NVC) M1 *Sphagnum auriculatum* bog pool community described by Rodwell (1991). *H. paludosa* is mentioned as rare species for M21 *Narthecium ossifragum*–*Sphagnum papillosum* valley mire (Averis et al., 2004). On Colonsay in the Inner Hebrides it is also associated with *Trichophorum cespitosum*–*Erica tetralix* wet heath (NVC M15a; K. J. Walker, personal communication). Frequent associates include *Eriophorum angustifolium*, *Molinia caerulea* and *Rhynchospora alba* which are associated with both M1 and M21 communities, whereas *Menyanthes trifoliata* is a constant species of M1 and *Narthecium ossifragum* and *Erica tetralix* are characteristic of M21. Other species often found with *H. paludosa*, are *Carex echinata*, *Juncus squarrosus*, *Pinguicula vulgaris*, *Potamogeton polygonifolius* (Foley & Clarke, 2005; Stroh, 2015). Mire plant communities in Britain differ mainly by species of sedges. For example, *Carex panicea* and *C. echinata* are constant in M15a, distinguishing the community from M21. M10 is characterised by *Carex dioica* together with *Pinguicula vulgaris*; M6 type is characterised by *Carex echinata* and *Sphagnum recurvum/auriculatum* (Elkington et al., 2002). Examples of the plant communities with *H. paludosa* from Scotland and world-wide are listed in Table 3.

At the European level, *Hammarbya paludosa* is assigned to bog and mire vegetation dominated by particular species, some of which are rare in the British Isles (e.g. *Scheuchzeria palustris* and *Pallavicinia lyellii*). Both on the European continent and the British Isles, circumpolar Boreal-montane species form plant communities where *Hammarbya paludosa* is present. Most wide spread are phytosociological classes *Scheuchzerio-Caricetea nigrae* and *Oxycocco-Sphagnetea* (Leuschner & Ellenberg, 2017). The species is widespread in mire communities of *Scheuchzerietalia palustris*

and *Rhynchosporion albae* alliances in Sweden (Diekmann, 1997), Pomerania, Poland (Sotek, 2010), Vologda Oblast, Russia (Philippov, 2015) and Ukraine (Didukh, 2009). In the Netherlands, *Hammarbya paludosa* is associated with communities dominated by bryophytes such as *Pallavicinio-Sphagnetum*, *Campylio-Caricetum dioicae*, *Carex rostrata*–[*scheuchzerieta*] and *Scorpidio-Caricetum diandrae* (van Dijk et al., 2015). In Asian locations of *H. paludosa* (e.g. in Primorye Territory, 44°94'96"N, 136°54'79"E), the species grows on the *Sphagnum*-dominated bogs together with *Eriophorum gracile* and large forbs as *Sanguisorba parviflora* and *Lobelia sessilifolia* (Vakhrameeva et al., 2008). From the British Isles to the far east of Asia, *Menyanthes trifoliata*, *Molinia caerulea*, *Rhynchospora alba* and species of *Drosera* and *Eriophorum* commonly occur in plant communities with *H. paludosa* (Table 3). Species from the Family Ericaceae are regular associates of *H. paludosa*: in the British Isles they include *Myrica gale*, *Calluna vulgaris* and *Erica tetralix*, whereas on continental Europe—*Vaccinium oxycoccos* and *V. uliginosum*. Wet meadow plant communities rarely include *H. paludosa* (Didukh, 2009).

4 | RESPONSE TO BIOTIC FACTORS

Hammarbya paludosa is a very weak competitor (Kirilova, 2019; Lieurade & Thomassin, 2011; Skogen, 1973). It occurs in habitats with sparse cover of other herbs as well as low and sparse shrubs. If the taller plants increase their cover, *H. paludosa* disappears from the community (Zhmylev et al., 2013). It grows in fens where the cover of herbs is 12%–25% at 10 cm height above the ground, and reduced to 5% at 50 cm height (van Dijk et al., 2015). In Tver Oblast, Russia, the cover of herbs in the habitat of *H. paludosa* varies from 29% to 55% (Khomutovskiy, 2014b) and from 4% to 45% in Kerzhenskii Nature reserve, Nizhniy Novgorod, Russia (Urbanavichute, 2019). Moderate trampling can reduce the vigour of competitive herbs and increase microhabitats for *H. paludosa*, as well as for some other rare and threatened plants such as *Liparis loeselii* and *Pinguicula lusitanica* (Clément & Proctor, 2009). Creating patches of bare ground in the habitats of *H. paludosa* is suggested in order to help establishment of the species' propagules (Becker, 2005; Gunnarsson et al., 2002; Kirilova, 2019; Lieurade & Thomassin, 2011; Urbanavichute, 2019; van Dijk et al., 2015).

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

In the British Isles *Hammarbya paludosa* is usually found growing as single plants (Figure 3a,c), scattered individuals (Figure 3f) or as very small groups (Figure 3b,e). As shown in Figure 4, one third of 35 Scottish populations consisted of one or two plants; 17% consisted of three to five, and on the Scottish mainland, only a population near Tyndrum had more than 100 plants, with 141 flowering and numerous others vegetative (S. Longrigg, personal observation). Population

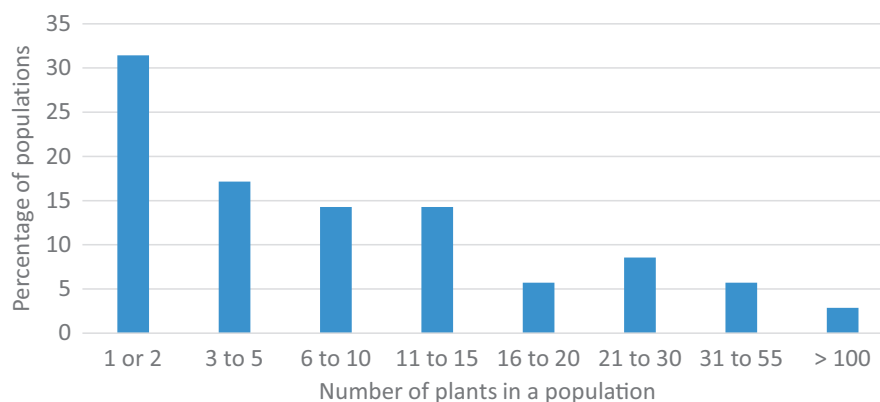
TABLE 3 (Continued)

Site	1	2	3	4	5	6	7	8	9	10
<i>Menyanthes trifoliata</i>	+								+	+
<i>Molinia caerulea</i>	+	+	+	+	+	+	+	+	+	
<i>Narthecium ossifragum</i>	+	+	+		+	+				
<i>Pedicularis palustris</i>		+			+					
<i>Phragmites australis</i>	+									
<i>Polygala serpyllifolia</i>	+									
<i>Potamogeton polygonifolius</i>	+	+				+				
<i>Rhynchospora alba</i>			+	+		+		+	+	
<i>Rhynchospora fusca</i>									+	
<i>Scheuchzeria palustris</i>								+	+	+
<i>Schoenus nigricans</i>	+				+					
<i>Scutellaria galericulata</i>								+		
<i>Succisa pratensis</i>					+					
<i>Tofieldia pusilla</i>								+		
<i>Trichophorum alpinum</i>								+		
<i>Trichophorum cespitosum</i>							+			
<i>Urticularia</i> sp.					+					
Bryophytes										
<i>Pleurozium schreberi</i>										+
<i>Sphagnum majus</i> , <i>S. fallax</i> , <i>S. denticulatum</i> , <i>S. papillosum</i> , <i>S. cuspidatum</i> , <i>S. magellanicum</i> , <i>S. annulatum</i>			+	+	+	+		+	+	+
<i>Thuidium delicatulum</i>										+

Sites of *Hammarbya paludosa* in Scotland (location and the author of the survey):

1. West end of Lochan a'Bhraghad, Colonsay SSSI (56°6'32"N, 6°9'33"W) (Lavery, 2007).
2. Carn Spiris, Colonsay (56°3'1"N, 6°14'29"W) (K. J. Walker, personal observations, 2019).
3. Resipole west and Laudale, Sunart SSSI (56°42'54"N, 5°44'32"W) (Strachan, 2012).
4. Kinlochewe (57°35'40"N, 5°20'53"W) (Green & MacDonald, 2007).
5. North East Coll Lochs and Moors SSSI (56°39'34"N, 6°30'18"W) (Griffith & Acton, 2009).
6. Glac Mhor, between Samhnan Insir and Kilmory (57°19'40"N, 4°58'41"W) (Loizou, 2010, based on information collected by K. J. Walker, 2009).
7. Creag Bhocan, Beinn Dubhchraig (56°23'50"N, 4°42'53"W) (McIntosh, 2006).
- 8–10. Compilation of data from several publications (Khomutovskiy, 2014b; Lieurade & Thomassin, 2011; Skogen, 1973; van Dijk et al., 2015; Whitfeld et al., 2015; Zhmylev et al., 2013).

FIGURE 4 Sizes of *Hammarbya paludosa* populations in Scotland. Data based on observations by S. Longrigg, with additions from McIntosh (2006), Lavery (2007), Green and MacDonald (2007), Griffith and Acton (2009), Loizou (2010) and Strachan (2012)



densities of *Hammarbya paludosa* fluctuate substantially, as was shown in annual monitoring of plants at several sites in Scotland for 4–18 years (Figure 5). Numbers of the flowering plants can show

two- to threefold decrease or increase in consecutive years. Such sharp increases in numbers, as in 2005–2006 and 2008–2009 on Conic Hill, 2009–2010 at Inverlochlarig, could not be attributed to

'reproduction waves' as increase in vegetative individuals should precede an increase in flowering plants (Khomutovskiy, 2014a). Peaks in numbers presumably occurred after a large proportion of plants in a population re-emerged after a prolonged dormancy. It is likely that *H. paludosa* can remain alive underground for 1–2 years (see below), however, conclusive proof requires annual observations of known and marked individuals. Vegetative individuals were present in most years in Inverlochlarig and Conic Hill populations, whereas on Beinn Challum they were recorded only once. Flowering plants consistently dominate in all observed sites. Only on one occasion, the number of vegetative individuals almost equalled the number of flowering ones in the Inverlochlarig population (Figure 5; S. Longrigg, personal observations).

The sizes of the populations in the other parts of the range are also generally small and very variable. In the Netherlands, five populations had less than 10 plants each, two populations 10–50 plants, and five more populations with up to 100 plants (van Dijk et al., 2015). Similarly sized populations were found in Poland (Jarzombkowski et al., 2014) and Germany (Becker, 2005). A population of 30 individuals scattered across 200 m² area of transitional bog was recorded in Romania (Bartók et al., 2019). A small population of *H. paludosa* with 13 flowering plants occupies an area of 16 m² in Volyn Region, Ukraine (Danylyk et al., 2018).

Single plants are scattered across the Shig bog in Arkhangelsk Oblast (Puchnina et al., 2015) and in Shichengskoe bog in Vologda Oblast (Philippov, 2015), in the north of European Russia. Large populations of more than 100 plants with high densities of 5–14 plants/m² are uncommon (Becker, 2005; Blinova, 2003; Bragina & Vakhrameeva, 2008; Seite & Durfort, 1995; Zhmylev et al., 2013). The majority of populations in different parts of the species' range comprise 10–50 plants, with a density of 0.2–3.0 individuals/m² (Gudžinskas, 2001; Harrap & Harrap, 2009; Jarzombkowski et al., 2014; Vakhrameeva et al., 2008; van Dijk et al., 2015). Two relatively large populations with up to 182 and 212 individual plants respectively, were monitored in Tver Oblast, Russia (Khomutovskiy, 2014a, 2014b). Spatial distribution in one of these populations at Srednee Lake is very uneven, groups of 3–10 plants being scattered across an area of 1840 m². Over a 6-year monitoring period, the fluctuations in numbers were mainly due to vegetative plants, while the number of flowering plants increases consistently apart from a small drop in 2010 (Figure 6).

H. paludosa is a very elusive plant that often evades detection during resurveys of former populations (e.g. Strachan, 2012). The species can re-appear in the same habitat after a gap of 1 (Lieurade & Thomassin, 2011) or 2 years (P. Zhmylev, personal observation). *H. paludosa* can spread

