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.


INTRODUCTION

Carnivorous plants, and especially the widespread genus *Drosera*, have fascinated and inspired researchers for centuries [264]. 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 Europe [142], 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 paludiculture [76]. *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 long [255, 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 petiole \(^{95}\), membranously adnate, fimbriate, 4–6 mm in length \(^{157}\), and each divided into about 7 teeth \(^{255}\). The laminae are initially helical involute \(^{101}\) 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 capsule \(^{1, 13, 127}\), 1-valved and split into 3 sections \(^{48, 209}\), double un-ranked raceme \(^{101, 261}\).

cymose raceme that terminates in a leafless, single or 3 (rarely 4 or 5) united carpels is superior, unilocular, \(3 \text{ mm long}^{54, 90, 157}\), and occasionally bears tentacles \(^{3}\). The 5 free petals are spatulate, obovate, white or pinkish, 4–7 × ≤ 3 mm \(^{54, 157, 5, 201}\), wedge-shaped and persistent in cleistogamous flowers \(^{48}\). The androecium includes 4–8 free, 4–5 mm long stamens with reddish, filiform filaments \(^{54, 256, 48, 195}\) and extrorse anthers \(^{256, 255}\). The pollen consists of \(1,395 \text{ m in Germany}^{167}; 2,000 \text{ m in Austria, France and Italy}^{86, 186, 179}, \text{ and oceanic climates}^{111, 44, 161}. \text{ In Europe, the species is found}

**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 sites \(^{192}\) in continental, oceanic and suboceanic regions \(^{91, 187}\). *D. rotundifolia* is highly adapted to the microclimatic conditions of peatlands \(^{41}\), 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

### GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

*Drösera rotundifolia* is probably one of the most widely distributed carnivorous plant species, appearing in most regions of the Holarctic (Figure 1; \(^{165, 206, 99, 78, 227, 199}\)). In northern Eurasia it is known from Iceland, the British Isles, Norway (up to 70° 65′ N \(^{163}\)), 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 \(^{90, 12}\), Italy and Corsica (as var. *corsica* (Maire) Briq.) \(^{179}\), the Balkan Peninsula \(^{86, 6, 57}\), the Caucasus \(^{113}\), Mongolia \(^{49}\), 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′ N \(^{239}\)), and from Alaska to California and Alabama, to 33° 97′ N \(^{88, 240}\). 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 m \(^{33}\), but has also been reported at about 900 m in Scotland \(^{105}\). In continental Europe it reaches altitudes of 1,100 m in Scandinavia \(^{149}\), 1,395 m in Germany \(^{167}\), 2,000 m in Austria, France and Italy \(^{186, 249, 179}\), and 2,100 m in Spain \(^{40}\). In Japan *D. rotundifolia* may be found up to 1,920 m \(^{81}\), and in Colorado (USA) up to about 3,000 m \(^{147}\).
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, 214. 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 Ca\(^2+\) and Mg\(^2+\) 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.

<table>
<thead>
<tr>
<th>Location</th>
<th>Soil pH</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Europe</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germany</td>
<td>3.6–4.3</td>
<td>Forst (1997)</td>
</tr>
<tr>
<td>Germany</td>
<td>4.6</td>
<td>Oltmanns (1996)</td>
</tr>
<tr>
<td>Germany</td>
<td>3.3–3.5</td>
<td>Huntke (2008)</td>
</tr>
<tr>
<td>Italy</td>
<td>4.4–4.9</td>
<td>Miserere <em>et al.</em> (2003)</td>
</tr>
<tr>
<td>North America</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maine</td>
<td>3.5–4.5</td>
<td>Davis &amp; Anderson (1991)</td>
</tr>
<tr>
<td>Virginia</td>
<td>3.5–3.7</td>
<td>Byers <em>et al.</em> (2007)</td>
</tr>
</tbody>
</table>

Table 2. pH, calcium (Ca\(^{2+}\)) and magnesium (Mg\(^{2+}\)) 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.

<table>
<thead>
<tr>
<th>Location</th>
<th>pH</th>
<th>Ca(^{2+})</th>
<th>Mg(^{2+})</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Europe</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Britain</td>
<td>3.5–4.4</td>
<td>2.4–24</td>
<td>1.2–7.0</td>
<td>Crowder <em>et al.</em> (1990)</td>
</tr>
<tr>
<td>Britain</td>
<td>4.54–5.22</td>
<td>1.2–2.5</td>
<td>0.09–1.05</td>
<td>Shimwell (2005)</td>
</tr>
<tr>
<td>Britain</td>
<td>6.5–6.8</td>
<td>5.5–7.1</td>
<td>3.50–3.70</td>
<td>Shimwell (2005)</td>
</tr>
<tr>
<td>Britain</td>
<td>4.8</td>
<td>14</td>
<td>8.7</td>
<td>Box <em>et al.</em> (2011)</td>
</tr>
<tr>
<td>Britain</td>
<td>5</td>
<td>17</td>
<td>6.6</td>
<td>Box <em>et al.</em> (2011)</td>
</tr>
<tr>
<td>Germany</td>
<td>4.6–5.1</td>
<td>NA</td>
<td>NA</td>
<td>Ellwanger (1996)</td>
</tr>
<tr>
<td>Italy</td>
<td>4.4–4.9</td>
<td>NA</td>
<td>NA</td>
<td>Miserere <em>et al.</em> (2003)</td>
</tr>
<tr>
<td>Italy</td>
<td>5.6</td>
<td>5.55 (± 0.43)</td>
<td>1.40 (± 0.11)</td>
<td>Gerdol <em>et al.</em> (2011)</td>
</tr>
<tr>
<td>Italy</td>
<td>6.1</td>
<td>8.27 (± 0.38)</td>
<td>1.91 (± 0.09)</td>
<td>Gerdol <em>et al.</em> (2011)</td>
</tr>
<tr>
<td>Netherlands</td>
<td>4.5 (± 0.07)</td>
<td>0.46</td>
<td>0.46</td>
<td>Adema <em>et al.</em> (2006)</td>
</tr>
<tr>
<td>Poland</td>
<td>4.0</td>
<td>0.75</td>
<td>0.18</td>
<td>Wojtuñ <em>et al.</em> (2013)</td>
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<tr>
<td>Spain</td>
<td>3.0</td>
<td>NA</td>
<td>NA</td>
<td>Fernández-Pascual (2016)</td>
</tr>
<tr>
<td>Spain</td>
<td>4.6</td>
<td>NA</td>
<td>NA</td>
<td>Fernández-Pascual (2016)</td>
</tr>
<tr>
<td>Sweden</td>
<td>3.9–4.4</td>
<td>NA</td>
<td>NA</td>
<td>Vinichuk <em>et al.</em> (2010)</td>
</tr>
<tr>
<td>North America</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canada</td>
<td>4.3–6.9</td>
<td>NA</td>
<td>NA</td>
<td>Pellerin <em>et al.</em> (2006)</td>
</tr>
<tr>
<td>Minnesota</td>
<td>3.9</td>
<td>0.8</td>
<td>NA</td>
<td>Glaser <em>et al.</em> (1990)</td>
</tr>
<tr>
<td>Minnesota</td>
<td>7.5</td>
<td>30</td>
<td>NA</td>
<td>Glaser <em>et al.</em> (1990)</td>
</tr>
<tr>
<td>Ohio</td>
<td>4.0–5.1</td>
<td>2.8 (± 0.8)</td>
<td>1.7 (± 0.3)</td>
<td>Andreas &amp; Bryan (1990)</td>
</tr>
<tr>
<td>Ohio</td>
<td>4.1–4.3</td>
<td>2.8 (± 0.8)</td>
<td>1.2 (± 0.4)</td>
<td>Andreas &amp; Bryan (1990)</td>
</tr>
<tr>
<td>Ohio</td>
<td>6.3–7.3</td>
<td>6.0 (± 1.3)</td>
<td>2.6 (± 0.7)</td>
<td>Andreas &amp; Bryan (1990)</td>
</tr>
</tbody>
</table>
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 concentrations
201, but is salt-intolerant 131 and growth is hampered
by raised salt concentrations 216.

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 Wiskskirchen & 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-
Sphagnetea Br.-Bl. & R. Tx. ex Westh. et al. 46 and
the Scheuchzerio-Caricetea 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-Sphagnetea,
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
ulinosum and Erica tetralix, as well as with Calluna vulgaris in dry areas 255, 207. In Scheuchzerio-
Caricetea fuscae Tx. 37 communities, the species is
found together with, for example, Rhynchospora
alba, R. fusca, Eriophorum angustifolium, Molinia
cærulea, Trichophorum cespitosum, Menyanthes
trifoliata and Sphagnum (e.g. Sphagnum fallax,
S. inundatum, S. cuspidatum) 214, 183.

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

<table>
<thead>
<tr>
<th>Plant communities</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sphagnion medii Kästner et Flössner 1933</td>
<td>Berg et al. (2004), Thébaud (2011)</td>
</tr>
<tr>
<td>Ericion tetralicis Schwickerath 1933</td>
<td>Berg et al. (2004)</td>
</tr>
<tr>
<td>Scheuchzerio-Caricetea fuscae Tx. 37</td>
<td>Borhidi (2003), Rodondi et al. (2009)</td>
</tr>
</tbody>
</table>
**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 sunlight \(^{257}\). 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 system \(^{48}\). 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 cells \(^{20}\). 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 petiole \(^{20}\). 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 plant \(^{257}\). In the case of the shoot tip being damaged, the top axillary shoot takes over the (regeneration) function of the terminal shoot \(^{257}\). If the peduncle is removed, buds can - in humid conditions - also appear on the stem \(^{257}\). Another form of vegetative reproduction occurs when roots develop below-ground suckers \(^{129}\), 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 reported \(^{218}\).

The axillary bud forms a secondary rosette beside or below the main rosette \(^{48}\), which is genetically identical to the parent plant \(^{261}\).

**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 cleistogamous flowers, whereas later, well-developed reproductive structures in chasmogamous flowers are formed. According to Goebel (1914), the occurrence of cleistogamous *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 hours \(^{54}\). *D. rotundifolia* flowers start opening if the temperature reaches 25–30 °C, but complete blooming requires at least 35 °C \(^{180}\).

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 scale \(^{176}\). In contrast, that little to no cross-pollination occurs has been inferred from pollen to ovule ratios and pollinator visitation \(^{159}\). After cross-pollination the corolla closes in the evening \(^{216}\). Self-pollination occurs in the closed flower, as the anthers empty their pollen onto the stigmas \(^{90}\).

Pseudo-cleistogamous flowers of *D. rotundifolia*, which are half open at midday but close within a short time, are also found \(^{54}\). These normally chasmogamous flowers develop as a consequence of habitat disturbance such as deficient light, high water level and strong water currents \(^{160}\).

The fruit of *D. rotundifolia* matures 5–7 weeks after flowering \(^{176}\). 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) \(^{15}\); 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 autumn \(^{48}\). 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/June \(^{71}\). In order to germinate, the seeds need cold stratification (by frost \(^{35}\)), sufficient light, and temperatures of 20–25 °C \(^{38,197,15}\). If dormancy break happens in summer, \(D. \ rotundifolia\) seeds are able to germinate in the same year as they are dispersed \(^{17}\). On peat, seeds usually germinate within 20–30 days \(^{176,39}\), with exposure to cold causing almost simultaneous germination over a period of two weeks \(^{48}\).

Campbell & Rochefort (2003) showed experimentally that germination in peat decreases rapidly if burial depth exceeds 5 mm. \(D. \ rotundifolia\) seeds germinate very effectively on \(Sphagnum\) moss \(^{199}\) 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 tract \(^{14}\). 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 \(^{124,33,244,171,18}\). 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 \(Drosera\) biomass \(^{70}\). 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 Switzerland \(^{60}\). 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 individuals \(^{75}\) and one picker collects about 40 kg of \(Drosera\) during the season, which begins in July and ends in August \(^{60}\). The pickers are paid 43 EUR kg\(^{-1}\) for raw \(Drosera\) material \(^{104}\).

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 Croatia \(^{162}\), 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 law \(^{67}\). In some states of the USA, \(D. \ rotundifolia\) is federally protected and listed as threatened or endangered \(^{242}\). 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 habitat \(^{75}\), 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 ‘Drosera 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 conditions 123, cultivation in glasshouses, and cultivation outdoors under seminatural conditions on peatlands 72.

**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 potential 201. Seeds, leaf rosettes, isolated leaves, roots, flowers and gemmae are all used as explants for establishing tissue cultures 201. 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 5.8 15. 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 organics 158. The culture media can be supplemented with casein hydrolysate, various nitrogen sources (in inorganic or organic form), coconut milk or grapevine exudate 201. 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 shoots 251.

*In vitro* cultures are susceptible to contamination 201, e.g. by fungi and bacteria 47, 11. Explant sterilisation can be carried out with commercial bleach, CaOCl, HgCl2 or NaOCl 201.

Propagation of *D. rotundifolia* on culture media may be achieved either by using seeds 98 or by caulogenesis from leaves 11, 252, 25, shoot rosettes 250, root and leaf explants 252, 1996, 26, shoot tips 108, 115, axillary shoots and internodes 243.

Kukuczanka & Czajstka (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 reported 251 of *D. rotundifolia*, using cytokinins (2iP), achieving about 20 shoots per leaf explant. In a later study 250 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 subculture 11. 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 seeds 25. The leaf tissue of *D. rotundifolia* grown *in vitro* is relatively thick, fibrous and mucilaginous 21.

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, 56 often, mainly for demonstration and decorative purposes 176. Successful indoor *Drosera* culture requires suitable temperature, humidity, shading and aeration 32. 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 autumn 213. 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⁻¹ 39. 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 substrate 39.

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 reported 72. 74. After overwintering for six months outdoors, the containers were transferred into a greenhouse in spring. The plants were fed at weekly intervals with milk powder and various fish feed preparations, red bloodworms and *Tubifex* worms 72. 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 year 72. 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’ 70. The first flowering and the first harvest took place in the second year. A further report 245 suggested that successful culture requires high humidity.

Few outdoor *D. rotundifolia* cultivation studies have been published in detail. One report 110 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 years 71. The plants showed more growth with regular artificial feeding 73, reaching an average fresh mass of 259 g m⁻² with feeding (milk powder) and 89 g m⁻² without feeding 71. 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 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 cycle 68.

A problem identified during these experiments was that weeds (*Polytrichum*, *Epilobium*, *Betula* and *Pinus silvestris*) 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 year 70.

**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. 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 (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.

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

<table>
<thead>
<tr>
<th>Location</th>
<th>Source</th>
<th>Associated species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Europe</td>
<td></td>
<td>Calluna vulgaris, Trichophorum cespitosum, Cephalozia connivens, Molinia careulea,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Erica tetralix, Narthecium angustifolium, Sphagnum tenellum, S. magellanicum.</td>
</tr>
<tr>
<td>Britain</td>
<td>Lindsay et al. (1983)</td>
<td>Agrostis curtisii, Erica tetralix, Betula spp., Potentilla erecta, Molinia caerulea,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aulacomnium palustre, Luzula campestre, Sphagnum cuspidatum, S. palustre, S. papillosum, S. auriculatum.</td>
</tr>
<tr>
<td>Britain</td>
<td>Lindsay et al. (1985)</td>
<td>Narthecium ossifragum, Vaccinium oxyccocos, Juncus bulbosus.</td>
</tr>
<tr>
<td>Britain</td>
<td>Millett et al. (2012a)</td>
<td>Molinia caerulea, Scirpus cespitosus, Erica tetralix, Calluna vulgaris, Sphagnum papillosum.</td>
</tr>
<tr>
<td>Country</td>
<td>Reference</td>
<td>Species</td>
</tr>
<tr>
<td>---------</td>
<td>-----------</td>
<td>--------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Finland</td>
<td>Galambosi et al. (2000b)</td>
<td>Pinus sylvestris, Betula sp., Ledum palustre, Calluna vulgaris, Empetrum nigrum, Vaccinium oxycoccos, Rubus chamaemorus, Andromeda polifolia, Carex sp., Eriophorum sp., Sphagnum sp.</td>
</tr>
<tr>
<td>Germany</td>
<td>Dierssen &amp; Dierssen (1984)</td>
<td>Scheuchzeria palustris, Carex limosa, Drosera x obovata, Sphagnum cuspidatum, S. majus.</td>
</tr>
<tr>
<td>Hungary</td>
<td>Borhidi (2003)</td>
<td>Lysimachia vulgaris, Betula pubescens, Carex elata, Menyanthes trifoliata, Peucedanum palustre, Sphagnum</td>
</tr>
</tbody>
</table>
- *Drosera flexuosa*, *S. cuspidatum*, *S. fallax*, *S. magellanicum*, *S. palustre*.

**Hungary**  
Borhidi (2003)  
*Eriophorum vaginatum*, *Salix aurita*, *Vaccinium oxycoccos*, *Hammarbya paludosa*, *Carex lasiocarpa*, *Sphagnum palustre*, *S. magellanicum*, *S. fuscum*, *S. recurvum*, *S. fimbriatum*.

**Italy**  
Miserere et al. (2003)  
*Potentilla erecta*, *Molinia caerulea*, *Scirpus sylvaticus*, *Calluna vulgaris*, *Sphagnum subnitens*, *S. papillosum*.

**Italy**  
Miserere et al. (2003)  
*Carex echinata*, *C. nigra*, *C. rostrata*, *Scirpus caespitosus*, *Viola palustris*, *Warnstorfia exannulata*, *Eriophorum angustifolium*, *Calliergon stramineum*, *Sphagnum subsecundum*.

**Italy**  
Gerdol et al. (2011)  
*Calluna vulgaris*, *Pinus mugo*, *Vaccinium microcarpum*, *V. myrtillus*, *V. uliginosum*, *Carex pauciflora*, *Eriophorum vaginatum*, *Melampyrum pratense*, *Sphagnum magellanicum*, *S. capillifolium*.

**Italy**  
Gerdol et al. (2011)  
*Eriophorum vaginatum*, *Molinia caerulea*, *Trichophorum caespitosum*, *Potentilla erecta*, *Dicranum bonjeanii*, *Sphagnum capillifolium*, *S. compactum*, *S. magellanicum*.

**Italy**  
Poto et al. (2013)  
*Drosera longifolia*, *Andromeda polifolia*, *Vaccinium microcarpum*, *Sphagnum magellanicum*, *S. majus*, *S. squarrosum*, *S. capillifolium*.

**The Netherlands**  
Adema et al. (2006)  
*Utricularia minor*, *Erica tetralix*, *Calluna vulgaris*, *Rhynchospora alba*, *Vaccinium oxycoccos*, *Sphagnum cuspidatum*, *S. magellanicum*, *S. palustre*, *S. fallax*.

**Norway**  
Nordbakken et al. (2004)  
*Mylia anomala*, *Kurzia pauciflora*, *Cladopodiella fluitans*, *Cephalozia loitlbersgeri*, *Sphagnum rubellum*, *S. fuscum*.

**Norway**  
Hansen (1967)  
*Andromeda polifolia*, *Rubus chamaenorus*, *Calluna vulgaris*, *Vaccinium oxycoccos*, *Myrica gale*, *Eriophorum sp.*, *Cladonia rangerifera*, *Betula nana*, *Sphagnum spp.*

**Serbia**  
Petronijević et al. (2009)  
*Eriophorum angustifolium*, *E. latifolium*, *Comarum palustre*, *Menyanthes trifoliata*, *Pedicularis palustris*, *Ranunculus lingua*.

**Spain**  
Prieto et al. (1985)  
*Erica makaiana*, *Aulacomnium palustre*, *Carex durieu*, *Nathecium ossifragum*, *Molinia careulea*, *Agrostis canina*, *Sphagnum subnitens*, *S. auricolatum*. 
Spain Prieto et al. (1985) | Eriophorum angustifolium, Eleocharis multicaulis, Molinia caerulea, Drosera intermedia, Sphagnum cuspidatum.
---
Sweden Millett et al. (2012b) | Sphagnum fuscum, S. balticum.

**North America**

Minnesota Glaser et al. (1990) | Scirpus hudsonianus, Cladium mariscoides, Parnassia palustris, Muhlenbergia glomerata, Scirpus caespitosus, Carex limosa, C. liva, Cladium mariscoides, Drosera
anglica, Utricularia intermedia, U. cornuta, Rhynchospora alba, Eleocharis compressa, Sarracenia purpurea, Menyanthes trifoliata, Vaccinium oxycoccos.


Other


