

Biology, ecology, use, conservation and cultivation of round-leaved sundew (*Drosera rotundifolia* L.): a review

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SUMMARY

Drosera rotundifolia is a perennial insectivorous herb which occupies open, wet, oligotrophic habitats such as acidic bogs and poor fens, and specifically grows in *Sphagnum*-dominated communities. Since mediaeval times the species has been collected from natural habitats and used as a remedy for coughs and pulmonary diseases. Due to the substantial decline of *Drosera* habitat, the plant has been protected in most European countries since the 1980s, which means that wild *D. rotundifolia* has become unavailable to the pharmaceutical industry. The persistent demand has stimulated research into the cultivation of *Drosera* in several European countries. These studies have shown that *Drosera* cultivation is time-consuming and not (yet) cost-effective, and there is a need for the development of cultivation methods. This article reviews the morphology, distribution, ecology and reproduction of *Drosera rotundifolia*; outlines its commercial use and nature conservation requirements; and describes previous research on its propagation and cultivation.

KEY WORDS: cultivation, distribution, *Drosera rotundifolia*, Droserae herba, *Sphagnum* spp.

INTRODUCTION

Carnivorous plants, and especially the widespread genus *Drosera*, have fascinated and inspired researchers for centuries²⁶⁴. Charles Darwin's comprehensive study on *Drosera*⁵¹ was followed by extensive work on the morphology, biology and ecology of the round-leaved sundew (*Drosera rotundifolia* L.)^{54, 90, 91, 48}.

Drosera has a long history as a remedy ('Droserae herba', 'Herba Droserae') for coughs and pulmonary diseases^{201, 14}. Nowadays, the air-dried or fresh plant^{58, 84} is used in 200–300 of the medications registered in Europe¹⁴², creating a continuing demand from pharmaceutical companies. For this purpose, the plants are still collected (as they traditionally have been) from natural habitats. Whereas collecting from the wild has contributed to the reduction of local populations, and even to their extinction^{245, 258}, *D. rotundifolia* and other *Drosera* species of wet, oligotrophic and acidic habitats have declined most as a result of land reclamation and drainage. *Drosera* species are strongly associated with *Sphagnum* mosses (see Appendix) and are characteristic for many *Sphagnum*-dominated communities. *Sphagnum* cultivation ('Sphagnum farming') to provide raw materials for horticultural growing media is a promising technology in paludiculture⁷⁶. *D. rotundifolia* occurs spontaneously on the Sphagnum farming pilot area at Hankhausen

(Lower Saxony, Germany), and this has stimulated research into whether it could be cultivated with *Sphagnum*. This article reviews aspects of the biology, ecology, propagation and cultivation of *D. rotundifolia* that are relevant to the prospect of growing it on Sphagnum farms. Its commercial use and nature conservation status are also discussed. What follows is in sections: Morphology, Geographical and altitudinal distribution, Ecology (climatic and hydrological conditions, soil conditions, communities), Reproduction (asexual reproduction, sexual reproduction), Commercial use, Conservation, Propagation and cultivation (*in vitro* propagation, indoor cultivation, outdoor cultivation), and Prospects.

MORPHOLOGY

Drosera rotundifolia is a small, clonal and perennial carnivorous (usually insectivorous) herb^{218, 261, 195, 117}. The roots are generally poorly developed and fibrous, consisting of a tap root with (1–) 3–5 (–6) fine, blackish and slightly divided branches with a length of (2–) 13–25 (–44) mm^{54, 205, 139, 261}. The 4–12 (–20) leaves are arranged in a basal rosette^{218, 195}. The leaves are (10–) 20–50 mm long²⁵⁵, horizontally spreading (but sometimes semi-erect) and long-petioled^{238, 19, 120}. The petioles are green, flat, hairy or sometimes glabrous^{157, 48, 85}, 10–30 (–50) mm long

and 6–10 mm wide^{209, 195, 120}. The stipules are usually united up to their centre with the petiole⁹³, membranously adnate, fimbriate, 4–6 mm in length¹⁵⁷, and each divided into about 7 teeth²⁵⁵. The laminae are initially helical involute¹⁰¹ and later orbicular to vertically oval, 4–10 × 5–18 mm, and abruptly narrowed into the petiole^{54, 209, 85}. The abaxial surfaces of the laminae are glabrous, lightish olive green to yellow-green; the adaxial surfaces are often reddish because of anthocyanins^{48, 5}.

The adaxial surface and the margin of the lamina are covered with digestive glands, glandular trichomes and tentacles^{127, 197}. The approximately 200 tentacles on each lamina are long-petioled, reddish, flexible and 1–5 (–6) mm long^{101, 24, 261, 258}, perpendicular to the surface and longest on the leaf margin⁴⁸.

The rosette has 1–5 (–7) terminal, erect, reddish, leafless, glabrous and initially epinastically inrolled flower stalks^{255, 217} of (1–) 5–20 (–30) cm length^{48, 202, 85, 63}. The inflorescence is one-sided, with a cymose raceme that terminates in a naked, single or double un-ranked raceme^{101, 261}.

The 1–15 (–25) flowers on each flowering scape are radially symmetric^{54, 215, 209}, androgynous¹²² and short-petioled (5–12 × ≤ 3 mm,^{93, 13, 261}). The pedicel is short (2 mm), and erect during anthesis^{54, 213}. The 5 sepals are united at the base, obtuse, remaining till ripening and 5 × ≤ 1.5 mm long^{54, 122, 5}. Their colour is green or brownish green, and black in the fruit^{204, 48}. The 5 free petals are spatulate, obovate, white or pinkish, 4–7 × ≤ 3 mm^{54, 157, 5, 201}, wedge-shaped and persistent in cleistogamic flowers⁴⁸. The androecium includes 4–8 free, 4–5 mm long stamens with reddish, filiform filaments^{54, 256, 48, 195} and white extrorse anthers^{256, 255}. The pollen consists of inaperturate tetrads 51–75 µm in diameter; the nexine is 2–3 (–4) µm thick, the sexine 1.5–3.5 µm high with dimorphic spinules^{185, 23}. Each flower produces only a few hundred pollen grains²¹⁰, and these remain in permanent tetrahedral tetrads^{222, 87}. The ovary of 3 (rarely 4 or 5) united carpels is superior, unilocular, 3 mm long^{54, 90, 157}, and occasionally bears tentacles⁴⁸. The styles are 2–5 partite¹⁵⁷, free, forked, straight or club-shaped, about 1.5–2 mm long^{54, 93, 48}. The 3 stigmas are papillate, whitish, club-shaped and 2-parted^{13, 255}. The ovules are 3–∞ in number, anatropous, tenuinucellate (embryo sac and epidermis not being separated by nucellar tissue) and bitegmic (having two integuments)^{91, 212}.

The fruit is a blackish-brown, smooth, loculicidal capsule^{1, 13, 127}, 1-valved and split into 3 sections^{48, 209}, 3–5 (–6) mm long and 1.7–2 mm wide^{101, 217, 195}. Each capsule contains 69 ± 95 seeds (SD, $n = 273$, B. Baranyai, unpublished data). For Finland,

averages of 90 (80–119) seeds *per* seedcase and 424 (63–816) seeds *per* plant have been reported⁷⁵. The seeds are yellowish-brown to blackish-brown, narrow ellipsoid, smooth, reticulate, shining with a metallic lustre, 1.5–1.7 mm long and 0.2–0.3 mm wide; the inner seeds are 0.3–0.5 mm × 0.2–0.3 mm^{80, 13, 27}. The seeds are endospermous, including endosperm and small basal embryos^{95, 212}. The average weight of 1,000 seeds is 0.2 g¹⁹⁴.

GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Drosera rotundifolia is probably one of the most widely distributed carnivorous plant species, appearing in most regions of the Holarctic (Figure 1; 105, 206, 99, 18, 227, 199). In northern Eurasia it is known from Iceland, the British Isles, Norway (up to 70° 65' N¹⁶³), north-western Russia and Siberia (50–65° N)^{94, 83} to the Kamchatka Peninsula and Manchuria^{262, 254}. The southern Eurasian distribution includes the Mediterranean mountain ranges of Portugal, Spain^{90, 40, 12}, Italy and Corsica (as var. *corsica* (Maire) Briq.)¹⁷⁹, the Balkan Peninsula^{86, 6, 57}, the Caucasus¹¹³, Mongolia⁴⁹, South Korea and Japan^{42, 103}. In arctic and temperate North America the species is found from Greenland and Newfoundland to the Canadian Northwest Territories (to 67° 97' N²³⁹), and from Alaska to California and Alabama, to 33° 97' N^{88, 240, 83}. Outliers in the distribution are known from Lebanon, Israel^{233, 49} and New Guinea (as subsp. *bracteata* Kern & Steen)²⁵⁵.