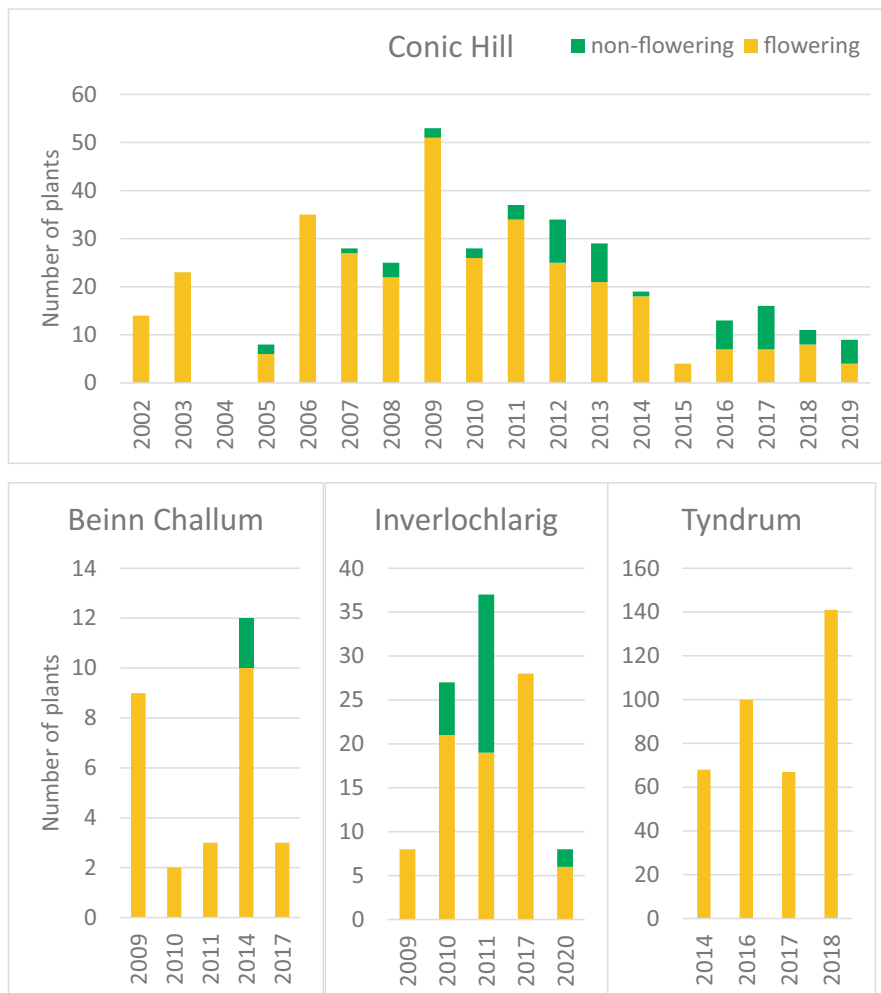


FIGURE 5 Dynamics of four populations of *Hammarbya paludosa* in Scotland. Observations by S. Longrigg, 2002–2019. Beinn Challum (56°25'25"N, 4°39'25"W). Plants were found on Conic Hill (56°5'32"N, 4°32'3"W) in 2004, but not counted. The Inverlochlarig population (56°19'54"N, 4°32'8"W) was surveyed by P. and Ph. Kingston in 2020. Vegetative plants are not presented for the Tyndrum population (56°26'44"N, 4°42'37"W) because there was no accurate count of them on the visits. No permission was needed for fieldwork

clonally by detaching ramets (bulbils) from the tips of its leaves that are then dispersed by water. If propagules germinate near the mother plant, very dense clumps of individuals can be formed (Stroh, 2015). Such clumps of 5–12 plants per 10 × 10 cm of the ground surface were found, for example, in Scotland (Figure 3e) and in the population of *H. paludosa* in Primorye Territory, Russia (I. Tatarenko, personal observation).

5.2 | Performance in various habitats

Some aspects of morphology of *H. paludosa* vary depending on the habitat. The length of the internodes on the rhizomes is controlled by the density of substratum: internodes are short or very short (0.1–0.3 cm) in plants growing on bare peat, sand or thin moss carpet overlaying rocks, but they extend up to 2–3 cm each on *Sphagnum*. Heights of the flower stalks show a negative correlation with latitude. In one of the most northern habitats in Murmansk Oblast, Russia, plant heights ranged from 4.0 to 6.5 cm (Blinova, 2003), whereas further south the variation in height is much greater, from 6 to 15 cm in France (Seite & Durfort, 1995), 8.9 to 20.7 cm in Tver Oblast, Russia (Khomutovskiy, 2014a) and 13.1 to 23.7 cm in Ukraine (Danylyk et al., 2018). Number of flowers per plant varied in Tver Oblast from 8 to 27 to 6 to 36 in different years (Khomutovskiy, 2014a).

5.3 | Effect of frost, drought, etc.

Hammarbya paludosa is very sensitive to droughts. Severe declines were reported following droughts during the onset of the main growth period in 2001 and 2002 in Murmansk Oblast, Russia (Blinova, 2008) and in 2010 in Moscow Oblast, Russia (Zhmylev et al., 2013). There are no observations on which parts of the plants are most affected by a lack of moisture. It is likely that pseudobulbs might remain dormant for 1–2 years, ensuring the plant reappearance in 1–2 years.

The species occurrence in the geographic areas with very low winter temperatures suggests that frost tolerance of the species is high, although the insulating properties of snow cover may offer protection.

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Hammarbya paludosa is an erect perennial with a single, slender, unbranched flowering stem. It is formed from an apical bud on a swollen terminal internode of the rhizome (Figure 7). In non-flowering individuals, this apical meristem remains dormant, with the potential for producing a vegetative propagule. An adult plant of *H. paludosa* has a short or long below-ground rhizome. Every annual segment of the rhizome consists of six internodes (Figure 7), their length controlled by the substratum. Leaf arrangement on the rhizome depends on the

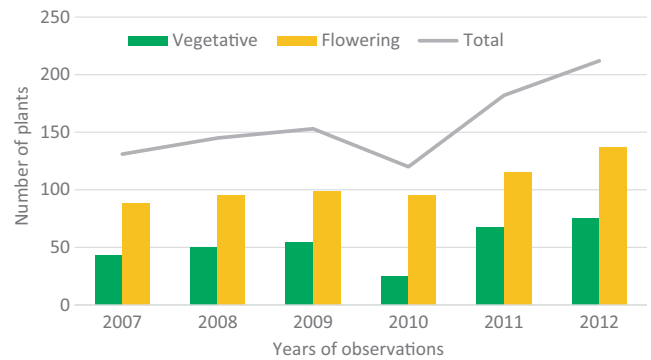


FIGURE 6 Population dynamics of *Hammarbya paludosa* in the bog at the Srednee Lake (Tver Oblast, Russia; 57°20'23"N, 32°59'20"E) in 2007–2012. Adapted from Khomutovskiy (2014a)

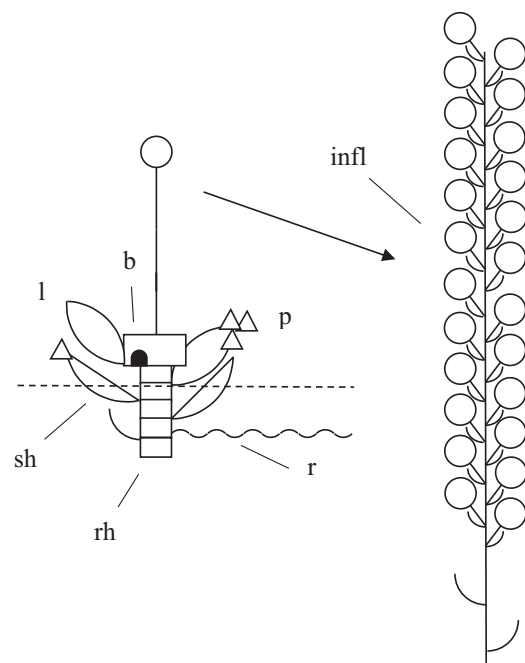


FIGURE 7 Diagram of an annual shoot of *Hammarbya paludosa*. Adapted from Tatarenko (2015). l—leaf, b—pseudobulb with renewal bud at a base, p—propagule, sh—sheath, rh—rhizome, r—root, infl—inflorescence

length of internodes: leaves form a basal rosette on dense substrata, but spread along an underground rhizome in *Sphagnum*, where only one to two upper leaves can be visible above the surface (Figure 3a). Leaf blades can be formed on four of five succulent sheath leaves carried by every annual segment of the rhizome (Figure 7). Formation of a leaf blade is controlled by light. Plants fully buried in *Sphagnum* might have all five leaves with no blades where the flower spikes are visible, but vegetative individuals are often not seen above the surface of *Sphagnum*. Plants grown on a dense substratum can have up to five leaf blades fully formed. This explains the differences in estimates of the number of leaves, from four to six in *H. paludosa* made by different authors (Bragina & Vakhrameeva, 2008; Ebel &

Müehlberg, 1991; Tatarenko, 1996). The top leaf can have a leaf primordium 1 mm long, which quickly withers away without forming a leaf blade (Ebel & Müehlberg, 1991). Margins of leaf blades can form vegetative propagules (bulbils) 0.05–0.15 cm in diameter.

The succulent sheaths of the leaves surround a terminal swollen green internode of the rhizome (Figure 3b). On dense substrata, where the rhizome is very short, the whole perennial structure resembles a bulb and is called a 'pseudobulb'. On *Sphagnum*, the rhizome is elongated and the terminal internode is encapsulated only by two upper sheaths. The pseudobulb lives for 1–2 (3) years (Harrap & Harrap, 2009; Käsermann & Moser, 1999; Lieurade & Thomassin, 2011; Reeves & Reeves, 1984; Seite & Durfort, 1995; Stroh, 2015; van Dijk et al., 2015). In a population in Leningrad Oblast, Russia, plants with up to five pseudobulbs were observed (Bragina & Vakhrameeva, 2008). The succulent sheath leaves can be up to 2 mm thick. There are large, empty cells which are arranged along the leaf ribs. These cells are dead at maturity and serve to retain air or water. Functionally, they might be similar to hyaline cells in *Sphagnum* leaves (Ebel & Müehlberg, 1991).

Hammarbya paludosa shoots grow sympodially from a very early stage of ontogenesis. Sympodial branching occurs from an axillary renewal bud formed at the base of the very first swollen internode (Figure 7). Other axillary meristems on the rhizome usually remain undeveloped. Branching of the rhizome is rare (Bragina & Vakhrameeva, 2008) although Bragina (2001a) observed development of two renewal buds on the rhizome instead of one bud. Zhmylev et al. (2013) describes a plant bearing two flower stalks, which could only be formed as a result of the rhizome branching. Monopodial growth can occur in non-flowering plants if an apical meristem on the swollen internode produces a vegetative propagule. In 11.5% of plants in a population in Leningrad Oblast, Russia, this meristem formed a terminal propagule on the 2-year-old pseudobulbs (Bragina, 2001a). The morphology of this propagule is identical to the ones developed on the leaves. Because of resources available directly from the pseudobulb, the terminal propagule can reach the size of 3 cm and develop its own pseudobulb and four leaves by the time it detaches itself from the mother plant at the end of the growing season (Bragina, 2001a). A similar method of vegetative reproduction via terminal propagule is described in *Malaxis monophyllos* (Ziegenspeck, 1936) and *Liparis japonica* (Tatarenko, 1996), taxa morphologically close to *Hammarbya* (Tatarenko, 2015).

Vegetative propagules were called 'foliar embryos' by Taylor (1967) because of their unusual morphology resembling protocorms (seedlings) of the species. Vegetative propagules form along the leaf margin as a result of endogenous proliferation of epidermal cells of the adaxial surface of the leaf (Bragina, 2001a). Meristem cells form a dome structure with a bundle of cells with high density cytoplasm in the middle. At the top of the dome, the primordium of the first leaf of a propagule starts growing. At the same time, an internal egg-shape part of the propagule is formed. The primary leaf of the propagule encapsulates the internal part and

serves for its protection and nutrient storage (Figure 8a–r). Cells of this leaf can proliferate again, forming propagules of the second order (Bragina, 2001a). This type of branching at the propagule level was also observed in a species closely related to *H. paludosa*, *Liparis makinoana*. It formed propagules bunched up to the third and fourth orders, while growing in axenic culture with high nutrient availability (Tatarenko, 2007).

Adventitious roots develop, one per internode along the rhizome, but not in all plants. In some populations, the plants have no roots, but multiple hair-like trichomes on the rhizome at the base of the leaves (Figure 8) on the first and second internodes (Rasmussen, 1995) or along the rhizome (Bragina, 2001a). In Minnesota as well as in Leningrad Oblast populations, a few plants had from one to four short (0.5–1.5 cm) roots (Bragina & Vakhrameeva, 2008; Reeves & Reeves, 1984). In a population on *Sphagnum* bog in Primorye Territory, Russia, adult plants had 1–3 long roots (3–4 cm). Internal growth of a root inside the old part of rhizome was described by Rasmussen (1995).

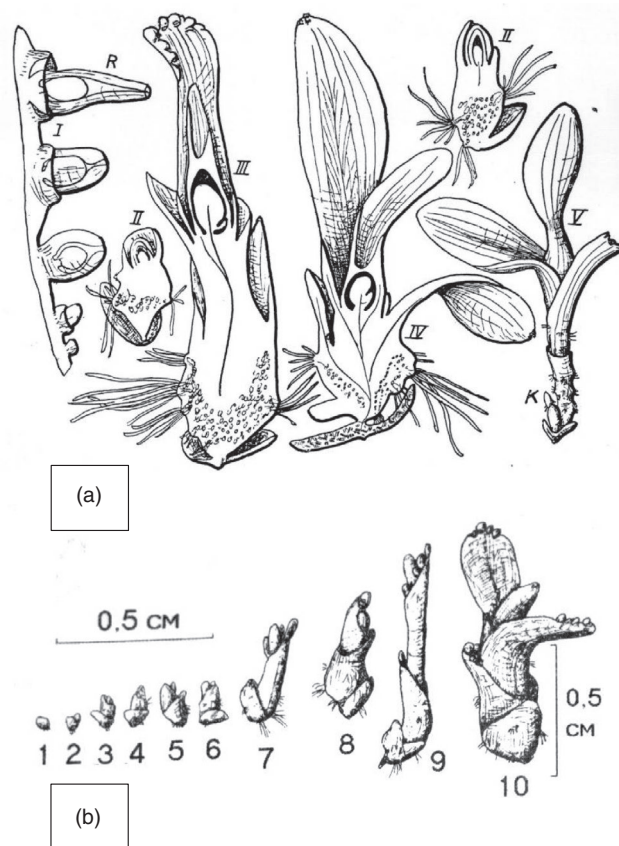


FIGURE 8 Different stages of development of the propagule detached from a leaf of *Hammarbya paludosa*. (a) Adapted from Irmish (1853): I—Development of a rim of leaf propagules, R—well-formed propagule, II—presumably 2-year-old propagule, fungus at the base, III—3-year-old propagule—small bulb, IV—4 years, V—5-year-old plant, K—bud. I–IV—strongly enlarged, V—slightly enlarged. (b) Adapted from Ziegenspeck (1936): 1–10 stages of development of a propagule after it detached from a leaf. Both (a) and (b) shows trichomes located at the bases of the propagules

6.2 | Mycorrhiza

The occurrence of *Hammarbya paludosa* in oligotrophic habitats provoked a suggestion of full dependence of the species on mycorrhizal fungi (Nilsson, 1979), even though all parts of the plant are green and presumably are able to photosynthesise. Fungi have been observed in different below-ground organs of the species. Mycorrhizal fungi were found in the roots of *H. paludosa* but occupation rate of the root cortical cells was relatively low (12%) in plants in Primorye Territory, Russia. Rhizomes of those plants contained no fungi (Tatarenko, 1995). In contrast, the rhizomes of plants collected in Murmansk Oblast, Russia, had rhizome cells occupied by fungal pelotons (Figure 9) (Dmitriev, 2017). Plants of *H. paludosa* studied by Rasmussen (1995) had internal mycorrhizal roots, growing along the old parts of the rhizome and covered by the leaf sheaths. Succulent sheaths themselves contained fungi in the basal parts (Rasmussen, 1995). Similar localisation of the thick internal roots was observed in *Liparis* sp., a genus close to *Hammarbya*. Internal roots in *Liparis* grew longitudinally through the remaining sheaths of the previous year's leaves. Both thick internal roots and sheaths were heavily occupied by mycorrhizal fungi, while very thin external roots were colonised at the rate of 5%–15% (I. Tatarenko, personal observation).

