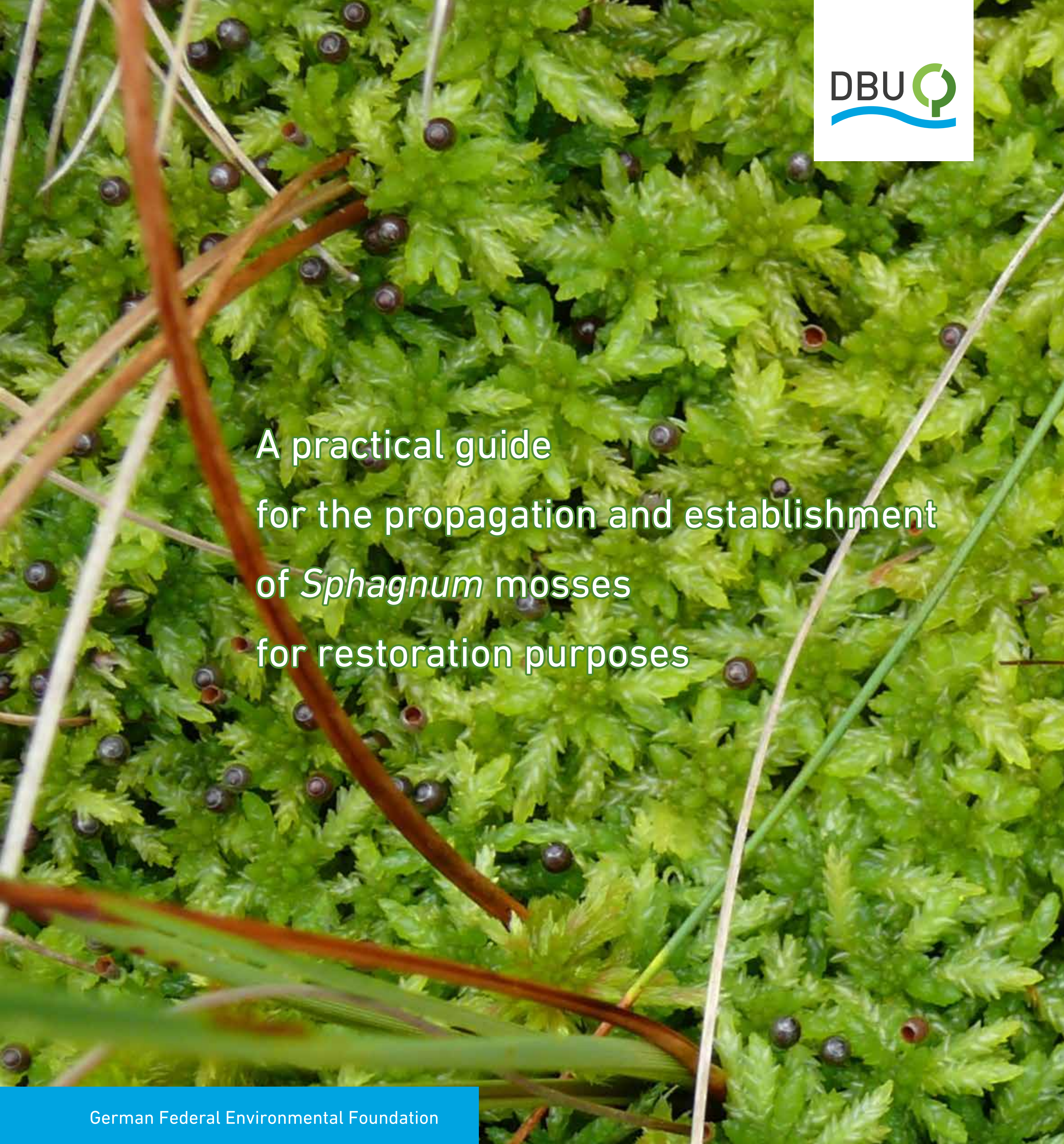

A practical guide for the propagation and establishment of *Sphagnum* mosses for restoration purposes

German Federal Environmental Foundation

Guide

Created within the joint projects

I. Development and testing of methods to establish *Sphagnum* mosses in rewetted cutover bogs after peat extraction, 2015 – 2019

II. Activation of raised bog regeneration through the establishment of *Sphagnum* mosses (AktiMoos), 2019 – 2022

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Part I: Development and testing of methods to establish *Sphagnum* mosses in rewetted cutover bogs after peat extraction

1 Introduction

1.1 Restoring raised and cutover bogs

The regulatory functions of peatlands and their related ecosystem services have received increasing attention in scientific and public discussion over the last decade, especially in the context of climate change (Joosten & Clarke 2002, Millennium Ecosystem Assessment 2005, Kimmel & Mander 2010). Undisturbed peatlands accumulate significant amounts of organic material as peat in the long term, meaning that peatlands are of great importance as a natural sink of atmospheric carbon (Gorham et al. 2012; Loisel et al. 2014). They thus play a vital role in mitigating the current increase of the greenhouse gas carbon dioxide in the atmosphere and thereby global warming (Limpens et al. 2008; IPCC 2014). Conversely, with vast amounts of carbon stored in peat, peatlands can also become a major source of greenhouse gases. These are released during exploitation, degradation and drainage, further accelerating global warming (Frolking et al. 2011). In addition to their impact on the Earth's climate, peatlands and raised bogs also contribute significantly at local and regional scale to the retention of water and nutrients in the landscape (Edom 2001). Furthermore, they provide habitats for many rare and highly specialized animal and plant species, which makes them particularly important for the conservation of biodiversity (Couwenberg & Joosten 2005). As such, regeneration efforts focus not only on preserving carbon stocks and the restarting peat formation processes, but also on restoring typical peatland communities.

In Lower Saxony, where the majority of Germany's peatland area is located, more than 90 % of peatlands and raised bogs have been destroyed or strongly degraded, e.g. by drainage with subsequent agricultural use or by industrial peat extraction (Couwenberg & Joosten 2001). In response, large-scale regeneration measures were carried out in some areas of degraded bogs during Germany's first peatland conservation program starting in the 1980s (NLWKN 2006). Up to now, these regeneration measures have primarily focused on rewetting, including blocking drainage ditches and constructing dams. This approach does not consider the trophic requirements and/or biotic components, and local restoration measures often differ significantly depending on the stakeholders involved. Due to the close relationships between vegetation, water regime and peat properties, which together control the overall ecosystem processes in peatlands (Ivanov 1981), holistic approaches are needed to at least partially restore essential functions regarding water, nutrient and carbon budgets within a reasonable period of time (Schumann & Joosten 2008). As explained below, the establishment of hummock-forming species of the genus *Sphagnum* plays a key role in the regeneration of ecosystem functions.

1.2 Shortcomings of current regeneration measures

Since the 1980s, former peat extraction sites in northern Germany have been undergoing regeneration and are gradually being rewetted. The majority of the regeneration areas in Lower Saxony (including about 14,000 ha of rewetted areas after industrial peat extraction; Schmatzler 2015), however, have not reached

Initial colonisation of a rewetted cutover site with cotton grass (*Eriophorum vaginatum*) and a hollow-inhabiting moss (*Sphagnum cuspidatum*).

the goal of a full regeneration of a self-sustaining ombrotrophic (i.e. rain-fed) or peat-accumulating ecosystem. Preliminary studies on more than 50 rewetted sites in northwestern Germany conducted by the Institute of Landscape Ecology at University of Münster have shown that many raised bog plant species, and in particular hummock-forming mosses, are still almost completely absent. In addition, nutrient-enrichment and/or unstable hydrological conditions (Price & Ketcheson 2009) remain the main reasons for the lack of success in re-establishing many bog-typical species (Gorham & Rochefort 2003).

Soil profiles of intact bogs are typically divided into two layers: The acrotelm, an upper, usually 10-50 cm thick layer of high hydraulic conductivity and incomplete water saturation in which peat is formed; and the catotelm, a permanently water-saturated, anoxic lower layer in which peat carbon is stored long-term.

After 20-30 years of succession with favourable hydrological conditions, floating mats develop, but cotton grass (*Eriophorum angustifolium*, *E. vaginatum*) and hollow-inhabiting mosses (*Sphagnum cuspidatum* and *S. fallax*) still dominate. Despite suitable site conditions, hummock-forming mosses and typical vascular plants for bogs (e.g. from the heather family) are still completely absent.

In contrast to strongly degraded bogs, intact and naturally nutrient-poor bogs with an existing acrotelm are characterized by permanently high water levels near the surface in a highly acidic environment (Rydin & Jeglum 2013). *Sphagnum* mosses regulate not only the hydrological but also the hydrochemical properties in the bog, creating conditions which are unfavourable for competing vegetation and vascular plants. To restore degraded and cutover bogs, the acrotelm must first be reconstituted to re-establish a stable water regime with constantly high groundwater levels (Timmermann et al. 2009). This process is usually initiated by rewetting the sites. However, rewetting is often initially done by permanent flooding, which creates shallow lakes, where only floating hollow-inhabiting species such as *S. cuspidatum* and *S. fallax* successfully colonise (Limpens et al., 2003). At the other extreme, conditions that are too dry and nutrient-rich trigger successional changes in species composition due to the spread of more competitive, invasive graminoids (*Molinia caerulea*, *Juncus effusus*) as well shrubs (*Betula pubescens*) (Tomassen et al., 2004).

Large fluctuations in water levels are extremely unfavourable for the establishment of hummock-forming mosses. This is particularly the case when flooding occurs for too long or too frequently, as is often practiced to suppress shrub encroachment.

Preliminary studies at the University of Münster confirmed that rewetting over 30 years allows the establishment of hollow-inhabiting moss species, but is otherwise often not sufficient to initiate a moss-dominated typical bog vegetation. This time period is obviously insufficient to get beyond initial stages of rewetting with establishment of only pioneer species such as *Sphagnum cuspidatum* and *Eriophorum vaginatum*. Particularly obvious is the almost complete absence of hummock-forming moss species such as *Sphagnum medium*, *S. papillosum* and *S. rubellum*, which act as ecosystem engineers and thus are of crucial importance for the regeneration of raised bog ecosystem functions. Due to the obvious lack of a spontaneous colonisation with hummock mosses, active introduction of these keystone species offers the possibility to accelerate the revegetation of rewetted areas (Schumann & Joosten 2008). However, this procedure has rarely been employed in Germany so far. Under the term »moss layer transfer technique«, this has already been successfully established in Canada even on larger scales (Quinty & Rochefort 2003).

Besides hummock mosses, typical dwarf shrubs for bogs such as bog-rosemary (*Andromeda polifolia*, pictured), bog cranberry (*Vaccinium oxycoccos*) and cross-leaved heath (*Erica tetralix*) are among the species that rely on active reintroduction. Even after 30 years, they usually do not recolonise spontaneously.

The reason why active introduction of hummock-forming mosses has rarely been applied in Central Europe is presumably that, unlike in Canada and because of the massive decline in raised bog habitats in Europe, only very few suitable donor sites are available for larger-scale species introduction measures. In addition, there is a lack of experimental evidence and of effective practical experience regarding the establishment of hummock mosses on rewetted areas in Central Europe under the local conditions. Knowledge on restoration from other countries such as Canada can be transferred to northwestern Germany only to a limited degree, as the bog remnants often have very different and very difficult starting conditions in terms of hydrology and peat degradation. Moreover, there is limited knowledge about restoration approaches that include the active propagation of *Sphagnum* mosses. Pilot projects related to this topic have so far been focused almost exclusively on the cultivation of mosses for economic use as a raw material for growing media in horticulture (*Sphagnum* farming) (Gaudig 2002, Gaudig et al., 2014).

1.3 Causes of dispersal limitation of *Sphagnum* mosses

Although *Sphagnum* mosses can form a long-lived spore bank of tens of thousands of individuals (Sundberg & Rydin 2000), this is apparently not a key factor for their re-establishment on rewetted cutover sites. This is presumably because the deeper fossil peat layers exposed at the surface of cutover peatlands are typically several thousand years old and therefore contain no viable spores. Recolonisation can thus only take place by the introduction of recently produced diaspores from other locations.

Residual peat deposits in restoration sites can be several thousand years old, and therefore no longer contain viable spores of *Sphagnum* moss or seeds of typical vascular plants. Recolonisation through immigration from the surrounding intensively used agricultural landscape is highly unlikely. If at all, there are only sparse and often isolated residual populations of typical bog species.

In Central Europe, peat extraction no longer occurs in semi-natural, living raised bogs with typical communities of flora and fauna. It is limited to former farmed areas and degraded bog remnants. After peat extraction has ceased, the remaining areas are usually large (several km^2) and homogeneously structured. The surroundings support no or only very small and strongly isolated relic populations, which usually are also degraded remnants of raised bog communities. Usually, the surrounding areas of restored extraction sites in northwestern Germany are dominated by intensive agricultural land-use. The almost complete absence of healthy source populations on the landscape level can thus be considered as a major cause for the lack of spontaneous recolonisation of hummock mosses and other typical raised bog species on restored areas. However, even under favourable environmental conditions with large semi-natural raised bogs adjacent to extraction sites, such as are found in Canada, spontaneous recolonisation on rewetted bare peat occurs only to a limited extent. This process is apparently very slow (Quinty & Rochefort 2003). Although *Sphagnum* mosses are able to produce a large number of spores and these can potentially be dispersed very effectively due to their small size, recolonisation of new (regeneration) areas via generative propagation is rarely observed for two reasons:

The majority of hummock mosses in northwestern Germany now no longer regularly produce spores (the picture shows small spore capsules of *S. papillosum*). Although spores can potentially be produced in large quantities and are highly mobile, the overall spore rain has decreased drastically due to the massive decline in the area of intact raised bogs in northwestern Germany. Spores of *Sphagnum* arriving today are more likely to come from southern Scandinavia or the British Isles than from northwestern Germany itself.

(1) The probability that *Sphagnum* mosses produce spores decreases with their vitality (Sundberg & Rydin 2002) and population size (Fenton & Bergeron 2006). Consequently, the production of spores (sporulation) is very rarely observed within the small residual populations of hummock mosses in northwestern Germany.
(2) The protonema, which develops from a haploid spore, is an extremely sensitive phase in the life cycle of *Sphagnum* mosses, so that adult moss plants can only develop under ideal conditions (Hajek & Vicherova 2014, Beike et al., 2015). Even under optimal conditions, significantly fewer than 1 % of spores germinate of most species (Sundberg & Rydin 2002). Successful germination of spores requires locally slightly increased phosphate availability in the substrate (e.g. provided by elk manure or leaf litter), stable moisture conditions, low levels of competition, and sites that offer protection against desiccation. These conditions for successful establishment of the protonema stage are extremely rare in industrially extracted peatlands. In early successional stages, unfavourable abiotic (micro-)site conditions mostly constrain establishment, while in later stages strong competition from vascular plants becomes increasingly important for future development. The complete failure of hummock mosses to re-establish on bare peat surfaces can be attributed to predominantly harsh microclimatic conditions during the extremely sensitive protonema stage. In contrast, the likelihood of successful establishment in later successional stages of rewetted cutover sites via spore rain is inevitably impeded by the massive reduction of vital spore sources due to habitat destruction and degradation.

Vegetative reproduction, which produces new moss plants by simple cell division or fragmentation, plays a significant role in the spread of *Sphagnum* mosses also in nature, and is probably even more important than sexual reproduction (Rydin & Jeglum 2013). However, for long-distance dispersal of

Neither the bare peat extraction sites nor the older regeneration stages mostly dominated by vascular plants and with high water level fluctuations offer suitable microsite conditions for the highly sensitive spore germination of *Sphagnum* moss. Accordingly, they reproduce and disperse almost exclusively vegetatively (short-distance dispersal by fragments).

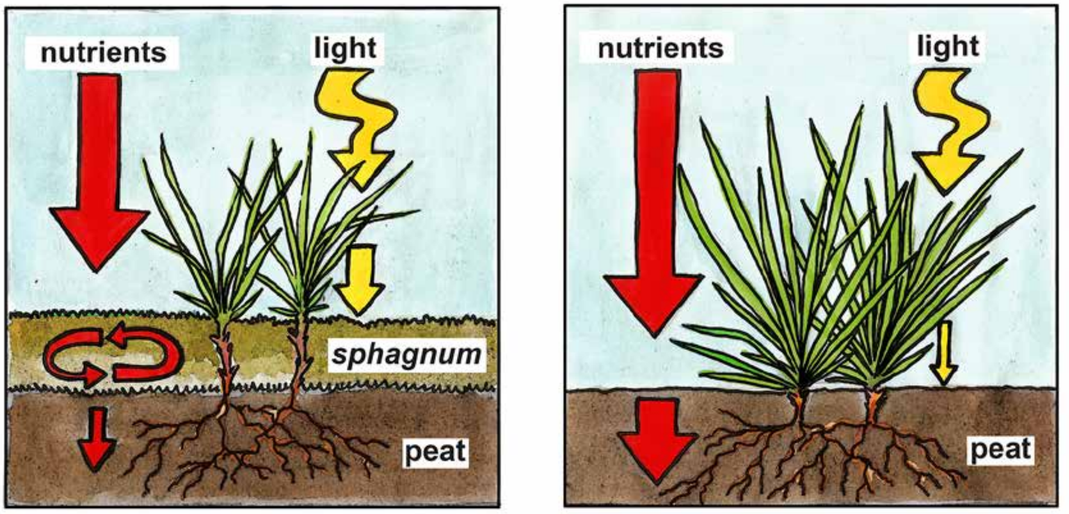
vegetative diaspores to occur, a dispersal vector is needed that connects the source of the plant material with prospective receptor sites. The recolonisation through hollow-inhabiting moss species often occurs quickly under suitable site conditions and can be considered unproblematic. Here, waterfowl and waders can be considered as effective dispersal vectors, which can disseminate living moss fragments over longer distances into newly created and not yet fully occupied habitats. Conversely, hummock-forming mosses that are adapted to drier microsites lack similarly effective dispersal vectors in Central Europe: in the boreal zone this role is played by large mammals such as moose and bears. Moreover, also for the vegetative dispersal path, the probability of diaspore arrival to a suitable microsite decreases rapidly with the decline of potential source populations.

Compact hummocks of *Sphagnum* mosses (the picture shows *S. papillosum*, *S. medium* and *S. rubellum* growing together with heather plants) are of central functional importance for the light, water and nutrient regimes of raised bogs. Without the establishment of these ecological key species, complete and sustainable regeneration of bogs is not possible.

1.4 Ecosystem importance of *Sphagnum* mosses

There are few other ecosystems where a single taxon shapes the light, water and nutrient budgets as raised bogs and hummock-forming *Sphagnum* mosses (referred to here as hummock mosses). As an ecosystem engineer, this species group is essential for the preservation as well as for the restoration of naturally functioning bogs. Without them, a targeted successional development from a peat extraction site towards an increasingly bog-like habitat is impossible.

Only communities dominated by hummock mosses are able to create the balance between water permeability and water storage capacity typical of bogs. This makes them a keystone species in bog restoration, as the objective is to create an acrotelm that stores large amounts of water but is at the same time not too wet. They are essential for important ecosystem functions such as peat formation, to re-establish a carbon sink or buffer against hydrological extremes. Hummock mosses are thus the crucial functional link between atmosphere, hydrology, peat deposits and plant communities, which constitute the complexity of raised bogs, and therefore determine the functioning and resilience of bog ecosystems. This becomes particularly evident also in the function of hummock mosses to act as a filter against atmospheric nutrient deposition (Lamers et al. 2000). In intact raised bogs dominated by hummock mosses, the living *Sphagnum* mosses absorb almost all the nutrients introduced via atmospheric deposition, such as nitrogen (N), potassium (K), calcium (Ca) and magnesium (Mg), and use them for their own growth (Fig. p.17, top left). Only a small proportion of nutrients is not retained and becomes available for uptake by roots of vascular plants. Hummock mosses thus reduce the above-ground competitive advantage of vascular plants for light by creating very unfavourable, nutrient-poor and acidic conditions below ground. As a result of the reduced vitality of vascular plants, *Sphagnum* mosses can even overgrow and completely outcompete non-specialised plants.



In the absence of the nutrient filter function of hummock mosses, atmospheric nutrients (particularly nitrogen) reach the roots of tall vascular plants and increase their vitality and dominance. Through shading and litter production, the vascular plants in turn impede the establishment of hummock mosses. This negative feedback can only be bridged through the targeted introduction of hummock mosses, which act as a nutrient filter (Illustration based on Rydin & Jeglum 2013).

If the soil surface is not completely covered by hummock mosses, nutrients can penetrate into deeper soil layers and reach the rhizosphere of the vascular plants (Lamers et al., 2000) (Fig. top right). Consequently, vascular plants increase their aboveground biomass production, and are able to outcompete mosses and other small species for light. The massive increase in vitality of vascular plants such as *Eriophorum vaginatum*, *E. angustifolium*, *Molinia caerulea* and *Betula pubescens* in bog regeneration areas in northwestern Germany is largely due to the lack of an effective nutrient filter, normally created by the presence of hummock mosses (Tomassen et al., 2003). This strong expansion of graminoids and the encroachment of shrubs and birch trees is probably the most serious problem in restoration, which can be counteracted only by a sustained establishment of hummock mosses. This situation is aggravated by increased atmospheric inputs of nitrogen from agriculture and industry, which in many

Strong dominance of *Eriophorum vaginatum*, *E. angustifolium* and *Molinia caerulea*, as well as shrub encroachment of downy birch (*Betula pubescens*), are currently major problems in the regeneration of raised bog ecosystems on rewetted peat extraction sites in northwestern Germany. A major cause is increased atmospheric nutrient deposition, which reach the root space of the vascular plants due to the lack of filtering by hummock mosses.

cases reach dimensions significantly greater than the natural filter capacity of a healthy hummock moss layer (Lamers et al 2000). It seems thus all the more important, from an ecosystem point of view, to support the establishment of hummock mosses through targeted introduction. This is the only way to minimise the negative outcomes caused by increased atmospheric nutrient inputs, such as the almost ubiquitous dominance of graminoids and shrub encroachment (Tomassen et al., 2004).

1.5 Active introduction of *Sphagnum* mosses

As mentioned above, hummock mosses play a key role for successful restoration of raised bogs. However, spontaneous colonisation of rewetted areas by hummock mosses has been rarely observed, even after more than 30 years. Active introduction of these target species therefore seems to be a logical strategy to initiate bog regeneration and to overcome its limited natural dispersal abilities. The active introduction of hummock mosses on degraded bogs is especially useful, as *Sphagnum* mosses have a self-sustaining effect. They are able to establish a microhabitat with appropriate hydrological and hydrochemical conditions to support their own growth. Also, due to their high water storage and capillary water transport capacities, they sustain stable wet conditions, yet though a highly porous structure avoid too wet conditions. The local acidification of the surrounding environment creates conditions that limit or suppress the establishment of competitors. Thus, the active introduction of hummock mosses also counteracts many common problems in the early phases of bog restoration (e.g. variable water levels, dominance of non-target species such as *Molinia* and *Betula*). If the establishment of hummock mosses is successful, the microsite conditions they create allow other typical raised bog species to establish.

1.6 Propagation of *Sphagnum* mosses for reintroduction

In contrast to e.g. Fennoscandia and Canada, the few remaining natural hummock moss populations in northwestern Germany and central Europe are mostly too small to provide enough donor material to actively repopulate rewetted cutover sites. As such, targeted propagation appears to be the only viable way to meet the demand whilst complying with peatland restoration regulations. Through targeted propagation, the need to collect species from small natural remnant populations can be reduced to an acceptable level.

Since remaining populations and thus sources of donor material are generally only found in nature conservation areas and are subject to strict species protection regulations (see below), the acquisition of small amounts of initial donor material for propagation can be challenging.

The legal framework differs between countries, therefore discussions with regional and national authorities and nature protection agencies are essential. This guide outlines the legal framework in Germany as an example, as it is not possible to cover the countless regulations different countries. Although regulations may be similar in other European countries, we urge readers to consult the relevant authorities in their countries.

1.7 Legal framework for the collection, propagation and cultivation of *Sphagnum* mosses – Germany as an example

Massive declines in the 20th century mean that numerous hummock moss species are now on the Red Lists of most of the federal states of Germany. Furthermore, all species of the genus *Sphagnum* are listed in Annex V of the EU Habitats Directive, meaning that their use is restricted, and only allowed if it is compatible with the maintenance of a favourable conservation status. To achieve this, special measures may be required in accordance with Article 14 of the Directive, such as: establishing an extraction quota, introducing a licencing system, temporary or local bans on collection of the species, or the establishment of a propagation program. These measures also include the continuation of monitoring of favourable conservation status according to Article 11.

The Habitats Directive explicitly allows special permits for restocking and reintroduction of species, including the artificial propagation of plants for this purpose, to aid research and education. Collection of biological material and permits are regulated in Articles 14 and 16 of the Habitats Directive.

The provisions of the Habitats Directive are implemented in the German Federal Nature Conservation Act, and are regulated as follows:

§ 39 (2) Subject to the provisions of laws on hunting and fishing, it shall be prohibited to remove wild plants and animals of species listed in Annex V of Directive 92/43/EEC from nature. The federal states may grant exceptions to Sentence 1 under the conditions set forth in § 45 (7) or Article 14 of Directive 92/43/EEC.

§ 45 (7) likewise explicitly refers to removal for propagation only in exceptional circumstances:

§ 45 (7) The competent authorities for nature conservation and landscape management, pursuant to the legislation of the Länder, and, in the case of introduction from other countries, the Federal Agency for Nature Conservation (BfN), may grant further exceptions from the prohibitions of Article 44, in individual cases:

[...]

3. for purposes of research, teaching, education, or reintroduction, or for the breeding operations or artificial propagation measures necessary for these purposes.

Most state laws, such as the Lower Saxony Implementation Act for the Federal Nature Conservation Act of 19.02.2010, adopt the provisions of the Federal Nature Conservation Act without any further additions or specifications.

In summary, the removal of *Sphagnum* mosses is generally possible for the purposes of propagation and reintroduction under federal and state law in Germany as well as under European law, but each individual case requires approval by the relevant authorities. This is particularly relevant for countries other than Germany, as the information above describes the legal framework in Germany only.

The common German name for *Sphagnum* is »bleaching moss«, which is derived from the property of these species to fade very strongly when they dry out until they appear almost white

2 Selection of propagation material

2.1 General aspects

When selecting moss species from the genus *Sphagnum* for bog regeneration, the species-specific characteristics and site requirements are - besides the availability of propagation material - of decisive importance for the success of reintroduction measures. Propagation should therefore always be accompanied by monitoring of the intended receptor sites to assess the chances of success and to be able to make a site-appropriate species selection. Of particular relevance are ombrotrophic (deriving their nutrients primarily from precipitation) mosses, which are able to initiate succession on periodically flooded, hollow moss-dominated areas and gradually grow out of the waterlogged hollows. Such species can tolerate water level fluctuations to some degree, with prolonged dry periods and intermittent flooding with more mineral-rich water until the acrotelm function has been successively re-established. Among the hummock mosses, particularly *S. papillosum* has such »pioneer characteristics«.

S. medium, *S. rubellum* and *S. capillifolium*, in contrast, are more sensitive to waterlogging and tend to colonise the higher areas of the hummocks. Other ombrotrophic hummock mosses such as *S. angustifolium* are currently rare in NW Germany and are therefore of minor importance in restoration. They are occasionally found in small numbers in stands of other dominant species.

The introduction of species that form floating mats, such as *S. cuspidatum* and *S. fallax*, is usually not necessary, since these common and non-threatened species usually succeed in colonising regeneration areas on their own. These species also tolerate somewhat higher nutrient levels, but are not able to effectively suppress vascular plants.

Other common minerotrophic mosses (which obtain their nutrients primarily from groundwater) such as *S. fimbriatum*, *S. palustre* and *S. squarrosum* are also not among the target species for raised bog regeneration and therefore do not require targeted propagation.

Distinguishing hummock-forming mosses from hollow-inhabiting and fen moss species

In contrast to the hollow mosses, hummock *Sphagnum* mosses are capable of growing above the water level and can survive moderate phases of drought largely unharmed.

In contrast to fen species, hummock mosses of raised bogs are adapted to to extremely low nutrient levels and to obtaining their nutrients solely through atmospheric deposition. They usually reach complete dominance as soon as water and nutrients are supplied exclusively via precipitation.

Table 1: Conservation categories of potential target species in peatland restoration. According to Hassel et al. (2018), the ombrotrophic form of the species formerly described in Europe as *S. magellanicum* is actually *S. medium*.

A. Ombrotraphent hummocks to lawns		**B. Ombro-/Mesotraphent floating mats**		**C. Minerotraphent hummocks to lawns**	
S. affine	•••	*S. majus*	•••	*S. subnitens*	••
S. fuscum	•••	*S. flexuosum*	•	*S. teres*	••
S. molle	••	*S. cuspidatum*	o	*S. centrale*	•
S. angustifolium	•	*S. fallax*	o	*S. riparium*	•
S. compactum	•			*S. warnstorfii*	•
S. medium	•	**D. Forest mosses**		*S. fimbriatum*	o
S. papillosum	•	*S. capillifolium*	•	*S. palustre*	o
S. rubellum	•	*S. russowii*	o	*S. squarrosum*	o

Species protection categories for northwestern Germany according to Meinunger & Schröder (2007), ecology according to Hölzer (2010)

••• = RL1, extremely rare, strictly protected

•• = RL2, very rare, highly protected

• = RL3, rare/endangered, protected; o = common/not endangered, not protected

A. Hummock-forming, ombrotrophic *Sphagnum* mosses = target species of this guide, adapted to nutrient-poor conditions, potentially peat-forming species

B. Floating, blanket or mat-forming species = in contrast to hummock-forming mosses, suitable to be reintroduced to intermittently flooded areas, with varying tolerance to minerals and nutrients

C. Minerotrophic species = transition mire and fen species tolerant of mineral-rich water (base-rich irrigation water)

D. Forest mosses = species frequently occurring in shady, humid forests, which are suitable for reintroduction to forested sites due to their shade tolerance

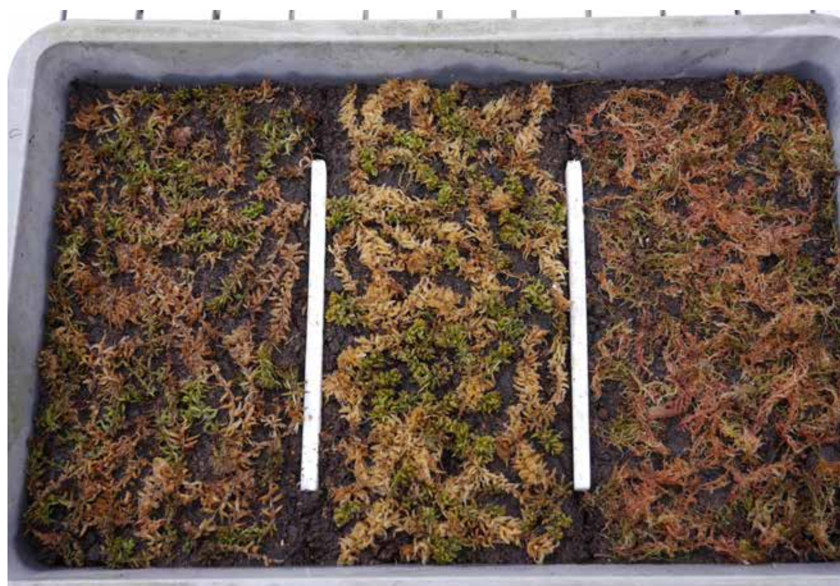
2.2 Biological and ecological characteristics of suitable hummock-forming moss species

All hummock *Sphagnum* mosses are at their optimum under consistently moist conditions, but differ in their tolerance to water level fluctuations and in nutrient and light requirements. *S. rubellum* has a relatively narrow range of optimal conditions under which it achieves high reproductive rates, but suffers greatly from the effects of water stress. *S. medium* also prefers permanently moist, not too wet conditions, but is much less sensitive to prolonged drought.

S. papillosum has proven to be the most robust of the species tested in our work and elsewhere. This species shows the greatest tolerance to water level fluctuations and nutrient inputs and is thus capable of establishing itself permanently on a rewetted area even under suboptimal conditions.

For species of the genus *Sphagnum*, as with all mosses, uniform moisture conditions are crucial for photosynthetic performance and thus growth, as the capitulae (the head-like branches at the apex of the moss stem) require a constant water content. Self-regulation of water supply occurs exclusively through the dense growth habit, capillary water upwelling and a water storage in the deeper, dead or no longer photosynthetically active parts of the plant. Since propagation begins with loose fragments, the individual plants or fragments are particularly sensitive to fluctuating water availability until they have accumulated more biomass and formed dense, self-stabilising structures.

In contrast to hollow species, hummock mosses are generally better able to avoid drought stress in during periods of low precipitation due to their compact growth and the resulting capillarity. If the water content in the capitulae falls below the optimal level, even if only slightly or if only for a short time,



Individual plants and fragments in a tray with approximately 4 cm of peat substrate. The mosses are very sensitive at this stage due to the limited contact with the substrate and because the moss layer has not yet formed a self-stabilizing unit as a hummock. In the example shown, the species (from left to right) *Sphagnum medium*, *S. papillosum* and *S. rubellum* were grown separately to investigate single species effects.

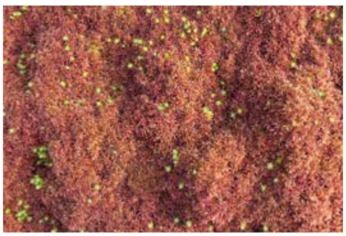
The formation of a dense moss layer allows a good capillary rise of water to the photosynthetically active green parts, and the mosses are able to withstand temporary water shortage. Their dense growth and acidification of the surroundings supress the growth of other plants.

they stop growing until the water supply improves. However, little decomposition and compaction occurs during such periods of growth stagnation. Only very severe desiccation results in persistent damage. Too high water levels or even submergence, especially with unsuitable water quality (see below) will lead to conditions under which hollow mosses become more competitive. Flooding during propagation therefore leads to a shift towards undesirable species that already have advantages under less favourable site conditions and often already establish themselves.

For later establishment success, but also already during propagation, it is thus crucial that the plants develop hydrologic self-regulation with regard to water quantity and quality. In this way, the living plant parts on the surface become increasingly independent of fluctuating conditions with simultaneous accumulation of dead biomass in deeper layers below.

As with all vegetation, *Sphagnum* requires suitable light and temperature conditions for optimal growth. Starting propagation in autumn is not recommended, as growth during the winter months is severely limited making the mosses layer vulnerable, and spring drought is unlikely to be a problem in propagation systems. In contrast, sods and fragments for establishment in the field can be brought to receptor sites in autumn. Under sub-optimal conditions in the field (no watering), water availability and especially spring drought can be the critical factor. Moreover, for sufficient supply of light, propagation plants should be set up outdoors and without shading.

Tabelle 2: Description and evaluation of target species. Based on observations of the authors and data in Meinunger & Schröder (2007) and Hölzer (2010). Following a recent scientific study, the ombrotrophic form of the species formerly described as *S. magellanicum* in Europe is now *S. medium* (Hassel et al. 2018).

S. rubellum »Red Bog-moss«	*S. medium* »Midway Bog-moss«	*S. papillosum* »Fat Bog-moss»
		
Ecological niche Base/flank of high hummocks, hollow edge **Traits** Susceptible to flooding and drying out Good capillarity High regeneration capacity	**Ecological niche** Low hummocks and ombrotrophic lawns **Traits** Acidophilic Low nutrient requirements Tolerates drought Tolerates shade	**Ecological niche** Temporary flushed lawns and low hummocks **Traits** Tolerates flooding and moderately mineral-rich water Tolerates drought
Assessment Demanding species, unsuitable for sites with high variation in water levels and mineral water influence	**Assessment** Robust to prolonged drought, problematic under excessively wet conditions and high nitrogen inputs	**Assessment** Robust species, greatest tolerance to drought, flooding and increased inputs of mineral-rich waters

When selecting species for hummock-forming moss propagation, the following criteria in particular should be considered:

- Importance of the source population for species conservation <-> Functional importance in the receptor site (as a nutrient filter and for peat formation)
- Availability (rarity) of the source population <-> High reproduction rates in cultivation.
- Water and substrate quality in propagation -> hummock-forming mosses grow best under ombrotrophic (acidic, low mineral content) and permanently moist conditions
- Prospects for sustainable establishment of propagated mosses -> Dependent on the receptor site and its management
- Long-term potential to reduce methane emissions and new peat formation in restored areas (on which areas is the greatest need for action, where can the greatest effects of hummock moss establishment be expected?)

Reduction of emissions of the potent greenhouse gas methane by hummock-forming mosses

Water saturation in peatlands also produces methane, a comparatively harmful greenhouse gas. Un- or poorly restored peatlands with high nutrient levels and inappropriate, easily decomposable vegetation (rushes, some sedge species, Poaceae and forbs) release comparatively large amounts of methane when water levels are high, which escapes into the atmosphere. Dead *Sphagnum* moss material, especially of the hummock-forming species, keeps methane formation low due to its resistance to decomposition and antimicrobial properties (via the high content of polyphenols). In addition, *Sphagnum* mosses form a symbiosis with methane-oxidizing bacteria on and inside the leaflets. A dense layer of *Sphagnum* mosses can therefore significantly reduce methane emissions from peatlands, further enhancing the positive climatic effect of sequestering carbon dioxide from the air. In contrast, dense coverage of sedge and rush species can lead to greatly increased emissions, as these and other species form air channels in their roots (aerenchyma), through which comparatively large amounts of methane are released.

2.3 Role of origin and local adaptations in hummock-forming mosses

As evidenced by many genetic studies (Stenøien & Såstad 1999, Gunnarson et al. 2005, Mikulaskova et al. 2015, Kyrkjeeide et al. 2016b, Yousefi et al. 2017), *Sphagnum* species are characterized by high local genetic diversity within populations and comparatively low genetic differentiation between populations. The latter is also true across larger geographic areas and even on a continental scale as shown, for example, by the low genetic differentiation of European and North American populations of *S. magellanicum* (Kyrkjeeide et al. 2016a). The reasons for this are, on the one hand, a particularly effective large-scale genetic exchange by means of mass-produced, highly mobile spores and, on the other hand, a slow rate of evolution that is apparently typical for the genus (Stenøien & Såstad 1999). For restoration and propagation, this means that particular care must be taken to ensure that local genetic diversity and thus adaptations to local environmental gradients (water level, pH, light) are considered in the selection of donor material, while regional differentiation is of much less importance. In Germany, there is a classification of regions based on landscape units with relatively homogenous genetic populations of wild vascular plants that is used to define seeds of regional provenance (Prasse et al. 2010). For vascular grassland plants it has been shown that these seed production regions represent a considerable proportion of the regional genetic variation within Germany (Bucharova et al. 2017, Durka et al. 2017). Despite the relatively low regional genetic differentiation in *Sphagnum* mosses, for practical reasons of acceptance by nature conservation authorities and NGOs this classification may be taken as the basis for selecting appropriate regional donor populations, although this may be overcautious. Considering that population genetic studies of *Sphagnum* mosses (e.g., Mikulaskova et al. 2014) showed a much lower overall regional geographic differentiation than for most vascular plants, in case of *Sphagnum* mosses, it seems to be more important to consider the local genetic diversity in the material used for propagation (Bucharova et al. 2019).

When collecting material for propagation from source populations, the following procedure is recommended:

1) Since potential donor areas are mostly protected areas, an official entry permit must be organized in advance.

2) Before collection, the target moss populations should be studied and their distribution mapped. Experts who are able to identify the different species of *Sphagnum* should be consulted.

3) Subsequently, a permit must be obtained from the relevant nature conservation authority detailing the location, type and extent of the removal for propagation purposes.

The particularly dense and compact hummocks of *S. papilllosum* can tolerate both surface desiccation and short-term waterlogging, making them particularly suitable for restoration areas with relatively unstable water levels.

4) The collection of donor material should be carried out over as large an area as possible of the range of the local population to ensure that, as far as possible, the full range of local genetic differentiation is preserved for propagation.

5) Accordingly, the collection at a particular location should not be spatially clumped, but rather as highly dispersed as possible.

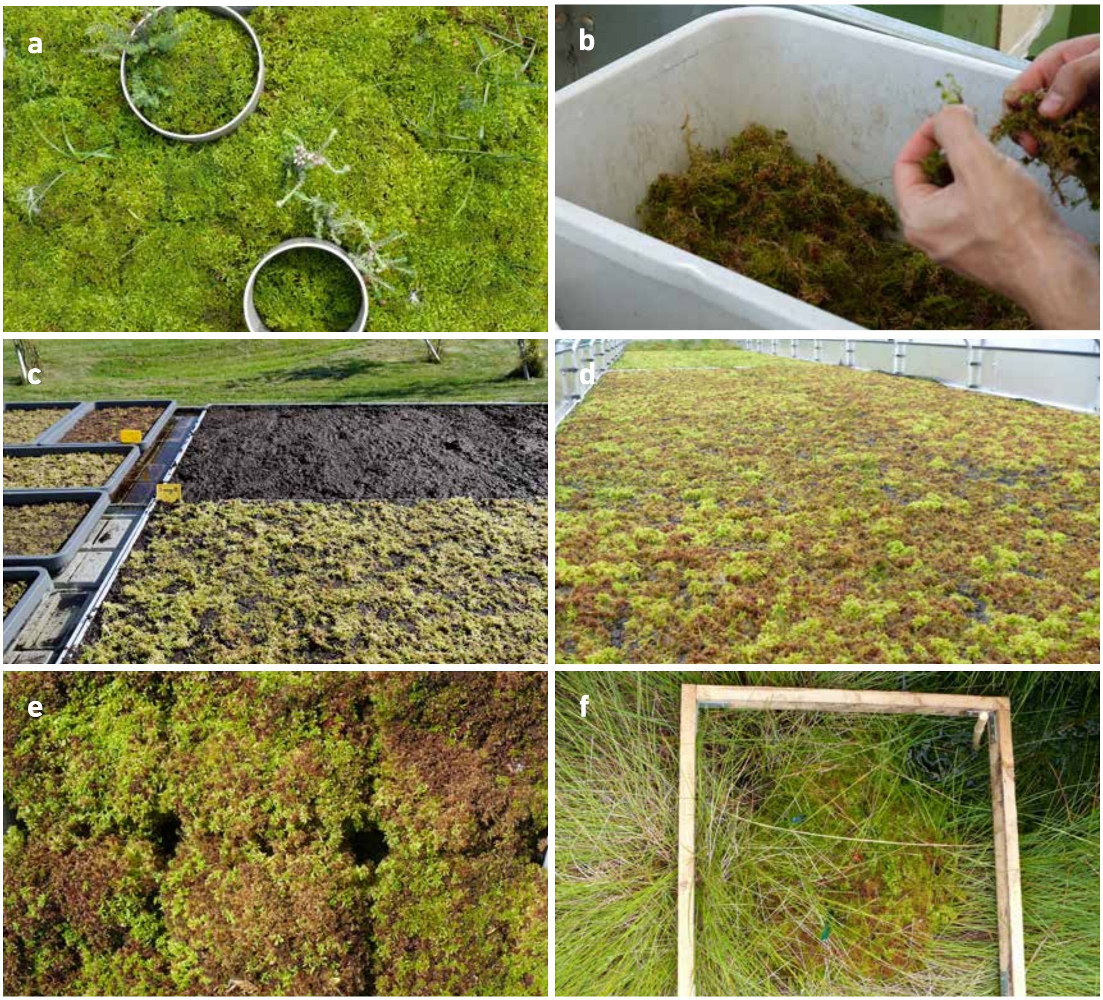
6) This can be achieved, for example, by removing plants from *Sphagnum* hummocks every 1-2 m along line transects. For this purpose, e.g. sampling cylinders of approx. 5 cm diameter can be used. In total, no more than 10-20 % of the area per *Sphagnum* cushion should be removed in order not to damage the donor areas too much.

7) During the collection itself, a *Sphagnum* expert should also be present. The expert can identify the dominant species, allowing them to be collected separately and later mixed into the desired ratios.

8) Optimally, at least 3-5 populations per landscape unit should be collected from nearby peatlands in order to cover the local genetic differentiation in the propagation material as completely as possible. This is especially true for smaller populations, which may already be genetically impoverished.

Ensuring a broad representation of local genetic diversity when obtaining donor material is especially important because subsequent propagation is exclusively vegetative and does not allow for any recombination. If material is used that is already genetically impoverished, undesirable founder effects can easily occur, which can significantly limit the fitness and adaptability of newly established populations (Bucharova et al. 2019).

To avoid cultivation effects, propagation plots or facilities should be designed so that the conditions are as close to natural as possible. This can minimize the risk of loss of important functional traits during propagation. The removal of small sods and natural propagation conditions can ensure that other target species of raised bog regeneration, such as white beak-sedge (*Rhynchospora alba*) or bog-rosemary (*Andromeda polifolia*) are propagated in addition to the hummock-forming mosses.



An example of moss propagation on irrigation tables for the production of donor material for active species introduction: (a) collection; (b) processing (separation, fragmentation, portioning); (c) fragments spread on a thin substrate layer; (d) moss cover after 4 months of growth; (e) fully grown, intact sods; (f) inoculated tussock of *Eriophorum vaginatum* in a restored area.

Sphagnum nursery on tables. A significant increase in moss biomass is already visible in the bottom right of the picture. The spreading of collected fragments in the bottom left took place shortly before the photo was taken. This picture also shows the irrigation system for overhead irrigation and the structures to fix bird exclusion nets. A control system for continuous flow irrigation from below can be seen on the side of the tables. The tables must have strong supports, because they have to carry 40-80 kg m^2 of load over long periods.

3 Water and substrate

The key to successful hummock *Sphagnum* moss propagation is to ensure consistently high water levels in the growing medium. This has been demonstrated in a large number of studies on *Sphagnum* moss growth and is confirmed by the University of Münster own results. Since the propagation set-up lacks a powerful, hydraulically connected and water-storing peat base, the water level must be regulated very precisely, i.e. water must be added or removed in a controlled manner depending on the conditions. While *Sphagnum* mosses from wet habitats (hollows) benefit from high water accumulation or overwatering, the water supply for hummock species must be kept constant in their optimum range, since both too wet and too dry conditions result in reduced growth. In addition, conditions that are too wet lead to undesirable shifts in species proportions towards hollow-inhabiting mosses, which are usually present in low densities in the donor material.

In a pilot experiment, commercially available greenhouse tables have proven to be the ideal set-up for hummock moss propagation on a smaller scale (10 m^2). The tables should be placed outdoors to acclimatise the mosses to the changing weather conditions in the field. Propagation in the greenhouse has proven to be less successful, as it results in increased fungal infestation or a massive spread of algae. Both have a strong negative effect on the growth rates or can even cause complete death of the mosses. Greenhouse tables allow the creation of beds for propagation with only a few cm of white peat substrate as a base. With a simple irrigation system (e.g., using floats) and appropriate overflows, the water level can be precisely adjusted. Nevertheless, wind can cause temporary drying of the moss capitulae, significantly reducing growth rates. Protective walls (e.g. metal sheets or plexiglass) about 20 cm high on the sides of the tables have proven to be an effective measure to reduce the wind speed near the surface and thus the water loss at the vegetation surface. To protect against disturbance by birds, the tables should be protected by netting.

An alternative to greenhouse tables, especially for propagation of hummock *Sphagnum* mosses on a larger scale (> 100 m^2), is propagation directly in the field. For successful propagation, however, it is essential to adjust the water levels as precisely as possible. This can be quite a challenge in the field and becomes more difficult as the size of the propagation area increases. The substrate must be prepared carefully to be able to set water levels on as level a surface as possible. Ensuring optimal water quality for good peat growth is equally much more difficult in the field, as the use of groundwater and surface water is often unavoidable, at least during the summer months. Use of water with suboptimal quality leads to reduced growth rates due to excessive nutrient or dissolved organic carbon levels. In the pilot trial, successful outdoor approaches used either level beds flooded with good quality water at regular intervals (ebb-and-flow technique) or an irrigation system (subsurface or overhead irrigation) in basins lined with waterproof sheeting with an appropriate overflow.
While ebb-and-flow irrigation is much more vulnerable and requires larger quantities of good quality water (artificial ponds or rainwater reservoirs), overhead irrigation systems are robust and comparatively easy to implement technically. Propagation areas with irrigation systems require appropriate control with pumps and, if necessary, filtration systems. A system in individual chambered beds simplifies field establishment and improves controllability of water supply in all approaches. If appropriate, mosses can be grown in boxes or trays to facilitate later removal as sods.

Suitable irrigation techniques for moss propagation

Propagation on tables	Propagation in the field
Propagation on a thin substrate layer *Flow irrigation* - Controlled water supply from below by regulation with floats and overflows (highly precise) *Overhead irrigation* - Spray hoses - use only rainwater! **Propagation on fresh substrates** - as an additional option: subsurface irrigation (laid in the substrate)	**Propagation on peat substrates** - Irrigable beds (controlled flooding) - Periodic flooding (ebb-and-flow method) - Surface irrigation (spray or drip hoses on the surface)

3.1 Irrigation techniques

Various irrigation techniques can be used to achieve the optimum water level for propagation, i.e. a water level that is as constant as possible a few cm below the capitulae. A constant high water level is very important especially in the beginning for the sensitive individual plants and fragments. As the moss becomes denser and the plants increase in length, the distance to the water surface changes. At the same time, the capillarity of the moss cover also improves, so that the water table usually does not need to be readjusted, or only slightly. However, it should be noted that evapotranspiration also increases with increasing growth.

3.1.1 Flow irrigation

The simplest method of irrigation is to set a constant water level through an overflow and an adjustable water inlet. This is very easy to set up, especially on greenhouse tables. The tables can be fitted with overflows at the appropriate height, and the water inflow can be controlled by a float, which are readily and inexpensively available from plumbing or gardening supply stores.

Constant flow irrigation under field conditions is more complicated. Not only does the substrate need to be reprofiled to provide a flat surface, but the subsoil must be sealed by plastic sheeting to minimize the influence of chemically unsuitable groundwater and to keep the irrigation water in the area. Depending on the size of the propagation area, multiple inlets and outlets may be needed.

Regulation of the water supply can also be achieved by creating individual beds at different heights and by controlling the duration of regular flooding (ebb-and-flow method). High variation in evaporation means that this technique is usually linked to larger fluctuations in the water supply, requiring regular monitoring to prevent prolonged unfavourable conditions, especially in the more sensitive initial phase. A layer of straw can also be applied to help prevent excessive water loss in the early stages. Overall, the variable water supply reduces growth performance compared to methods that allow more precise regulation of irrigation. However, the lower biomass accumulation is offset by significantly reduced labour and material inputs.

3.1.2 Overhead irrigation

Overhead irrigation in principle is advisable wherever possible, especially via timed irrigation control in the early morning hours to maintain a uniform water supply to the moss capitulae. This promotes uniform growth and high reproductive rates.

Due to the higher demands on technical equipment the high demands on water quality, overhead irrigation should be used selectively and for a limited period of time. For example, this type of irrigation is recommended at the beginning of propagation as long as capillary connection to the substrate has not yet been established by the individual plants or fragments. The effect and necessity therefore also depends very much on the precipitation conditions; while in wet seasons it is not necessary, in hot and dry summers the benefit is clear. In addition, overhead irrigation can be useful as distance to the water level increases and capillarity decreases and evaporation becomes high. Generally, however, hummock mosses can already be harvested for further propagation or establishment in the field after such vigorous growth.

For overhead irrigation, it is important to use excellent quality water (rainwater), since evaporation directly in the moss cover leads to a significant accumulation of dissolved substances, making toxicity effects more likely. In addition, prolonged standing storage of the irrigation water can lead to algal growth, which is particularly problematic with overhead irrigation and must be avoided at all costs.

3.1.3 Irrigation in the field

In general, the same irrigation techniques can be used in the field as for table propagation. However, for precise control of irrigation, especially in the case of flooding, it may be necessary to seal the bottom of the propagation areas or beds, for example with plastic sheeting. Otherwise, the water usually

Propagation system in the field with flow irrigation in a bed with a waterproof layer underneath. In the picture, irrigation is provided by drip hoses laid in the substrate. In the foreground and the background, large quantities of moss mixtures were propagated. In the middle part, trials were carried out with different variants, including individual species and various mixtures in trays.

cannot be maintained at a constant level. In addition, sealing low-lying propagation areas reduces the influence of groundwater, which can impair propagation success due to excessive mineral and/or nutrient inputs.

After a time-consuming initial setup of the controlled flooding system through sealing the beds and flattening the surface, the operating expense is comparatively low and a uniform water supply can be ensured.

Irrigation by periodic flooding (ebb-and-flow method) can work well in the in the field if the establishment of beds or basins is possible, since it incurs relatively low technical costs. The water inflow and outflow can be regulated with simple piping and rotatable elbows. Since the supply is operated only periodically, this can be done manually. However, considerable effort may be required to set up the beds or basins, and suitable conditions and appropriate reservoirs of water (ponds or similar) are required.

Spray or drip irrigation can be used alone or in combination with flooding. If sufficient water is available, irrigation of the beds can suppress groundwater influence. In most cases, however, it is advisable to seal the beds to reduce the water demand. Since irrigation requires water filtration, the system requires more effort to maintain, especially if the water is obtained from open reservoirs. As with overhead irrigation on tables, very good water quality (rainwater) is required for outdoor sprinkler irrigation, otherwise salinisation or even toxic effects from dissolved salts and nutrients may occur. It may be necessary to temporarily stop irrigation if the water quality is insufficient.

Propagation area in the field with periodic flooding (ebb-and-flow irrigation). The cascade-like arrangement of the beds means that the water from the reservoir (mainly rainwater; not shown in the picture) can be used particularly effectively for irrigation. Simple, rotatable pipe brackets can be used to regulate the inflow and outflow.

Table 3: Summary of irrigation techniques

Flow irrigation – stable, high level	Flow irrigation – unstable	Overhead irrigation/ additional sprinkling
AIM: Continuous water supply from below via automated flow irrigation on tables or via periodic activation of drip irrigation in shallow basins or sealed basins.	AIM: Watering from below via manually activated inlets.	AIM: sprinkling irrigation from above, aiming at efficient use of limited resources, e.g. when stable flow irrigation is not or only partially possible (for reasons of limited water availability or load-bearing capacity and permeability of the sublayer).
Benefits/Purpose Simple and precise regulation of the water level, particularly on a thin substrate/peat layer with an impermeable sublayer. **Disadvantages/Problems** To achieve an optimal water supply, flat and stable surfaces are required. High water consumption due to permanent evapotranspiration (in warm periods). **Optimisation/Solution** Careful preparation of the substrate and its base (e.g. on height-adjustable tables) promotes growth. Availability of large reservoirs as well as recycling run-off water during long and heavy rain events may help to minimize risk of water shortage (however, strongly nutrient-enriched or algae-infested water may offset benefits).	**Benefits/Purpose** Does not require complex technical installations and electricity. Sufficient for occasional irrigation on thick substrates with a large water storage capacity as well as in periods of low evapotranspiration. **Disadvantages/Problems** Reduction of growth resulting from frequent drying/wetting cycles. Frequency and intensity of occurrence depends on substrate properties, precipitation frequency and microclimate. Frequent water level changes are counterproductive. **Optimisation/Solution** If a regular, manual water supply is not feasible, shading or wind protection measures should be taken.	**Benefits/Purpose** Comparatively low water consumption. Less heavy for the supporting tables. **Disadvantages/Problems** More technically demanding and maintenance-intensive. Good water quality is important, otherwise there is high risk of excessive uptake of dissolved substances from the irrigation water. **Optimisation/Solution** Since the mosses are usually moistened from above in the early morning hours, an adequate water supply from below is necessary even during the day to maintain high propagation rates. If the rainwater quality is poor, it may be necessary to temporarily deactivate sprinklers.
Conclusion/Recommendation High initial effort needed. When a functioning system is established, however, it can be expected that less effort will follow to maintain an automated irrigation (e.g. via routine supervision and occasional readjustments) than to manually keep an ebb/flow irrigation operating on a regular basis.	**Conclusion/Recommendation** Suitable for small propagation systems. In the case of patchy moss layers and in periods of high evapotranspiration, care must be taken to avoid frequent changes in moisture levels (on thin substrate layers). However, movable tables can be pushed into the shade depending on the weather.	**Conclusion/Recommendation** