Untersuchungen zur Machbarkeit der Kultivierung von *Drosera rotundifolia* für medizinale Zwecke auf wiedervernässten Hochmoorflächen in Deutschland mit besonderer Berücksichtigung der Co-Nutzung bei der Torfmooskultivierung

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Untersuchungen zur Machbarkeit der Kultivierung von *Drosera rotundifolia* für medizinale Zwecke auf wiedervernässten Hochmoorflächen in Deutschland mit besonderer Berücksichtigung der Co-Nutzung bei der Torfmooskultivierung

Balázs Baranyai

Kedves szüleim
köszönöm nektek
a sokéves támogatásotokat
és
hogy mindig ott voltatok nekem.
A disszertációmat nektek ajánlom.

Meine lieben Eltern,
ich danke Euch
für Eure langjährige Unterstützung
und
dass ihr immer
für mich da gewesen seid.
Ich widme euch meine Dissertation.

Es steht ein Blümlein wunderfein
Im stillen Moos auf weiter Heid'-
Und sprosset dort im Sonnenschein
In stiller Blumen Seligkeit.-
Die weißen Sternlein wiegt der Wind,
Die runden Blättchen ruhn gar lind
Auf weichem, zartem bleichem Moos
Und funkelnd strahlt an jedem Blatt
Im hellem Mittagssonnenglanz,
Dem frisch gefall'nen Taue gleich,
Ein zarter Drüsen-Perlenkranz.

Ein Bienchen kommt durchs Heideland
Und sieht das holde Blümchen blühn –
Hat sich sein Herzlein gleich verbrannt,
Kann nimmer weiter heimwärts ziehn,
Und Blümlein auf der stillen Heid',
Das hört sein Liebeslied und spricht
Mit leiser Stimm', voll Traurigkeit:
»Ich hab' kein Herz, ich liebe nicht,
Drum fliehe fort, verlasse mich,
Bevor sich naht das Abendbrot –
Denn wagtest du zu freien mich,
Dein erster Kuß wär' auch dein Tod.«

Doch Bienlein war ein junges Blut,
Gar frisch und kühn, voll Lebensmut,
Und küßt' in heißer Liebesglut
Des Blümchens süße Perlenflut. –
Und als der erste Mondenstrahl
Sich durch das düstre Nebelgrau
Der weiten stillen Heide stahl, -
Da lag das Bienlein tot im Tau.

Anton Kerner von Marilaun,
deutscher Naturforscher, 1908

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Inhalt

Zusammenfassung (dt. Abstract)

Der rundblättrige Sonnentau (*Drosera rotundifolia* L.) ist typisch für nährstoffarme Hochmoore und nimmt eine besondere Rolle im Moor-Ökosystem ein. Die Pflanzenart gilt in vielen europäischen Ländern als gefährdet bzw. stark gefährdet. Ihre Gefährdung lässt sich auf drei Ursachen zurückführen:

1) Seit Jahrzehnten führt die Bewirtschaftung der europäischen Moore und die damit einhergehende Entwässerung und Düngung zu einem deutlichen Rückgang der von *Drosera*-Arten bevorzugten oligotrophen, nassen und sauren Standorte.
2) Bereits im Mittelalter waren *Drosera*-Arten als Heilpflanzen bekannt und wurden hauptsächlich zur Behandlung von Atemwegserkrankungen (Asthma, Bronchitis, Keuchhusten etc.) eingesetzt.
3) Obwohl seit den 1920er Jahren bereits immer wieder Kultivierungsversuche mit *Drosera*-Arten durchgeführt wurden, konnte bisher keine Methode für den großflächigen Anbau von Sonnentau realisiert werden, um die von der Pharmaindustrie benötigten Mengen des *Drosera*-Rohstoffs zu produzieren. Daher werden bis heute europäische und nicht europäische *Drosera*-Arten immer noch in großen Mengen in natürlichen Mooren gesammelt.

Die zunehmende Zerstörung der natürlichen Moore und die Sammlung für arzneiliche Zwecke stellen zusammen eine ernsthafte Bedrohung für den Erhalt von *D. rotundifolia* dar. Die Torfmooskultivierungsflächen in Deutschland sind in vieler Hinsicht vergleichbar mit intakten Hochmooren. Das nährstoffarme Milieu der kultivierten Torfmoose dient als Lebensraum für heimische *Drosera*-Arten, wie *Drosera rotundifolia* L. und *Drosera intermedia* Hayne. Daher bieten diese Kulturflächen eine neue Alternative für den Anbau von *Drosera*-Arten.

In vier Studien wurde die Eignung von Torfmoosrasen für den *Drosera*-Anbau untersucht, mit Schwerpunkt auf den Anbau von *Drosera rotundifolia* auf Torfmooskultivierungsflächen. In der ersten Studie wurde das Wissen über die Morphologie, Verbreitung, Ökologie, Reproduktion, Nutzung, den Schutz und den Anbau von *D. rotundifolia* erstmals zusammenfassend diskutiert, um eine wissenschaftliche Grundlage für einen erfolgreichen Anbau auf Torfmoosrasen zu schaffen. Basierend auf diesen Kenntnissen konzentriert sich die zweite Studie auf die Keimfähigkeit von *D. rotundifolia* und die Überlebensrate von jungen *Drosera*-Pflanzen auf Torfmoosrasen unter natürlichen, naturnahen und künstlichen Bedingungen. Die dritte Studie fokussiert auf den Gehalt pharmakologisch wirksamer Inhaltsstoffe angebauter und „wild wachsender" *D. rotundifolia*- sowie *D. intermedia*-Pflanzen auf Torfmooskultivierungsflächen. Die vierte Studie untersucht die Biomasseproduktivität und den Ertrag, d. h. den Biomasseanteil der geerntet wird, von beiden o. g. *Drosera*-Arten auf Torfmooskultivierungsflächen.

Die generierten Daten und Erkenntnisse der vier Studien wurden in vier wissenschaftlichen Artikeln zusammengefasst, wovon zwei bereits veröffentlicht und zwei eingereicht sind.

Die wichtigsten Ergebnisse dieser Studien sind die Folgenden:

i) *Drosera rotundifolia* ist sehr stark mit *Sphagnum*-dominierten Pflanzengemeinschaften verbunden, welche durch Entwässerung europaweit zurückgegangen bzw. verschwunden sind. Dadurch ist *D. rotundifolia* in den meisten europäischen Ländern eine seltene und geschützte Pflanzenart geworden.
ii) Verschiedene *Drosera*-Arten, u. a. *D. rotundifolia*, *D. intermedia*, *D. anglica* und *D. madagascariensis*, werden immer noch von Pharmaunternehmen verwendet. Die Pflanzen werden in der freien Natur gesammelt, weil deren Anbau zeitaufwendig und (noch) nicht effizient ist. Daher ist die Entwicklung von Anbaumethoden erforderlich.
iii) Die selbstentwickelte „Torf-Gefäß-Methode" ergab sich als die meist geeignete *Drosera*-Anbau-Methode durch das spezielle Mikroklima des *Sphagnum*-Rasens, das konkurrenzarme Milieu und den permanent nassen *Sphagnum*-Torf in den Pflanzgefäßen.
iv) In den Feldversuchen wurden bei der Aussaat sehr niedrige Keimungsraten < 1 % registriert. Deshalb sind für den Anbau mit Aussaat große Mengen an Samen erforderlich.
v) Die Entfernung von Gefäßpflanzen zeigte im ersten Jahr eine positive Korrelation mit der Anzahl der *Drosera*-Keimlinge und führte im zweiten Jahr zu einer höheren Anzahl überlebender *Drosera*-Pflanzen.
vi) Auf Torfmooskultivierungsflächen wachsende *Drosera-rotundifolia*-Pflanzen wiesen eine 7- bis 8-mal höhere Konzentration von 7-Methyljuglon auf als *D. madagascariensis*, die hauptsächlich für 'Droserae herba' verwendet wird.
vii) Für *Drosera rotundifolia* gab es bezüglich der Tageszeit keine signifikanten Unterschiede in den Konzentrationen bioaktiver Inhaltsstoffe. Dies bedeutet, sie kann ganztägig zwischen 7 und 16 Uhr gesammelt werden. Die höchsten Konzentrationen bioaktiver Inhaltsstoffe wurden für *D. rotundifolia* und *D. intermedia* bei 13 bis 24 Monate alten blühenden Pflanzen festgestellt
viii) Im Vergleich zu natürlichen Mooren Mittel- und Nordeuropas, zeigte *D. rotundifolia* auf den Torfmooskultivierungsflächen eine 3-34 Mal höhere Biomasseproduktivität (275 kg ha^{-1} a^{-1}) und einen 2-21 Mal höheren Ertrag (214 kg ha^{-1} a^{-1}).
ix) Der höchste Ertrag von *D. rotundifolia* und *D. intermedia* wurde im Juli und August dokumentiert. In diesen Monaten erreichen die Pflanzen ihr höchstes Gewicht. Auf Torfmooskultivierungsflächen erreichte *D. rotundifolia* einen viermal höheren Ertrag als *D. intermedia*. Deshalb ist *D. rotundifolia* für den Anbau zu bevorzugen.
x) Für eine langfristige nachhaltige Produktion von *Drosera* wird die Ernte von mindestens 12 Monate alten Pflanzen empfohlen.

Abstract

The round-leaved sundew (*Drosera rotundifolia* L.) is typical for nutrient-poor raised bogs and plays a special role in the ecosystem. In many European countries, this plant species is considered endangered or highly endangered. This can be attributed to three causes:

1) For decades the management and therewith drainage and fertilization of European peatlands have led to a significant decline of wet, oligotrophic and acidic habitats, which are favoured by *Drosera* species.
2) Already in the Middle Ages, *Drosera* species were used as medicinal plants mainly for the treatment of respiratory diseases (asthma, bronchitis, whooping cough etc.).
3) Cultivation experiments with *Drosera* species have been conducted since 1920. Nevertheless, no method for the large-scale cultivation of sundew has yet been realized to produce the quantities of the *Drosera* raw material required by the pharmaceutical industry. Therefore, large quantities of European and non-European *Drosera* species are still being collected in natural peatlands.

The increasing destruction of the natural bogs and the collection for medicinal purposes together pose a serious threat to the conservation of *D. rotundifolia*. *Sphagnum* farming areas in Germany are in many respects comparable to intact raised bogs, and the nutrient-poor environment of the cultivated *Sphagnum* serves as a habitat for native *Drosera* species, such as *Drosera rotundifolia* L. and *Drosera intermedia* Hayne. Therefore, these cultivated areas offer a new alternative for the cultivation of *Drosera* species.

The suitability of *Sphagnum* lawn for *Drosera* cultivation was investigated in four studies, with a focus on the cultivation of *Drosera rotundifolia* in *Sphagnum* farming areas.In the first study, the available knowledge on the morphology, distribution, ecology, reproduction, use, protection and cultivation of *D. rotundifolia* is comprehensibly discussed to provide a scientific basis for the successful cultivation on *Sphagnum* lawn. Based on this knowledge, the second study focuses on the germination rate of *D. rotundifolia* and the survival rate of young *Drosera* plants on *Sphagnum* lawn under natural, near-natural and artificial conditions. The third study focuses on the content of pharmacologically active substances in cultivated and wild growing *D. rotundifolia* and in *D. intermedia* plants from *Sphagnum* farming areas. The fourth study investigates biomass productivity and yield of both above-mentioned *Drosera* species on *Sphagnum* farming areas.

The generated data and findings of the four studies were summarized in four scientific articles, two of which have already been published and two of which have been submitted.

The main results of these studies are as follows:

i) *Drosera rotundifolia* is strongly associated with *Sphagnum*-dominated plant communities, which have declined or disappeared throughout Europe due to drainage. As a result *D. rotundifolia* has become a rare and protected plant species in most European countries.
ii) Several *Drosera* species, including *D. rotundifolia*, *D. intermedia*, *D. anglica* and *D. madagascariensis*, are still used by pharmaceutical companies. The plants are collected in natural peatlands, because their cultivation is time-consuming and not (yet) efficient. Therefore, the development of cultivation methods is necessary.
iii) The self-developed „peat pot method" turned out to be the most suitable *Drosera* cultivation method because of the special microclimate of the *Sphagnum* lawn, the low-competitive environment and the permanently wet *Sphagnum* peat in the plant pots.
iv) In the field with sowing very low germination rates < 1 % were recorded. Therefore large quantities of seeds are required for cultivation with sowing.
v) The removal of vascular plants showed a positive correlation with the number of *Drosera* seedlings in the first year and led to a higher number of surviving *Drosera* plants in the second year.
vi) *D. rotundifolia* plants growing in the *Sphagnum* farming area showed a 7 to 8 times higher concentration of 7-methyljuglon than *D. madagascariensis*, which is mainly used for ‚Droserae herba'.
vii) With respect to the daytime there were no significant differences in the concentrations of bioactive constituents in *Drosera rotundifolia*. This means that the material can be collected throughout the day between 7 and 16 o'clock. The highest concentrations of bioactive ingredients of *D. rotundifolia* and *D. intermedia* were found in 13 to 24 month old flowering plants.
viii) Compared to natural bogs of Central and Northern Europe, biomass productivity of *D. rotundifolia* on *Sphagnum* farming areas was 3-34 times higher (275 kg ha^{-1} yr^{-1}) and the harvestable yield 2-21 times higher (214 ha^{-1} yr^{-1}).
ix) The highest yield of *D. rotundifolia* and *D. intermedia* was documented in July and August. In these months, the plants reach their highest weight. On *Sphagnum* farming areas *D. rotundifolia* yields were 4 times higher than for *D. intermedia*. *D. rotundifolia* should therefore be preferred for cultivation.
x) For a long-term sustainable production of *Drosera*, harvesting of plants older than 12 months old is recommended.

Autorenbeiträge zu jedem Kapitel

Die vorliegende Dissertation besteht aus zwei veröffentlichten und zwei eingereichten Manuskripten (Kapitel 2-5), denen das Kapitel 1 mit allgemeiner Einführung, einem Überblick der Hauptergebnisse und einer Abschlussdiskussion vorausgeht.

Kapitel 1 Einführung, Methoden, Ergebnisse, Diskussion und Ausblick. – B. Baranyai hat dieses Kapitel komplett selbst geschrieben.

Kapitel 2 Baranyai, B. & Joosten, H. (2016) Biology, ecology, use, conservation and cultivation of round-leaved sundew (*Drosera rotundifolia* L.): a review. Mires and Peat, Vol. 18 Art. 18, S. 1–28. – Das Manuskript wurde in erster Linie durch B. Baranyai mit erheblichen Beiträgen von H. Joosten geschrieben.

Kapitel 3 Baranyai, B., Krebs, M., Oehmke, C., Joosten, H. (eingereicht, 01/2020). Germination and seedling survival of *Drosera rotundifolia* L. cultivated on *Sphagnum*: Influence of cultivation method, seed density, *Sphagnum* species and vascular plant cover. Mires and Peat. – B. Baranyai führte die Keimungsversuche inklusive der Datenaufnahme von *Drosera rotundifolia* im Freiland (Deutschland, Ungarn) und im Gewächshaus (Deutschland) durch. Das Datenmanagement und die statistische Auswertung wurden gemeinsam von B. Baranyai und M.Krebs realisiert. Das Manuskript wurde in erster Linie durch B. Baranyai mit erheblichen Beiträgen von M. Krebs, C. Oehmke und H. Joosten geschrieben.

Kapitel 4 Baranyai, B., Bäcker, C., Reich, C., Lindequist, U. (2016) The production of 7-methyljuglone, plumbagin and quercetin in wild and cultivated *Drosera rotundifolia* and *Drosera intermedia*. Mires and Peat, Vol. 18 Art. 19, S. 1–8. – B. Baranyai sammelte die Sonnentau-Proben aus dem Freiland und stellte sie für die Analyse bereit. B. Baranyai und C.Bäcker führten die HPLC-Analysen mit Hilfe von C. Reich durch. C. Bäcker und C. Reich werteten die Daten aus. B. Baranyai und C. Bäcker schrieben die erste Fassung des Manuskripts, alle Autoren lasen und editierten den Text.

Kapitel 5 Baranyai, B., Krebs, M., Oehmke, C., Joosten, H. (eingereicht, 03/2020). Biomass productivity and yield of *Drosera* on cultivated *Sphagnum* in NW Germany. Mires and Peat. – B. Baranyai sammelte die *Drosera* Pflanzen. Alle Pflanzendaten wurden von B. Baranyai aufgenommen. Das Datenmanagement und die statistische Auswertung wurden gemeinsam von B. Baranyai und M. Krebs vorgenommen. Das Manuskript wurde in erster Linie durch B. Baranyai mit erheblichen Beiträgen von M. Krebs, C. Oehmke und H. Joosten geschrieben.

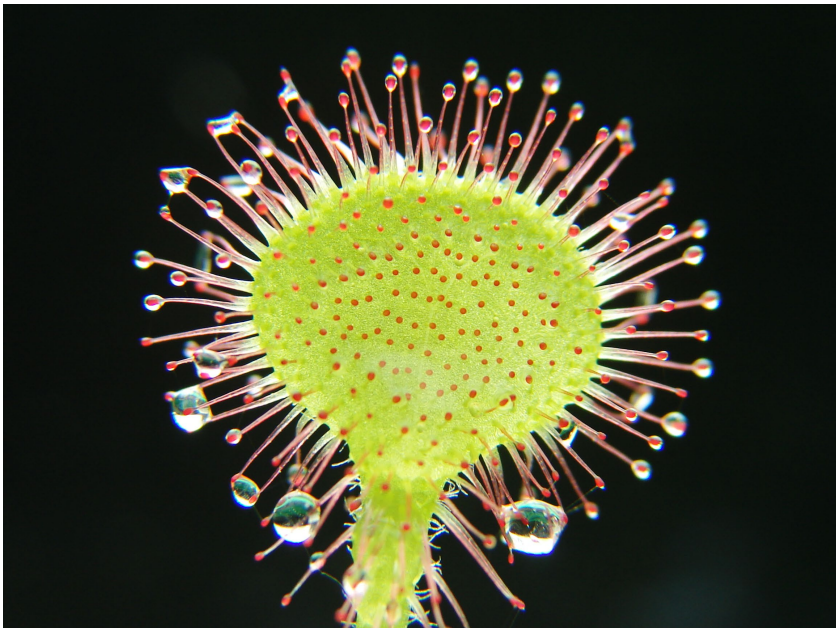
Balázs Baranyai - Ich bestätige die Autorenbeitragsangaben.

Greifswald, _____

(Datum) Prof. Dr. Dr. h.c. Hans Joosten

1
Einführung, Methoden, Ergebnisse, Diskussion und Ausblick

Balázs Baranyai



1.1 Problemdarstellung und Begründung der Studie

Die Arzneidroge 'Droserae herba' (Sonnentaukraut) wird schon seit langem erfolgreich in der Therapie von Hustenerkrankungen (u. a. Reizhusten, Asthma oder Bronchitis) eingesetzt (Cygan 1989, Frohne 1994). Heutzutage werden *Drosera*-Pflanzen in frischem oder getrocknetem Zustand für 'Droserae herba' aufgearbeitet (Šamaj *et al.* 1999, Babula *et al.* 2009) und in 200-300 registrierten Arzneimitteln in Europa verwendet, zumeist in Hustenmitteln (MacKinnon 2009). Weiterhin werden in der Pharmaindustrie homöopathische Auszüge von *Drosera*-Pflanzen als Homöopathikum »Drosera« genutzt (Metzger 1951).

Als Stammpflanze für 'Droserae herba' diente ursprünglich nur *Drosera rotundifolia* L. (Schier & Schultze 1987). Jedoch mit dem Rückgang ihres Vorkommens auf natürlichen Moorstandorten wurden zunehmend andere heimische *Drosera*-Arten (*D. intermedia* HAYNE, *D. longifolia* L. [= *D. anglica* HUDS.]) für arzneiliche Zwecke gesammelt (Melzig *et al.* 2001, Hiller & Loew 2009). In Folge der Zerstörung der natürlichen Lebensräume (Hochmoore, Zwischenmoore bzw. sauer-arme Niedermoore) und der intensiven Sammlung für arzneiliche Zwecke, sind diese *Drosera*-Arten in einigen europäischen Ländern seit den 1980er Jahren unter Schutz gestellt (**Kapitel 2**).

Die natürliche Knappheit und die erschwerte, rechtlich zulässige Beschaffung von *Drosera*-Rohstoff zwang die Pharmaindustrie, sich auf Herkunftsregionen zu konzentrieren, wo noch ausreichend Lebensräume vorhanden sind und eine Wildsammlung der *Drosera*-Arten möglich ist (Lange 1998, TRAFFIC 2002), d. h. auf Finnland (für *Drosera rotundifolia*) und Ost-Afrika und Madagaskar (für *Drosera madagascariensis*). Diese Länder exportierten in den letzten Jahren die größten Mengen an *Drosera*-Rohstoff (**Kapitel 2**). Jedoch haben die außereuropäischen *Drosera*-Arten sehr geringere Konzentrationen der wertvollen bioaktiven Inhaltsstoffe (Krenn *et al.* 1995, 1998).