Propagules formed on the leaf margins of *H. paludosa* are not infected with the fungi at the moment of their separation from a mother plant (Fuchs & Ziegenspeck, 1927, cited in Rasmussen, 1995). Trichomes occur on the bases of the primordial leaves of propagules after separation (Bragina & Vakhrameeva, 2008). Mycorrhizal fungi penetrate both protocorms and vegetative propagules via trichomes (Rasmussen, 1995; Kulikov & Filippov, 2001). Mycorrhiza can be restricted to trichomes only, as it has been observed in rootless orchid species like *Ephippianthus sachalinensis* and *Myrmechis japonica* (Tatarenko, 1996, 2007). Such mycorrhizal localisation is also possible in young plants of *H. paludosa* sampled, which had no roots and no mycorrhiza within the rhizomes (Tatarenko, 1995).

Information about mycorrhizal localisation in plants of *Hammarbya paludosa* is still scarce. Plants from four geographical locations described above showed different below-ground organs being occupied by symbiotic fungi. However, there is no suggestion that populations of the species differ in mycorrhizal localisation. The differences are more likely to be explained by the variation between individual plants.

In an experiment with unripe seeds from green pods of *H. paludosa* *in vitro*, no germination occurred on fungus-free media (Andronova et al., 2000). In symbiotic culture, fungi obtained from adult plants of *H. paludosa* displayed no specificity to the species, and stimulated germination in several other orchid species not closely related to *Hammarbya* (Kulikov & Filippov, 2001). Symbionts of *H. paludosa* were recently identified in two different populations: in Hungary (Illyés et al., 2009) and in Murmansk Oblast, in the extreme north of Russia (Dmitriev, 2017). Strains of the genus *Tulasnella* were identified as the most common symbionts of *H. paludosa* in both habitats. Illyés et al. (2009) described anamorphic strains of *Tulasnella* as *Epulorhiza* '1'. These two strains were found in protocorms of *H. paludosa* germinated near the adult plants growing on the floating mat ferns at the lake shore. According to Illyés et al. (2009), fungi from this specific habitat differ from other strains of *Epulorhiza* named in the publication as *Epulorhiza* '2', which were found in orchids in the other types of wetland habitats.

A basidiomycete fungus, *Ceratobasidium cornigerum* (Bourdot) D.P. Rogers, commonly forms mycorrhiza with many different orchid species (Smith & Read, 2008). It was identified as a symbiont of *H. paludosa* in the Murmansk population (Dmitriev, 2017), but not in the Hungarian population. Two species of ascomycete, *Meliniomyces* spp. (Figure 9c) and *Varicosporium elodeae* Kegel were observed as endophytes in the rhizomes of *H. paludosa* in the Murmansk population. The same two species were present in the roots of another boreal-montane orchid species *Pseudorchis albida* in oligotrophic meadows in Czechia (Kohout et al., 2013).

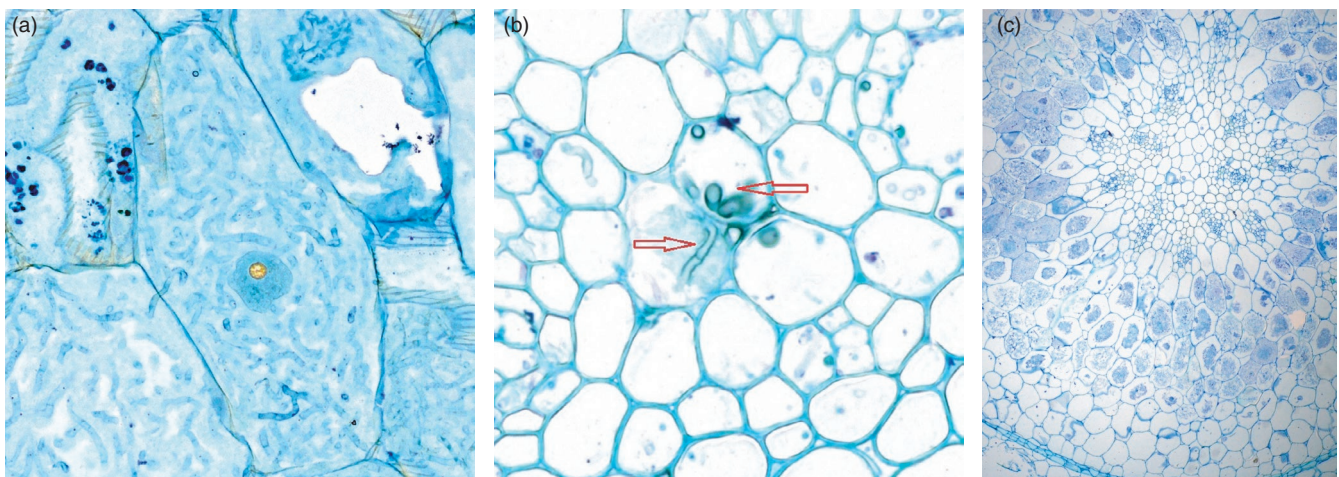


FIGURE 9 Cross sections of the rhizome of *H. paludosa*. (a) An enlarged nucleus in the cell occupied by mycorrhizal fungus (x400); (b) Hyphae of endophyte fungus *Meliniomyces* sp. (x400); (c) Abundant pelotons in the cortex cells (x100). Adapted from Dmitriev (2018)

All four fungal symbionts of *H. paludosa* found in the Murmansk population have been recorded as symbionts of other vascular plants elsewhere. Species of *Tulasnella* form mycorrhiza with a mycotrophic liverwort *Aneura mirabilis* and several coniferous and broadleaved trees (Bidartondo et al., 2003). *Ceratobasidium cornigerum* forms mycorrhiza with the orchid *Rhizanthella gardneri* as well as with ectomycorrhizal shrubs from the genus *Melaleuca* (Bougoure et al., 2010). The mycelium of *Meliniomyces* spp. forms a network with Ericaceae and ectomycorrhizal trees (Lukešová et al., 2015). The Ericaceae genera of *Calluna*, *Empetrum* and *Vaccinium* have *Meliniomyces* spp. as their mycorrhizal symbionts (Hambleton & Sigler, 2005). *Varicosporium elodeae*, during an asexual part of its life cycle, acts as a saprotroph occurring in oligotrophic lakes (Thornton, 1963). However, during a sexual part of the life cycle, this species can become a parasite and/or endophyte of terrestrial plants (Chauvet et al., 2016). Involvement of *Hammarbya paludosa* into the fungal network with other plants has not been studied but the fact that *H. paludosa* shares its symbionts with Ericaceae and trees suggests the possibility of it being connected by soil fungi to other vascular plants. If so, that implies *H. paludosa* could be a mixotrophic species, which receives carbon not only from its own photosynthesis but also from other autotrophic plants via mycorrhizal fungi.

In recent years, the occurrence of mixotrophy in orchids was confirmed not only for species from shaded habitats (Preiss et al., 2010), but also for the species growing in the open (Liebel, 2016). Mixotrophy in *Hammarbya paludosa* was tested by using $^{13}\text{C}/^{15}\text{N}$ stable isotope analysis (Dmitriev, 2018). Stable isotope signature (δ) as a ratio between heavy and light isotopes can be a marker of an organism's trophic strategy because heavy isotopes accumulate in consumers' tissues and show higher values compared to a source of nutrients (Tiunov, 2007). For plants, it was shown that enrichment in ^{13}C is typical for mycoheterotrophs (fully heterotrophic plants feeding entirely on their mycorrhizal fungi), and ^{15}N enrichment can reflect mixotrophy (partial heterotrophy of green plants capable of photosynthesis themselves); high N/C ratio is observed as a result of mixotrophy (Selosse et al., 2017). To test whether *H. paludosa* has mixotrophy, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and N/C ratio were measured in plants collected in the Murmansk population. The values obtained were compared with species of different trophic strategies growing in the same habitat (Dmitriev, 2018; Table 4). Insectivorous plants were found to have a higher level of $\delta^{15}\text{N}$

than *Hammarbya paludosa*, which agrees with their trophic strategy. Significance of the differences in isotope values was tested with *t* tests. *H. paludosa* had higher values of $\delta^{15}\text{N}$ compared to plants with ericoid mycorrhiza ($n_1 = 38$, $n_2 = 21$, $df = 57$, $p = <0.01$) and ectomycorrhiza ($n_1 = 38$, $n_2 = 12$, $df = 48$, $p = <0.01$). The N/C ratio was higher in *H. paludosa* than in plants with ericoid ($n_1 = 38$, $n_2 = 21$, $df = 57$, $p = 0.01$) and arbuscular mycorrhiza ($n_1 = 38$, $n_2 = 69$, $df = 105$, $p = <0.01$). Values obtained from *H. paludosa* were similar to two other orchid species from the same habitat (Table 4). An increase in $\delta^{15}\text{N}$ and high N/C ratio was observed in several orchids as a result of mixotrophy (Selosse et al., 2017). Mixotrophy is a suggested trophic strategy of *H. paludosa* also (Dmitriev, 2018). Isotope tests in other populations of the species would confirm how widely it is involved in the nutrient exchange with other plant groups across its extensive geographical range.

Relationships of *H. paludosa* with mycorrhizal fungi remain poorly understood even after two focused studies by Illyés et al. (2009) and Dmitriev (2017, 2018). Dmitriev suggested several symbionts being involved in mycorrhiza with *H. paludosa*, however, their number is likely to increase after studying more populations from different parts of the species' range. Localisation of the symbionts in different organs: roots, root hairs, trichomes, rhizomes and leaf bases and old leaf sheaths should be taken into the account in the future mycorrhizal research on *Hammarbya paludosa*, because different mycorrhizal fungi could use different parts of the plants in different habitats.

6.3 | Perennation: Reproduction

Perennation organs are the short-lived pseudobulbs, with a life span of 1–2(3), very rarely up to 5 years (Bragina & Vakhrameeva, 2008). That suggests an individual plant is also short-lived. The Raunkiaer life-form of *H. paludosa* was identified as hemicryptophyte (Stroh, 2015), which is true in most of its habitats. However, when it grows in *Sphagnum*, a renewal bud is located well below the surface of the substratum, such that it is a geophyte. An opposite interpretation of plants which are entirely situated in the moss cushions is as epiphytes (Delforge, 2006; Luer, 1975). An epiphytic origin of the entire tribe Malaxidae has been suggested by Cameron (2005). The terrestrial clade of the

Mycorrhiza type (number of species studied)	$\delta^{13}\text{C}$, ‰	$\delta^{15}\text{N}$, ‰	N/C
Ectomycorrhiza (4)	-30.82 ± 0.81^A	-4.42 ± 2.20^C	0.03 ± 0.01^F
Ericoid mycorrhiza (7)	-29.78 ± 1.37^A	-7.08 ± 1.36^C	0.02 ± 0.00^G
Arbuscular mycorrhiza + non-mycorrhizal (24)	-28.46 ± 1.42^B	-0.01 ± 2.68^D	0.03 ± 0.01^G
Non-mycorrhizal, insectivorous (3)	-28.17 ± 2.08^A	0.99 ± 1.39^E	0.03 ± 0.02^F
Orchid mycorrhiza (2)	-29.83 ± 1.38^A	0.36 ± 0.48^D	0.03 ± 0.00^F
<i>Hammarbya paludosa</i> (mixotrophic?)	-29.47 ± 2.47^A	-0.33 ± 1.42^D	0.04 ± 0.03^F

TABLE 4 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and N/C ratio in *Hammarbya paludosa* and in autotrophic species with different trophic strategies from the same habitat (*Sphagnum* bog in Kandalaksha District, Murmansk Oblast, Russia; 67°07'23.9"N, 32°37'28.4"E). Adapted from Dmitriev (2018)

tribe, which includes *H. paludosa*, still retains adaptations to an epiphytic environment such as a green (photosynthesising) pseudobulb and water storing cells in the leaf sheaths.

Plants survive winter conditions as pseudobulbs. Each plant has only one developed axillary renewal bud at the base of a swollen internode (Figure 7; Tatarenko, 2015). Despite having five buds on each annual growth of the rhizome (Pladias, 2020), intensive sympodial branching of the rhizome is rarely observed. Propagules, which form on leaves and from the apical meristem on the swollen internode, are the main means of vegetative reproduction. Reproduction by propagules formed on the leaves, dominates the species reproduction strategy (Blinova, 2003; Harrap & Harrap, 2009; Käsermann & Moser, 1999; Seite & Durfort, 1995). Tiny propagules 0.05–0.3 cm long-form along the margins of any or all lower leaves (Figure 3b), occasionally on the bracts, during the summer. The number of propagules per leaf varies from 2 to 40 (Bragina & Vakhrameeva, 2008; Khomutovskiy, 2014a; Reeves & Reeves, 1984; Taylor, 1967). In some populations, no plants bear propagules on their leaves (Rakosy, 2014; Tatarenko, 1996; Zhmylev et al., 2013).

Six years of observations on marked individual plants of *Hammarbya paludosa* in the population in Tver Oblast, Russia, revealed that young plants remain vegetative for 1–3 years before the first flowering. The flowering period lasts for 3–5 years, and most plants have 1–2-year gaps in flowering. Three individuals flowered and set seed pods annually in all 6 years (Khomutovskiy, 2014a).

6.4 | Chromosomes

The chromosome number in *Hammarbya paludosa* is reported as $2n = 28$ (Hagerup, 1944; Kliphuis, 1963; Tanaka, 1965; Taylor & Mulligan, 1968).

6.5 | Physiological data

No data are available.

6.6 | Biochemical data

Two alkaloids of the class amino ester glucosides of alkylated p-hydroxybenzoic acids have been isolated from *Hammarbya paludosa*. The more complex alkaloid was named paludocine (Lindström et al., 1971), and the simpler one as hammarbine (Lindström et al., 1972).

7 | PHENOLOGY

Hammarbya paludosa is a summer-green species. Reeves and Reeves (1984) reported that exposure of the plants to a temperature of 5.5°C for 6 weeks promoted subsequent development of an inflorescence within 2 weeks after the temperature was increased

to 18°C. In the British Isles, the species flowers from late June to September, occasionally into October (Stroh, 2015). Across the species' continental range, plants flower from July to the beginning of August and fruits are set in August–September (Vakhrameeva et al., 2008). The perianth remains green during pod development and dries together with the pods when seeds ripen after a month. *H. paludosa* has a 2-year period of within-bud development of the shoot. An apex of the new annual shoot appears in spring as a group of meristematic cells; it remains inactive for a year and then starts growing very quickly in the next spring to form a new shoot and inflorescence inside the bud by the beginning of July. This bud proliferates into an aerial shoot next spring, and young roots appear at the base of the pseudobulb at the same time (Vakhrameeva et al., 2008).

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

H. paludosa is amphimictic. Bisexual flowers are arranged along the erect stem into an elongated inflorescence. Self-pollination is physically restricted by location of the pollinia below the column. Experimental field study, with eight plants being bagged to exclude access to flowers by pollinators, was carried out in Minnesota by Reeves and Reeves (1984). No pods were formed in bagged plants in contrast to the high rate of fruiting in the control, unbagged plants. This study suggested that flowers of *H. paludosa* are not self-compatible, however, Argue (2012) did not find that evidence was statistically robust.

The flowers produce a small amount of nectar and a weak sweet smell of cucumber (Reeves & Reeves, 1984). Highly accessible nectar attracts many species of Diptera to the flowers. Gnats and small flies are recorded as visitors of *H. paludosa* in British populations (Harrap & Harrap, 2009).

In Minnesota, several species of Diptera were recorded on the flowers (Table 5). However, there was no confirmation that any of those species carried pollinia of the orchid (Reeves & Reeves, 1984). Two species of Hymenoptera (Table 5) are noted as visitors to the flowers of *H. paludosa* in France (Seite & Durfort, 1995).

Only a gnat species, *Phronia digitata* Hackman (Diptera, Mycetophilidae), has been documented as a definite pollinator of *Hammarbya paludosa* (Rakosy, 2014; Reeves & Reeves, 1984). *Phronia digitata* has a Holarctic range, which fully overlaps with the range of *H. paludosa* in North America (Gagné, 1975), but in Europe, distribution of *Phronia digitata* is restricted to northern Russia (Karelia) and Scandinavia (Kjærandsen et al., 2007). Another gnat species pollinating *H. paludosa* is *Sciara hemerobioides* (Diptera, Sciaridae—'black fungus gnat') (Stroh, 2015) and records for it in NBN Atlas (2020) match well with the distribution of *H. paludosa* in the British Isles.

Polyembryony, the development of several embryos per a seed, has been reported in *H. paludosa* (Bragina, 2001b).

8.2 | Hybrids

None known.

8.3 | Seed production and dispersal

Fruiting percentage in *Hammarbya paludosa* varies between populations and also between years. In some populations 64%–90% of flowers set seeds. However, numbers are usually much lower (Harrap & Harrap, 2009; Käsermann & Moser, 1999; Khomutovskiy, 2014a; Kjærandsen et al., 2007; Rakosy, 2014; Reeves & Reeves, 1984; Seite & Durfort, 1995). In Primorye Territory, the fruiting rate was as low as 7.6% (Tatarenko, 1996), in Leningrad Oblast in Russia it ranged from 0% to 26.6% (Bragina, 2001a), but reached 75% in small population in Ukraine (Danylyk et al., 2018). The average number of seeds per capsule is $1449 \pm 294(\text{SE})$ in Leningrad Province (Bragina, 2001a). Seeds are dispersed by wind and water (Nilsson, 1979).

8.4 | Viability of seeds: germination

Seeds of *Hammarbya paludosa* are globose, light-brown and tiny. Their length is 232–236 μm and their diameter is 173–206 μm

(Bragina, 2001a). Greater variation in seed size was recorded in Tver Oblast (Table 6). *Hammarbya paludosa* is listed among species with known seed dormancy (Baskin & Baskin, 2014), however, no details on length of their dormancy are given. Seeds extracted from green, unripe pods failed to germinate on asymbiotic media *in vitro* (Andronova et al., 2000; Mamaev et al., 2004).

An *in situ* experiment on germination of seeds of *H. paludosa* under natural conditions was carried out in Bábta, Gelénes, in Hungary by Illyés (2011). A method of seed germination in mesh packets (mesh size 85–100 μm) buried in the substratum (Rasmussen & Whigham, 1993) was applied. Illyés (2011) provides no information about seed collection and storage before their application. Packets with seeds were buried in peat on floating mats in spring and retrieved in autumn. Germination was successful and protocorms of *H. paludosa* were obtained from the packets, however, the seed germination rate was not reported (Illyés, 2011).

8.5 | Seedling morphology

Seedlings of *Hammarbya paludosa* have never been described. Protocorms (initial stages of seedling development in orchids) were obtained for the study of mycorrhizal fungi (Illyés, 2011), but their morphology was not documented. Seedlings of *Liparis japonica*, a species whose vegetative morphology is very close

Group	Family	Genus/species
Diptera	Mycetophilidae	^{1,2} <i>Phronia digitata</i> Hackman
		¹ <i>Mycetophila</i> sp.
		² <i>Neuratelia</i> sp.
	Helomyzidae	¹ <i>Allophylla laevis</i> Loew
	Culicidae	¹ <i>Aedes</i> sp.
	Scathophagidae	¹ <i>Megaphthalma</i> sp.
	Sphaeroceridae	¹ <i>Copromyza atra</i> Meigen
Hymenoptera	Muscidae	¹ <i>Schoenomyza</i> sp.
	Sciaridae	² <i>Sciara hemerobioides</i> Scopoli
	Perilampidae	¹ <i>Perilampus muesebeckii</i> Smulyan
		Cynipidae

TABLE 5 Insect visitors to the flowers of *Hammarbya paludosa* recorded in Minnesota¹ (Reeves & Reeves, 1984) and in France² (Seite & Durfort, 1995)

Seed characteristics	Range	Mean	Variation coefficient, %
Seed length (μm)	213–320	267	9.71
Seed width (μm)	142–226	159	12.5
Length:width ratio	1.02–2.39	1.35	15.5
Seed volume ($\mu\text{m}^3 \times 10^3$)	1280–4230	2176	25.2
Embryo volume ($\mu\text{m}^3 \times 10^3$)	59–251	150	31
Seed volume:embryo volume ratio	5.1–28.1	15.6	32.7
Air volume inside a seed (%)	87.6–96.45	92.9	2.5

TABLE 6 Sizes of seeds and embryos of *Hammarbya paludosa* in Tver Oblast. Adapted from Khomutovskiy (2014a)

to *H. paludosa*, were found to be very similar to the 'seedlings' of *H. paludosa*, which developed from the vegetative propagules (I. Tatarenko, personal observations). At 1-year-old 'seedlings' that have developed from propagules are tiny at 0.3–2.9 cm tall. They have very thin shoots bearing trichomes (Figure 8a), but no roots (Bragina, 2001a; Rasmussen, 1995). Bragina (2001a) carried out a detailed study on the very first stages of ontogenesis of *Hammarbya paludosa* plants. 'Seedlings' at the different stages are shown in Figure 10. Very young 'seedlings' have two to three leaves with no leaf blades, but propagules formed at the tips (Figure 10a). The primordium of a primary root is formed, but the root does not elongate (Figure 10b). An apical pseudobulb is formed at the top of the 'seedling' shoot (Figure 10d) from the apical meristem (Figure 10c), which indicates the beginning of the juvenile stage of plant ontogenesis.

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

None known.

9.2 | Plant parasites and diseases

None known.

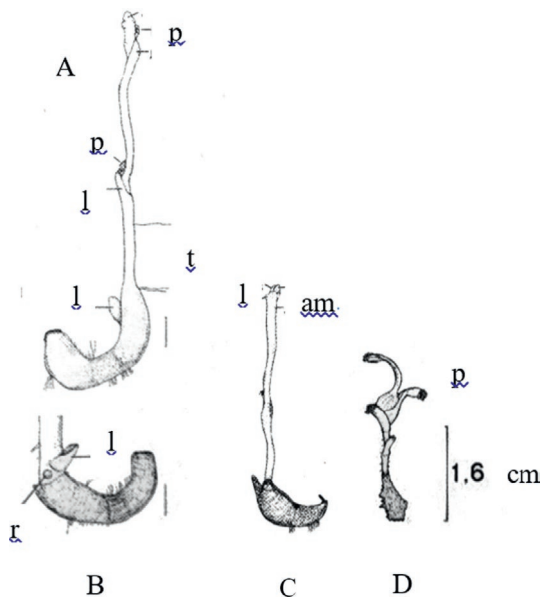


FIGURE 10 First stages of development of the leaf propagules of *Hammarbya paludosa*. (a) Young 'seedling' with three primordial leaves, propagules on their tips, and trichomes; (b) Basal part of the 'seedling' with a primordial root; (c) 'Seedling' with an apical meristem; (d) Juvenile plant with apical pseudobulb. l—leaves, r—root apex, t—trichomes, p—propagules, am—shoot apical meristem. Adapted from Bragina (2001a)

10 | HISTORY

According to Foley and Clarke (2005) and Harrap and Harrap (2009), the first British record of *Hammarbya paludosa* as '*Bifolium palustre*' was made by John Parkinson in 1640. The original description by Parkinson (1640), suggests that *Bifolium palustre* looked similar to *Bifolium vulgare* (*Neottia ovata*, in modern nomenclature), but 'lesser' in size. Roots of *Bifolium palustre* are described as 'long runner and creeper', which matches well with the morphology of other small two-leaved green orchids, but not with *H. paludosa*. The flowering period of *Bifolium palustre* in May–June (Parkinson, 1640) is characteristic of *Neottia cordata* and *Liparis loeselii*, but 2 months ahead of flowering time of *H. paludosa*. The absence of drawings of *Bifolium palustre* in historic publications complicates identification of the plant. There is a possibility that the name *Bifolium palustre* was indiscriminately applied to not one but several species which can grow in marshy habitats: *H. paludosa*, *N. cordata*, *L. loeselii* and *Herminium monorchis*. The latter grows in dry chalk grasslands in England, but elsewhere, it can form extensive populations in fens and wetlands, so, potentially, could have occurred in wetland habitats in England in the past.

With a lack of old herbarium specimen, expert evaluation of *Bifolium palustre* being an old name for *H. paludosa* (Foley & Clarke, 2005) has been based on historic locations, where the species was recorded through time. John Parkinson found the species on the 'low wet grounds between Hatfield and S. Albones', and 'in divers places of Romney Marsh' (1640). In 1684, Mr Dent and Mr Dale reported the species 'on the boggy and fenny grounds near Gamlingay in Cambridgeshire' (Ray, 1690). The species had been repeatedly recorded in Gamlingay area until 1855 under different Latin names from *Bifolium palustre* to *Malaxis paludosa*, but retaining the English name of Marsh Twayblade. This provides confirmation that the Gamlingay population of the species was indeed *Hammarbya paludosa*. Under the name of *Ophrys palustris* the species was recorded on Hilton Moor, Cambridgeshire by Dr Th. Manningham (Blackstone, 1746). The species was found in 'turfy bogs on the north side of Norwich' by Smith and Sowerby (1793). Some populations with long historical records can still be found. At one site in Cumbria *H. paludosa* was refound in 2020, 135 years after it was discovered there by F. C. M. Ropper in 1885 (Baker, 1887). However, two other historic locations in the area have changed too much and do not support the species any more (Gendle et al., 2020).

Targeted searches for the species in suitable habitats in Scotland in recent years have also resulted in finding new populations in 10-km grid squares where *Hammarbya paludosa* had not been recorded in the past (S. Longrigg, personal observations).

11 | CONSERVATION AND MANAGEMENT

Hammarbya paludosa is a scarce species in the British Isles (Porter, 1994), listed as Vulnerable in the England Red Data List (Stroh et al., 2014), and Endangered in Wales (Dines, 2008), although the overall species conservation category in Great Britain is 'Least Concern' due to its

relative frequency in Scotland. In Wales, it is a species 'of principal importance for the purpose of conserving biodiversity' covered under Section 42 (Wales) of the NERC Act (2006) and therefore needs to be taken into consideration by a public body when performing any of its functions with a view to conserving biodiversity. In Northern Ireland, plants are protected from intentional picking, removal or destruction and from selling (in whole or part) and from advertising for sale (The Wildlife [Northern Ireland] Order, 1985). The species is assigned Threat number 8 (rare but not endangered) in the Irish Red Data Book (Curtis & McGough, 1988). Walker and Preston (2006) linked the substantial retreat of *H. paludosa* from southern Britain to habitat destruction which began over 200 years ago. The most negative effects come from drainage, overgrazing (particularly in the uplands) and undergrazing (mainly in the lowlands) (Stroh, 2015). Species populations in southern England are at further risk due to habitat fragmentation.

Hammarbya paludosa is listed in IUCN Red Data List (Maiz-Tome, 2017) and many national and regional Red Data Lists in Europe and in Russia. The species' decline has been recorded in European countries over the last 40 years (Damgaard et al., 2020). For example, out of 80 locations of the species historically known in Pomerania, Poland, only seven remained after the 1990s (Sotek, 2010). Similar to the British Isles, drainage of bogs and mires has been a major threat to *H. paludosa* in Europe. Acidification is another big threat badly affecting floating fens—the main habitats of *H. paludosa* in the Netherlands (Bootsma et al., 2002).

Conservation management for the species should support appropriate hydrological regimes in the habitats. Grazing is required in many habitats for maintenance of an open sward and to create patches of bare soil for the germination of propagules. Nevertheless, grazing pressure should not lead to the erosion or excessive poaching of vulnerable peat soils and vegetation (Stroh, 2015). Attempts at conservation via cultivation in a botanic garden were not successful in Ekaterinburg Botanical Garden (Mamaev et al., 2004).

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS

I.T. wrote the manuscript, P.Z. compiled information on the species' distribution world-wide and did extensive literature search; E.V. wrote the 'Mycoorrhiza' section; S.L. provided data on species distribution in Scotland.

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DATA AVAILABILITY STATEMENT

This manuscript does not use data.

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