In the British Isles, *D. rotundifolia* occurs from sea level up to 670 m³³, but has also been reported at about 900 m in Scotland¹⁰⁵. In continental Europe it reaches altitudes of 1,100 m in Scandinavia¹⁴⁹; 1,395 m in Germany¹⁶⁷; 2,000 m in Austria, France and Italy^{186, 249, 179}; and 2,100 m in Spain⁴⁰. In Japan *D. rotundifolia* may be found up to 1,920 m⁸¹, and in Colorado (USA) up to about 3,000 m¹⁴⁷.

ECOLOGY

Climatic and hydrological conditions

Globally, *D. rotundifolia* grows in both continental and oceanic climates^{111, 44, 161}. In Europe, the species is closely connected to wet and oligotrophic sites¹⁹² in continental, oceanic and suboceanic regions^{91, 187}. *D. rotundifolia* is highly adapted to the microclimatic conditions of peatlands⁴¹, including the “higher air humidity compared to mineral soils, greater frequency of mists and dew, notably greater frequency of ground frost, lower air temperatures and

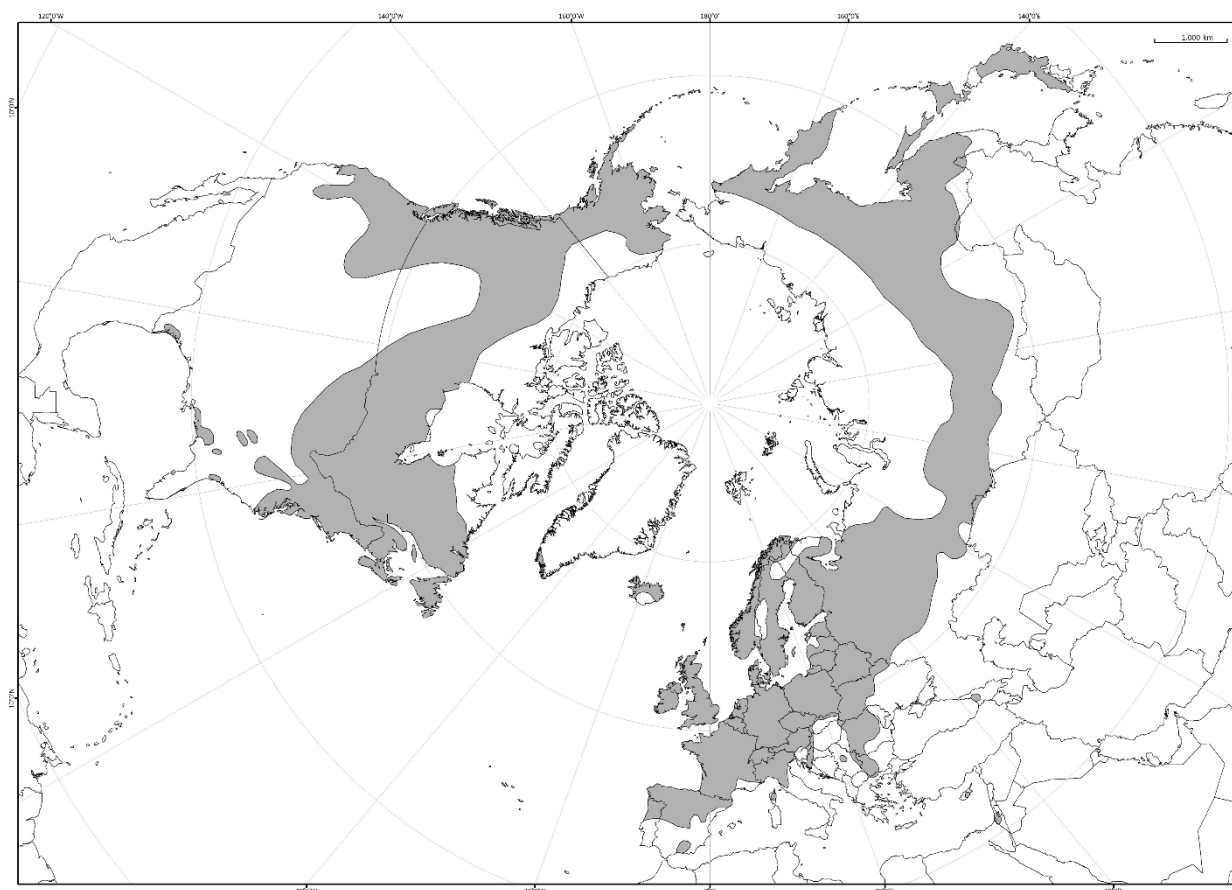


Figure 1. The distribution of *D. rotundifolia* in the Holarctic (based on ^{149, 105, 224, 48, 255, 30, 126, 237, 8, 261, 40, 113, 86, 145, 241, 77, 166}).

lower topsoil temperatures in the summer period” ¹⁰⁷.

Amongst the European species of sundew, *D. rotundifolia* grows in the highest locations within the bog microrelief ^{138, 137}, i.e. on rather high *Sphagnum* hummocks ¹⁹⁹, where it does not form basal rosettes and its long axis and petioles grow fast enough to evade competition with the rapidly growing *Sphagnum* mosses ^{48, 218}. The species has generally larger leaves in the shade ²³². The length of the slender vertical axis of *D. rotundifolia* was about 3 cm in full sun and up to 5 cm in shade ²⁶¹.

The species avoids waterlogged places with perennial standing water ^{228, 261}. As a hemicryptophyte with frost-resistant hibernacula (winterbuds) ^{164, 230, 197}, it can survive ground frosts. It tolerates strong wind on vertical faces and at high altitudes, but is smaller in such places ⁴⁸.

Soil conditions

Drosera rotundifolia flourishes in continuously moist acid soils which are poor in nutrients (N, P, K, Ca and Mg; ^{186, 2, 141}) and lime ²⁰⁸, with various granulometric structures ^{114, 230}. Its main substrates are living *Sphagnum* moss and humus, i.e. peat, raw

humus or moder ^{131, 220, 197}. The species also grows on moist acidic sand, e.g. in dune valleys along the Baltic Sea coast ^{91, 219, 200}, on silicate bedrock deficient in bases and lime (e.g. granite, lime-free sandstone) and on dolomite rocks that are wet from freshwater seepage ^{13, 209, 134}. Other habitats include sand and clay mining areas ²⁵⁵; the edges of ponds, springs or streams on mineral soil ^{219, 255, 66}; freshly cut peat surfaces ¹³⁹; and, rather rarely, constantly damp or mouldering logs ^{48, 255}.

The soils where *D. rotundifolia* thrives are uniformly acidic at the surface, with soil pH 3.3–5.0 in central Europe and 3.5–4.5 in North America (Table 1), though it is sometimes found in rich fens (see below). A Canadian study found the species on loamy sand with a pH of 6.1 ²¹⁹. Water pH values range from 3.0 to 6.5 with outliers of 7.5 (Table 2). The concentrations of Ca²⁺ and Mg²⁺ ions in the surface water and groundwater of *D. rotundifolia* habitats differ from region to region but are generally low (Table 2).

The growth and growth form of *D. rotundifolia* are influenced by the (hydro)chemical conditions of the habitat. For example, calcium is toxic to

Table 1. pH values for wetland soils with *Drosera rotundifolia* in central Europe and North America.

Location	Soil pH	Source
<u>Europe</u>		
Germany	3.6–4.3	Forst (1997)
Germany	4.6	Oltmanns (1996)
Germany	3.3–3.5	Huntke (2008)
Hungary	4–5	Borhidi (2003)
Italy	4.4–4.9	Miserere <i>et al.</i> (2003)
<u>North America</u>		
Maine	3.5–4.5	Davis & Anderson (1991)
Virginia	3.5–3.7	Byers <i>et al.</i> (2007)

Table 2. pH, calcium (Ca²⁺) and magnesium (Mg²⁺) concentrations (mg L⁻¹) in water of wetlands with *Drosera rotundifolia*. (Some publications list more than one site, e.g. Fernández-Pascual (2016): Los Cándanos pH 3.0 and La Veiga Cimera pH 4.6). NA = not available.