Die zunehmenden Schwierigkeiten bei der Beschaffung von qualitativ hochwertigem *Drosera*-Rohstoff haben in den letzten Jahrzehnten zu unterschiedlichen Kultivierungs- und Anbauexperimenten geführt (Šamaj *et al.* 1999, Krenn & Kartnig 2005, Banasiuk *et al.* 2012). So wurden Anbauversuche in Gewächshäusern, unter naturnahen Bedingungen im Freiland auf Torf, oder in-vitro unter sterilen Laborbedingungen durchgeführt (Wawrosch *et al.* 1996, Galambosi *el al.* 1998, 2000a, Bruzzese *et al.* 2010, Galambosi & Galambosi 2013). Trotz erfolgreicher Versuche und funktionierender Methoden existierte bis vor kurzem keine *Drosera*-Anbaufläche in Europa (**Kapitel 2**). Die Ursache hierfür liegt vor allem in hohen Qualitätsansprüchen der Pharmaindustrie. Sie fordert, dass die Anzucht der *Drosera*-Pflanzen aus Samen (generativ) auf Torf geschieht (Westphal 2016), keine chemische Behandlung oder Düngung stattfinden (Länger & Schiller, 2004, HAB 2014) und die Pflanzen Mindestkonzentrationen von bioaktiven Inhaltsstoffen enthalten (z.B.: für Naphthochinon-Derivate 0,14-0,22 %, Wichtl 2009). Ein weiteres Hindernis ist, dass die bisher getesteten Vermehrungs- und Anbaumethoden sehr zeit- und kostenaufwendig sind (Baranyai 2016).

Seit 2004 erforscht die Universität Greifswald in zahlreichen Projekten die Kultivierung von Torfmoosen auf degradierten Hochmoorstandorten (Krebs *et al.* 2012), im Rahmen eines landwirtschaftlichen Konzepts zur Biomasseproduktion auf

nassen und wiedervernässten Moorböden bei gleichzeitigem Torferhalt: der Paludikultur (palus = lat. „Sumpf, Morast“) (Wichtmann *et al.* 2016). Auf der im Frühjahr 2011 eingerichteten, 4 ha großen Torfmooskultivierungsfläche des „MOOSGRÜN“-Projektes („Torfmooskultivierung auf Hochmoorgrünland“) im Hankhauser Moor (Niedersachsen) gedeihen neben *Sphagnum*-Arten spontan auch konkurrenzschwache Pflanzenarten, wie *Drosera rotundifolia*, *D. intermedia* und *Erica tetralix* (**Kapitel 2 und 5**, Gaudig & Krebs 2016). Durch diese Beobachtung, ergab sich die Frage, ob die *Drosera*-Arten auf vitalem *Sphagnum*-Rasen erfolgreich kultiviert werden könnten. Dies wurde bisher nicht untersucht.

1.2 Zielsetzung und Fragestellung

Ziel des Promotionsvorhabens war es, eine erfolgreiche, nachhaltige *Drosera*-Anbaumethode auf Torfmooskulturen zu entwickeln.

Dazu ergaben sich unterschiedliche wissenschaftliche Fragestellungen, u.a. ob sich Torfmoosrasen verschiedener *Sphagnum*-Arten für den Anbau von *Drosera*-Arten (mit dem Schwerpunkt auf *Drosera rotundifolia* und *D. intermedia*) eignen und ob die angebauten *Drosera-rotundifolia*-Pflanzen die pharmakologisch wirksamen Inhaltsstoffe (7-Methyljuglon, Plumbagin) in ausreichender Konzentration enthalten und den Qualitätsansprüchen der verarbeitenden Industrie genügen. Es sollte weiterhin das Biomassepotential von *Drosera* auf Torfmooskulturen abgeschätzt werden, in dem die Produktivität bzw. Erträge der dort vorkommenden Populationen untersucht wurden.

Die Kombination von Torfmooskultivierung und *Drosera*-Anbau in Paludikultur könnte Landnutzern eine alternative und nachhaltige Bewirtschaftungsmöglichkeit bieten, die auch die Ziele des Moorschutzes berücksichtigt und eine Annäherung zwischen landwirtschaftlicher Nutzung und Artenschutz auf bisher entwässerten Moorböden ermöglicht. Die nachfolgenden Forschungsfragen wurden angegangen:

1. Welche Umweltbedingungen sind für die Vermehrung von *Drosera* optimal? Welche Erkenntnisse wurden bisher zum *Drosera*-Anbau erhoben?
2. Welche neuen Pflanz- bzw. Aussaatmethoden können für den kommerziellen und nachhaltigen *Drosera*-Anbau auf Torfmoosrasen entwickelt werden? Wie beeinflussen verschiedene *Sphagnum*-Arten und konkurrierende Gefäßpflanzen die Keimungsdauer und das Wachstum der *Drosera-rotundifolia*-Pflanzen?
3. Können die *Drosera*-Pflanzen auf Torfmoosen die Anforderungen der Pharmaindustrie, hinsichtlich bioaktiver Inhaltsstoffe, erfüllen? Durch welche Faktoren wird der Wirkstoffgehalt von *Drosera* beeinflusst z.B. Erntezeit (Monat) und Tageszeit, bzw. Alter der Pflanze etc.?
4. Sind *Drosera*-Arten auf Torfmooskultivierungsflächen im Vergleich zu natürlichen Standorten produktiver? Bei welcher Erntezeit und welchem Lebensalter werden die höchste Produktivität als auch die höchsten Erträge von *D. rotundifolia* und *D. intermedia* auf Torfmooskultivierungsflächen erreicht? Wie kann eine nachhaltige Ernte von *Drosera*-Arten in Torfmooskultivierungsflächen erfolgen und langfristig hohe Erträge gesichert werden?

1.3 Wissenschaftlicher Hintergrund und Stand der Forschung

Drosera rotundifolia - der rundblättrige Sonnentau

Der rundblättrige Sonnentau (*Drosera rotundifolia* L.) ist eine insektenfressende Pflanzenart und gehört zu der Familie der Sonnentaugewächse (Droseraceae). Die einzelne Pflanze hat eine typische Größe von 5 bis 20 cm und ein Gewicht von ≤ 1 g (**Kapitel 5**, Király *et al.* 2011). Wegen seines Vorkommens in fast allen Regionen der Holarktis ist sie wahrscheinlich die am häufigsten verbreitete insektenfressende Pflanzenart weltweit (**Kapitel 2**). In den kontinentalen, ozeanischen und subozeanischen Regionen Europas ist die Art an nasse und oligotrophe Standorte gebunden (Hegi 1961, Rameau *et al.* 2008, Rodondi *et al.* 2010). Bevorzugt wächst sie auf sehr sauren, nährstoffarmen Torfböden, selten auf nähstoffarmem, humosem oder torfhaltigem, nassen Sand (Auster & Schafer 1957, Swales 1975). Der pH-Wert des Bodens übersteigt selten einen Wert von 5,0 (**Kapitel 2**). Ökologisch betrachtet ist *D. rotundifolia* eine konkurrenzschwache Moorpflanzenart, welche offene, sonnige Stellen, mit gleichmäßiger und dauerhafter Feuchtigkeit benötigt (Diels 1906, Geißler 1987, Crowder *et al.* 1990).

In Mitteleuropa tritt die Art überwiegend in zwei pflanzensoziologischen Klassen auf: in der Oxycocco-Sphagnetea Br.-Bl. und R. Tx. ex Westh. *et al.* 46 und in der Scheuchzerio-Caricetea fuscae Tx. 37 (**Kapitel 2**). In diesen Klassen kommt sie insbesondere gemeinsam mit *Sphagnum*-Arten vor. Eine Illustration der engen Vergesellschaftung mit *Sphagnum,* ist die Auflistung von 26 *Sphagnum*-Arten mit denen *Drosera rotundifolia* in 14 Ländern assoziiert ist (**Kapitel 2**).

Drosera rotundifolia ist als einzige der drei heimischen *Drosera*-Arten in der Lage mit dem jährlichen Höhenwachstum der raschwüchsigen *Sphagnum*-Arten mitzuhalten (Hegi 1923). Am Ende der Vegetationsperiode bildet die Pflanze eine achselbürtige Endknospe (Winterknospe), die von niederblattähnlichen Hüllblättern umschlossen ist (Siegfried *et al.* 1971, Ruprecht & Kutzelnigg 2011). Zu Beginn der neuen Vegetationszeit treibt die Winterknospe einen mit Schuppenblättern besetzten Spross nach oben bis die Oberfläche des Torfmoospolsters wieder erreicht wird, worauf die neue Blattrosette entsteht (Ruhland 1959).

Die natürliche Reproduktion der einheimischen *Drosera*-Arten, unter anderem bei *D. rotundifolia*, findet sowohl über eine asexuelle Vermehrung (vegetativ), als auch mittels sexueller Vermehrung (generativ) statt (Murza & Davis 2003, Hoyo & Tsuyuzaki 2015). Die generative Reproduktion via Samen ist allerdings die dominierende Reproduktionsmethode (**Kapitel 2**).

Drosera rotundifolia blüht im Mittsommer, zwischen Juni und August (Király *et al.* 2011, Bäumler 2012), in den Höhenlagen auch im Mai oder Oktober (Crowder *et al.* 1990, Strid & Tan 2002).

Abhängig vom Standort produziert die Pflanze eine unterschiedliche Anzahl an Samenkapseln und unterschiedliche Samenmengen pro Kapsel (**Kapitel 2 und 3**). Nach 5 bis 7 Wochen sind die Pflanzensamen einer Kapsel reif und verbreiten sich anemochor, zooochor oder hydrochor (Swales 1975, Phillips 1985, Crowder *et al.* 1990, Wolf *et al.* 2006). Nach Kinzel (1913) sind die einheimischen *Drosera*-Arten ausgesprochene Lichtfrostkeimer. Das Keimen des Samens erfolgt nur bei

Lichtzutritt und nach natürlicher Stratifikation (Schulz 1965, Braem 2002). Auf *Sphagnum* keimen *D. rotundifolia* Samen besonders effektiv (Rydin & Jeglum 2013). Dennoch eine rasche Abnahme der Keimfähigkeit kann sich ergeben, wenn die Samen durch Wasser (z.B. Regenwasser, Bewässerung) in den *Sphagnum*-Rasen eingewaschen werden und mit zunehmender Versenkungstiefe die Lichtverfügbarkeit abnimmt (**Kapitel 2**).

Sammlung als Arzneipflanze

In Europa werden die frischen und zu Beginn der Blüte gesammelten ganzen *Drosera*-Pflanzen, inklusive Wurzeln (*Planta tota recens, cum florere inciperet, collecta*) als Rohstoff für die Pharmaindustrie verwendet (**Kapitel 2**, Voegele, A. und Raiser, M., persönliche Mitteilung). Ursprünglich wurde als Stammpflanze für 'Droserae herba' (Sonnentaukraut) nur *D. rotundifolia* L. zugelassen, aber nach dem zweiten Weltkrieg wurden, auch die anderen heimischen Arten *D. anglica* HUDS. und *D. intermedia* HAYNE zunehmend verwendet (DAB 1953, Schier & Schultze 1987).

Aufgrund der starken Einschränkung des Lebensraumes europäischer *Drosera*-Arten durch die Trockenlegung der Moorgebiete kam es zum Rückgang der Populationen, in deren Folge die Arten unter Schutz gestellt wurden. Dies führte zu Engpässen bei der Belieferung von Pharmaunternehmen. Deshalb wurden in verschiedenen pharmakologischen Monografien auch außereuropäische, wie afrikanische und asiatische *Drosera*-Arten, zugelassen (**Kapitel 2**, Krenn & Kartnig 2005).

Auf dem europäischen Markt werden schätzungsweise 6 bis 20 t *Drosera*-Rohstoff aus natürlichen Ressourcen pro Jahr gehandelt (Galambosi 2002). Davon ist der größte Teil *D. madagascariensis* DC. mit ca. 2 bis 20 t, welche in natürlichen Mooren Madagaskars raubabgebaut werden. Der restliche Anteil von ca. 1 bis 3 t ist *D. rotundifolia* und wird aus finnischen Mooren gesammelt (**Kapitel 2**, Galambosi & Jokela 2002). Die außereuropäischen *Drosera*-Arten, wie *D. madagascariensis* oder *D. peltata* weisen jedoch eine wesentlich geringere Konzentration bioaktiver Inhaltsstoffe als *D. rotundifolia* auf (**Kapitel 4**, Krenn *et al.* 1995). Deshalb wird auf dem europäischen Kräutermarkt bis heute bevorzugt *D. rotundifolia* von natürlichen Moorstandorten gehandelt (**Kapitel 2 und 4**)[1].

Erhalt und Schutzstatus

Die Zerstörung der Lebensräume der *Drosera*-Arten führte zu einem starken Rückgang der natürlichen *Drosera*-Populationen (**Kapitel 2 und 4**). Demzufolge gelten sie in einigen europäischen Ländern, als gefährdete, im Bestand verletzliche oder seltene Pflanzenarten (Lange 1998, Khela 2012).
In Ungarn gilt *D. rotundifolia* als gefährdet (Király 2007), in Kroatien als stark gefährdet (Nikolic & Topic 2005). In Deutschland wurden alle heimischen

1 *Bemerkung des Autors: Die geringere Inhaltsstoffkonzentrationen dieser Pflanzen führt zu größeren Erntemengen und damit zu einer zusätzlichen Gefährdung ihrer natürlichen Populationen. Dadurch werden sowohl die Nachhaltigkeit, als auch das Gestatten von Wildsammlungen auf lange Sicht in Frage gestellt.*

Drosera-Arten auf Grund der starken Einschränkung ihres Lebensraums auf die „Rote Liste" gesetzt: *Drosera longifolia* als stark gefährdet, und *D. intermedia* sowie *D. rotundifolia* als gefährdet (Ludwig & Schnittler 1996). Alle *Drosera*-Arten sind durch das Bundesnaturschutzgesetz (BNatSchG 2009) besonders geschützt. Wilde Populationen sind nach der Bundesartenschutzverordnung (BArtSchV 2005) ebenfalls geschützt. Zudem besteht z.B. in Deutschland ein gesetzliches Sammelverbot (Frohn 2010). Derzeit ist in Europa die Sammlung von *Drosera*-Arten nur in Finnland unter Sonderbedingungen gestattet (**Kapitel 2**, Galambosi *et al.* 2000b). Im Falle eines landwirtschaftlichen Anbaus von *Drosera* in Deutschland wird die Art als medizinische Nutzpflanze behandelt, und mit ihrer Herkunft aus dem „Anbau" unterliegt sie nicht mehr dem Naturschutz. Trotzdem muss bei örtlichen Behörden eine Sondergenehmigung zum Anbau, zum Sammeln und zur Vermarktung einer geschützten Pflanzenart erfolgen.

1.4 Alternative Anbaumethoden für Sonnentau und deren Probleme

Die ersten Kultivierungsexperimente mit *Drosera*-Arten (Himmelbaur 1926, Velenovský 1928, Rudolf 1938) wurden wegen der Übersammlung der Pflanze durchgeführt. Grund war eine erhöhte Nachfrage nach 'Droserae herba' Anfang des 20. Jahrhunderts. Diese Anbauversuche konzertierten sich allerdings nur auf in-situ-Versuche, genauer, auf blankem Torf der natürlichen Moorstandorte von *D. rotundifolia* (**Kapitel 2**).

Seit der zweiten Hälfte des 20. Jahrhunderts befassen sich mehrere Forschungsinstitute mit der Ausarbeitung von Vermehrungs- und Anbaumethoden europäischer und außereuropäischer *Drosera*-Arten für medizinische Zwecke (**Kapitel 2**). Eine dieser Methoden ist die in-vitro-Vermehrung, womit man innerhalb kurzer Zeit große Mengen genetisch einheitlicher Pflanzen gewinnen kann (Krenn & Kartnig 2005). Bisher wurde für 21 *Drosera*-Arten eine in-vitro-Vermehrung erforscht (Reichling *et al.* 1995, Šamaj *et al.* 1999, Kim & Jang 2004, Jayaram & Prasad 2008, Thaweesak *et al.* 2011, Banasiuk *et al.* 2012, Taraszkiewicz *et al.* 2012). Im Vergleich zu anderen Pflanzenarten kann man die *Drosera*-Arten sehr gut mit dieser Methode vermehren und gleichzeitig eine hohe Vermehrungsrate erzielen (Wawrosch, C., persönliche Mitteilung). Für die Pharmaindustrie ist die in-vitro-Vermehrung aus ökonomischer und ökologischer Sicht jedoch uninteressant, z.B. da die Pflanzen künstlich mit Nährstoffen versorgt werden und genetisch identisch sind (Krenn & Kartnig 2005, Krenn, L., persönliche Mitteilung).

Seit den 1950er Jahren wurden mit *D. rotundifolia* und *D. anglica* Kulturversuche unter Gewächshaus- und Freilandbedingungen durchgeführt. Für eine erfolgreiche *Drosera*-Kultur im Gewächshaus ist eine gleichbleibende Temperatur, Luftfeuchte, Beschattung und Belüftung notwendig (Braem 2002). Eine konsequente Sicherung dieser Bedingungen erhöht allerdings den Kostenaufwand (Baranyai 2013).

Bisher wurden nur wenig detaillierte Studien bezüglich Freilandanbau von *D. rotundifolia* veröffentlicht (**Kapitel 2**). Jopke (1954) berichtet über einen Anbauversuch in einem ehemaligen Torfstich. Er erreichte hohe Erträge (genaue Zahlen sind nicht angegeben). Ebenso erzielte Galambosi *et al.* (2000a) in Finnland hohe

Erträge mit *D. rotundifolia* und *D. anglica* in ungedüngten Torfbeeten im Freiland. Hierbei wurden, anders als bei bisherigen Versuchen, die Pflanzen mit proteinhaltigen Substanzen (z.B. Mückenlarven, Milchpulver) per Hand „gefüttert", was einen positiven Effekt bezüglich Wachstum, Lebenszyklus der Pflanzen, Gewicht und Ertrag erzeugte (Galambosi *et al.* 1998, 1999).

In den meisten Anbauversuchen gab es jedoch „schwerwiegende Probleme" mit konkurrierenden Pflanzenarten *Polytrichum*, *Epilobium*, *Juncus*, *Carex* und Keimlingen von *Betula* bzw. *Pinus sylvestris* (z.B. Jopke 1954, Galambosi 2002), die die Produktivität von *Drosera* negativ beeinflussen. Jopke (1954) konnte nur hohe Erträge erzielen, wenn er diese vollständig entfernte. Galambosi *et al.* (2000a) berichtete sogar, dass *Drosera*-Jungpflanzen durch die gezielte Entfernung von begleitenden Arten beschädigt werden können.

Galambosi (2002) beobachtete ein weiteres Problem: in *Drosera*-Kulturen mit einer starken Pflanzendichte wurden durch die Entnahme erntereifer Exemplare, die restlichen, noch nicht erntereifen Jungpflanzen und nicht blühende Pflanzen beschädigt, was einen geringeren Ertrag für das kommende Jahr zur Folge hatte. Allerdings besteht laut B. Galambosi (persönliche Mitteilung) seitens der Pharmaindustrie kein Interesse an *Drosera*-Pflanzen, die, wie oben beschrieben, künstlich ernährt werden. Der Rohstoffbedarf der Arzneimittelhersteller in Deutschland wird bisher nur durch Importe aus Wildsammlungen gedeckt (**Kapitel 2 und 4**).

Zusammenfassend sind drei Gründe ausschlaggebend, warum es bisher noch keinen großflächigen kommerziellen *Drosera*-Anbau gab (**Kapitel 2**, Baranyai 2016):

1. die anspruchsvollen ökologischen und technischen Anforderungen der *Drosera*- Arten,
2. der hohe Zeit- und Kostenaufwand um die *Drosera*-Kulturen in Stand zu halten,
3. die ausreichende Verfügbarkeit von *Drosera*-Rohstoff durch Importe von außer-europäischen *Drosera*-Arten aus Wildsammlungen.

1.5 Methoden

Literaturrecherche & Grundlagen

Um eine gute Datengrundlage für die Studie zu erlangen, wurde die Arbeit mit einer umfassenden Literaturrecherche und dem Aneignen von „Know How" über den Anbau von *Drosera*-Arten begonnen. Es wurde Kontakt mit insgesamt 67 Drogengroßhändlern und Arzneimittelherstellern sowie 27 Forschenden verschiedener Universitäten und Botanischer Gärten aus sieben verschiedenen Ländern (A, CH, D, FIN, HU, RUS, S) aufgenommen, und diese um Rat - in Bezug auf *Drosera*-Anbau und 'Droserae herba' - befragt. Während eines Pilotanbau-Versuches (2012/2013) wurde offensichtlich, dass die Literaturrecherche sich nicht nur auf die potenzielle Vermehrung und auf mögliche Anbaumethoden konzentrieren sollte, sondern auch auf die Biologie der Pflanze. Deshalb wurden auch Umweltbedingungen definiert, unter denen die Pflanze *D. rotundifolia* vorkommt und sich natürlicherweise vermehren kann. Erweitert mit Informationen über deren Schutzstatus und

Verwertung als Rohstoff für die Pharmaindustrie wurde ein noch umfassenderes Bild über *D. rotundifolia* mit Informationen aus 264 Fachpublikationen zusammengestellt (**Kapitel 2**).

Anbau & Vermehrung

Die Ergebnisse der Literaturrecherche und die Kommunikation mit Handelsvertretern der Pharmaindustrie zeigten, dass nicht nur an den *Drosera*-Rohstoff, sondern auch an die Anbaumethode hohe Ansprüche gestellt werden. Unter Betrachtung dieser Ansprüche wurde die Eignung von Torfmoosrasen für den Anbau von Sonnentau getestet. Dazu wurden zwei Ausbringungsmethoden mit „Torf-Pads" und „Torf-Gefäßen" eigens entwickelt. *Drosera*-Samen wurden darin, als auch als lose Aussaat in Mischung mit Torfmoospulver, auf *Sphagnum palustre* und *S. papillosum* Torfmoosrasen ausgesät (2013/2014). Im Versuch wurden 150 × 150 cm große Dauerquadrate angelegt (Freiland) bzw. Vermehrungsschalen verwendet (Gewächshaus), auf denen die Torf-Pads und Torf-Gefäße jeweils mit 3, 6 und 9 Samen, und für die Aussaat mit 10, 50 und 100 Samen (per 10 × 10 cm Plots) ausgebracht wurden, je randomisiert in 6 Wiederholungen. Die Versuche wurden an drei Standorten durchgeführt: (1) natürlich: „Fekete-tó" bei Szentgotthárd-Farkasfa (Ungarn), (2) naturnah: Torfmooskultivierungsflächen bei Hankhausen (Deutschland) und (3) künstlich: unter künstlich imitierten Umweltbedingungen im Gewächshaus der Universität Greifswald (Deutschland).

Auf den natürlichen und naturnahen Standorten im Freiland wurde der Einfluss von konkurrierenden Pflanzenarten untersucht, in dem auf jeweils einem Dauerquadrat die Gefäßpflanzen einmal im Monat vollständig entfernt wurden (Dauerquadrat mit Gefäßpflanzen vs. Dauerquadrat ohne Gefäßpflanzen). Auf den drei Standorten (natürlich, naturnah und künstlich) wurden insgesamt 11.136 *D. rotundifolia* Samen ausgebracht: 9.408 Samen per Aussaat und 1.728 Samen in Pflanzgefäßen. Die Keimlinge wurden einzeln registriert und deren Wachstum und Vitalität über einen Zeitraum von zwei Jahren beobachtet und dokumentiert (**Kapitel 3**).

Qualitätsuntersuchungen

Der Anbau von *D. rotundifolia* für arzneiliche Zwecke ist nur dann erfolgreich, wenn die Anforderungen an deren Wirkstoffzusammensetzung und – gehalte erfüllt sind. Daher wurde in Kooperation mit Kollegen aus dem Institut für Pharmazie der Universität Greifswald die Quantität bioaktiver Inhaltsstoffe, 7-Methyljuglon, Plumbagin und Quercetin, ermittelt. Für die Studie wurden angebaute Pflanzen aus dem Pilot-Anbauversuch (*D. rotundifolia*) analysiert, als auch "wilde" Pflanzen, die sich spontan auf der Torfmooskultivierungsfläche ansiedelten (*D. rotundifolia* und *D. intermedia*). Es wurden insgesamt 44 Proben aus beiden *Drosera*-Arten im Juli und im August 2014 in *Sphagnum palustre* und *S. papillosum* auf der Torfmooskultivierungsfläche gesammelt. Um zu bestimmen, in welchem Monat, zu welcher Tageszeit und bei welchem Alter der *Drosera*-Pflanzen die höchsten Inhaltsstoffkonzentrationen auftreten, wurden die Proben am Vormittag (7:00–8:00) und am Nachmittag (15:00–16:00) am gleichen Tag gesammelt, und drei Altersklassen (≤ 6, 6–12 und 13–24 Monate alt) zugeordnet (**Kapitel 4**).

Produktivität und Ertrag

Um die Eignung des Lebensraums Torfmooskultivierungsfläche für *Drosera*-Anbau zu untersuchen wurden 46 Quadrate (1 × 1 m) auf *Sphagnum palustre* und auf *S. papillosum* zufallsbedingt markiert (2013/2014). Aus diesen Quadraten wurden insgesamt 5907 Exemplare von *D. rotundifolia* und 301 von *D. intermedia* gesammelt und deren morphologische Daten aufgenommen, wie z.B. Pflanzengewicht, Blatttyp- und zahl. Aktive und nicht aktive Blätter wurden unterschieden: aktive Blätter sind gesund und in der Lage Insekten zu fangen. Nicht aktive Blätter sind zu junge oder tote bzw. braune Blätter, die noch nicht, oder nicht mehr fähig sind, Insekten zu fangen. Weiterhin wurden Stiellängen aller Blätter, Wurzellängen der Pflanzen, Zahl der Blütenstängel und Pflanzenalter (vier Altersklassen: 0-3, 3-6, 6-12, 12-24, >24 Monate) gemessen. Es wurden insgesamt 72.192 morphologische Daten gesammelt. Anhand dieser Daten wurde die Biomasseproduktivität (gesamte Biomassemenge aller Pflanzen mit und ohne Blüte, pro Pflanze oder pro Flächeneinheit), der potenzielle Ertrag (Biomassemenge der Pflanzen in Blüte pro Flächeneinheit), die Pflanzendichte pro m^2 und das durchschnittliche Gewicht einer *Drosera*-Pflanze bestimmt (**Kapitel 5**).

1.6 Ergebnisse und Diskussion

Literaturrecherche & Grundlagen

Die Literaturrecherche zeigt erstmalig ein umfassendes, gesamtes Bild über die Morphologie, Verbreitung, Ökologie und Reproduktion von *Drosera rotundifolia*, die ihre kommerzielle Nutzung als Heilpflanze, ihren Schutzstatus und die früheren Forschungen zu ihrer Vermehrung und Kultivierung in verschiedenen Ländern einschließt (**Kapitel 2**).

Mit Hilfe einer aktualisierten Verbreitungskarte von *D. rotundifolia* in der Holarktis, zeigte sich, dass die Verbreitung der Pflanze mit feuchten und oligotrophen Biotopen korreliert, die von *Sphagnum* dominiert werden (**Kapitel 2**). Die *Sphagnum*-Pflanzen bewirken durch die Produktion großer Mengen organischer Säuren sowie durch Kationenaustausch ein Absenken des pH-Wertes und schaffen sich somit eine Umgebung in der sie überleben können, gleichzeitig aber konkurrierende Arten verdrängen. Es wird dadurch eine nährstoff- und, konkurrenzarme, sonnige sowie immer nasse Umgebung geschaffen, welche von *D. rotundifolia* bevorzugt wird (**Kapitel 2**).

Die Ursachen für den Rückgang der natürlichen *D. rotundifolia*-Populationen sind häufig komplex und miteinander verbunden, aber in verschiedenen Ländern jedoch nicht unbedingt ähnlich. Die Lebensräume von *D. rotundifolia* nehmen in mehreren Ländern stetig ab; weiterhin stellt die Sammlung von Pflanzen aus natürlichen Populationen eine zusätzliche Bedrohung für die Art dar. Zum Beispiel müssen die *Drosera*-Sammler in Finnland Sammelrichtlinien einhalten (**Kapitel 2**), die lediglich Empfehlungen und nicht rechtsverbindlich sind. Darüber hinaus ist es nicht immer möglich, die Einhaltung der Richtlinien zu überwachen, und die selektive Sammlung größerer Individuen kann in kleinen Populationen leicht

zu einer Verschlechterung des genetischen Genpools führen. In Madagaskar, als zweites Beispiel, gibt es keine Sammelrichtlinien, und es wird nicht erwartet, dass ähnliche Richtlinien - wie in Finnland - in naher Zukunft umgesetzt werden. Aus den natürlichen *Drosera*-Populationen werden wahrscheinlich auch in Zukunft große Mengen an Pflanzen entnommen, zumindest bis es keine langfristige Lösung für einen *Drosera*-Anbau gibt.

Es existiert bisher in Europa keine *Drosera*-Anbaufläche, welche die erforderlichen Mengen für die Industrie bereitstellen kann. Ursachen dafür sind die Schwierigkeiten der Massenproduktion von *Drosera*-Arten, wie die große Zeit- und Kostenaufwendungen jahrelanger Haltung und Pflege, die speziellen Lebens- und Produktionsbedingungen sowie die hohen Qualitätsansprüche an die Arzneidroge 'Droserae herba' (**Kapitel 2, 3 und 4**). Diese Qualitätsansprüche und die weiteren speziellen Anforderungen der Pharmaindustrie beziehen sich nicht nur auf die Inhaltstoffkonzentrationen der Pflanzen, sondern auch auf die verwendbaren Pflanzsubstrate und Vermehrungsmethoden (**Kapitel 3**).

Um langfristig einen Rückgang der natürlichen Populationen verhindern zu können, müssen zeit- und kosteneffiziente Anbaumethoden in engem Kontakt mit der Pharmaindustrie als Abnehmer entwickelt und umgesetzt werden (**Kapitel 2 und 4**).

Anbau & Vermehrung

Eine Alternative bietet die neue klima- und umweltfreundliche Landnutzungsform Paludikultur, d. h. der Anbau von Moorpflanzen auf ehemaligen entwässerten und degradierten Moorstandorten, insbesondere von *Sphagnum*-Arten (Torfmooskultivierung „*Sphagnum* farming") (**Kapitel 2**).

Auf den von *Sphagnum*-Arten dominierten naturnahen Torfmooskultivierungsflächen vermehren sich natürlicherweise *D. rotundifolia* und *D. intermedia* Pflanzenarten in großer Zahl (**Kapitel 5**). Da das jährliche Wachstum der Torfmoose mit dem des Sonnentaus konkurriert, ist man bisher davon ausgegangen, dass beide Arten zusammen nicht kultiviert werden können (Galambosi, B., persönliche Mitteilung). Durch unsere Anbauversuche im Gewächshaus und im Freiland wurde erstmalig festgestellt, dass ein natürlicher oder etablierter Torfmoosrasen von *S. palustre* und *S. papillosum* für einen *Drosera*-Anbau geeignet ist (**Kapitel 2 und 3**, Baranyai, 2016).

Im Gewächshaus wurden die höchsten Keimraten gemessen, wahrscheinlich aufgrund der kontrollierten Umweltbedingungen: optimale Temperatur, Feuchtigkeit, Beschattung und Belüftung, und das Fehlen von Gefäßpflanzen (**Kapitel 3**). Trotz der höchsten Keimraten würde der Anbau im Gewächshaus den Marktanforderungen nicht entsprechen, da das begrenzte Angebot an Insekten eine zusätzliche künstliche Fütterung der *Drosera*-Pflanzen erfordern würde (**Kapitel 2 und 3**).

Der Anbau in natürlichen Mooren erfordert eine große Fläche, würde das natürliche Moorökosystem beeinträchtigten und ist auch mit dem Naturschutzrecht nicht zu vereinbaren. Die naturnahen Torfmooskultivierungsflächen können demgegenüber ausreichend groß angelegt werden. Im Vergleich zu den natürlichen Mooren konnten höhere Pflanzdichten pro Fläche, als auch höhere Pflanzengewichte auf kultiviertem Torfmoosrasen erzielt werden (**Kapitel 5**). Zudem besteht

hier aufgrund der großen Fläche und Erträge die Möglichkeit eine Auswahl der größten Pflanzen für die Ernte vorzunehmen (**Kapitel 3 und 5**).

Von den drei getesteten Anbaumethoden ergab sich die Methode Torf-Pads als nicht anwendbar, weil die Torf-Pads zu anfällig für die Umweltbedingungen waren (**Kapitel 3**). Bei der Aussaatmethode wurde eine sehr kleine Keimungsrate (< 1 %) dokumentiert (**Kapitel 3**). Es wird vermutet, dass die kleinen *Drosera*-Samen zwischen Mai und Juni durch das Regenwasser in tiefere Torfmoosschichten eingewaschen wurden; da ist die Lichtintensität geringer und nimmt folglich die Keimfähigkeit schnell ab (**Kapitel 2**). Dies wird durch die signifikant höheren Keimungsraten der Aussaat im Gewächshaus bestätigt (**Kapitel 3**). Die Aussaatmethode ist nur dann im Freiland vorteilhaft, wenn man große Mengen von Samen ausbringt. Unsere Anbauexperimente zeigten, dass *D. rotundifolia* in biologisch abbaubaren Zellulose-Torfgefäßen mit nur wenigen Samen im Innen- und Außenbereich auf vitalem *Sphagnum* erfolgreich kultiviert werden kann (**Kapitel 3**). Es wurde beobachtet, dass die Torfgefäße innerhalb von zwei Monaten vollständig von *Sphagnum* überwachsen waren. Dieses schnelle Überwachsen führte zu einer Mikrohöhlung um die kleinen und tiefen Torfgefäße, die den Samen bessere Keimbedingungen in Form von indirektem Sonnenlicht und einem warm-feuchten Mikroklima verschaffte (**Kapitel 2 und 3**, Crowder *et al.* 1990).

Hinsichtlich konkurrierender Pflanzenarten wurde festgestellt, dass die regelmäßige Entfernung im ersten Versuchsjahr einen signifikanten positiven Einfluss auf die Samenkeimung in beiden Pflanzgefäß-Typen hatte. Die Entfernung von konkurrierenden Pflanzenarten erhöhte auch die Überlebensrate der *Drosera*-Pflanzen im zweiten Wachstumsjahr erheblich. Durch die Entfernung entsteht eine helle und offene Oberfläche bzw. Umgebung mit geringer Konkurrenz, die für die Insektenerbeutung (Nährstoffaufnahme) und das Pflanzenwachstum von *D. rotundifolia* optimal ist (**Kapitel 3 und 5**).

Qualitätsuntersuchungen

Die Qualitätsuntersuchungen haben erstmalig bewiesen, dass es keinen Unterschied der Inhaltsstoffkonzentrationen zwischen auf der Torfmooskultivierungsfläche angebauten und „wild wachsenden" *D. rotundifolia* gibt. Weiterhin zeigte sich, dass die auf der Torfmooskultivierungsfläche wachsenden *D. rotundifolia* Pflanzen eine 7- bis 8-mal höhere Konzentration von 7-Methyljuglon aufweisen als *D. madagascariensis* DC, die derzeit für 'Droserae herba' meist verwendete Pflanzenart. Zudem konnte erstmalig nachgewiesen werden, dass auch nicht blühende *D. rotundifolia*-Pflanzen zwischen Juli bis August die geforderten Inhaltsstoffkonzentrationen erreichen. Aus Sicht dieser Ergebnisse ist eine Einschränkung der Ernte auf blühende Pflanzen nicht zwingend. Bezüglich der Tageszeit wurden keine signifikanten Konzentrationsunterschiede der Inhaltsstoffe festgestellt. Dies bedeutet, dass es keinerlei Einschränkungen für das Sammeln während des ganzen Tages, zwischen 7 und 16 Uhr gibt. Die höchsten Konzentrationen bioaktiver Inhaltsstoffe wurden in *Drosera rotundifolia* und *D. intermedia* Pflanzen festgestellt die 13 bis 24 Monate alt sind und blühen (**Kapitel 4**).

Produktivität und Ertrag

In den Torfmooskultivierungsflächen lag die durchschnittliche Biomasseproduktivität (FM = Frischmasse) bei *D. rotundifolia* wesentlich höher, 28 g pro m², als bei *D. intermedia*, 7 g pro m². Der durchschnittliche Ertrag (FM), d. h. nur blühende Pflanzen für pharmakologische Zwecke, betrug bei *D. rotundifolia* 21 g pro m² und *D. intermedia* 4 g pro m². Damit entsprach die erntbare Biomassemenge von *D. rotundifolia* etwa 80% der gesamten Biomasse auf der Fläche.

Die ermittelte Biomasseproduktivität von *D. rotundifolia* war 3- bis 34-mal höher als in borealen (Schweden, Finnland) bzw. 3-mal höher als in nemoralen Mooren (Deutschland). Es wurde weiterhin ein 2- bis 21-mal höherer Frischertrag von *D. rotundifolia* registriert als auf finnischen Moorstandorten. Auf den Torfmooskultivierungsflächen wurden deutlich weniger Pflanzen von *D. intermedia* als von *D. rotundifolia* gefunden. Die Biomasseproduktivität von *D. intermedia* war geringer als in natürlichen Mooren in Deutschland (**Kapitel 5**).

Im Juli und August erreichten beide *Drosera*-Arten ihr Wachstumsmaximum, welches mit der Entwicklung einer oder mehrerer Blütenstängel mit Blüten und einer höheren Anzahl von Blättern mit längeren Blattstielen sowie Wurzeln einhergeht (**Kapitel 5**). Die mindestens ein Jahr alten *Drosera*-Pflanzen zeigten im Juli und August sowohl das höchste Gewicht pro Pflanze als auch den höchsten Hektarertrag, bzw. die höchsten Konzentrationen bioaktiver Inhaltsstoffe. Damit ist diese Altersgruppe optimal zur Ernte geeignet (**Kapitel 4 und 5**). Um langfristig eine stabile Population zu gewährleisten, wird ein nachhaltiges Erntemanagement empfohlen, in welchem nur Pflanzen gesammelt werden, die mindestens ein Jahr alt sind (**Kapitel 5**). Die Erträge der Folgejahre verringern sich bei einer substanziellen Ernte von sehr kleinen Pflanzen, da diese einerseits kaum Ertrag im aktuellen Jahr bringen, als auch keine Erträge in Folgejahren erzeugen können.

1.7 Ausblick

Zusammenfassend kann festgestellt werden, dass die Torfmooskultivierungsflächen in Deutschland ein sehr großes Potenzial für den Anbau des *Drosera*-Rohstoffs haben, vornehmlich für *D. rotundifolia* bzgl. Quantität als auch Qualität. Das kontinuierliche Flächenmanagement erzeugt ideale Umweltbedingungen, die die Ausbreitung von *Drosera*-Pflanzen fördern und eine natürliche Vermehrung ermöglichen. Der durchgehend offene und konstant feuchte *Sphagnum*-Rasen und die geringe Konkurrenz durch Begleitpflanzen sind für das Pflanzenwachstum als auch für den Insektenfang (Nährstoffaufnahme) optimal. Eine Kombination aus Torfmooskultivierung und Zellulose-Torfgefäßen als Pflanzmethode ist besonders geeignet, um *Drosera* mit größerer Beschaffungssicherheit zu produzieren. Durch die Ernte von *Drosera*-Pflanzen im Juli und August, die älter als 12 Monate alt sind, können die Bestände auch in den Folgejahren produktiv gehalten werden. Diese Erkenntnisse ermöglichen ein Anbau- und Erntemanagement, das dem Prinzip der Nachhaltigkeit entspricht.

Eine Co-Nutzung von *D. rotundifolia* und Torfmoos von Torfmooskultivierungsflächen wäre nur soweit zu empfehlen, wenn durch ein gezieltes *Drosera*-

Management auf der Fläche das Torfmooswachstum (als Hauptnutzung) nicht negativ beeinflusst wird. Die Ernte von Torfmoos zur kommerziellen Nutzung steht der Ernte von Sonnentau insofern entgegen, das sie die Population vernichtet. Deshalb sollte Torfmoos nur auf Teilflächen in bestimmten Zeiträumen (alle 3 Jahre) geerntet werden, damit die Sonnentaupflanzen sich wieder natürlicherweise ausbreiten können. Bisher ist aber nicht untersucht worden, in wieweit eine Co-Nutzung von Torfmoosen und Sonnentau auch ökonomisch tragfähig ist.

Für die Hauptnutzung von Sonnentau auf Torfmoosen in Paludikultur, wurde mit den Erfahrungen des Autors in Nordostdeutschland 2017 eine Firma gegründet, mit dem Ziel, die Pharmaindustrie mit nachhaltig angebautem *Drosera rotundifolia*-Rohstoff in Bio-Qualität zu versorgen. Unter der Leitung des Autors (als ehem. Geschäftsführer und Leiter für Heilpflanzenanbau) wurde in einem ehemaligen Torfabbaugebiet (5,6 Hektar) ein Wasserspeicher und eine 3,5 Hektar große „*Drosera-Sphagnum*-Kultur" angelegt. Die „*Drosera-Sphagnum*-Kultur" wurde im Mai 2019 fertig gestellt. Bis September 2019 konnte sich schon ein kleiner *Drosera*-Bestand entwickeln, aber höhere Erträge wurden im ersten Jahr noch nicht erreicht.

Paludikultur, als nasse, landwirtschaftliche Nutzungsform auf Hochmoor, hat ein hohes Potenzial für den kommerziellen Anbau von *Drosera* in der nemoralen Zone. Dazu sind allerdings nur ausgewählte Flächen, die die Anforderungen an Infrastruktur, Wasserregime, Bodentyp, Wiedervernässungspotential, und gesetzliche Rahmenbedingungen entsprechen, geeignet. Daneben ist ein kontrolliertes Wasser- bzw. Pflegemanagement nötig, um *Drosera* im großen Maßstab zu produzieren. Für die Planung, Einrichtung und Betreuung ist Fachpersonal erforderlich. Aus unserer Sicht könnten diese Anbausysteme auch auf andere Regionen in Europa übertragen werden, z.B. auf die boreale Zone. Dazu wäre aber weitere Forschung notwendig.

Ein erfolgreicher Anbau von *D. rotundifolia* auf Torfmooskulturen kann folgende positive Effekte erzielen:

1. Der *Drosera*-Anbau könnte die Gewinnung von ‚Droserae herba' ermöglichen bei gleichzeitigem Schutz der Wildpopulationen in Europa und auch weltweit. Die Anbauflächen können dabei gleichzeitig als „Genpool" zum Erhalt der Art beitragen.
2. Der in wiedervernässten Hochmooren durchgeführte kommerzielle Anbau von *D. rotundifolia* könnte durch seine kontrollierten Bedingungen eine gleichbleibend hohe Qualität gewährleisten (z.B.: Bio-Qualität), die der Arzneimittelindustrie genügt.
3. In moorreichen Regionen, die sich gerade in peripheren bzw. strukturschwachen Regionen befinden, könnte der Anbau von *D. rotundifolia* als potenzielle Paludikultur-Pflanzenart, mit der Entwicklung von Produkten und dem Verkauf von Biomasse, Arbeitsplätze schaffen und Einkommensalternativen für Landwirte und verarbeitendes Gewerbe bieten.
4. Der *Drosera*-Anbau als Form von Paludikultur (nasse Bewirtschaftung von Mooren) würde den Torfboden erhalten, Treibhausgasemissionen im Vergleich zur konventionellen, entwässerungsbasierten Moorbewirtschaftung verringern, und Lebensraum für geschützte Arten bieten.

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2

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 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], 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

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and 6–10 mm wide [209, 195, 120]. The stipules are usually united up to their centre with the petiole [93], 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 laminas 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 margin [48].

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], androgynous [122] 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 flowers [48]. 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 grains [210], 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 tentacles [48]. The styles are 2–5 partite [157], 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 $3-\infty$ 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 reported [75]. 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 g [194].

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′ 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, 40, 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, 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 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].

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

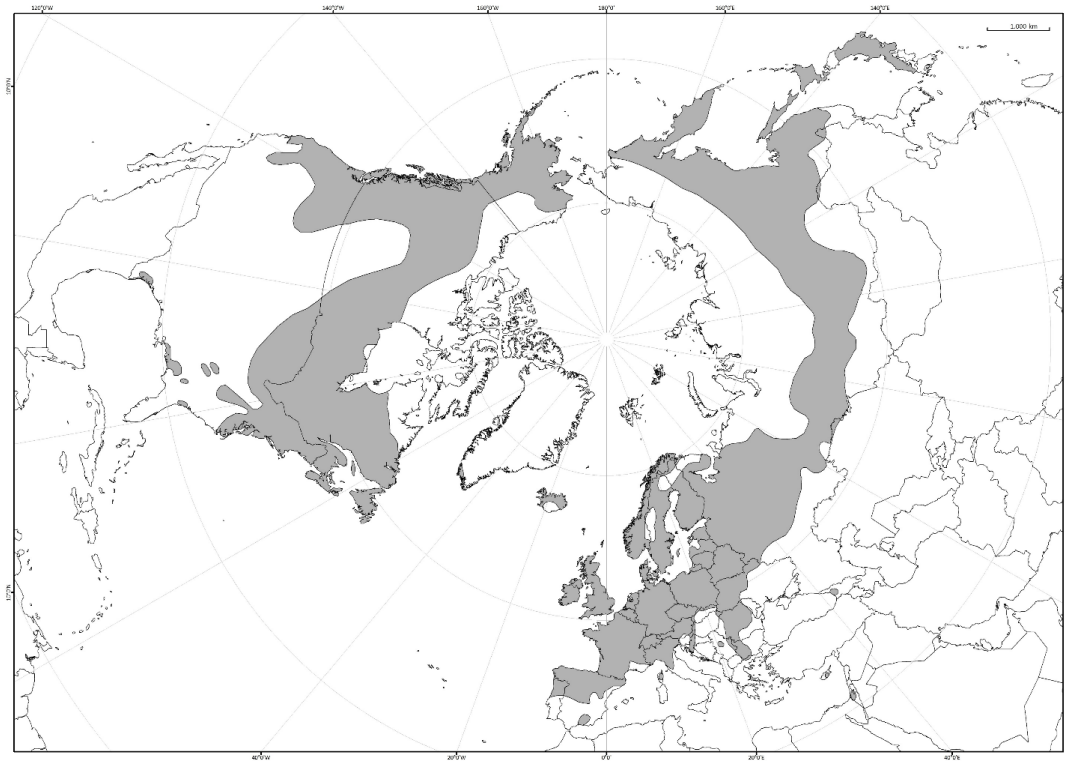

Figure 1. The distribution of *D. rotundifolia* in the Holoarctic (based on [149, 105, 224, 48, 255, 30, 126, 237, 8, 261, 40, 113, 86, 145, 241, 77, 166]).

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 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.

Location	Soil pH	Source
Europe		
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 *et al*. (2003)
North America		
Maine	3.5–4.5	Davis & Anderson (1991)
Virginia	3.5–3.7	Byers *et al*. (2007)

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.

Location	pH	Ca^{2+}	Mg^{2+}	Source
Europe				
Britain	3.5–4.4	2.4–24	1.2–7.0	Crowder *et al*. (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 *et al.* (2011)
Britain	5	17	6.6	Box *et al.* (2011)
Germany	4.6–5.1	NA	NA	Ellwanger (1996)
Italy	4.4–4.9	NA	NA	Miserere *et al.* (2003)
Italy	5.6	5.55 (± 0.43)	1.40 (± 0.11)	Gerdol *et al.* (2011)
Italy	6.1	8.27 (± 0.38)	1.91 (± 0.09)	Gerdol *et al.* (2011)
Netherlands	4.5 (± 0.07)	0.46	0.46	Adema *et al*. (2006)
Poland	4.0	0.75	0.18	Wojtuń *et al*. (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 *et al*. (2010)
North America				
Canada	4.3– 6.9	NA	NA	Pellerin *et al*. (2006)
Minnesota	3.9	0.8	NA	Glaser *et al.* (1990)
Minnesota	7.5	30	NA	Glaser *et al.* (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 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 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-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 uliginosum* 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 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 mats [111].

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-Sphagnetea Br.-Bl. & R. Tx. ex Westh. *et al*. 46	Weber (1995), Schubert *et al.* (2001)
Sphagnion medii Kästner et Flössner 1933	Berg *et al*. (2004), Thébaud (2011)
Ericion tetralicis Schwickerath 1933	Berg *et al*. (2004)
Oxycocco-Ericion tetralicis Nordhagen ex Tx.1937	Pott (1995), Schaminée *et al*. (1995)
Scheuchzerio-Caricetea fuscae Tx. 37	Borhidi (2003), Rodondi *et al.* (2009)
Scheuchzerion palustris Nordhagen ex Tx. 1937	Linder-Effland (2002), Huntke (2008)
Caricion fuscae Koch 1926 em. Klika 1934	Oberdorfer (1992), Borhidi (2003), Berg *et al*. (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. *et al*. 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 *et al*. 1946	Linder-Effland (2002)

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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 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 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) [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 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

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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 [32]), 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 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, 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* 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 '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 conditions [123], cultivation in glasshouses, and cultivation outdoors under semi-natural 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, $HgCl_2$ 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].

Kukułczanka & Cząstka (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, 50] 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

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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 glasshouse 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' [97]. The first flowering and the first harvest took place in the second year. A futher 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 [71]. In the cultivation with 9 m^2 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].

Table 4. Fresh yields of *Drosera rotundifolia* in peat beds (total 54 m^2) 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**

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 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

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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.

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

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

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

		flexuosum, *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.*
Neatherland	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 loitlesbergeri*, *Sphagnum rubellum*, *S. fuscum.*
Norway	Hansen (1967)	*Andromeda polifolia*, *Rubus chamaemorus*, *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 durieui*, *Nathecium ossifragum*, *Molinia careulea*, *Agrostis canina*, *Sphagnum subnitens*, *S. auriculatum.*

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

North America

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

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

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3
Germination and seedling survival of *Drosera rotundifolia* L. cultivated on *Sphagnum*: Influence of cultivation method, seed density, *Sphagnum* species and vascular plant cover

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Mires and Peat (eingereicht im Januar 2020)

Germination and seedling survival of *Drosera rotundifolia* L. cultivated on *Sphagnum*: Influence of cultivation method, seed density, *Sphagnum* species and vascular plant cover

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SUMMARY

Round-leaved sundew (*Drosera rotundifolia* L.) is a drug commonly collected for treating respiratory diseases. The species is collected from the wild, because in- and outdoor cultivation experiments have not yet resulted in commercial cultivation options. We studied seed germinability and seedling survival of *Drosera rotundifolia* cultivated on *Sphagnum palustre* and *S. papillosum* lawns under natural, semi-natural (*Sphagnum* farming fields) and greenhouse conditions. The plants were cultivated with and without vascular plants in inserted cellulose pots and paper mesh bags as well as directly sown. Seed germination was most successful in cellulose pots, whereas direct sowing only led to a germination rate < 1%. Different *Sphagnum* species and the mowing of vascular plants had no significant effect on seed germination, but did increase the survival of plants in the second growing year. Cultivation of *Drosera rotundifolia* in bio-degradable cellulose holders on *Sphagnum* meets the requirements of the pharmaceutical industry and has many ecological benefits compared to collection from the wild.

KEY WORDS: sundew, Droserae herba, medicinal plant, cultivation methods, Paludiculture

INTRODUCTION

The European *Drosera* species have a long history in their use for treating respiratory diseases (Šamaj *et al*. 1999, Babula *et al*. 2009), with the drug 'Droserae herba' being traditionally prepared from the dried above-ground parts of *D. rotundifolia* (Egan & van der Kooy 2013, Baranyai & Joosten 2016). Severe decline has resulted in all native European *Drosera* species currently being endangered. Currently mainly non-European *Drosera* species are used for pharmaceutical purposes, despite their substantially lower content of pharmacologically active compounds (Krenn *et al*. 1995, 1998, Baranyai & Joosten 2016).

The increasing difficulties in procuring high-quality drugs has in recent years led to various in- and outdoor experiments to cultivate *Drosera* (Wawrosch *et al*. 1996, Galambosi *el al*. 1998, 2000a, Šamaj *et al*. 1999, Galambosi 2002, Krenn *et al*. 2005, Bruzzese *et al*. 2010, Banasiuk *et al*. 2012, Galambosi & Galambosi 2013, Baranyai & Joosten 2016), but those trials have not yet resulted in widespread sundew

Important reasons for *Drosera* not yet being cultivated are the requirements set by the pharmaceutical industry, which demands

a) minimum content of bioactive compounds (e.g. naphthoquinone: > 0.14 %),
b) plants from peat substrate (no in vitro cultivation),
c) no use of fertilizer nor any other chemical treatment,
d) no genetically identical (cloned), unnatural and artificially fed *Drosera* plants,
e) high purity of the biomass (≤ 3% plant material other than *Drosera*, and among *Drosera* ≤ 10 % other species than *D. rotundifolia*),
f) full transparency and continuous documentation of the cultivation process (ÖAB 9 1960, EB 6 1989, Blaschek 1998, Franke 1999, Länger & Schiller 2004, Wichtl 2009, HAB 2014, Westphal 2016, Baranyai & Joosten 2016).

Other reasons are the high costs and time requirement of sundew propagation and cultivation (Baranyai *et al*. 2016).

Over the last decade, the cultivation of *Sphagnum* has emerged as a climate- and environment-friendly land use alternative on rewetted, formerly drained and degraded bog land (Gaudig *et al*. 2014, 2018, Beyer & Höper 2015, Muster *et. al.* 2015, Gaudig & Krebs 2016, Günther *et al*. 2017). Sphagnum cultivation ('Sphagnum farming', Gaudig *et al*. 2014, Krebs *et al*. 2014) has created large artificial habitats where *D. rotundifolia* occurs spontaneously. Pilot studies have furthermore shown that, on living *Sphagnum*, *Drosera rotundifolia* develops better than on sand (B. Baranyai, unpublished data) and contains concentrations of bioactive compounds that exceed the required pharmacological minimum of 0.14 % (Baranyai *et al*. 2016).

This paper reports on seed germination and seedling survival of *D. rotundifolia* cultivated in living *Sphagnum* using different cultivation methods. We hypothesize that Sphagnum farming areas constitute a suitable habitat for *Drosera* cultivation.

MATERIALS AND METHODS

We cultivated *Drosera* under natural, semi-natural and greenhouse conditions. Cultivation under natural conditions was studied in Fekete-to (Western Hungary, 46º53′07″ N, 16º53′07″ E), a transitional mire (600 m^2) situated at 275 m a.s.l. (Kol 1967). Mean annual rainfall is 760–800 mm, mean annual temperature 9.1–9.8 ºC (Dövényi 2010). Vegetation is dominated by *Sphagnum palustre* L. and *S. fallax* H. Klinggr., accompanied by *Carex elata* All., *Eriophorum angustifolium* Honck, *Drosera rotundifolia*, *Calluna vulgaris* (L.) Hull and *Polytricum formosum* (Hedw.) G.L.Sm. *Drosera rotundifolia* grows on *Sphagnum* hummocks with a low (10 %) cover of vascular plants.

Cultivation under semi-natural conditions was studied in a Sphagnum farm on rewetted, former bog grassland near Rastede (NW Germany 53º15′80″ N, 08º16′05″ E, 0.5 m below sea level, Gaudig *et al*. 2014, 2018, Temmink *et al*. 2017). Mean annual precipitation is 778 mm, mean annual temperature 8.7 ºC (Climate-Data.org 2018). The vegetation is dominated by *Sphagnum palustre*, *S. papillosum* Lindb. and *S.*

fallax, with a coverage of 95 % (Wichmann *et al*. 2015). Co-occurring vascular plants include *Juncus effusus* L., *Drosera rotundifolia*, *D. intermedia*, *Juncus bulbosus* L., *Carex canescens* L., *Rhynchospora alba* (L.) Vahl, *Eriophorum angustifolium*. and *Erica tetralix* L. The vascular plants are regularly mown in the growing season.

Cultivation under greenhouse conditions was studied in a greenhouse in the Botanical Garden of Greifswald University (NE Germany, 54º09′38″ N, 13°36′70″ E) using 35.5 × 22 × 5 cm containers filled with a mixture of 25 % medium humified (von Post scale H5) *Sphagnum* peat and 75 % *Sphagnum* biomass fragments from the Rastede farm. Light levels were manually adjusted by lamps (Photosynthetic Photon Flux Density in winter 79 ± 5 μmol m^{-2} s^{-1}, in summer 119 ± 8 μmol m^{-2} s^{-1}) to accommodate for the dormancy period of *Drosera rotundifolia*. Air temperatures were maintained constant at 24 ± 2.0 °C in summer and 15 ± 2.0 ºC in winter. Humidity was on average 87.2 ± 12.9 % and plants were well-watered to simulate naturally moist conditions.

Seed capsules of *Drosera rotundifolia* were collected in September 2013 by hand from 30 randomly selected mature plants per site (20,172 seeds in Rastede with mean number of seeds per capsule 71 ± 31, n = 285, 20,698 seeds in Fekete-to with mean number of seeds per capsule 76 ± 26, n = 273) and stored in a hermetically sealed flask at 4 ± 2 ºC. Seed capsules were opened directly before start of experiments in April 2014. Seeds (mean length 1.78 ± 0.21 mm, mean width 0.20 ± 0.04 mm, n = 170) were counted at room temperature, mixed with dry grinded *Sphagnum* biomass (1:10, Galambosi *et al*. 2000a) and evenly sown in various numbers (10, 50 or 100 seeds) over plots of 10 × 10 cm (direct seed sowing). Seeds (3, 6 or 9 seeds per pot/bag) were also seeded in bio-degradable cellulose Boller pots (Ø 4.5 cm, depth 5 cm; Romberg & Sohn GmbH, Germany) and bio-degradable paper mesh bags (Ø 6 cm, depth 0.8 cm; with an 2 × 2 cm X-shaped incision in the centre of the adaxial surface; SENSEO® Pads, Douwe Egberts Retail Germany GmbH, Germany) filled with 100% medium humified *Sphagnum* peat. Pots and bags were carefully placed in the *Sphagnum* lawn to avoid disturbance of the lawn and covering of the pots/bags. Plots, pots and bags were labelled with wooden sticks to allow easy retrieval.

Experiments were done in *Sphagnum* lawns dominated by *Sphagnum palustre* or *S. papillosum* (under semi-natural und greenhouse conditions) or *S. palustre* (under natural conditions). Under natural and semi-natural growing conditions, two 150 × 150 cm permanent quadrats (100 cm from each other) were laid-out and protected against disturbance with a wooden frame (170 × 170 × 170 cm) and a bird net. In one permanent quadrat, vascular plants were allowed to grow whereas in the other quadrat aboveground plant material was removed monthly using hedge shears. In the greenhouse all vascular plants were removed. Spontaneously established *Drosera rotundifolia* plants were removed. Six replicates per treatment were installed randomly within the permanent quadrats at the natural and semi-natural sites and in the greenhouse (random distribution of all treatments within one container replicated for six containers).

The replicates covered an area of 3825 cm^2 for direct seed sowing, 1114 cm^2 for cellulose pots and 1980 cm^2 for paper mesh bags in the outside experiments, and 2409 cm^2 for both the cellulose pots and the paper mesh bags in the greenhouse experiments. All results are expressed in m^{-2}.

The experiment started in April 2014. Germination (plants/seed) was monitored monthly from May to September 2014 and plants survival from April to August 2015. The survival rate is the percentage surviving in August 2015 of all plants that had germinated until September 2014.

Data analysis included a detailed data exploration before (after Zuur *et al*. 2009). Group differences for germination and survival were analysed with the non-parametric Kruskal Wallis test and a multiple comparison test after Siegel & Castellan (1988), and the R package pgirmess after Giraudoux (2010).

To analyse the effects of treatments we applied a generalised linear model with a Poisson distribution to take the high number of seeds that did not germinate into account. We analysed the response variable 'germination rate' (percentage of deployed seeds germinated) with as explanatory variables: cultivation conditions (greenhouse, natural and semi-natural), cultivation method (cellulose pots, paper bags, direct sowing), number of seeds (3, 6, 9 seeds; 10, 50 or 100 seeds), *Sphagnum* species (*S. papillosum*, *S. palustre*), and vascular plants (removed and not removed).

We applied Spearman's rank correlation test to analyse the relation of survival rate and number of germinated plantlets for the single cultivation methods.

Statistical data exploration, computation and figure design were done with the software R (v3.1.3, R Development Core Team 2009) and the packages AED (Zuur *et al*. 2009), pgirmess (Giraudoux 2010) and stats (R Development Core Team 2009)

RESULTS

Germination

In total only a small fraction of seeds (4.7 %) did germinate, i.e. 12.2 %, under greenhouse, 2.8 under semi-natural and 1.1 % under natural conditions (Table 1). Mean germination rates with cellulose pots were higher than with paper mesh bags and direct seed sowing (Figure 1). Direct sowing showed a substantially lower germination rate under semi-natural and natural conditions compared to greenhouse conditions (Figure 1). The differences between all cultivation conditions and methods are statistically significant (Table A1).

For cellulose pots and paper bags, generally higher germination rates were observed with 3 and 6 seeds than with 9 seeds (Figure 2), but differences were not statistically significant (n = 287, Kruskal-Wallis, χ^2 = 2.93, d.f. = 2, P = 0.23). For direct seed sowing under natural conditions no seeds were found to germinate in the 10 and 50 seeds variants, whereas for 100 seeds a very small germination rate of 0.3 ± 0.2 %, was recorded (Figure 2). Under greenhouse and semi-natural conditions, proportionally more seedlings were observed for direct seed sowing with 10 seeds (Figure 2), but differences with the 50 and 100 seeds variants were not significant (Figure 2). Germination rate of *Drosera* did not significantly differ on *Sphagnum palustre* and *S. papillosum* for all implied cultivation conditions and methods (Table A1).

Under natural and semi-natural conditions, significantly larger germination rates were found when aboveground vascular plants had been removed, with 2.5 times higher rates in cellulose pots (Table A2). In contrast, three times more seeds germinated in paper mesh bag when vascular plants were present (except for one treatment under semi-natural condition on *S. papillosum*) (Table A2).

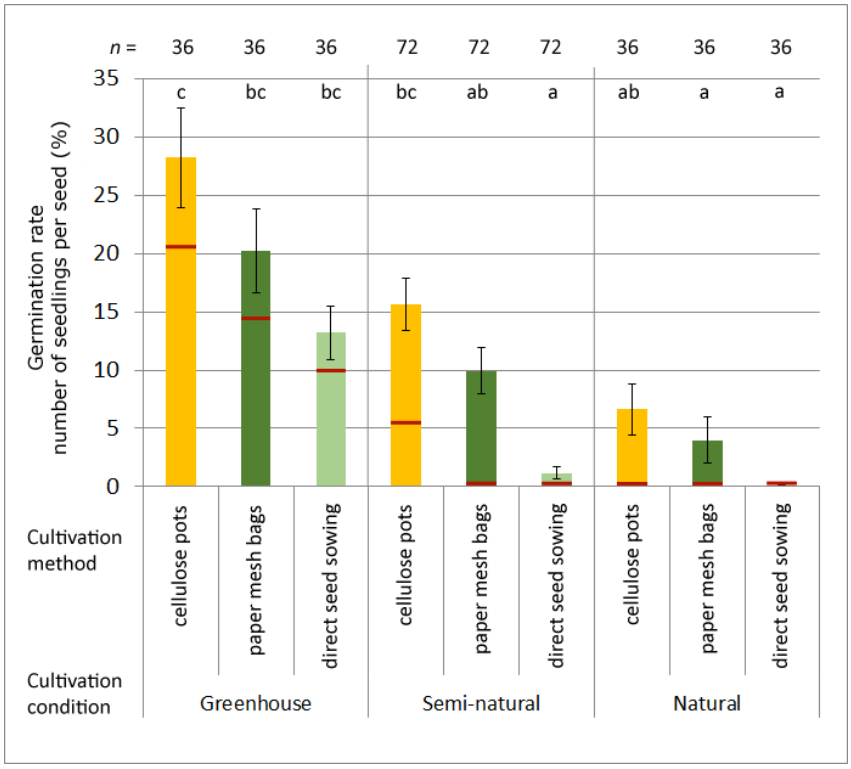

Figure 1. Germination rate (number of seedlings as percentage of number of deployed *Drosera rotundifolia* seeds) for the different cultivation conditions and methods. Vertical bars show the means, the whiskers the SE, the red lines the medians. Number of replicates is written above each bar. Values with different letters differ significantly ($P \leq 0.05$). Differences in germination rate for cultivation conditions and methods were analysed with the non-parametric Kruskal Wallis test after Siegel & Castellan (1988) after a significant overall Kruskal Wallis test: $\chi^2 = 109.34$, d.f. = 8, $P = <0.001$.