Location	pH	Ca ²⁺	Mg ²⁺	Source
<u>Europe</u>				
Britain	3.5–4.4	2.4–24	1.2–7.0	Crowder <i>et al.</i> (1990)
Britain	4.54–5.22	1.2–2.5	0.09–1.05	Shimwell (2005)
Britain	6.5–6.8	5.5–7.1	3.50–3.70	Shimwell (2005)
Britain	4.8	14	8.7	Box <i>et al.</i> (2011)
Britain	5	17	6.6	Box <i>et al.</i> (2011)
Germany	4.6–5.1	NA	NA	Ellwanger (1996)
Italy	4.4–4.9	NA	NA	Miserere <i>et al.</i> (2003)
Italy	5.6	5.55 (± 0.43)	1.40 (± 0.11)	Gerdol <i>et al.</i> (2011)
Italy	6.1	8.27 (± 0.38)	1.91 (± 0.09)	Gerdol <i>et al.</i> (2011)
Netherlands	4.5 (± 0.07)	0.46	0.46	Adema <i>et al.</i> (2006)
Poland	4.0	0.75	0.18	Wojtuń <i>et al.</i> (2013)
Spain	3.0	NA	NA	Fernández-Pascual (2016)
Spain	4.6	NA	NA	Fernández-Pascual (2016)
Sweden	3.9–4.4	NA	NA	Vinichuk <i>et al.</i> (2010)
<u>North America</u>				
Canada	4.3– 6.9	NA	NA	Pellerin <i>et al.</i> (2006)
Minnesota	3.9	0.8	NA	Glaser <i>et al.</i> (1990)
Minnesota	7.5	30	NA	Glaser <i>et al.</i> (1990)
Ohio	4.0–5.1	2.8 (± 0.8)	1.7 (± 0.3)	Andreas & Bryan (1990)
Ohio	4.1–4.3	2.8 (± 0.8)	1.2 (± 0.4)	Andreas & Bryan (1990)
Ohio	6.3–7.3	6.0 (± 1.3)	2.6 (± 0.7)	Andreas & Bryan (1990)

D. rotundifolia but the toxicity depends on the pH of the soil^{198,4}. The species responds to higher nitrogen and phosphorus supply by growing to a smaller size and producing fewer leaves and flowers *per plant*²¹⁶. *D. rotundifolia* can tolerate low salt concentrations²⁰¹, but is salt-intolerant¹³¹ and growth is hampered by raised salt concentrations²¹⁶.

Communities

In the following account, the nomenclature of plant communities in Europe follows Mucina *et al.* (in prep.); the taxonomy and nomenclature of Spermatophyta follows Wisskirchen & Haeupler (1998) and Moss (1983); for Bryophyta we follow Frahm & Frey (2004); and for the genus *Sphagnum* we follow Michaelis (2011).

The main habitats of *D. rotundifolia* are acidic bogs and poor fens, but the species has also been recorded from intermediate-rich and extreme-rich fens^{221, 261, 18}. It grows primarily in *Sphagnum*-dominated communities^{131, 191, 151}. Species in wetlands supporting occurrences of *D. rotundifolia* are listed in the Appendix.

In central Europe, *D. rotundifolia* occurs mainly in two phytosociological classes, the Oxycocco-Sphagnetes Br.-Bl. & R. Tx. ex Westh. *et al.* 46 and the Scheuchzerio-Caricetes fuscae Tx. 37. Furthermore, the species is represented in the

Montio-Cardaminetea Br.-Bl. et Tx. ex Klika 48, the Vaccinio-Piceetea Br.-Bl. in Br.-Bl. *et al.* 1939 and the Alnetea glutinosae Br.-Bl. & R. Tx ex Westhoff *et al.* 1946 (Table 3). In the Oxycocco-Sphagnetes, *D. rotundifolia* is mainly associated with *Sphagnum* (e.g. *Sphagnum magellanicum*, *S. fuscum*, *S. rubellum*), *Eriophorum vaginatum* and *Andromeda polifolia* together with *Oxycoccus palustris*, *Narthecium ossifragum*, *Vaccinium uliginosum* and *Erica tetralix*, as well as with *Calluna vulgaris* in dry areas^{255, 207}. In Scheuchzerio-Caricetes fuscae Tx. 37 communities, the species is found together with, for example, *Rhynchospora alba*, *R. fusca*, *Eriophorum angustifolium*, *Molinia caerulea*, *Trichophorum cespitosum*, *Menyanthes trifoliata* and *Sphagnum* (e.g. *Sphagnum fallax*, *S. inundatum*, *S. cuspidatum*)^{214, 183}.

In Japan *D. rotundifolia* has been recorded from communities of lawns, hummocks, hollows and floating mats¹¹¹.

In North America *D. rotundifolia* typically flourishes on bogs and occupies the margins of acidic ponds and floating peat mats in fens throughout Canada and in many states of the USA^{172, 147}. The species occurs in central Alberta (Canada) in an extreme-rich fen, with *Scorpidium scorpioides*, *Drepanocladus revolvens*, *Campylium stellatum* and *Tomenthypnum nitens*²²¹.

Table 3: List of central European plant communities that include *Drosera rotundifolia*.

Plant communities	References
Oxycocco-Sphagnetes Br.-Bl. & R. Tx. ex Westh. <i>et al.</i> 46	Weber (1995), Schubert <i>et al.</i> (2001)
Sphagnion medii Kästner et Flössner 1933	Berg <i>et al.</i> (2004), Thébaud (2011)
Ericion tetralicis Schwickerath 1933	Berg <i>et al.</i> (2004)
Oxycocco-Ericion tetralicis Nordhagen ex Tx. 1937	Pott (1995), Schaminée <i>et al.</i> (1995)
Scheuchzerio-Caricetes fuscae Tx. 37	Borhidi (2003), Rodondi <i>et al.</i> (2009)
Scheuchzerion palustris Nordhagen ex Tx. 1937	Linder-Effland (2002), Huntke (2008)
Caricion fuscae Koch 1926 em. Klika 1934	Oberdorfer (1992), Borhidi (2003), Berg <i>et al.</i> (2004)
Caricion davallianae Klika 1934	Anthes (2002), Conradi & Friedmann (2013)
Montio-Cardaminetea Br.-Bl. et Tx. ex Klika 48	Borhidi (2003)
Vaccinio-Piceetea Br.-Bl. in Br.-Bl. <i>et al.</i> 1939	Pietsch (1985), Oberdorfer (1992), Wagner (2000)
Salicion cinereae Th. Müller et Görs ex Passarge 1961	Borhidi (2003)
Alnetea glutinosae Br.-Bl. & R. Tx ex Westhoff <i>et al.</i> 1946	Linder-Effland (2002)

REPRODUCTION

D. rotundifolia possesses the ability to reproduce both asexually (vegetatively) and sexually (generatively)^{159, 103}.

Asexual reproduction

Asexual reproduction can occur by the development of new buds on the adaxial surface of the lamina, on the petiole, in the axils of the leaves and on the flower stalks, as well as by means of root suckers^{164, 20, 257, 121, 4}.

The production and development rate of buds is affected by humidity, temperature, and - in respect of lamina buds - physiological leaf age^{20, 257}. Shoots grow under conditions of constantly high air and soil humidity and indirect sunlight²⁵⁷. The exogenous buds on the leaves usually form on the lower part of a tentacle stalk, probably from all tissues except the lower epidermis, but the bud is not connected to the parental vascular system⁴⁸. Buds develop preferentially in the centre of a lamina, where (*per lamina*) 4–5 and rarely 10 buds may originate^{208, 257}. Bud development takes 14–30 days^{20, 92, 257}. The roots of the buds form endogenously and shoot growth starts from epidermal cells²⁰. The appearance of buds on the leaves can be observed from early spring until late autumn^{164, 146}. These buds develop on old adult leaves which are partially or completely detached from the axis (of the leaf)¹⁶⁴. It is only when the petiole of the lamina is detached from the axil that buds can develop on the surface of the petiole²⁰. If the mother plant is mechanically damaged, e.g. by rot, fungal decay, or invertebrate attack, the apical dominance is lifted and within 14 days an axillary bud develops on the undamaged lower part of the plant²⁵⁷. In the case of the shoot tip being damaged, the top axillary shoot takes over the (regeneration) function of the terminal shoot²⁵⁷. If the peduncle is removed, buds can - in humid conditions - also appear on the stem²⁵⁷. Another form of vegetative reproduction occurs when roots develop below-ground suckers¹²⁹, and when the plants produce new ramets from axillary buds^{218, 103}. In a Swedish subarctic bog, 1.57 ± 0.8 (max. 4; SD, $n = 93$) ramets *per D. rotundifolia* plant were reported²¹⁸.

The axillary bud forms a secondary rosette beside or below the main rosette⁴⁸, which is genetically identical to the parent plant²⁶¹.

Sexual reproduction

D. rotundifolia reproduces sexually^{48, 218} by producing seeds from its hermaphroditic flowers^{61, 261}, and this is the main method of reproduction.

Under natural conditions, sexual reproduction is mostly autogamous (self-pollinating)^{127, 159, 261}. Initially the plant forms small unopened cleistogamic flowers, whereas later, well-developed reproductive structures in chasmogamous flowers are formed. According to Goebel (1914), the occurrence of cleistogamic *Drosera* flowers is caused by intense light and high temperature, rather than by lack of visiting insects. A high proportion of cleistogamous flowers in a population may lead to significant inbreeding^{82, 231}. Chasmogamous flowers bloom in midsummer, i.e. mainly in June, July and August^{154, 143, 120, 18} but, depending on the altitude, flowering may also occur in May or October^{48, 217}. The flower opens only in direct sunlight, for two or three hours on a single day^{116, 54, 193, 19, 18}. If the calyx is not fully open, withering can take at least five hours⁵⁴. *D. rotundifolia* flowers start opening if the temperature reaches 25–30 °C, but complete blooming requires at least 35 °C¹⁸⁰.

During long periods of rainfall and cool sunny days the chasmogamous flowers remain closed^{101, 54}. Usually, only one or two flowers bloom *per* flowering scape, so blooming flowers and mature capsules can co-occur on the same flower scale¹⁷⁶. In contrast, that little to no cross-pollination occurs has been inferred from pollen to ovule ratios and pollinator visitation¹⁵⁹. After cross-pollination the corolla closes in the evening²¹⁶. Self-pollination occurs in the closed flower, as the anthers empty their pollen onto the stigmas⁹⁰.

Pseudo-cleistogamous flowers of *D. rotundifolia*, which are half open at midday but close within a short time, are also found⁵⁴. These normally chasmogamous flowers develop as a consequence of habitat disturbance such as deficient light, high water level and strong water currents¹⁶⁰.

The fruit of *D. rotundifolia* matures 5–7 weeks after flowering¹⁷⁶. The number of capsules on a single flowering scape and seed production differ among populations. Finnish plants had, on average, 4.75 capsules *per* scape ($n = 110$) and 90 seeds *per* capsule ($n = 432$)⁷⁵; and Hungarian plants 9.3 ± 2.2 capsules *per* scape (SD, $n = 30$) and 76.0 ± 26.0 seeds *per* capsule (SD, $n = 279$) (B. Baranyai, unpublished data). Depending on the time of pollination, seeds are released from July onwards, but mostly in autumn⁴⁸. Dispersal of the small seeds is anemochorous, zoochorous, and hydrochorous (by wind, animals, and water)^{219, 48, 261, 197}. The seed has a sack-shaped husk (testa) which enables it to fly on the wind, even as far as 10 km^{102, 35, 197}. The testa has ribs or striae which make the seed waterproof and able to float for several months^{13, 48, 146}, which promotes dispersal by

stream water. The seeds remain viable for 1–5 years^{181, 229}. Germination occurs in May/June⁷¹. In order to germinate, the seeds need cold stratification (by frost³²), sufficient light, and temperatures of 20–25 °C^{39, 197, 17}. If dormancy break happens in summer, *D. rotundifolia* seeds are able to germinate in the same year as they are dispersed¹⁷. On peat, seeds usually germinate within 20–30 days^{176, 39}, with exposure to cold causing almost simultaneous germination over a period of two weeks⁴⁸.

Campbell & Rochefort (2003) showed experimentally that germination in peat decreases rapidly if burial depth exceeds 5 mm. *D. rotundifolia* seeds germinate very effectively on *Sphagnum* moss¹⁹⁹ but their ability to germinate decreases rapidly if they are washed into the *Sphagnum* carpet, as burial depth increases and light flux declines (B. Baranyai, unpublished data).

COMMERCIAL USE

The above-ground parts of *Drosera* are used in Europe as a medicine for treatment of diseases of the respiratory tract¹⁴. Traditionally, *D. rotundifolia* L. was used for the drug ‘*Droserae herba*’; but since this species became rare, *D. intermedia* Hayne and *D. anglica* Huds. have been used as substitutes^{148, 96}. Asian and African *Drosera* species (*D. indica* L., *D. burmanii* Vahl, *D. peltata* Smith, *D. ramentacea* Burch. ex Herv. et Sond. and *D. madagascariensis* DC.) are also officially permitted for pharmaceutical purposes in European countries^{124, 53, 244, 171, 18}. Currently, the commercial source of ‘*Droserae herba*’ is mainly *D. madagascariensis* DC.²⁶³, which has notably lower concentrations of naphthoquinones (the active ingredient) than does *D. rotundifolia*^{124, 18}.

The annual demand for pharmacological use on the European market is currently 6–20 tons of air-dried *Drosera* biomass⁷⁰. This consists mostly of *D. madagascariensis* (from Madagascar, East Africa) at 2–20 t yr⁻¹, followed by *D. rotundifolia* (from Finland) at 1–3 t yr⁻¹ and *D. peltata* (from eastern Asia, India, Malaysia and China) at 0.1–0.5 t yr⁻¹^{69, 244, 258}. The market shares of other *Drosera* species are insignificant. Thus, Finland (*D. rotundifolia*) and Madagascar (*D. madagascariensis*) have been the countries most engaged in export of *Drosera* drugs in recent years. In both of these countries, plants are harvested from wild populations^{263, 104}. The collection of *D. rotundifolia* has also been reported from Spain, France, Sweden and Norway^{247, 132}.

Drosera rotundifolia is collected in 13 regions of

northern Finland (64–68 °N)¹⁰⁰, and most of the harvest is exported to Switzerland⁶⁰. The pickers are specially trained Finnish youths (4H-Young Organization); or temporary immigrants, mainly Asian berry pickers^{75, 9}. One kilogram of freshly collected *Drosera* biomass contains approximately 5,000–10,000 flowering individuals⁷⁵ and one picker collects about 40 kg of *Drosera* during the season, which begins in July and ends in August⁶⁰. The pickers are paid 43 EUR kg⁻¹ for raw *Drosera* material¹⁰⁴.

The prices for fresh *D. rotundifolia* drug on the European market are 80–120 (–900) EUR kg⁻¹ and for air-dried drug 1000–1200 EUR kg⁻¹. The change in weight from fresh *D. rotundifolia* drug to air-dried is 8:1 (12–24 months old *D. rotundifolia* plants with flower stem dried at 40 °C for 72 hours in a Memmert Cleanroom drying oven) (B. Baranyai, unpublished data).

CONSERVATION

The destruction of *Drosera* habitats (especially mires), as well as their eutrophication, leads to the reduction of natural *Drosera* populations^{132, 197, 15}. Hence, the European *Drosera* species are listed as endangered, vulnerable or rare in many European countries^{132, 117}. For example, *Drosera rotundifolia* is critically endangered in Croatia¹⁶², endangered in Greece and Hungary^{119, 177}, and vulnerable in Bulgaria and Germany^{140, 175}. In Switzerland, collecting is allowed only for scientific purposes and with a special permit issued by the cantonal and federal administrations. The fine for collecting without permission is up to 1,000 CHF (970 EUR) in most cantons (A. Bedolla, personal communication). In France, all native *Drosera* species (*D. anglica*, *D. intermedia* and *D. rotundifolia*) are protected at national level. Harvesting, use, transport or trade of wild *Drosera* specimens requires special permission from the Ministry in charge of nature conservation (F. Muller, personal communication). In Germany, commercial collection of *Drosera* species is prohibited by law⁶⁷. In some states of the USA, *D. rotundifolia* is federally protected and listed as threatened or endangered²⁴². In Finland, on the other hand, natural populations of *D. rotundifolia* are protected from over-collection by guidelines developed by the organisation “4H”. For example, pickers are requested to leave 5–10 flowering plants per square metre on the habitat⁷⁵, which maintains a sufficiently high population density and contributes to natural regeneration by seed dispersal.

PROPAGATION AND CULTIVATION

The first cultivation experiments with *D. rotundifolia*^{97, 245, 196} arose from over-collection in its natural habitat as the demand for ‘*Droserae herba*’ increased in the first part of the 20th century. More recently, in response to the sustained demand from pharmaceutical companies since nature protection measures curtailed the availability of wild material, several European research institutes have tested a variety of *Drosera* propagation and cultivation technologies^{74, 132}. These include *in vitro* propagation under sterile laboratory conditions¹²³, cultivation in glasshouses, and cultivation outdoors under semi-natural conditions on peatlands⁷².

In vitro propagation

In vitro micropropagation allows rapid clonal propagation of genetically identical copies of a single plant under sterile conditions^{144, 133, 15}. *Drosera* species are well suited for *in vitro* micropropagation because of their high regeneration potential²⁰¹. Seeds, leaf rosettes, isolated leaves, roots, flowers and gemmae are all used as explants for establishing tissue cultures²⁰¹. So far, *in vitro* propagation has been carried out with 21 *Drosera* species^{189, 201, 118, 109, 225, 15, 223}.

Drosera rotundifolia explants can be cultured on Murashige-Skoog (MS) or Reinert-Mohr (RM) medium^{158, 190, 201}. The optimal pH of the medium is between 5.5 and 5.8¹⁵. According to Crouch & van Staden (1988) and Perica & Berljak (1996), the best medium for *in vitro* multiplication of *Drosera* is the MS medium, which is a mixture of macronutrients, micronutrients, vitamins and organics¹⁵⁸. The culture media can be supplemented with casein hydrolysate, various nitrogen sources (in inorganic or organic form), coconut milk or grapevine exudate²⁰¹. Natural or synthetic growth regulators such as auxins (e.g. 1-naphthaleneacetic acid (NAA)) and cytokinins (e.g. 6-benzylaminopurine (BAP)) may significantly increase the rates of regeneration and callus formation^{28, 47, 123, 15}, although BAP may cause morphological abnormalities in newly formed shoots²⁵¹.

In vitro cultures are susceptible to contamination²⁰¹, e.g. by fungi and bacteria^{47, 11}. Explant sterilisation can be carried out with commercial bleach, CaOCl₂, HgCl₂ or NaOCl²⁰¹.

Propagation of *D. rotundifolia* on culture media may be achieved either by using seeds⁹⁸ or by caulogenesis from leaves^{11, 252, 25}, shoot rosettes²⁵⁰, root and leaf explants^{252, 1996, 26}, shoot tips^{108, 115}, axillary shoots and internodes²⁴³.

Kukulczanka & Czastka (1988) reported

germination of sterilised *D. rotundifolia* seeds on RM medium after 16–24 days at 20–25 °C. Clapa *et al.* (2010) achieved high multiplication rates on modified MS medium with coconut water, MS medium with 5 mg L⁻¹ kinetin, and hormone-free MS gelled with agar. Bobák *et al.* (1995) reported an average regeneration rate of 18.3 shoots *per* explant from isolated leaves on MS medium without growth regulators, or on media supplemented with 10⁻⁸ M NAA. Banasiuk *et al.* (2012) reported 3–12 plants *per* leaf explant after 6–8 weeks on MS medium supplemented with growth regulators. Micropropagation is reported²⁵¹ of *D. rotundifolia*, using cytokinins (2iP), achieving about 20 shoots *per* leaf explant. In a later study²⁵⁰ using a two-step culture system with liquid and semi-solid media, averages of 27.4 shoots *per* leaf explant and 53.3 shoots *per* shoot explant were recorded. *Drosera rotundifolia* plantlets produced extensive root systems after 6–8 weeks in subculture¹¹. Young shoots with 3–7 leaflets rooted spontaneously on a growth-regulator-free medium within 38 days of culture, and isolated mature plants produced viable seeds²⁵. The leaf tissue of *D. rotundifolia* grown *in vitro* is relatively thick, fibrous and mucilaginous²¹.

After acclimatisation, *in vitro* cultivated plantlets of *D. rotundifolia* are able to grow under outdoor conditions and in non-sterile substrates (e.g. horticultural soil, black peat, peatmoss), showing significant growth and low mortality^{251, 253, 236, 133}.

Indoor cultivation

Indoor cultivation of *Drosera* has been described^{213, 39, 32, 130, 16, 50} often, mainly for demonstration and decorative purposes¹⁷⁶. Successful indoor *Drosera* culture requires suitable temperature, humidity, shading and aeration³². Conventionally, seeds, leaf cuttings or root cuttings are used^{135, 130, 16}. For germination and undisturbed development, *D. rotundifolia* requires acidic to subneutral (pH 3.5–6.5) substrates^{32, 130}. The structural stability of the substrate (e.g. *Sphagnum* moss or *Sphagnum* peat) can be improved by mixing it with lime-free sand or very small proportions of vermiculite or perlite^{39, 32, 130}. Furthermore, *Drosera* plants need 10,000–15,000 lx of artificial light for 14–16 hr day⁻¹ in summer, and 8,500 lx for 8–12 hr day⁻¹ in winter after gradually reducing the light flux in autumn²¹³. A warm-humid microclimate is ideal; i.e. a summer temperature of 15–25 °C (< 40 °C) and a winter temperature between 3 °C and 8 °C^{213, 39, 16} with (40–) 60–70 % relative humidity^{130, 36}. The irrigation water should have a pH of 5–6, a total hardness of 0–5 °dH, and an electrical conductivity of 50–100 µS cm⁻¹³⁹. Germination of *Drosera* species occurs at 20–25 °C, 2–3 weeks after

seeding. After three months the seedlings are pricked out and transplanted into fresh substrate³⁹.

Cultivation of *D. rotundifolia* by sowing seeds on non-fertilised and fertilised commercial peat (pH 3.5–4.5) in 5 × 5 cm containers has been reported⁷². After overwintering for six months outdoors, the containers were transferred into a glasshouse in spring. The plants were fed at weekly intervals with milk powder and various fish feed preparations, red bloodworms and *Tubifex* worms⁷². The fresh yield of entire *D. rotundifolia* plants was 1,209–1,863 g m⁻² in the second growing year and 735–1,149 g m⁻² in the third year⁷². The results confirmed that protein feed had a positive effect on growth, life cycle, fresh plant weight, and yield^{74,72}.

Outdoor cultivation

Seeds of *D. rotundifolia* were sown in *Sphagnum*-free peat and natural ‘suitable raised bogs’⁹⁷. The first flowering and the first harvest took place in the second year. A further report²⁴⁵ suggested that successful culture requires high humidity.

Few outdoor *D. rotundifolia* cultivation studies have been published in detail. One report¹¹⁰ is of experiments in beds at an abandoned peat-cutting site. The beds were 2 m wide and separated by 1 m wide flooded channels from which the experiments could be accessed by boat. In the middle of each bed, a 0.3 m wide strip was left as a seed source to ensure natural reseeding. The water level was maintained at a constant depth of 0.05 m below the surface in order to provide continuous humidity, and no fertiliser was applied. *D. rotundifolia* produced high yields in pure culture only if weeds (*Juncus*, *Carex*, *Rhynchospora*, *Sphagnum*) were completely removed, but biomass production was not recorded.

Cultivation of *Drosera rotundifolia* and *D. anglica* was studied in southern Finland between 1992 and 2002^{73, 71, 70}. In the first experiments, *Drosera* plants were propagated in raised peat beds (size 3 × 1 × 0.7 m) filled with unfertilised peat (pH 3.5), using a drip irrigation system with tap water (pH 7)⁷¹. In a larger-scale pilot cultivation (1999–2004) the size of the peat beds was 9 × 1 m. Seeds were collected from natural sites, cold stratified, mixed with sand (ratio 1:10) and sown directly into the beds. The plants were artificially fed with natural proteins (e.g. fish food, milk powder). Flowering started in the second and third growing years⁷¹. The plants showed more growth with regular artificial feeding⁷³, reaching an average fresh mass of 259 g m⁻² with feeding (milk powder) and 89 g m⁻² without⁷¹. In the cultivation with 9 m² beds, the total fresh yield in years 3–6 was 836 g m⁻² (Table 4) with the highest yields in the second (489 g m⁻²) and third (212

Table 4. Fresh yields of *Drosera rotundifolia* in peat beds (total 54 m²) between 1999 and 2004 in Mikkeli, Finland. Source: Galambosi & Galambosi (2013).

Year	Fresh Yield	
	g m ⁻²	%
1999	-	-
2000	-	-
2001	75	9
2002	489	58,5
2003	212	25,3
2004	69	7,2
total	836	100

g m⁻²) harvest years. After collecting all sundew plants the top 5 cm layer of peat could be replaced with new peat and the beds used for the next 5–6 year growing cycle⁶⁸.

A problem identified during these experiments was that weeds (*Polytrichum*, *Epilobium*, *Betula* and *Pinus sylvestris* seedlings) in the beds reduced the productivity of *Drosera* and increased the risk of inadvertently removing young *Drosera* plants whilst weeding^{71, 70}. Also, especially if the density of *Drosera* was high, young and non-flowering plants could be damaged during harvesting, reducing the yield in the following year⁷⁰.

PROSPECTS

Drosera rotundifolia is one of the most common carnivorous plants in the world. This species is distributed contiguously across the Temperate and Boreal zones, as well as part of the Subarctic zone, from Europe, northern and central Asia to Japan and North America, and is scattered around the Mediterranean (Figure 1). Its distribution is correlated with wet and oligotrophic biotopes dominated by *Sphagnum*. As a result of human intervention (reclamation, nitrogen pollution) in the last 100 years, these habitats have decreased in extent, causing *D. rotundifolia* to be restricted to isolated communities which are sensitive to anthropic impacts.

From the early twentieth century onwards, the phyto-pharmacological properties of *D. rotundifolia* have been increasingly recognised and the plants have been collected in ever larger quantities for medical purposes. With the significant decline of *D. rotundifolia* populations in Europe, pharmaceutical producers have focused increasingly

on other native *Drosera* species such as *D. intermedia* and *D. anglica*. Since the 1980s, over-harvesting and habitat losses have led to the protection of these species in many European countries, forcing the pharmacological sector to use non-European *Drosera* species as substitute drugs and as feedstock for medicinal products. Today, *D. madagascariensis* is the most imported and most used *Drosera* species in Europe. It is collected from the native populations of Madagascar in an unsustainable way, which causes a threat to the species. Furthermore, the drug derived from *D. madagascariensis* is of low quality because it contains smaller amounts of active ingredients than *D. rotundifolia* does^{124, 18}. Therefore, *D. rotundifolia* is still preferred on the herbal market and is still collected from wild habitats.

Since the second half of the 20th century, research in Europe has addressed the propagation and cultivation of European and non-European *Drosera* species for medicinal purposes. However, despite positive results, *Drosera* species are not yet commercially cultivated. Compared with other plant species, sundews can be propagated very successfully *in vitro* and can achieve high propagation rates (C. Wawrosch, personal communication). Plants propagated *in vitro* are, however, rejected by the pharmaceutical industry because they are genetically identical (cloned), unnatural and artificially fed⁽¹²³⁾, L. Krenn, personal communication). The Finnish methods for indoor and outdoor cultivation are practicable and demonstrate that cultivation can replace collection from the wild. However, the cultivated *Drosera* product must again fit the requirements of the pharmaceutical industry. At least one company is not interested in cultivated, artificially fed plants (B. Galambosi, personal communication).

The reasons why *Drosera* has not yet been commercially cultivated include: a) the high cost and time requirements for maintaining *Drosera* cultures; b) the specific ecological and technical requirements of *Drosera* cultivation; and c) the current availability of sufficient material from the wild.

At present, the largest *Drosera* drug exporter in Europe is Finland. To protect natural *D. rotundifolia* populations, the Finnish organisation “4H” has developed guidelines for collectors in order to prevent over-exploitation. These guidelines are, however, merely recommendations and are not legally binding. Moreover, it is not always possible to monitor compliance with the guidelines, and the selective collection of larger individuals can easily lead to genetic drift in small populations. There are no such guidelines in Madagascar, and it is not

expected that guidelines will be implemented there in the near future.

In summary, the causes of the decline of natural *D. rotundifolia* populations are often complex and interrelated, but are not necessarily similar in different countries. However, the native habitats of *D. rotundifolia* are steadily diminishing in several countries, and the collection of plants from natural populations poses an additional threat to the species. In order to prevent natural populations from declining in the long term, cultivation methods that are time- and cost-effective must be developed and implemented.

Recently, *Sphagnum* cultivation (‘Sphagnum farming’) was established as a new alternative for commercial production of *Drosera* raw material in a sustainable way for commercial pharmacological purposes.

ACKNOWLEDGEMENTS

We thank John Couwenberg and Christoph Wawrosch for their comments; Liselotte Krenn, Raimo Heikkilä, Angéline Bedolla and Francis Muller for information; Cosima Tegetmeyer for help with the distribution map; Jenny Schulz, Livia Nagy and Judith Kiss for revising the English; and the Deutsche Bundesstiftung Umwelt (DBU) for financial support.

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Submitted 30 Nov 2015, final revision 15 Jly 2016
 Editor: R.S. Clymo

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Appendix. Common vegetation associates reported from wetlands supporting *Drosera rotundifolia* L.

Location	Source	Associated species
<u>Europe</u>		
Britain	Lindsay <i>et al.</i> (1983)	<i>Calluna vulgaris</i> , <i>Trichophorum cespitosum</i> , <i>Cephalozia connivens</i> , <i>Molinia caerulea</i> , <i>Erica tetralix</i> , <i>Narthecium angustifolium</i> , <i>Sphagnum tenellum</i> , <i>S. magellanicum</i> .
Britain	Box <i>et al.</i> (2011)	<i>Agrostis curtisii</i> , <i>Erica tetralix</i> , <i>Betula</i> spp., <i>Potentilla erecta</i> , <i>Molinia caerulea</i> , <i>Aulacomnium palustre</i> , <i>Luzula campestre</i> , <i>Sphagnum cuspidatum</i> , <i>S. palustre</i> , <i>S. papillosum</i> , <i>S. auriculatum</i> .
Britain	Lindsay <i>et al.</i> (1985)	<i>Empetrum nigrum</i> , <i>Calluna vulgaris</i> , <i>Eriophorum vaginatum</i> , <i>Erica tetralix</i> , <i>Drosera anglica</i> , <i>Sphagnum inbricatum</i> , <i>S. rubellum</i> , <i>S. tenellum</i> , <i>S. papillosum</i> .
Britain	Shimwell (2005)	<i>Narthecium ossifragum</i> , <i>Vaccinium oxycoccos</i> , <i>Juncus bulbosus</i> .
Britain	Shimwell (2005)	<i>Molinia caerulea</i> , <i>Nardia scalaris</i> , <i>Carex viridula</i> ssp. <i>oedocarpa</i> , <i>Sphagnum auriculatum</i> , <i>S. subnitens</i> , <i>S. fallax</i> .
Britain	Shimwell (2005)	<i>Eriophorum angustifolium</i> , <i>Narthecium ossifragum</i> , <i>Carex viridula</i> ssp. <i>oedocarpa</i> , <i>Carex panicea</i> , <i>Sphagnum fallax</i> .
Britain	Millett <i>et al.</i> (2012a)	<i>Molinia caerulea</i> , <i>Scirpus cespitosus</i> , <i>Erica tetralix</i> , <i>Calluna vulgaris</i> , <i>Sphagnum papillosum</i> .
Britain	Kritzler <i>et al.</i> (2016)	<i>Betula pubescens</i> , <i>Carex rostrata</i> , <i>Empetrum nigrum</i> , <i>Erica tetralix</i> , <i>Eriophorum angustifolium</i> , <i>Juncus squarrosus</i> , <i>Narthecium ossifragum</i> , <i>Plagiothecium undulatum</i> , <i>Pleurozium schreberi</i> , <i>Sphagnum cuspidatum</i> , <i>S. fimbriatum</i> , <i>S. palustre</i> , <i>S. recurvum</i> , <i>S. tenellum</i> .
Croatia	Topić & Stančić (2006)	<i>Carex echinata</i> , <i>C. flava</i> , <i>C. lepidocarpa</i> , <i>Sphagnum</i> sp.
Estonia	Paal <i>et al.</i> (2016)	<i>Rubus chamaemorus</i> , <i>Aulacomnium palustre</i> , <i>Equisetum fluviatile</i> , <i>Succisa pratensis</i> , <i>Peucedanum palustre</i> , <i>Carex nigra</i> .
Estonia	Triisberg <i>et al.</i> (2011)	<i>Betula nana</i> , <i>Calluna vulgaris</i> , <i>Andromeda polifolia</i> , <i>Empetrum nigrum</i> , <i>Eriophorum vaginatum</i> , <i>Ledum palustre</i> , <i>Oxycoccus palustris</i> , <i>Pleurozium schreberi</i> , <i>Sphagnum capillifolium</i> , <i>S. fuscum</i> , <i>S. magellanicum</i> .

Finland	Galambosi <i>et al.</i> (2000b)	<i>Pinus sylvestris</i> , <i>Betula</i> sp., <i>Ledum palustre</i> , <i>Calluna vulgaris</i> , <i>Empetrum nigrum</i> , <i>Vaccinium oxycoccos</i> , <i>Rubus chamaemorus</i> , <i>Andromeda polifolia</i> , <i>Carex</i> sp., <i>Eriophorum</i> sp., <i>Sphagnum</i> sp.
Germany	Dierssen & Dierssen (1984)	<i>Scheuchzeria palustris</i> , <i>Carex limosa</i> , <i>Drosera</i> x <i>obovata</i> , <i>Sphagnum cuspidatum</i> , <i>S. majus</i> .
Germany	Forst (1997)	<i>Potentilla palustris</i> , <i>Carex rostrata</i> , <i>Agrostis canina</i> , <i>Viola palustris</i> , <i>Aulacomnium palustre</i> , <i>Sphagnum squarrosum</i> , <i>S. fimbriatum</i> .
Germany	Oltmanns (1996)	<i>Rhynchospora alba</i> , <i>Andromeda polifolia</i> , <i>Vaccinium oxycoccos</i> , <i>Erica tetralix</i> , <i>Drosera intermedia</i> , <i>Sphagnum magellanicum</i> .
Germany	Huntke (2008)	<i>Odontoschisma sphagni</i> , <i>Molinia caerulea</i> , <i>Eriophorum angustifolium</i> , <i>Erica tetralix</i> , <i>Vaccinium oxycoccos</i> , <i>Andromeda polifolia</i> , <i>Sphagnum cuspidatum</i> , <i>S. papillosum</i> .
Germany	Huntke (2008)	<i>Drosera intermedia</i> , <i>Rhynchospora alba</i> , <i>Cephalozia macrostachya</i> , <i>Odontoschisma sphagni</i> , <i>Molinia caerulea</i> , <i>Eriophorum angustifolium</i> , <i>Erica tetralix</i> , <i>Vaccinium oxycoccos</i> , <i>Sphagnum pulchrum</i> , <i>S. cuspidatum</i> , <i>S. tenellum</i> .
Germany	Ellwanger (1996)	<i>Trientalis europaea</i> , <i>Eriophorum angustifolium</i> , <i>Oxycoccus palustris</i> , <i>Picea abies</i> , <i>Potentilla erecta</i> , <i>Sphagnum fallax</i> , <i>S. papillosum</i> .
Germany	Ellwanger (1996)	<i>Nardus stricta</i> , <i>Viola palustris</i> , <i>Carex nigra</i> , <i>Potentilla erecta</i> , <i>Calliargon stramineum</i> , <i>S. fallax</i> , <i>S. russowii</i> .
Hungary	Borhidi (2003)	<i>Brachythecium rivulare</i> , <i>Bryum pseudotriquetrum</i> , <i>Calliargonella cuspidata</i> , <i>Myosotis palustris</i> , <i>Cirsium palustre</i> , <i>Doronicum austriacum</i> , <i>Sphagnum contortum</i> , <i>S. subsecundum</i> .
Hungary	Borhidi (2003)	<i>Pycnus flavescens</i> f. <i>monostachys</i> , <i>Rhynchospora alba</i> , <i>Potentilla erecta</i> , <i>Carex echinata</i> , <i>Sphagnum contortum</i> , <i>S. recurvum</i> .
Hungary	Borhidi (2003)	<i>Carex canescens</i> , <i>C. nigra</i> , <i>Epilobium palustre</i> , <i>Sphagnum recurvum</i> , <i>S. palustre</i> , <i>S. subsecundum</i> .
Hungary	Borhidi (2003)	<i>Lysimachia vulgaris</i> , <i>Betula pubescens</i> , <i>Carex elata</i> , <i>Menyanthes trifoliata</i> , <i>Peucedanum palustre</i> , <i>Sphagnum</i>

		<i>flexuosum</i> , <i>S. cuspidatum</i> , <i>S. fallax</i> , <i>S. magellanicum</i> , <i>S. palustre</i> .
Hungary	Borhidi (2003)	<i>Eriophorum vaginatum</i> , <i>Salix aurita</i> , <i>Vaccinium oxycoccos</i> , <i>Hammarbya paludosa</i> , <i>Carex lasiocarpa</i> , <i>Sphagnum</i> <i>palustre</i> , <i>S. magellanicum</i> , <i>S. fuscum</i> , <i>S. recurvum</i> , <i>S. fimbriatum</i> .
Italy	Miserere <i>et al.</i> (2003)	<i>Potentilla erecta</i> , <i>Molinia caerulea</i> , <i>Scirpus sylvaticus</i> , <i>Calluna vulgaris</i> , <i>Sphagnum subnitens</i> , <i>S. papillosum</i> .
Italy	Miserere <i>et al.</i> (2003)	<i>Carex echinata</i> , <i>C. nigra</i> , <i>C. rostrata</i> , <i>Scirpus caespitosus</i> , <i>Viola palustris</i> , <i>Warnstorfia exannulata</i> , <i>Eriophorum</i> <i>angustifolium</i> , <i>Calliergon stramineum</i> , <i>Sphagnum</i> <i>subsecundum</i> .
Italy	Gerdol <i>et al.</i> (2011)	<i>Calluna vulgaris</i> , <i>Pinus mugo</i> , <i>Vaccinium microcarpum</i> , <i>V. myrtillus</i> , <i>V. uliginosum</i> , <i>Carex pauciflora</i> , <i>Eriophorum</i> <i>vaginatum</i> , <i>Melampyrum pratense</i> , <i>Sphagnum</i> <i>magellanicum</i> , <i>S. capillifolium</i> .
Italy	Gerdol <i>et al.</i> (2011)	<i>Eriophorum vaginatum</i> , <i>Molinia caerulea</i> , <i>Trichophorum</i> <i>caespitosum</i> , <i>Potentilla erecta</i> , <i>Dicranum bonjeanii</i> , <i>Sphagnum capillifolium</i> , <i>S. compactum</i> , <i>S. magellanicum</i> .
Italy	Poto <i>et al.</i> (2013)	<i>Drosera longifolia</i> , <i>Andromeda polifolia</i> , <i>Vaccinium</i> <i>microcarpum</i> , <i>Sphagnum magellanicum</i> , <i>S. majus</i> , <i>S. squarrosus</i> , <i>S. capillifolium</i> .
Netherlands	Adema <i>et al.</i> (2006)	<i>Utricularia minor</i> , <i>Erica tetralix</i> , <i>Calluna vulgaris</i> , <i>Rhynchospora alba</i> , <i>Vaccinium oxycoccos</i> , <i>Sphagnum</i> <i>cuspidatum</i> , <i>S. magellanicum</i> , <i>S. palustre</i> , <i>S. fallax</i> .
Norway	Nordbakken <i>et al.</i> (2004)	<i>Mylia anomala</i> , <i>Kurzia pauciflora</i> , <i>Cladopodiella fluitans</i> , <i>Cephalozia loitlesbergeri</i> , <i>Sphagnum rubellum</i> , <i>S. fuscum</i> .
Norway	Hansen (1967)	<i>Andromeda polifolia</i> , <i>Rubus chamaemorus</i> , <i>Calluna</i> <i>vulgaris</i> , <i>Vaccinium oxycoccos</i> , <i>Myrica gale</i> , <i>Eriophorum</i> <i>sp.</i> , <i>Cladonia rangerifera</i> , <i>Betula nana</i> , <i>Sphagnum spp.</i>
Serbia	Petronijević <i>et al.</i> (2009)	<i>Eriophorum angustifolium</i> , <i>E. latifolium</i> , <i>Comarum</i> <i>palustre</i> , <i>Menyanthes trifoliata</i> , <i>Pedicularis palustris</i> , <i>Ranunculus lingua</i> .
Spain	Prieto <i>et al.</i> (1985)	<i>Erica makaiana</i> , <i>Aulacomnium palustre</i> , <i>Carex durieui</i> , <i>Nathecium ossifragum</i> , <i>Molinia careulea</i> , <i>Agrostis canina</i> , <i>Sphagnum subnitens</i> , <i>S. auriculatum</i> .

Spain	Prieto <i>et al.</i> (1985)	<i>Eriophorum angustifolium</i> , <i>Eleocharis multicaulis</i> , <i>Molinia caerulea</i> , <i>Drosera intermedia</i> , <i>Sphagnum cuspidatum</i> .
Spain	Prieto <i>et al.</i> (1985)	<i>Erica tetralix</i> , <i>Calluna vulgaris</i> , <i>Aulaconium palustre</i> , <i>Sphagnum capillifolium</i> , <i>S. recurvum</i> .
Spain	Prieto <i>et al.</i> (1985)	<i>Scirpus caespitosus</i> , <i>Narthecium ossifragum</i> , <i>Sphagnum tenellum</i> , <i>S. papillosum</i> .
Sweden	Vinichuk <i>et al.</i> (2010)	<i>Eriophorum vaginatum</i> , <i>Empetrum nigrum</i> , <i>Andromeda polifolia</i> , <i>Carex rostrata</i> , <i>Menyanthes trifoliata</i> , <i>Vaccinium oxycoccos</i> , <i>Sphagnum papillosum</i> , <i>S. angustifolium</i> , <i>S. magellanicum</i> .
Sweden	Breeuwer <i>et al.</i> (2009)	<i>Andromeda polifolia</i> , <i>Calluna vulgaris</i> , <i>Erica tetralix</i> , <i>Eriophorum vaginatum</i> , <i>Vaccinium oxycoccos</i> , <i>Rynchospora alba</i> , <i>Sphagnum cuspidatum</i> , <i>S. magellanicum</i> , <i>S. tenellum</i> , <i>S. balticum</i> , <i>S. rubellum</i> .
Sweden	Redbo-Torstensson (1994)	<i>Eriophorum vaginatum</i> , <i>Andromeda polifolia</i> , <i>Vaccinium oxycoccos</i> , <i>Sphagnum fuscum</i> , <i>S. rubellum</i> .
Sweden	Svensson (1995)	<i>Empetrum hermaphroditum</i> , <i>Rubus chamaemorus</i> , <i>Vaccinium microcarpum</i> , <i>Betula nana</i> , <i>Sphagnum fuscum</i> .
Sweden	Millett <i>et al.</i> (2012b)	<i>Sphagnum fuscum</i> , <i>S. balticum</i> .

North America

Canada	Pellerin <i>et al.</i> (2006)	<i>Chamaedaphne calyculata</i> , <i>Kalmia angustifolia</i> , <i>K. polifolia</i> , <i>Ledum groenlandicum</i> , <i>Rubus chamaemorus</i> , <i>Vaccinium oxycoccos</i> , <i>Sarracenia purpurea</i> , <i>Sphagnum fuscum</i> , <i>S. rubellum</i> , <i>S. angustifolium</i> , <i>S. capillifolium</i> , <i>S. magellanicum</i> .
Canada	Pellerin <i>et al.</i> (2006)	<i>Myrica gale</i> , <i>Dasiphora floribunda</i> , <i>Andromeda polifolia</i> var. <i>glaucophylla</i> , <i>Rhamnus alnifolia</i> , <i>Vaccinium oxycoccos</i> , <i>Trichophorum caespitosum</i> , <i>Campylium stellatum</i> , <i>Sphagnum warnstorffii</i> , <i>S. fuscum</i> , <i>S. capillifolium</i> , <i>S. rubellum</i> , <i>S. russowii</i> .
Canada	Swales (1975)	<i>Erigeron strigosus</i> , <i>Leucanthemum vulgare</i> , <i>Solidago nemoralis</i> , <i>Betula populifolia</i> , <i>Polygonum cilinode</i> , <i>Chrysanthemum leucanthemum</i> .
Minnesota	Glaser <i>et al.</i> (1990)	<i>Scirpus hudsonianus</i> , <i>Cladium mariscoides</i> , <i>Parnassia palustris</i> , <i>Muhlenbergia glomerata</i> , <i>Scirpus cespitosus</i> , <i>Carex limosa</i> , <i>C. livida</i> , <i>Cladium mariscoides</i> , <i>Drosera</i>

		<i>anglica</i> , <i>Utricularia intermedia</i> , <i>U. cornuta</i> , <i>Rhynchospora alba</i> , <i>Eleocharis compressa</i> , <i>Sarracenia purpurea</i> , <i>Menyanthes trifoliata</i> , <i>Vaccinium oxycoccos</i> .
Minnesota	Glaser <i>et al.</i> (1990)	<i>Picea mariana</i> , <i>Thuja occidentalis</i> , <i>Carex gynocrate</i> , <i>C. leptalea</i> , <i>Ledum groenlandicum</i> , <i>Sarracenia purpurea</i> , <i>Sphagnum angustifolium</i> , <i>S. magellanicum</i> , <i>S. capillifolium</i> , <i>S. russowi</i> , <i>S. warnstorffii</i> .
Minnesota	Glaser <i>et al.</i> (1990)	<i>Carex lasiocarpa</i> , <i>Utricularia intermedia</i> , <i>Equisetum fluviatile</i> , <i>Potentilla palustris</i> , <i>Carex chordorrhiza</i> , <i>Menyanthes trifoliata</i> , <i>Sarracenia purpurea</i> , <i>Sphagnum angustifolium</i> , <i>S. magellanicum</i> , <i>S. warnstorffii</i> .
Maine	Davis & Anderson (1991)	<i>Chamaeaphne calyculata</i> , <i>Rhynchospora alba</i> , <i>Eriophorum spissum</i> , <i>Vaccinium oxycoccos</i> , <i>Eriophorum virginicum</i> , <i>Kalmia angustifolia</i> , <i>Sphagnum rubellum</i> , <i>S. fuscum</i> , <i>S. magellanicum</i> .
Virginia	Byers <i>et al.</i> (2007)	<i>Vaccinium oxycoccos</i> , <i>Rhynchospora alba</i> , <i>Photinia melanocarpa</i> , <i>P. pyrifolia</i> , <i>Vaccinium myrtilloides</i> , <i>V. macrocarpon</i> , <i>Sphagnum rubellum</i> , <i>S. fallax</i> , <i>S. papillosum</i> , <i>S. flexuosum</i> , <i>S. cuspidatum</i> , <i>S. recurvum</i> , <i>S. magellanicum</i> .
Virginia	Byers <i>et al.</i> (2007)	<i>Pinus rigida</i> , <i>Picea rubens</i> , <i>Rubus hispidus</i> , <i>Gaultheria procumbens</i> , <i>Coptis trifolia</i> , <i>Rhynchospora alba</i> , <i>Sphagnum rubellum</i> , <i>S. magellanicum</i> , <i>S. fallax</i> , <i>S. papillosum</i> .
<u>Other</u>		
Iceland	Dijkema & Wolff (1983)	<i>Potentilla erecta</i> , <i>Pedicularis silvatica</i> , <i>Gentiana pneumonathe</i> , <i>Carex panicea</i> , <i>Sphagnum subsecundum</i> , <i>S. compactum</i> .
Japan	Julve (1999)	<i>Eriophorum vaginatum</i> , <i>Sanguisorba tenuifolia</i> var. <i>alba</i> , <i>Carex pauciflora</i> , <i>C. middendorffii</i> , <i>Geum pentapetalum</i> , <i>Tilingia ajanensis</i> , <i>Sasa senanensis</i> , <i>Sphagnum magellanicum</i> , <i>S. papillosum</i> .
Japan	Julve (1999)	<i>Ledum palustre</i> subsp. <i>diversipilosum</i> , <i>Empetrum nigrum</i> subsp. <i>japonicum</i> , <i>Vaccinium oxycoccos</i> , <i>Chamaedaphne calyculata</i> , <i>Scheuchzeria palustris</i> , <i>Carex middendorffii</i> , <i>Sphagnum fuscum</i> , <i>S. magellanicum</i> , <i>S. papillosum</i> .
Japan	Hoyo & Tsuyuzaki (2015)	<i>Carex middendorffii</i> , <i>Drosera anglica</i> , <i>Sphagnum papillosum</i> .