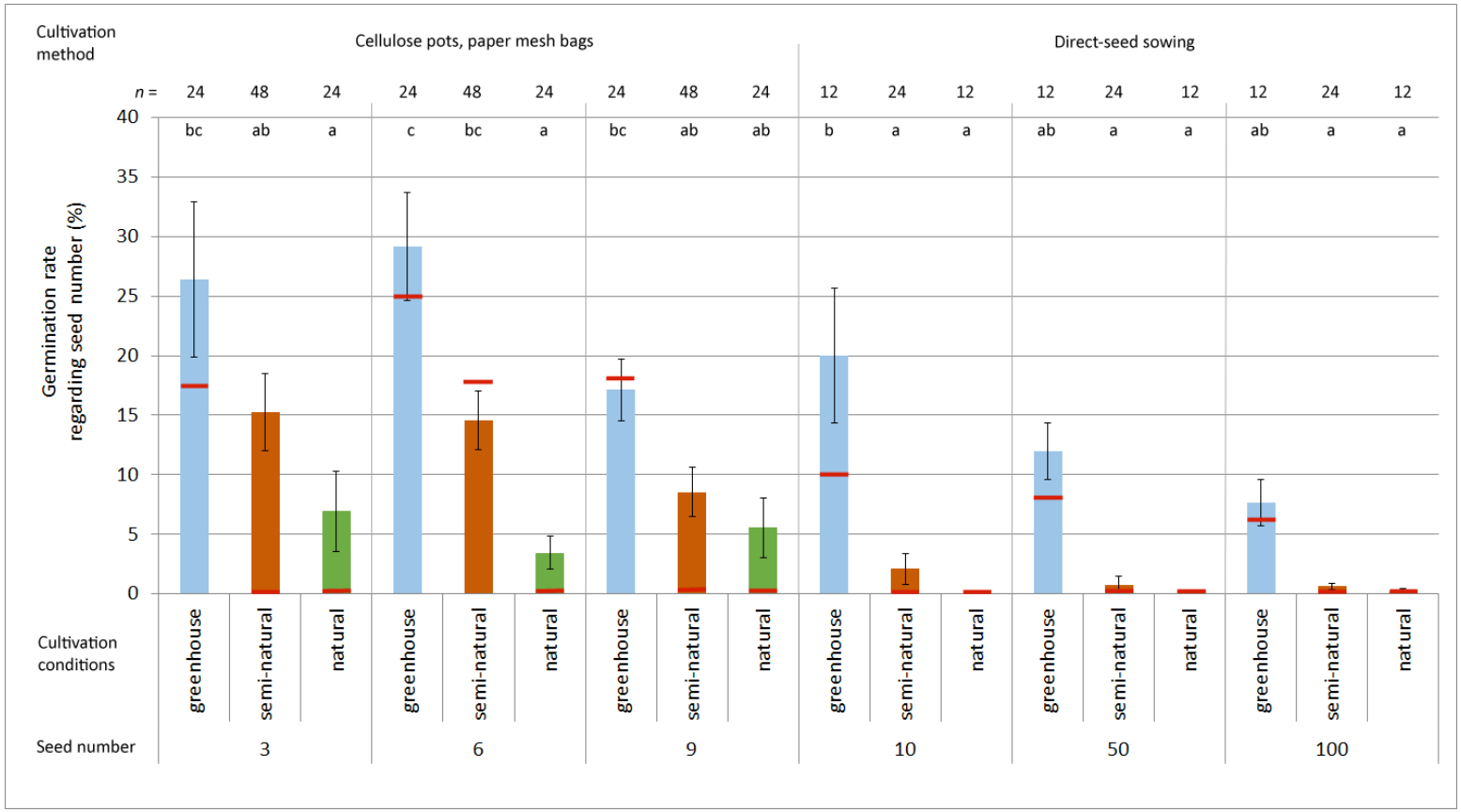

Figure 2. Mean germination rate (number of seedlings as percentage of number of deployed *Drosera rotundifolia* seeds) for the different treatments cultivation conditions, methods and seed number (see Table A2). Vertical bars show the means, the whiskers the SE, the red lines the medians. Number of replicates is written above each bar. Values with different letters differ significantly ($P \leq 0.05$). Differences in the germination rate for cultivation condition and seed number were analysed with the non-parametric Kruskal Wallis test after Siegel & Castellan (1988) after a significant overall Kruskal Wallis test: $\chi^2 = 111.69$, d.f. = 17, *P*-value = <0.001.

Survival

The survival rates for *Drosera* seedlings after one year were highest in the greenhouse with cellulose pots (91%), under semi-natural conditions with direct sowing (93%) and under natural conditions quite similar between cellulose pots (73%) and direct sowing (67%) (Table 1). No relation was found between *Drosera* survival rate and seed numbers (3, 6 and 9, Kruskal-Wallis test $\chi^2 = 0.58$, d.f. = 2, $P = 0.75$ and 10, 50, 100 seeds, Kruskal-Wallis test $\chi^2 = 1.84$, d.f. = 2, $P = 0.39$). Likewise, no relation could be established between the survival rate and the number of germinated plantlets (Spearman' rank correlation: cellulose pots $P = 0.37$, paper mesh bags $P = 0.84$ and direct seed sowing $P = 0.39$). Removal of vascular plants increased seedling survival significantly, e.g. at the Sphagnum farming site Hankhausen (Kruskal-Wallis test $\chi^2 = 7.33$, d.f. = 1, $P = 0.01$).

Table 1. Total number and percentage of deployed *Drosera rotundifolia* seeds germinated in the same year, and surviving plants and survival rate in the following year for the various cultivation conditions and methods.

Cultivation condition	Method	Deployed seeds	Germinated seeds	Surviving plants and survival rate
Greenhouse	cellulose pots	216	55 (25.5%)	50 (90.9%)
	paper mesh bags	216	43 (20.0%)	30 (69.8%)
	direct seed sowing	1920	188 (9.8%)	135 (71.9%)
Semi-natural	cellulose pots	432	64 (14.8%).	32 (50.0%)
	paper mesh bags	432	37 (8.6%)	18 (48.6%)
	direct seed sowing	3840	29 (0.8%)	27 (93.1%)
Natural	cellulose pots	216	15 (6.9%)	11 (73.3%)
	paper mesh bags	216	7 (3.2%)	4 (57.1%)
	direct seed sowing	1920	3 (0.2%)	2 (66.7%)
Total	All	9408	441 (4.7%)	309 (70,1%)

Plant densities

Average plant density, as calculated from the surviving plants (Table 1) and the size of all replicates (see Methods) was 124.5–280.2 plants m^{-2} in the greenhouse, 70.6 and 143.6 plants m^{-2} (with the highest values achieved with cellulose pots) under semi-natural conditions (Sphagnum farming), and 5.2–98.7 plants m^{-2} under natural conditions.

DISCUSSION

Cultivation method

Highest germination rates were obtained with cellulose pots (Table 1, Figure 1). We observed that cellulose pots were completely overgrown by *Sphagnum* within two months, whereas with bags this took at least one month longer. The fast overgrowth resulted in a micro-hollow around the small and deep cellulose pots, which provided the seeds with better germination conditions, in the form of indirect sunlight and a warm-humid microclimate (Crowder *et al*. 1990, Baranyai & Joosten 2016). In contrast, intensive sunlight on the thin paper bags lead to strong dehydration of the peat filling and hampered *Drosera* seed germination. In the Sphagnum farm and under natural conditions the bags were furthermore partly lifted out of the *Sphagnum* lawn by upward-growing vascular plants (*Juncus* sp. and *Carex* sp.). In general, germination rates were lowest under natural conditions with direct sowing. This is probably caused by the more compact *Sphagnum* lawn compared to the Sphagnum farm. Directly sown seeds are washed by the rain into deeper layers of the *Sphagnum* carpet, where light intensity is lower and consequently germinability rapidly decreases (Baranyai & Joosten 2016). The few seeds that did not wash in and remained on top of the *Sphagnum* lawn (Figure 3) did germinate and their seedlings had a high survival rate (Table 1). This shows that *D. rotundifolia* is highly adapted to live and hibernate in *Sphagnum* moss and its associated plant communities (Crowder *et al*. 1990, Baranyai & Joosten 2016).

Cultivation conditions

Highest germination rates were recorded in the greenhouse (Figures 1, 2, Table 1), probably because of the prevailing optimal temperature, humidity, shading and aeration conditions and the absence of vascular plants. The highest calculated plant density under semi-natural conditions was achieved with cellulose pots (143.6 plants m^{-2}). The production of 1 kg fresh *Drosera* drug (2,000–5,000 flowering individuals, Galambosi 2018) with cellulose pots in Sphagnum farming fields would require 1800–4500 cellulose pots and 14–35 m^2. Plant density under natural conditions (5.2–98.7 plants m^{-2}) is similar to density in natural peatlands in Finland (3.8–100.7 plant m^{-2}, Galambosi *et al*. 2000b).

Figures 3. *Drosera rotundifolia* seeds fixed between the leaves of *Sphagnum palustre* (left); germinating *D. rotundifolia* seed (right), picture: Balazs Baranyai.

Cultivation in the greenhouse would not comply with market demands, because the limited supply of prey would require additional artificial feeding of the *Drosera* (Baranyai & Joosten 2016).

We found no significant differences in *Drosera* germination rate between *Sphagnum palustre* and *S. papillosum* (Table A1). Whereas cellulose holders (pots and bags) work similarly well in lawns of both species, we observed that direct sowing under semi-natural conditions lead to higher germination rates in *S. palustre* (Table A2). This may relate to morphological differences between the species (Crum 1984) as the spreading branch leaves of *S. palustre* (Figure 3) provide a better footing of the small seeds of *Drosera* than the somewhat more imbricate leaves of *S. papillosum*. Whether *Drosera* seeds remain better in the upper parts of the *S. palustre* lawn where better exposure sunlight allow better germination, needs to be addressed in further research.

Regular removal of aboveground vascular plants in the first year had a significant positive influence on seed germination in cellulose pots on living *Sphagnum*. The removal did also substantially increase the survival rate of plants in the second growing year. These findings are not surprising: *Drosera rotundifolia* seeds need direct light flux for germination (Schmid 1912). In the second growing year, the *Drosera* plants reach the surface of the *Sphagnum* lawn, a bright environment, with little competition, which is optimal for insect capture (nutrient uptake) and plant growth (Schmid 1912, Crowder *et al*. 1990, Schulze & Schulze 1990).

Conclusion

This is the first study in which germination and survival of *Drosera rotundifolia* on *Sphagnum* moss as a growing substrate were studied from the perspective of producing sundew for industrial pharmacological applications.

Our cultivation experiments show that *Drosera rotundifolia* can be successfully cultivated indoors and outdoors on living *Sphagnum* in bio-degradable cellulose holders with only few seeds. *Drosera* cultivation on Sphagnum farming sites offers better possibilities for producing sundew raw material than cultivation under greenhouse and natural conditions. Cultivation under natural conditions requires a large area and infringes upon the natural mire ecosystem. Cultivation furthermore is more advantageous than collection from the wild, because of higher plant density, smaller production areas and the possibility to select cultivation areas without nature conservation restrictions e.g. former peat extraction sites or drained peat meadows and therewith improving agricultural land use. The cultivation of *Drosera rotundifolia* on Sphagnum farming fields (Sphagnum paludiculture) provides new opportunities for the industrial production of sundew raw material and offers synergies with climate and biodiversity protection initiatives.

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Appendix

Table A1. Results of the generalised linear modelling of the germination rate (percentage of deployed seeds germinated) for the treatments: cultivation conditions, cultivation method (direct seed sowing = DSS, cellulose pot = CP, paper mesh bag = PMB), number of seeds, *Sphagnum* species, vascular plants. The seed numbers differed between direct seed sowing (DSS, seed numbers: 10, 50 and 100) and the cellulose pot (CP) and paper mesh bag (PMB, with seed numbers: 3, 6 and 9). Seed numbers were classified as low (3 for CP and PMB and 10 for DSS); medium (6 for CP and PMB and 50 for DSS) and high (9 for CP and PMB and 100 for DSS). Presence/absence of vascular plants was only tested for natural and semi-natural conditions, as in the greenhouse all vascular plants had been removed. *SE*: *standard error; Z*: standard scores; *P*: level of significance. Null deviance: 10,783 on 431 degrees of freedom, Residual deviance: 7,730 on 423 degrees of freedom.

Treatment		*Factor*	*Estimate of the slope*	*SE*	*Z*	*P*
Cultivation condition	greenhouse	natural	-1.57	0.055	-26.36	≤0.001
		semi-natural	-0.65	0.036	-18.41	≤0.001
Cultivation method	cellulose pot	paper mesh bag	-0.40	0.032	-12.40	≤0.001
		direct seed sowing	-1.44	0.047	-30.73	≤0.001
Seed number	low seed number	medium seed number	-0.09	0.034	-2.87	≤0.01
		high seed number	-0.54	0.039	-14.04	≤0.001
Sphagnum species	*S. palustre*	*S. papillosum*	-0.017	0.031	-0.56	0.58
Vascular plants	Present	Removed	0.40	0.042	9.53	≤0.001

Appendix

Table A2. Number of germinated seedlings in September 2014 and number of surviving plants in August 2015) for the different cultivation conditions and methods. Total number of deployed *D. rotundifolia* seed per treatment = 108 (pot and bags) and 960 (seed sowing). *Vascular plants-Yes*: vascular plants are present; *No*: plants were removed.

Cultivation condition	*Sphagnum* species	Vascular plants	Cellulose pot		Paper mesh bag		Direct seed sowing	
			Germinated seedlings	Survived plants	Germinated seedlings	Survived plants	Germinated seedlings	Survived plants
Greenhouse	*S.palustre*	No	29	28	26	19	130	93
	S.papillosum	No	26	22	17	11	58	42
Semi-natural	*S.palustre*	No	18	9	6	5	23	22
		Yes	5	4	11	3	0	0
	S.papillosum	No	19	14	15	8	5	4
		Yes	22	5	5	2	1	1
Natural	*S.palustre*	No	14	10	3	2	2	2
		Yes	1	1	4	2	1	0

4
The production of 7-methyljuglone, plumbagin and quercetin in wild and cultivated *Drosera rotundifolia* and *Drosera intermedia*

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The production of 7-methyljuglone, plumbagin and quercetin in wild and cultivated *Drosera rotundifolia* and *Drosera intermedia*

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SUMMARY

The recent establishment of *Sphagnum* farming areas has created large artificial habitats where *Drosera* grows under semi-natural conditions. Here we test the suitability, for pharmaceutical purposes, of two *Drosera* species collected from such areas. We measured the concentration of the biologically active compounds 7-methyljuglone, plumbagin and quercetin in *Drosera rotundifolia* and *D. intermedia*. All three compounds were found in pharmacologically suitable concentrations with 7-methlyjuglone characteristic for *D. rotundifolia* and plumbagin for *D. intermedia*. The concentrations required for pharmacological purposes were achieved within one year, but higher concentrations occurred in older plants and plants in flower. Concentrations did not differ between plants collected in the morning and in the afternoon. *Drosera* plants cultivated under semi-natural conditions are suitable as sources of raw materials for industrial pharmacological applications.

KEY WORDS: collection, cultivation, flavonoids, Droserae herba, naphthoquinones

INTRODUCTION

The European *Drosera* species, round-leaved sundew (*Drosera rotundifolia* L.) and oblong-leaved sundew (*Drosera intermedia* Hayne) are mainly found in nutrient-poor, acid, open wetlands (Juniper *et al*. 1989, Crowder *et al*. 1990, Ellison & Gotelli 2009). The carnivorous plant traps its prey with sticky, sugar-rich mucin droplets exuded from glandular leaf hairs and then digests its prey enzymically (Darwin 1875, Barthlott 2004, Carow 2009). Nitrogen and phosphorous, in particular, are sourced from captured insects. Numerous *Drosera* species are used for medicinal purposes because they produce valuable secondary metabolites, among which the most abundant are two different 1,4-naphthoquinones (Figure 1), namely 7-methyljuglone (5-hydroxy-7-methyl-1,4-naphthoquinone) and plumbagin (5-hydroxy-2-methyl-1,4-naphthoquinone) (Kämäräinnen *et al*. 2003). The concentration of these two naphthoquinones differs among *Drosera* species (Krenn & Kartnig 2005). In *D. rotundifolia* 7-methyljuglone is the dominant quinone and plumbagin occurs in only trace amounts. In *D. intermedia* it is the other way round, with plumbagin dominant and 7-methyljuglone occurring in trace amounts only. *Drosera* also contains flavonoids such as quercetin (Šamaj *et al*. 1999) (Figure 1). Many of these secondary metabolites are used in the pharmaceutical, cosmetics and food industries (Banasiuk *et al*. 2012). Several naphthoquinones have been reported to exhibit a wide range of physiological and pharmacological properties. Extracts and tinctures of *Drosera* have anti-inflammatory and spasmolytic effects and are utilised in various medications to treat respiratory diseases (Finnie & van Staden 1993, Blumenthal *et al*. 1998, Krenn *et al*. 2004, Babula *et al*. 2009).

The drug Droserae Herba is traditionally prepared from the dried above-ground parts of *D. rotundifolia* (Egan & van der Kooy 2013). The plants are collected at the beginning of the flowering season, from July to August (HAB 2014, Király *et al*. 2011). Extracts and tinctures from *Drosera rotundifolia* and *D. intermedia* are also used in various medications for the treatment of coughs and pulmonary diseases. In Europe alone some 200–300 registered medications exist that contain *Drosera* as an ingredient (MacKinnon 2009). According to Galambosi (2002) the annual requirement of the European pharmaceutical industry for air-dried *Drosera* biomass is 6–20 tons, of which 1–3 tons is *D. rotundifolia* (Galambosi & Jokela 2002). The increased demand for *D. rotundifolia* and *D. intermedia* in the first part of the 20th century and the destruction of their habitat led to over-exploitation of the wild populations. As the plants have become increasingly rare, they are presently

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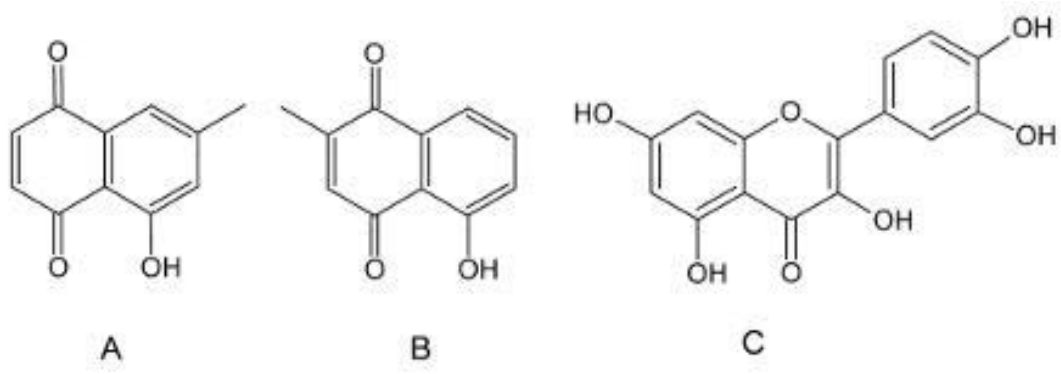

Figure 1. Bioactive compounds from *Drosera* species: (A) 7-methyljuglone, (B) plumbagin, (C) quercetin.

replaced by Asian and African species of *Drosera* (e.g. *D. burmanii* Vahl, *D. peltata* Smith and *D. madagascariensis* DC.) that are officially permitted to be used for pharmaceutical purposes in European countries (Krenn *et al*. 1995, van Wyk *et al*. 2004, Paper *et al*. 2005).

Nowadays, the main commercial source for pharmaceutical sundew material is *D. madagascariensis* DC., which has notably lower concentrations of active ingredients (e.g. 1,4-naphthoquinones, flavonoids and ellagic acid derivatives) compared to *D. rotundifolia* (Krenn *et al*. 1995, Blaschek 1998, Zehl *et al*. 2011, Bäumler 2012).

Current research is increasingly focusing on propagation and cultivation (mainly *in vitro*) of European and non-European sundews. However, these cultivation methods are time-consuming and costly. Recently, the establishment of *Sphagnum* farming areas (Gaudig *et al*. 2014, Krebs *et al*. 2014) has created large artificial habitats where *Drosera* grows in semi-natural conditions. In this article we report work on *Drosera* plants from a *Sphagnum* farming area. Our purposes are:

1. to quantify the biologically active compounds 7-methyljuglone, plumbagin and quercetin;
2. to assess whether the plants have the required minimum concentration of naphthoquinone derivatives; and
3. to determine whether the concentrations of biologically active compounds differ:
   a. over the course of the day;
   b. over the course of the main flowering season (July–August);
   c. with plant age; and
   d. between wild and cultivated populations.

The aim is to identify the most promising populations and harvesting times for sundew.

MATERIALS AND METHODS

Plant material

Entire green parts and roots of *Drosera rotundifolia* and *D. intermedia* were collected in July and August from an artificially established *Sphagnum palustre* L. and *S. papillosum* Lindb. lawn on a rewetted raised bog area near Rastede, NW Germany (53° 15′ 80″ N, 08° 16′ 05″ E). Most of the *Drosera* plants collected (Samples 1–40, 'wild') had germinated from seeds imported, unplanned, with the *Sphagnum* material. A small number of plants (Samples 41–44, 'cultivated') had been established by sowing seeds in cellulose germinating pots placed in the *Sphagnum* lawn. Both 'wild' and 'cultivated' plants were harvested in 2014. A voucher specimen of each species was deposited in the University of Greifswald herbarium under Nos. GFW 51151 (*D. intermedia* Hayne) and GFW 51152 (*D. rotundifolia* L.). Plants of three age groups (≤6 months, 6–12 months, 13–24 months) were harvested at two different times of day (7:00–8:00 h and 15:00–16:00 h) during July and August 2014 (Table 1). Individual plants were grouped by age category using descriptions and images in Nitschke (1860), Drude (1891), Diels (1906) and Bertsch (1912), supplemented by our own observations at the study site.

Extract preparation

The plant material was dried at 40 °C for 72 hours in a Memmert Cleanroom drying oven and ground in a hand-powered drug mill to produce a fine powder. This material (200 mg of each plant) was extracted

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Table 1: Comparison of the 19 test groups. Core criteria are highlighted in bold: **G1** and **G2**: wild *versus* cultivated; **G3–G6**: for both *Drosera* species collection time 07–08 h *versus* 15–16 h; **G7–G12**: for both *Drosera* species plant age ≤ 6 *versus* 6–12 *versus* 13–24 months; **G9**, **G12**, **G13**: for (partially) both *Drosera* species in bloom *versus* not in bloom, **G14–G19**: age of plant at collection. Abbreviations: **x** = naphthoquinone concentration based on either plumbagin or 7-methyljuglone; **7-MJ** = 7-methyljuglone; **P** = plumbagin; **Flav**. = quercetin; **rot** = *Drosera rotundifolia*, **int** = *D. intermedia*.

Group	Samples included	n	Species[1]	Type	Collection time		Age (months)	In flower (%)	Concentration in % dry weight			
					Hour of day	Month			Naphthoquinone	P	7-MJ	Flavonoid
G1	13–16	4	rot	**wild**	07–08	July/August	6–12	0	0.140 ± 0.042		x	0.100 ± 0.055
G2	41 –44	4	rot	**cultivated**	07–08	July/August	6–12	0	0.131 ± 0.022		x	0.097 ± 0,031
G3	2,3,9,10,17,19	6	**rot**	wild	**15–16**	July/August	6–24	0	0.140 ± 0.021		x	0.095 ± 0.027
G4	5,6,13,14,21,23	6	**rot**	wild	**07–08**	July/August	6–24	0	0.147 ± 0.031		x	0.111 ± 0.049
G5	25,27,29,31,33,35	6	**int**	wild	**15–16**	July/August	6–24	0	0.908 ± 0.141	x		0.044 ± 0.013
G6	26,28,30,32,34,36	6	**int**	wild	**07–08**	July/August	6–24	0	0.938 ± 0.125	x		0.044 ± 0.005
G7	2,4,6,7	4	**rot**	wild	15–16 / 07–08	July/August	**≤6**	0	0.129 ± 0.028		x	0.110 ± 0.024
G8	9–12	4	**rot**	wild	15–16	July/August	**6–12**	0	0.143 ± 0.034		x	0.077 ± 0.034
G9	21–24	4	**rot**	wild	07–08	July/August	**13–24**	**30–40**	0.158 ± 0.025		x	0.141 ± 0.038
G10	25–28	4	**int**	wild	15–16 / 07–08	July/August	**≤6**	0	0.752 ± 0.439	x		0.038 ± 0.003
G11	29–32	4	**int**	wild	15–16 / 07–08	July/August	**6–12**	0	0.812 ± 0.155	x		0.048 ± 0.012
G12	33–36	4	**int**	wild	15–16 / 07–08	July/August	**13–24**	**30–40**	0.946 ± 0.091	x		0.047 ± 0.008
G13	37–40	4	**rot**	wild	07–08	July/August	13–24	**60–70**	0.184 ± 0.077		x	0.106 ± 0.045
G14	1,2,5,6	4	rot	wild	15–16 / 07–08	**July**	**≤6**	0	0.109 ± 0.040		x	0.080 ± 0.054
G15	3,4,7,8	4	rot	wild	15–16 / 07–08	**August**	**≤6**	0	0.153 ± 0.026		x	0.087 ± 0.030
G16	9,10,13,14	4	rot	wild	15–16 / 07–08	**July**	**6–12**	0	0.137 ± 0.023		x	0.088 ± 0.033
G17	11,12,15, 16	4	rot	wild	15–16 / 07–08	**August**	**6–12**	0	0.172 ± 0.068		x	0.090 ± 0.059
G18	17,18,21, 22	4	rot	wild	15–16 / 07–08	**July**	**13–24**	0	0.145 ± 0.037		x	0.116 ± 0.030
G19	19,20,23, 24	4	rot	wild	15–16 / 07–08	**August**	**13–24**	0	0.161 ± 0.111		x	0.111 ± 0.057

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three consecutive times (3 hours each) with 10 ml of methanol using a magnetic stirrer (1000 rpm) at room temperature in darkness. The three extracts of each sample were combined, evaporated to dryness, lyophilised and stored at -20 °C.

General analytical procedures

For analytical liquid chromatography-mass spectrometry (LC-MS), a Shimadzu system (pumps LC-20AD, column oven CTO-10ASVP, autosampler SIL-10AF, DAD SPD-M20AD, LCMS-8030 mass spectrometer) using LabSolutions LCMS 5.75 SP2 software was utilised under the following conditions: Synergy 4 µ PolarRP 250 x 4.6 mm (Phenomenex) HPLC column, sample concentration 6 mg ml^{-1} (extract/methanol), injection volume 25 µl, oven temperature 25 °C, gradient elution with acetonitrile/water each acidified with 0.05 % formic acid, gradient sequence (time in min / % acetonitrile) 0/13, 5/16, 26/19.3, 50/80, 51/100, 52/13, 57/13, detection at 254 nm, MS ionisation mode ESI (for quercetin) and Atmospheric Pressure Chemical Ionization (APCI) (for 7-methyljuglone and plumbagin). A single determination was made for each individual sample.

The presence of 7-methyljuglone, plumbagin and quercetin was identified with the help of reference samples and comparison of retention times, UV-spectra and mass spectral data. Quantities were determined by manual integrated peak areas of HPLC-chromatograms using linear equations obtained from calibration with reference samples. Only the main naphthoquinone compounds that could be unambiguously identified by the analysis are included (*D. rotundifolia*: 7-methyljuglone; *D. intermedia*: plumbagin).

Statistical analysis

The results were combined into 19 groups (n = 4 or 6, Table 1) and concentration expressed as mean ± SD. Differences between groups were determined using one-way ANOVA (choosing $P < 0.05$ as statistically significant) and the Kruskal-Wallis test, using R version 3.1.3 (R Development Core Team 2015).

RESULTS

The wild grown (G_1) and cultivated (G_2) *D. rotundifolia* plants showed no statistically significant differences in naphthoquinone (NQ) and flavonoid (Fl) concentration (NQ: $\chi^2 = 0.083$, d.f. = 1, $P = 0.772$, Fl: $\chi^2 = 0$, d.f. = 1, $P = 1$, Kruskal-Wallis test) (Table 2). Highly significant differences were found between the two species (G_3–G_6) in both NQ and Fl concentration ($n = 22$, $P < 0.001$), with *D. intermedia* having six times higher concentrations of NQ than *D. rotundifolia*. No statistically significant differences were found between plants collected at different times during the day (Table 3).

Both species ($G_7 - G_{12}$), showed a consistent increase in NQ and Fl concentrations with age (e.g. *D. rotundifolia* with 0.129, 0.143 and 0.158 % NQ concentration for plants ≤ 6, 6–12, and 13–24 months old, respectively. However the differences between the age classes were not significant ($F = 0.98$; $n = 12$; $P = 0.410$, ANOVA). The NQ concentration also increased with the amount of flowering plants in the sample ($G_{18–19} < G_9 < G_{13}$) but again the differences were not statistically significant ($F = 0.70$; $n = 16$; $P = 0.510$).

In flowering plants the Fl concentration is lower ($G_{18–19} < G_9 > G_{13}$) and the NQ concentration higher ($G_{18–19} < G_9 < G_{13}$) than in non-flowering *Drosera* plants (Table 4). The difference between G_9 (flowering *D. rotundifolia*) and G_{12} (flowering *D. intermedia*) is statistically significant for both NQ and Fl (NQ and Fl: $\chi^2 = 5.333$, d.f. = 1, $P = 0.029$). From July to August, the concentration of bioactive compounds tends to increase (G_{14}–G_{19}, Table 1), but the differences are not statistically significant (NQ and Fl: $n = 24$, $P > 0.05$).

DISCUSSION

This is the first analysis of the concentrations of plumbagin, 7-methyljuglone and quercetin in sundew as a function of time of day and plant age. The time of collection of wild plants determines the concentration and quality of the bioactive compounds and thence the market price of the pharmaceutical drug Droserae Herba. This study shows that the concentration of bioactive compounds in cultivated plants does not differ from those in plants growing spontaneously ('wild'), and are constant over the day so that plants may be collected at any time of day without loss of quality. The concentrations in both *D. rotundifolia* and *D. intermedia* do not differ between July and August, but do increase with age (although not significantly).

The required concentration of naphthoquinones for pharmacological purposes is 0.14–0.22 % (Wichtl 2009). This study shows (Table 1) that, in this semi-natural area, individual *D. rotundifolia* plants may reach this concentration within 12 months, but the majority of plants require 13–24 months. In *D. intermedia* the naphthoquinone (plumbagin) concentration (Table 1) is 1.3–1.6 times the required pharmacological minimum of 0.6 % (Krenn *et al*.

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Table 2: List of individual samples of *Drosera rotundifolia* and *Drosera intermedia*.

No.	Species	Type	Age (months)	Collection time		No.	Species	Type	Age (month)	Collection time	
				Hour of day	Month					Hour of day	Month
1	*D. rotundifolia*	wild	≤6	7:00–8:00	July	23	*D. rotundifolia*	wild	13–24	15:00–16:00	August
2	*D. rotundifolia*	wild	≤6	7:00–8:00	July	24	*D. rotundifolia*	wild	13–24	15:00–16:00	August
3	*D. rotundifolia*	wild	≤6	7:00–8:00	August	25	*D. intermedia*	wild	≤6	7:00–8:00	July
4	*D. rotundifolia*	wild	≤6	7:00–8:00	August	26	*D. intermedia*	wild	≤6	15:00–16:00	July
5	*D. rotundifolia*	wild	≤6	15:00–16:00	July	27	*D. intermedia*	wild	≤6	7:00–8:00	August
6	*D. rotundifolia*	wild	≤6	15:00–16:00	July	28	*D. intermedia*	wild	≤6	15:00–16:00	August
7	*D. rotundifolia*	wild	≤6	15:00–16:00	August	29	*D. intermedia*	wild	6–12	7:00–8:00	July
8	*D. rotundifolia*	wild	≤6	15:00–16:00	August	30	*D. intermedia*	wild	6–12	15:00–16:00	July
9	*D. rotundifolia*	wild	6–12	7:00–8:00	July	31	*D. intermedia*	wild	6–12	7:00–8:00	August
10	*D. rotundifolia*	wild	6–12	7:00–8:00	July	32	*D. intermedia*	wild	6–12	15:00–16:00	August
11	*D. rotundifolia*	wild	6–12	7:00–8:00	August	33	*D. intermedia*	wild	13–24	7:00–8:00	July
12	*D. rotundifolia*	wild	6–12	7:00–8:00	August	34	*D. intermedia*	wild	13–24	15:00–16:00	July
13	*D. rotundifolia*	wild	6–12	15:00–16:00	July	35	*D. intermedia*	wild	13–24	7:00–8:00	August
14	*D. rotundifolia*	wild	6–12	15:00–16:00	July	36	*D. intermedia*	wild	13–24	15:00–16:00	August
15	*D. rotundifolia*	wild	6–12	15:00–16:00	August	37	*D. rotundifolia*	wild	13–24	15:00–16:00	July
16	*D. rotundifolia*	wild	6–12	15:00–16:00	August	38	*D. rotundifolia*	wild	13–24	15:00–16:00	July
17	*D. rotundifolia*	wild	13–24	7:00–8:00	July	39	*D. rotundifolia*	wild	13–24	15:00–16:00	August
18	*D. rotundifolia*	wild	13–24	7:00–8:00	July	40	*D. rotundifolia*	wild	13–24	15:00–16:00	August
19	*D. rotundifolia*	wild	13–24	7:00–8:00	August	41	*D. rotundifolia*	cultivated	6–12	15:00–16:00	July
20	*D. rotundifolia*	wild	13–24	7:00–8:00	August	42	*D. rotundifolia*	cultivated	6–12	15:00–16:00	July
21	*D. rotundifolia*	wild	13–24	15:00–16:00	July	43	*D. rotundifolia*	cultivated	6–12	15:00–16:00	August
22	*D. rotundifolia*	wild	13–24	15:00–16:00	July	44	*D. rotundifolia*	cultivated	6–12	15:00–16:00	August

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Table 3: ANOVA of differences in concentration of naphthoquinones and flavonoid in *Drosera rotundifolia* (G_3–G_4) and *Drosera intermedia* (G_5–G_6) collected at different time of day (G3/G5 = 15–16h, G4/G6 = 07–08h). SS = type III sum of squares; *F* = Fisher's F-value; *P* = probability of significance. Mean values and SE are given in Table 1.

Groups	Naphthoquinone			Flavonoid		
	SS	*F*	*P*	SS	*F*	*P*
G3–G4	< 0.001	0.238	0.635	< 0.001	0.534	0.481
G5–G6	< 0.001	0.004	0.948	< 0.001	0.022	0.882

1995) and 135 times more, than the concentration of Droserae Herba sourced from *D. madagascariensis* DC. (Melzig *et al*. 2001). The 7-methyljuglone concentration from samples of flowering *D. rotundifolia* was 6.6–7.6 times higher, than from *D. madagascariensis* DC. (e.g.: 0.024 % in Melzig *et al*. 2001). Maximum concentrations are reached in the samples with 60–70 % flowering plants. Plants younger than one year old can be collected for pharmacological purposes during the flowering season, but efforts are better aimed at collecting older plants, particularly those in flower.

In conclusion, *Drosera* plants cultivated in cellulose germinating pots, placed in the *Sphagnum* lawn, showed no difference in either quality and quantity in regard to the concentration of the biologically active compounds, nor in the time needed for harvest, compared to the *Drosera* plants that occur spontaneously on the Sphagnum farming area. On Sphagnum farming sites cultivated *Drosera* offers new opportunities for the industrial production of *Drosera* under semi-natural conditions.

Table 4: The percentage distribution of naphthoquinone and flavonoid (= quercetin) concentration in 13–24 month-old *D. rotundifolia* plants, with different amount of flowering plants (G18–G19 = 0 %, G9 = 30–40 %, G13 = 60–70 %). Arrowheads show direction of decreasing concentration.

Group	n	Concentration % dry weight	
		Naphthoquinone	Flavonoid
G18–G19	8	0.153	0.113
-	-	∧	∧
G9	4	0.158	0.141
-	-	∧	∨
G13	4	0.184	0.106

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5
Biomass productivity and yield of *Drosera* on cultivated *Sphagnum* in NW Germany

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Mires and Peat (eingereicht im März 2020)

Biomass productivity and yield of *Drosera* on cultivated *Sphagnum* in NW Germany

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SUMMARY

Drosera from *Sphagnum* farms is a new and sustainable alternative to supplying the pharmaceutical industry with fresh *Drosera* raw material collected from the wild. *Sphagnum* farms provide large artificial habitats where *Drosera* species grow under semi-natural conditions. We measured 'biomass productivity' (total biomass of flowering and non-flowering plants) and 'yield' (only flowering plants) of *Drosera rotundifolia* and *D. intermedia* collected from cultivated *Sphagnum palustre* and *S. papillosum* lawn. In the studied sites 136 ± 122 plants m^{-2} (n = 46) were recorded with an average fresh weight of 0.21 ± 0.17 g/plant of *D. rotundifolia* (n = 5907) and 0.33 ± 0.26 g/plant of *D. intermedia* (n = 301). Fresh biomass productivity on *Sphagnum* farming areas was 275.0 ± 261.5 kg ha^{-1} yr^{-1} and fresh yield 214.2 ± 191.7 kg ha^{-1} yr^{-1}. Therewith fresh biomass productivity was 3 - 34 times and yield 2 - 21 times higher compared to natural habitats in Central and Northern Europe. The results of this study showed for *D. rotundifolia* the highest yields in July/August, when the highest proportion of flowering plants per area was recorded. For sustainable production, the annual selective harvest of plants older than 12 months is recommended.

KEY WORDS: sundew, peat moss, sustainable *Drosera* production, harvest date, plant age, biomass production, yield, paludiculture

INTRODUCTION

The herbaceous insectivorous genus *Drosera* L. (Droseraceae) is with 218 species present throughout the world (Carow 2005). In Central Europe, *Drosera rotundifolia* L., *D. intermedia* Hayne, *D. anglica* Hudson and their natural hybrids occur in nutrient-poor, strongly acidic to base-rich wetlands, often as pioneers (Crowder *et al*. 1990). These sundews are very small in size (0.02 - 0.6 g per plant) and their population densities vary greatly in nature (Galambosi *et al*. 2000a, b).

Only few studies report on *Drosera* biomass productivity and/or yield in Europe. For *Drosera rotundifolia* productivities were found of 1 - 5 kg dry weight ha^{-1} yr^{-1} in mire communities in S Finland (Vasander 1981, Liedenpohja 1981), of 6 - 11 kg dry weight ha^{-1} yr^{-1} in an ombrotrophic bog in central Sweden (Backéus 1985). Thum (1986) found productivities for *D. rotundifolia* of 13 kg dry weight ha^{-1} yr^{-1} and for *D. intermedia* of 15 kg dry weight ha^{-1} yr^{-1} on a small terrestrialization mire in SE Germany.

Galambosi *et al*. 2000b estimated a yield of *D. rotundifolia* between 10-111 kg fresh weight ha^{-1} yr^{-1} in nine mires in SE and N Finland.

Drosera plants have been used for centuries in the therapy of pulmonary diseases (Šamaj *et al*. 1999, Babula *et al*. 2009). Originally *D. rotundifolia* was the main constituent of the pharmaceutical drug ′Droserae herba′ (Baranyai *et al*. 2016), but its shrinking occurrences have resulted in other species (*D. intermedia*, *D. anglica*, *D. madagascariensis*) being increasingly used (Melzig *et al*. 2001, Hiller & Loew 2009, Baranyai & Joosten 2016). Currently, *Drosera rotundifolia* and *D. intermedia* are included in the European Red List of Threatened Plant Species (Khela 2012) and continuing collection from the wild may lead to further population reduction of these and other *Drosera* species (Baranyai & Joosten 2016).

Propagation and cultivation of *Drosera* have been tested, but the methods hitherto applied failed to be cost-effective (Baranyai 2016).

Over the last decade, the cultivation of *Sphagnum* has emerged as a climate-friendly land use alternative for drained and degraded bog land (Gaudig *et al*. 2014, 2018, Wichtmann *et al*. 2016). Such '*Sphagnum* farms' aim to produce raw material for horticultural growing media (Krebs *et al*. 2012) but also provide new habitats for *Drosera rotundifolia* L. and *D. intermedia* Hayne (Baranyai *et al*. 2016).

This study determines the potential of cultivated *Sphagnum* as production site for *Drosera*, investigates biomass productivity and harvestable yield of *D. rotundifolia* and *D. intermedia*, assesses the relationship between *Drosera* density and weight, and determines the optimum time and development stage for harvesting *Drosera*.

MATERIALS AND METHODS

The study was carried out on a 20 × 200 m large part of the Rastede *Sphagnum* farm (NW Germany, 53°15′80″ N, 08°16′05′′ E, 0.5 m below sea level, Gaudig *et al*. 2014, Temmink *et al*. 2017). Mean annual precipitation is 778 mm, mean annual temperature 8.7 °C (Climate-Data.org 2016). The study site consisted of two parts: one with *Sphagnum papillosum* (71% cover) and *S. fallax* (29%), the other with *S. palustre* (42%) and *S. fallax* (58%) with an average lawn height of 8.3 cm (maximum 22.4 cm, Wichmann *et al*. 2015). In low quantities *S. cuspidatum* and *S. fimbriatum* were found. Dominant vascular plant species (total cover < 25%) were *Juncus effusus* L. and *Drosera rotundifolia* L, additional species were *Drosera intermedia* Hayne, *Juncus bulbosus* L., *Carex canescens* L., *Rumex acetosella* L. s.l., *Rhynchospora alba* (L.) Vahl, *Eriophorum angustifolium* Honck., *Erica tetralix* L. and various Poaceae (Gaudig & Krebs 2016).

Whole *D. rotundifolia* and *D. intermedia* plants (incl. roots) were collected from randomly selected 1×1 m quadrates (n = 46) between the 14th and 18th of each month from June to September 2013 (monthly two quadrats in each type of *Sphagnum* vegetation) and from May to September 2014 (monthly three quadrats in each type of *Sphagnum* vegetation), and stored in a plastic bag (500 ml) at 8 ºC (± 4 ºC) for maximally one week until further processing. Only plants were collected that were visible at and over the moss surface.

On the day of harvest, we immediately measured the fresh weight of all individual *D. rotundifolia* and *D. intermedia* plants using a Kern EMB 600-2 precision balance (KERN & SOHN GmbH, Balingen, Germany).

Thereafter we assigned all plants to plant age classes (0-3, 3-6, 6-12, 12-24, >24 months) that was developed after descriptions and images of Nitschke (1860), Drude (1891), Diels (1906) and Bertsch (1912), see examples (Appendix: Figures A1-A3).We recorded 72.192 morphological data in total for this study measuring the following parameters: fresh weight of individual plants, total number of active/non-active leaves and flowering stems, length of the roots, and the petiole length from axil to the margin of the lamina. Active leaves are healthy and able to catch insects, or currently with insects, in comparison to non-active leaves, that are too young (not opened) or too old (dying off, brown) to catch insects.

We distinguished between flowering and non-flowering specimen as only the former contain commercially interesting concentrations of pharmaceutical compounds (Baranyai *et al*. 2016). We define 'biomass productivity' as the total *Drosera* biomass of the plots, including non-flowering and flowering plants as well as above-ground plant parts and roots. The biomass of flowering plants, including above-ground plant parts and roots, we considered to be collectable 'yields'. As flowers had sometimes been removed by mechanical weed control, we treated plants with (mature) stalks (but without flower) also as flowering plants.

We used boosted regression trees (BRT, Elith *et al*. 2008, Friedman 2001) for testing dependence of biomass productivity on age, harvest month, and peat moss species. We used 10-fold cross validation for model development and validation. Explanatory variables that did not improve the performance of the model were removed. A Pearson correlation test was used to explore the relationship between total fresh weight and the number of plants of *Drosera* per m^2. Differences between *Drosera* and *Sphagnum* species, and different years were determined using one-way ANOVA (choosing $P < 0.05$ as statistically significant) and the Kruskal-Wallis test, using R version 3.1.3 (R Development Core Team 2009).

RESULTS

Number of plants

The number of all *D. rotundifolia* plants (flowering/non-flowering) varied significantly with *Sphagnum* species ($\chi^2 = 4$; df = 4; $P = 0.406$; Kruskal-Wallis test), with an average of 189.9 ± 133.5 plants m^{-2} in *Sphagnum palustre* and 78.8 ± 76.8 plants m^{-2} in *S. papillosum* (Table 3). We registered on *S. papillosum* four times less *Drosera intermedia* plants (21.6 ± 25.4 plants m^{-2}, $n = 23$) than *D.rotundifolia*. In *S. palustre* plots no *D. intermedia* plants were registered.

The number of flowering *D. rotundifolia* plants for all months in both years (2013/14) were 67.9 ± 58.6 plants m^{-2} on both *Sphagnum* species, 92.4 ± 66.3 plants m^{-2} on *S. palustre* and 41.7 ± 37.6 plants m^{-2} on *S. papillosum* (Table 3). The highest density of flowering *D. rotundifolia* plants was recorded on *S. palustre* in July (122.8 ± 63.1 plants m^{-2}), the lowest on *S. papillosum* in August (19.0 ± 14.7 plants m^{-2}). On *S. papillosum*, four times less flowering *D. intermedia* plants (9.8 ± 11.2 plants m^{-2}, $n = 23$) occurred compared to flowering *D. rotundifolia*. In May 2014, no flowering *Drosera* plants were registered on both *Sphagnum* species.

D. rotundifolia density increased moderately from 2013 (128.1 ± 137.9 plants m^{-2}, n = 16) to 2014 (156.1 ± 120.6 plants m^{-2}, n = 30), whereas *D. intermedia* density dropped moderately (2013: 33.8 ± 16.8 plants m^{-2}, n = 8 and 2014: 16.8 ± 30.2 plants m^{-2}, n = 15).

Fresh plant weight

For 2013/14, the average weight of *D. rotundifolia* plants did not significantly differ between *S. palustre* (0.21 ± 0.17 g/plant) and *S. papillosum* plots (0.20 ± 0.16 g/plant) ($P < 0.05$, Figure 3, Table 1). The weight of flowering *D. rotundifolia* (0.32 ± 0.18 and 0.30 ± 0.16 g/plant) was twice as high than that of non-flowering plants (0.13 ± 0.11 and 0.13 ± 0.12 g/plant) for both years, respectively, Table 1). The plant weight of *D. rotundifolia* on *S. palustre* was 27% higher in 2013 than in 2014 (Table 1). On *S. papillosum* it was reversed with 5 % lower plant weight in 2013 than in 2014. Weights of *D. rotundifolia* plants were lower (0.20 ± 0.16 g/plant) on *S. papillosum* than those of *D. intermedia* (0.33 ± 0.26 g/plant) (Table 1 and 2).

Similar to *D. rotundifolia*, *D. intermedia* showed twice as much average plant weight of flowering than of non-flowering plants for both years. The total plant weight of *D. intermedia* was 6 % lower in 2014 than in 2013 (Table 2).

Mature plants of *D. rotundifolia* had a significantly higher total weight than younger plants (Figure 3). With increasing plant age, plant average weight increased proportionally (Figure 3). Morphological data showed that mature plants have more leaves, mostly flowering stems, and longer roots and petioles (Table A1 and A2 in the Appendix).

Average weight of *D. rotundifolia* plants was 0.48 ± 0.19 g/plant for plants older than 24 months (n = 709), 0.30 ± 0.10 g/plant for plants of 12-24 months old (n = 1516), 0.17 ± 0.07 g/plant for plants 6-12 months old (n = 1727), 0.08 ± 0.05 g/plant for plants 3-6 months old (n = 1391) and 0.02 ± 0.01 g/plant for plants 0-3 months old (n = 566). Average plant weight from both *Drosera* species increased from May to June, especially for plants older than 24 months, reached a maximum from June to August and decreased until September (Table A1-A3 in the Appendix). The same trend for plant weight per month was found for flowering *D. rotundifolia* plants, except that no flowering plants occurred in May (Figure A5 in the Appendix).

The number of plants per 1 m^2 was not correlated with the fresh weight of *Drosera* plants (*D. rotundifolia*: df = 5637; t = -2.84; P = 0.997; *D. intermedia*: df = 292; t = -1.59; P = 0.943), implying that higher plant densities do not cause lighter plants.

Table 1: Fresh weight of individual *Drosera rotundifolia* plants. Flowering = with mature stalk, Non-flowering = without stalk. harvest dates: June – September 2013 and May – September 2014 (n = 23 per *Sphagnum* species: 2013: 2 plots × 4 months, 2014: 3 plots × 5 months).

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		Sphagnum palustre			*Sphagnum papillosum*		
	year	Number of plants	Weight g ± SD	Weight 2013/14 g ± SD	Number of plants	Weight g ± SD	Weight 2013/14 g ± SD
Flowering	2013	622	0.35 ± 0.17	0.32 ± 0.18	88	0.28 ± 0.13	0.30 ± 0.16
	2014	1128	0.31 ± 0.18		537	0.30 ± 0.16	
Non-flowering	2013	725	0.18 ± 0.11	0.13 ± 0.11	100	0.12 ± 0.07	0.13 ± 0.12
	2014	1895	0.11 ± 0.11		812	0.13 ± 0.13	
Total	2013	1347	0.26 ± 0.17	0.21 ± 0.17	188	0.19 ± 0.13	0.20 ± 0.16
	2014	3023	0.19 ± 0.19		1349	0.20 ± 0.17	

Table 3: Biomass production of *Drosera rotundifolia* on *S. palustre* and *S. papillosum*. flowering = with stalk(s), non-flowering = without stalk(s), total = flowering + non-flowering plants, harvest dates: June – September 2013 and May – September 2014 (n = 23 per *Sphagnum* species: 2013: 2 plots × 4 months, 2014: 3 plots × 5 months).

		Number of plants N m^{-2} ± SD	Biomass per plant g ± SD	Biomass per plot g m^{-2} ± SD	Number of plants per kg ± SD
S. palustre	Flowering	92.4 ± 66.3	0.31 ± 0.18	29.6 ± 22.41	3,187 ± 692
	Non-flowering	113.9 ± 76.8	0.13 ± 0.11	14.94 ± 9.86	7,626 ± 2,009
	Total	189.9 ± 133.5	0.21 ± 0.17	39.29 ± 30.31	5,407 ± 1,953
S.papillosum	Flowering	41.7 ± 37.6	0.30 ± 0.16	12.52 ± 10.15	3,194 ± 536
	Non-flowering	48.0 ± 57.4	0.13 ± 0.12	5.82 ± 6.82	7,781 ± 2,130
	Total	78.8 ± 76.8	0.19 ± 0.16	15.27 ± 12.60	5,051 ± 1,172
S. palustre + *S.papillosum*	Flowering	67.9 ± 58.6	0.31 ± 0.17	21.42 ± 19.17	3,188 ± 604
	Non-flowering	86.7 ± 79.9	0.13 ± 0.11	11.21 ± 10.16	7,730 ± 2,043
	Total	135.6 ± 122.0	0.20 ± 0.17	27.50 ± 26.15	5,233 ± 1,611

Table 2: Fresh weight of individual *Drosera intermedia* plants in *Sphagnum papillosum*. flowering = with stalk(s), non-flowering = without stalk(s), harvest dates: June – September 2013 and May – September 2014 (n = 23: 2013: 2 plots × 4 months, 2014: 3 plots × 5 months).

	Year	Number of plants	Weight g ± SD	Weight 2013/14 g ± SD
Flowering	2013	68	0.46 ± 0.24	0.47 ± 0.29
	2014	40	0.48 ± 0.35	
Non-flowering	2013	66	0.22 ± 0.17	0.25 ± 0.21
	2014	127	0.27 ± 0.23	
Total	2013	134	0.34 ± 0.24	0.33 ± 0.26
	2014	167	0.32 ± 0.28	

Total fresh biomass and yield

Biomass productivity of *D. rotundifolia* showed a moderate but not statistically significant ($P > 0.05$) decrease from 31.8 ± 37.2 g m^{-2} in 2013 (n = 16) to 29.7 ± 21.8 g m^{-2} in 2014 (n = 30). Average biomass production was 15.3 ± 12.6 g m^{-2} in *S. papillosum* against 39.3 ± 30.3 g m^{-2} in *S. palustre* (n = 46, $P < 0.001$) for both years (Table 3). Biomass productivity of *D. intermedia* was 7.1 ± 7.9 g m^{-2} (2013/14). The fresh yield (i.e. the biomass of flowering plants) of *D. rotundifolia* was 21.4 ± 19.2 g m^{-2} over all observations plots (Table 3). The highest yields of *D. rotundifolia* were reached on *S. palustre* in July (42.1 ± 22.8 g m^{-2}) and August (39.5 ± 26.1 g m^{-2}) (n = 20, $P > 0.05$) (Figure 1). Yields of *D. rotundifolia* were not significantly different between years: 21.9 ± 25.6 g m^{-2} in 2013 and 22.1 ± 15.8 g m^{-2} in 2014, respectively (n = 40, $P > 0.05$). However, for both years *D. rotundifolia* yield was significant higher on *S. palustre* (31.3 ± 24.6 g m^{-2}) than on *S. papillosum*: (12.5 ± 10.2 g m^{-2}, n = 40, $P < 0.05$).

Generally, the fresh yield of *D. intermedia* was substantially lower than that of *D. rotundifolia*. The highest yields of *D. intermedia* were measured in July and August, but differences are not significant (5.1 ± 4.9 g m^{-2} and 6.0 ± 6.1 g m^{-2}, respectively, n = 10, $P > 0.05$) (Figure 2). For both years, *D. intermedia* yield on *S. papillosum* was 4.4 ± 4.8 g m^{-2}. The yield of *D. intermedia* reached 7.2 ± 6.6 g m^{-2} in 2013 and 2.7 ± 2.8 g m^{-2} in 2014. We found no *D. intermedia* plants on *S. palustre* in 2013 and 2014.

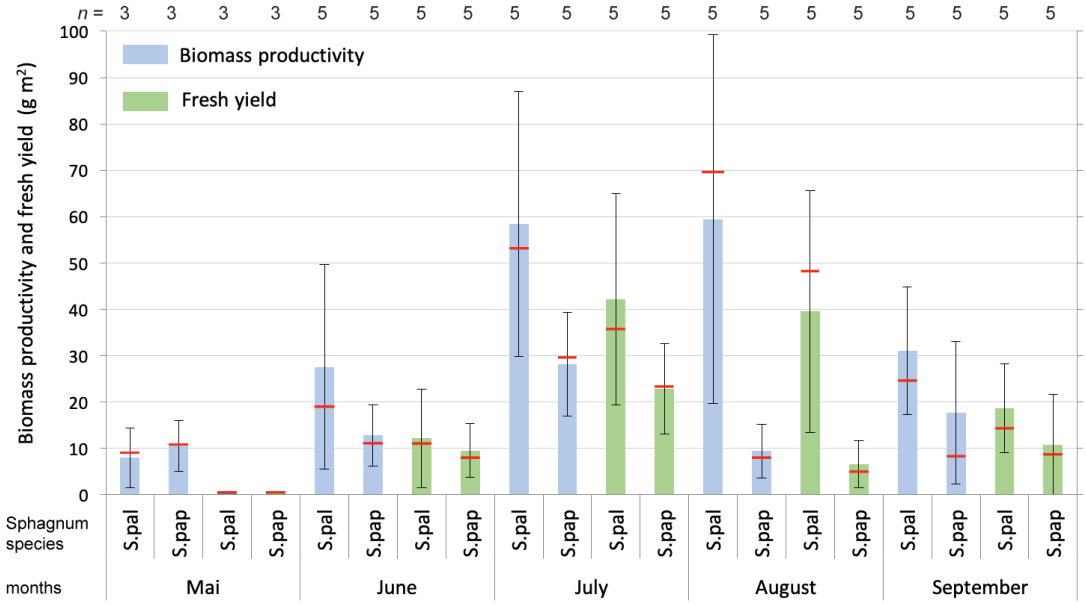

Figure 1: Biomass productivity and fresh yield of *Drosera rotundifolia* on *Sphagnum palustre* (S.pal) and *S. papillosum* (S.pap) between May/June – September in 2013 and 2014. Vertical bars show the means, the whiskers the SD, the red lines the medians. Number of replicates is written above each bar.

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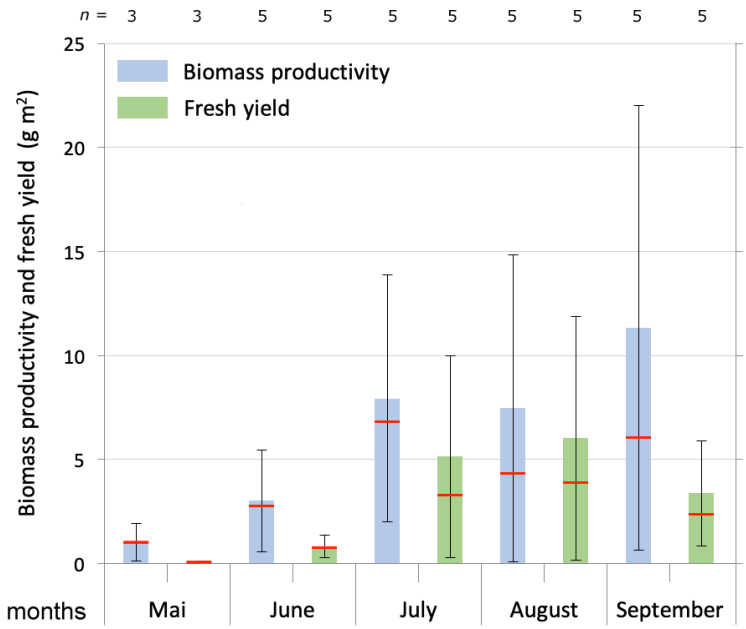

Figure 2. Biomass productivity and fresh yield of *Drosera intermedia* on *Sphagnum papillosum* between May/June – September in 2013 and 2014. Vertical bars show the means, the whiskers the SD, the red lines the medians. Number of replicates is written above each bar.

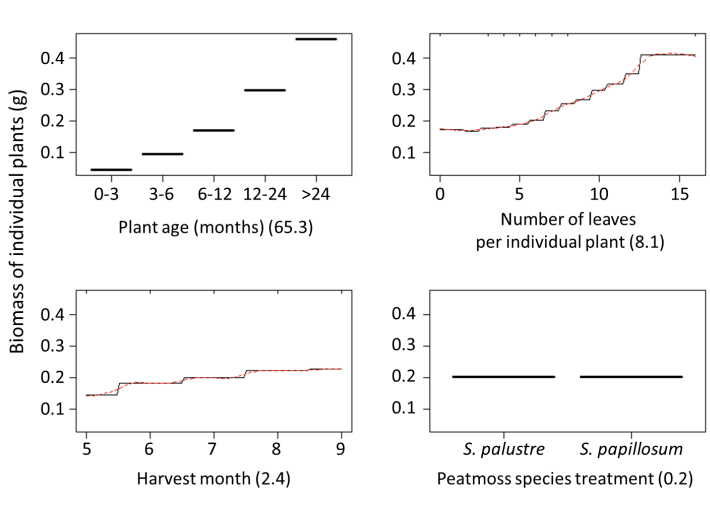

Figure 3: Boosted regression tree model of biomass productivity of *Drosera rotundifolia* (response variable) and predictor/ explanatory variables plant age, number of leaves per individual plant, harvest month and peat moss species. Percentages indicate the absolute contribution of the variable to the biomass productivity. The boosted regression tree model was performed with 5907 observations and 4 predictors, using Gaussian distribution, with tree complexity = 5 (sets the complexity of individual trees, interaction order), learning rate = 0.01 (sets the weight applied to individual trees, shrinkage factor), bag fraction = 0.75 (sets the proportion of observations used in selecting variables). The final model was fitted with a number of 1200 trees with an explained deviance = 0.7654.

DISCUSSION

This is the first study to assess biomass production and yield of *D. rotundifolia* and *D. intermedia* from the perspective of producing *Drosera* raw material for medicinal purposes on *Sphagnum* farming fields in Germany. The study shows that average plant numbers m^{-2} and biomass productivity as well as yield differ significantly for the two investigated *Sphagnum* species (*S. papillosum* < *S. palustre*), whereas no significant differences were observed for the average weight of individual plants. No correlation was found between the fresh weight of individual plants and their density (number m^{-2}).

This study shows that fresh biomass productivity of *Drosera rotundifolia* on *Sphagnum* farming fields was higher in comparison to natural habitats: 3 - 34 times higher than in boreal (Sweden, Finland) and 3 times higher than in nemoral mires (Germany), respectively (Vasander 1981, Liedenpohja 1981, Backéus 1985, Thum 1986). We found considerably less *D. intermedia* plants on the study area than *D. rotundifolia*. Biomass productivity of *D. intermedia* of this s,tudy reached 71 kg fresh weight ha^{-1} yr^{-1}. If we suppose that the dry weight : fresh weight ratio of *D. intermedia* is comparable to *D. rotundifolia* (app. 8:1, Baranyai & Joosten 2016) the biomass productivity of this study is app. 9 kg dry weight ha^{-1} yr^{-1}. It is slightly lower than the values of Thum (1986), also from Germany (15 kg ha^{-1} yr^{-1}). Other studies for productivity, yield and dry weight : fresh weight plant ratios of *D. intermedia* were not found for Europe.

Fresh yield of *D. rotundifolia* was 2 - 21 times higher (214.2 kg ha^{-1} yr^{-1}, Table 3), compared to Finnish peatlands (10 - 111 kg ha^{-1} yr^{-1}, Galambosi *et al*. 2000b). These findings are not surprising: The *Sphagnum* farming area provides, with its continuous openness (by regular mowing of vascular plants), constant wetness (by sophisticated water management) and *Sphagnum* dominated vegetation (Gaudig *et al*. 2018), a particularly attractive environment for *D. rotundifolia* (Baranyai & Joosten 2016). In natural mires, the higher cover of vascular plants outcompetes *Drosera* by shading and litterfall, and reduces insect availability (nutrient supply).

The production of one kg fresh *Drosera* drug in *Sphagnum* farming fields would require 3,188 ± 604 flowering plants (Table 3), this is on the lower range compared to peatlands in Spain (2,500-16,000 flowering plants, Lange 1998) or Finland (5,000–10,000 flowering plants, Galambosi *et al*. 2000b).

All studies, including ours, show a great variety in yield and productivity, with high standard deviations. Galambosi *et al*. (2000a) also found a great variety in plant density in natural peatlands, a phenomenon we could confirm for the *Sphagnum* farming fields in our study. To produce reliable data, many replicates are required of comparable sites (environments, peatland types), also with respect to climatic conditions. Currently, data on *Drosera* productivity and yield are extremely rare, and additionally some of them include various peatland types and habitats.

Concerning biomass production and yield, this study shows that the optimum harvest time for *D. rotundifolia* is July and August (Figure 1). In the middle of summer both *Drosera* species reach their growth maximum, which culminates in the development of one or more flowering stems with flowers, more leaves with longer petioles, and more roots (Table A1-A3 in the Appendix). For that reason, both *Drosera* species reach the highest biomass weight per plant as well as the highest yield per hectare in July and August.

The largest weight of the non-flowering and flowering *D. rotundifolia* was reached by plants of >24 months old, followed with a short distance by plants of 12-24 months old. Plants of 6-12 months old will reach that 2-3 times larger weight one year later (Figure A4 and Figure A5 in the Appendix). Our study implies that, in order to ensure a long-term stable population and a sustainable harvest, only plants should be collected, that are at least 12 months old. These findings are in harmony with results of Baranyai *et al*. (2016), who found that *Drosera* flowering plants older than 12 months reach the required concentrations of bioactive compounds for medicinal purposes also in July and August.

In conclusion, the present results clearly show that *Drosera* species occur in high abundances in *Sphagnum* farming areas. To allow a long-term sustainable production of *Drosera*, constantly high biomass yields of flowering plants are required every year. This study shows that these conditions are ensured when plants are harvested in July/August that are more than 12 months old.

Sphagnum farming areas, as wet agricultural land use systems, have a high potential for commercial cultivation of *Drosera* under controlled conditions in the nemoral zone. In our opinion, such cultivation could also be applied in other regions of Europe, e.g. in the boreal zone, but this would require further research. Additionally, cost/benefit analysis must show whether the cultivation of *D. rotundifolia* together on/with *Sphagnum* is economically feasible. A cost-efficient production of European *Drosera* species (e.g.

D. rotundifolia and *D. intermedia*) could totally or partly substitute the hitherto wild collected *Drosera* material.

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Appendix

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Figure A1. *Drosera intermedia* plants ordered by age classes a) 0-3, b) 3-6, c) 6-12, d) 12-24 and e) >24 months old. Collected on *Sphagnum* farming area (Rastede, NW Germany) in *Sphagnum papillosum* lawn. Collected and determined by Balázs Baranyai. Date: 17th August 2014.

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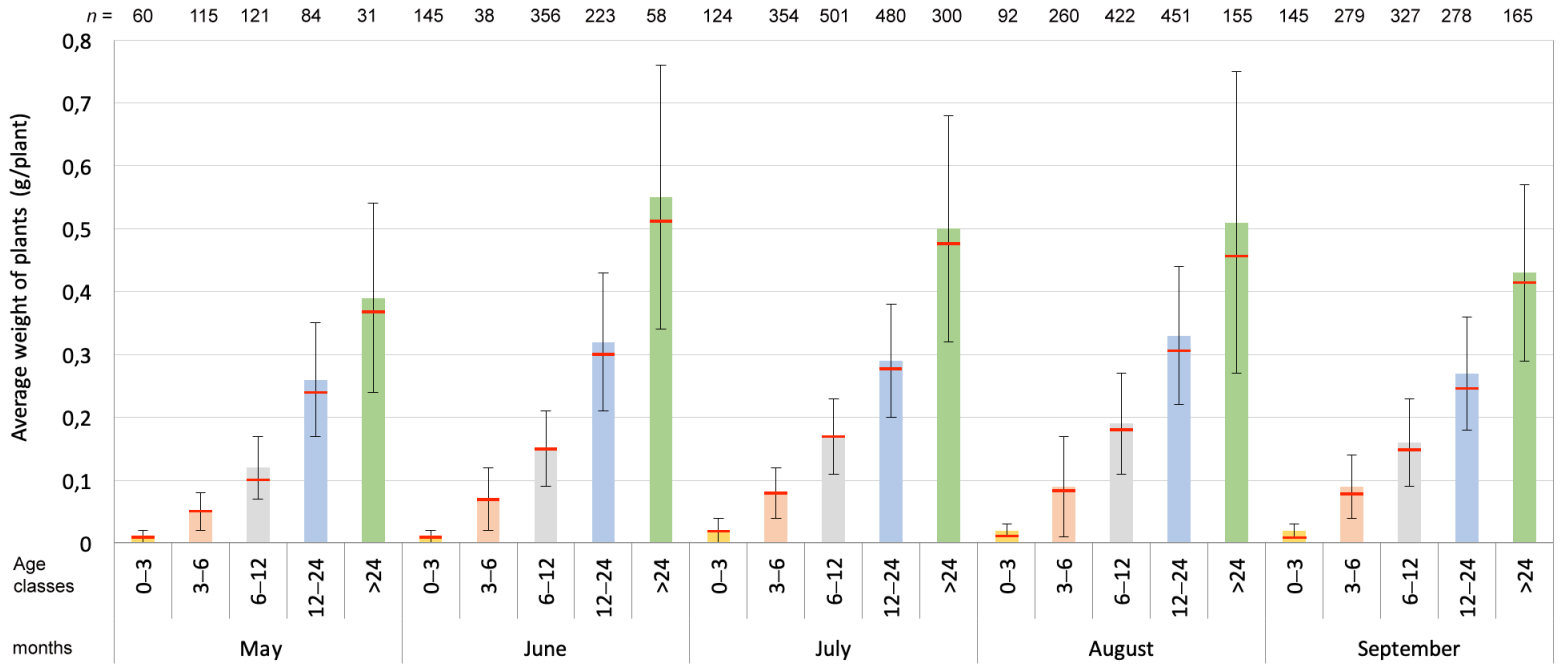
Figure A2. *Drosera rotundifolia* plants ordered by age classes a) 0-3, b) 3-6 and c) 6-12 months old. Collected on *Sphagnum* farming area (Rastede, NW Germany) in *Sphagnum palustre* lawn. Collected and determined by Balázs Baranyai. Date: 17th August 2014.

Figure A3. *Drosera rotundifolia* plant age classes d) 12-24 and e) >24 months old with two rosettes from the previous year (2013) and the year of collection (2014). Collected on *Sphagnum* farming area (Rastede, NW Germany) in *Sphagnum palustre* lawn. Collected and determined by Balázs Baranyai. Date: 17th August 2014.



350 Figure A4. Fresh weight of individual *Drosera rotundifolia* plants (flowering and non-flowering) growing on *Sphagnum palustre* and on *S. papillosum* ordered by age class (0-3, 3-6, 6-12, 12-24, >24 months old), collected between May/June – September in 2013 and 2014. Vertical bars show the means, the whiskers the SD, the red lines the medians. Number of replicates (n) is written over each bar.

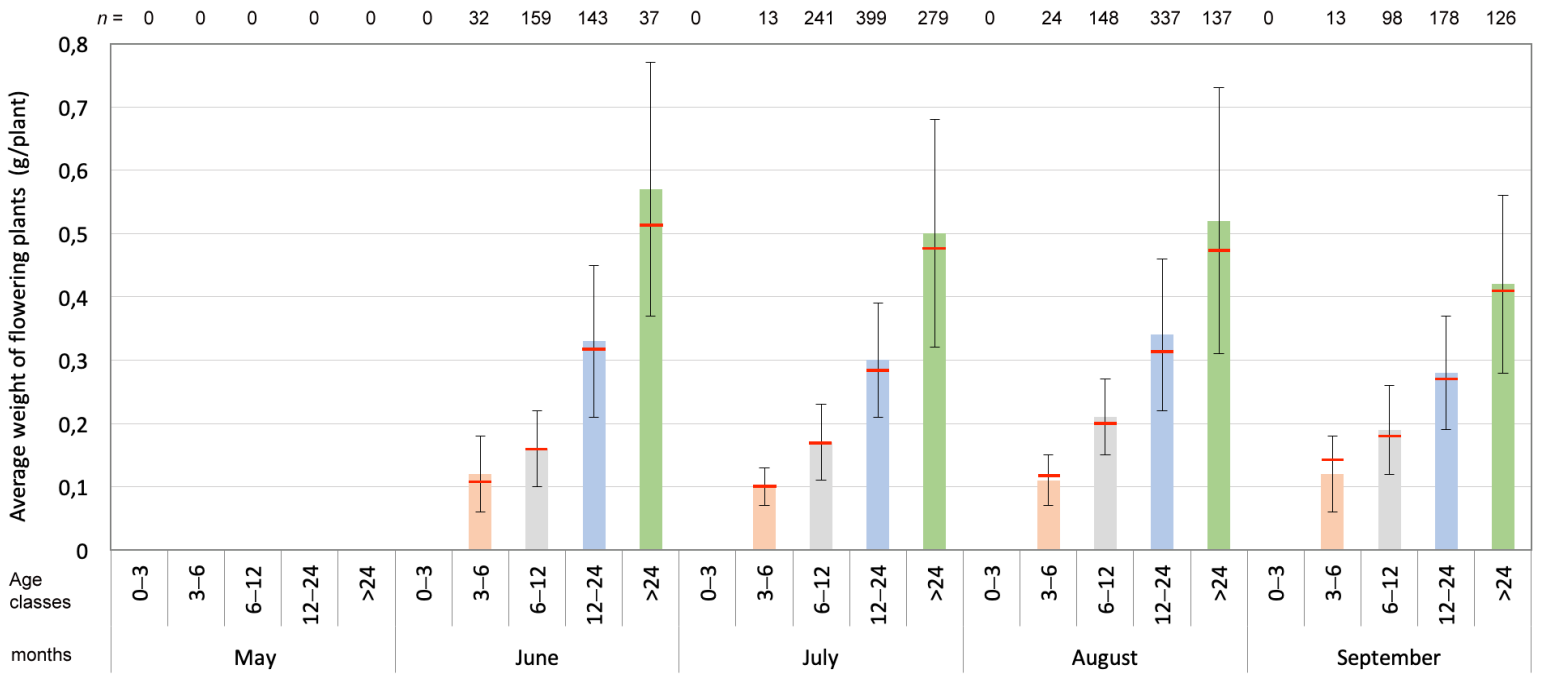


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Figure A5. Fresh weight of individual flowering *Drosera rotundifolia* plants growing on *Sphagnum palustre* and on *S. papillosum* ordered by age class (0-3, 3-6, 6-12, 12-24, >24 months old), collected between May/June – September in 2013 and 2014. Vertical bars show the means, the whiskers the SD, the red lines the medians. Number of replicates (n) is written over each bar.

Table A1. Morphological features of *Drosera rotundifolia* growing in 2013 and 2014 on cultivated *Sphagnum palustre*. *n* = Number of individual plants

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	Age class month	n	Fresh weight g ± SD	Total number of leaves N ± SD	Active leaves N ± SD	Non-active leaves N ± SD	Petiole length mm ± SD	Number of flower stems N ± SD	Length of roots mm ± SD
Mai	0-3	28	0.02 ± 0.03	3.46 ± 0.74	2.36 ± 0.62	1.11 ± 0.50	9.39 ± 2.90	0.0 ± 0.0	12.53 ± 7.13
	3-6	79	0.05 ± 0.03	4.59 ± 0.91	3.09 ± 0.82	1.51 ± 0.73	14.51 ± 2.92	0.0 ± 0.0	18.02 ± 5.84
	6-12	61	0.10 ± 0.04	5.26 ± 0.96	3.57 ± 0.81	1.69 ± 0.72	16.81 ± 2.94	0.0 ± 0.0	27.51 ± 12.33
	12-24	37	0.25 ± 0.09	7.08 ± 1.52	4.69 ± 1.09	2.39 ± 0.90	20.77 ± 3.15	0.0 ± 0.0	23.35 ± 11.35
	>24	10	0.39 ± 0.20	7.70 ± 2.00	5.60 ± 1.65	2.10 ± 0.74	22.10 ± 3.88	0.0 ± 0.0	30.93 ± 19.56
June	0-3	128	0.01 ± 0.01	3.62 ± 0.84	2.24 ± 0.70	1.39 ± 0.66	11.75 ± 4.66	0.0 ± 0.0	17.25 ± 8.23
	3-6	330	0.07 ± 0.05	4.96 ± 1.15	3.30 ± 0.95	1.66 ± 0.79	19.10 ± 5.70	0.08 ± 0.28	22.02 ± 9.64
	6-12	284	0.15 ± 0.06	6.12 ± 1.26	4.25 ± 1.15	1.87 ± 0.91	26.03 ± 5.86	0.45 ± 0.51	27.97 ± 12.26
	12-24	153	0.30 ± 0.11	7.29 ± 1.69	5.10 ± 1.43	2.20 ± 1.11	31.73 ± 6.24	0.61 ± 0.61	28.79 ± 13.84
	>24	43	0.51 ± 0.19	8.58 ± 2.14	5.88 ± 1.66	2.70 ± 1.57	31.68 ± 5.38	0.70 ± 0.77	33.04 ± 16.01
July	0-3	70	0.03 ± 0.02	3.46 ± 0.76	1.94 ± 0.63	1.51 ± 0.76	11.07 ± 4.05	0.00 ± 0.00	20.05 ± 11.35
	3-6	254	0.08 ± 0.04	4.59 ± 1.06	2.76 ± 0.81	1.83 ± 0.84	17.17 ± 5.40	0.03 ± 0.17	24.26 ± 10.40
	6-12	338	0.17 ± 0.05	5.43 ± 1.24	3.34 ± 0.95	2.09 ± 0.92	22.59 ± 5.87	0.39 ± 0.51	28.23 ± 11.74
	12-24	335	0.29 ± 0.09	6.11 ± 1.44	3.87 ± 1.14	2.25 ± 1.08	28.82 ± 5.09	0.87 ± 0.50	31.14 ± 12.63
	>24	221	0.51 ± 0.19	7.67 ± 1.93	4.92 ± 1.72	2.74 ± 1.36	35.31 ± 5.99	1.35 ± 0.67	37.99 ± 15.96

Table A1. Morphological features of *Drosera rotundifolia* growing in 2013 and 2014 on cultivated *Sphagnum palustre*.

	Age class month	n	Fresh weight g ± SD	Total number of leaves N ± SD	Active leaves N ± SD	Non-active leaves N ± SD	Petiole length mm ± SD	Number of flower stems N ± SD	Length of roots mm ± SD
August	0-3	81	0.02 ± 0.01	3.46 ± 0.57	1.90 ± 0.68	1.56 ± 0.59	9.99 ± 3.76	0.0 ± 0.0	23.52 ± 12.62
	3-6	231	0.10 ± 0.04	4.36 ± 0.89	2.81 ± 0.77	1.55 ± 0.78	17.07 ± 5.33	0.10 ± 0.33	31.59 ± 14.15
	6-12	385	0.20 ± 0.08	5.12 ± 1.13	3.41 ± 0.84	1.71 ± 0.84	21.59 ± 6.12	0.40 ± 0.57	33.96 ± 13.00
	12-24	389	0.32 ± 0.12	5.87 ± 1.39	4.04 ± 1.26	1.83 ± 0.95	27.73 ± 6.15	1.11 ± 0.86	37.50 ± 14.58
	>24	142	0.51 ± 0.25	7.53 ± 1.87	5.18 ± 1.64	2.35 ± 1.00	34.51 ± 7.12	1.50 ± 0.91	35.55 ± 13.14
September	0-3	66	0.02 ± 0.01	2.97 ± 0.93	1.95 ± 0.79	1.03 ± 0.65	8.47 ± 3.76	0.0 ± 0.0	17.82 ± 7.66
	3-6	186	0.09 ± 0.05	2.74 ± 1.29	1.91 ± 1.04	0.87 ± 0.85	15.37 ± 4.59	0.06 ± 0.24	32.67 ± 14.16
	6-12	210	0.16 ± 0.07	4.06 ± 2.29	2.96 ± 1.67	1.16 ± 1.15	19.45 ± 4.85	0.33 ± 0.52	37.31 ± 17.10
	12-24	187	0.27 ± 0.09	3.82 ± 2.25	2.92 ± 1.84	0.96 ± 1.05	23.31 ± 5.78	0.87 ± 0.75	42.44 ± 15.67
	>24	124	0.43 ± 0.13	5.21 ± 3.04	3.96 ± 2.50	1.28 ± 1.50	27.82 ± 6.50	1.49 ± 1.09	48.27 ± 16.16

Table A2. Morphological features of *Drosera rotundifolia* growing in 2013 and 2014 on cultivated *Sphagnum papillosum*. *n* = Number of individual plants

	Age class month	n	Fresh weight g ± SD	Total number of leaves N ± SD	Active leaves N ± SD	Non-active leaves N ± SD	Petiole length mm ± SD	Number of flower stems N ± SD	Length of roots mm ± SD
Mai	0-3	32	0.01 ± 0.00	3.47 ± 0.76	2.34 ± 0.60	1.13 ± 0.49	8.65 ± 2.29	0.0 ± 0.0	13.83 ± 7.25
	3-6	36	0.06 ± 0.04	4.77 ± 1.11	3.09 ± 0.85	1.69 ± 0.83	13.01 ± 2.55	0.0 ± 0.0	17.91 ± 11.08
	6-12	60	0.13 ± 0.05	5.92 ± 1.42	3.93 ± 1.16	1.98 ± 0.85	14.76 ± 2.95	0.0 ± 0.0	28.90 ± 10.91
	12-24	47	0.27 ± 0.09	7.26 ± 2.07	4.68 ± 1.55	2.57 ± 1.21	18.98 ± 3.74	0.0 ± 0.0	37.17 ± 14.32
	>24	21	0.40 ± 0.13	9.05 ± 2.18	5.48 ± 1.78	3.57 ± 1.57	20.44 ± 3.14	0.0 ± 0.0	29.78 ± 18.06
June	0-3	17	0.02 ± 0.01	4.12 ± 0.93	2.53 ± 0.80	1.59 ± 0.62	10.15 ± 2.73	0.0 ± 0.0	12.99 ± 6.85
	3-6	53	0.08 ± 0.05	5.08 ± 1.40	3.30 ± 1.17	1.77 ± 0.82	16.39 ± 4.41	0.08 ± 0.27	22.22 ± 9.91
	6-12	72	0.16 ± 0.07	6.15 ± 1.46	4.00 ± 1.16	2.15 ± 0.93	20.47 ± 4.98	0.46 ± 0.56	27.76 ± 15.36
	12-24	70	0.37 ± 0.12	7.40 ± 1.30	5.24 ± 1.45	2.16 ± 1.09	26.54 ± 5.51	0.96 ± 0.52	37.09 ± 17.54
	>24	15	0.65 ± 0.22	8.20 ± 1.47	6.47 ± 1.73	1.73 ± 1.16	28.30 ± 6.22	1.60 ± 0.63	38.49 ± 15.26
July	0-3	54	0.02 ± 0.01	3.31 ± 0.79	2.06 ± 0.83	1.25 ± 0.52	7.70 ± 2.96	0.0 ± 0.0	17.55 ± 8.24
	3-6	100	0.08 ± 0.03	4.77 ± 1.10	3.17 ± 0.90	1.61 ± 0.79	14.15 ± 4.39	0.05 ± 0.22	23.87 ± 9.49
	6-12	163	0.16 ± 0.06	4.99 ± 1.31	3.15 ± 1.16	1.83 ± 0.88	19.69 ± 5.41	0.71 ± 0.50	23.76 ± 9.88
	12-24	145	0.29 ± 0.09	5.82 ± 1.56	3.81 ± 1.33	2.01 ± 1.08	25.20 ± 6.07	1.25 ± 0.64	29.94 ± 12.74
	>24	79	0.46 ± 0.14	6.56 ± 2.09	4.35 ± 1.64	2.21 ± 1.06	29.34 ± 6.89	1.62 ± 0.70	37.92 ± 14.94

365 Table A2. Morphological features of *Drosera rotundifolia* growing in 2013 and 2014 on cultivated *Sphagnum papillosum*.

	Age class month	n	Fresh weight g ± SD	Total number of leaves N ± SD	Active leaves N ± SD	Non-active leaves N ± SD	Petiole length mm ± SD	Number of flower stems N ± SD	Length of roots mm ± SD
August	0-3	11	0.01 ± 0.01	3.18 ± 0.60	2.18 ± 0.75	1.00 ± 0.63	7.35 ± 2.15	0.0 ± 0.0	15.99 ± 5.11
	3-6	29	0.09 ± 0.05	4.69 ± 0.81	3.24 ± 0.95	1.45 ± 0.78	13.68 ± 3.05	0.07 ± 0.26	25.49 ± 11.77
	6-12	37	0.18 ± 0.06	5.68 ± 1.38	3.92 ± 1.01	1.76 ± 0.76	17.22 ± 4.50	0.30 ± 0.46	31.89 ± 14.48
	12-24	62	0.33 ± 0.10	6.48 ± 1.26	4.65 ± 1.01	1.84 ± 0.98	22.96 ± 4.08	1.08 ± 0.71	38.88 ± 16.91
	>24	13	0.56 ± 0.11	7.08 ± 1.26	5.00 ± 0.82	2.08 ± 0.76	27.16 ± 3.22	2.23 ± 0.73	55.75 ± 17.85
September	0-3	79	0.02 ± 0.01	3.03 ± 0.75	2.22 ± 0.65	0.81 ± 0.60	8.31 ± 4.44	0.00 ± 0.00	16.62 ± 8.90
	3-6	93	0.08 ± 0.04	3.28 ± 1.12	2.59 ± 0.95	0.70 ± 0.79	12.18 ± 2.99	0.02 ± 0.15	24.50 ± 10.48
	6-12	117	0.17 ± 0.07	3.24 ± 1.28	2.49 ± 0.97	0.76 ± 0.85	16.30 ± 5.33	0.30 ± 0.50	34.86 ± 15.63
	12-24	91	0.27 ± 0.11	3.42 ± 1.64	2.75 ± 1.09	0.66 ± 0.93	18.28 ± 4.31	0.96 ± 0.95	36.30 ± 12.57
	>24	41	0.42 ± 0.19	6.10 ± 3.22	4.34 ± 2.25	1.76 ± 1.45	22.16 ± 7.01	1.07 ± 0.88	38.94 ± 16.71

Table A3. Morphological features of *Drosera intermedia* growing in 2013 and 2014 on cultivated *Sphagnum papillosum*. In September 2013 and 2014 the length of roots was not measured. *n* = Number of individual plants

	Age class month	n	Fresh weight g ± SD	Number of flower stems ± SD	Length of roots mm ± SD		n	Fresh weight g ± SD	Number of flower stems N ± SD	Length of roots mm ± SD		n	Fresh weight g ± SD	Number of flower stems N ± SD
Mai	3-6	1	0.06 ± 0.00	0.0 ± 0.0	15.7 ± 0.00	July	8	0.07 ± 0.04	0.0 ± 0.0	19.20 ± 6.96	September	12	0.06 ± 0.03	0.0 ± 0.0
	6-12	4	0.11 ± 0.05	0.0 ± 0.0	37.03 ± 11.99		29	0.20 ± 0.10	0.43 ± 0.50	18.32 ± 8.73		34	0.14 ± 0.07	0.12 ± 0.41
	12-24	4	0.39 ± 0.11	0.0 ± 0.0	44.98 ± 19.73		26	0.35 ± 0.14	0.85 ± 0.55	19.94 ± 8.03		44	0.36 ± 0.19	0.18 ± 0.50
	>24	0	-	-	-		23	0.70 ± 0.24	1.09 ± 0.83	33.74 ± 17.11		19	0.66 ± 0.32	0.63 ± 0.60
June	3-6	24	0.10 ± 0.06	0.04 ± 0.20	18.88 ± 7.74	August	2	0.13 ± 0.01	0.0 ± 0.0	28.70 ± 8.20				
	6-12	2	0.17 ± 0.05	0.0 ± 0.0	26.05 ± 3.32		8	0.18 ± 0.05	0.13 ± 0.35	49.22 ± 19.79				
	12-24	14	0.28 ± 0.20	0.0 ± 0.0	21.96 ± 9.59		24	0.33 ± 0.16	0.67 ± 0.56	50.59 ± 14.19				
	>24	5	0.50 ± 0.11	0.80 ± 0.84	20.50 ± 6.03		19	0.68 ± 0.25	1.68 ± 0.89	70.81 ± 9.37				

Curriculum Vitae & Veröffentlichungen

Curriculum Vitae

Liste der Veröffentlichungen des Autors

Peer-reviewed

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Eigenständigkeitserklärung

Hiermit erkläre ich, dass diese Arbeit bisher von mir weder an der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Greifswald noch einer anderen wissenschaftlichen Einrichtung zum Zwecke der Promotion eingereicht wurde.
Ferner erkläre ich, dass ich diese Arbeit selbstständig verfasst und keine anderen als die darin angegebenen Hilfsmittel und Hilfen benutzt und keine Textabschnitte eines Dritten ohne Kennzeichnung übernommen habe.

Greifswald, den _____

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(Promovend)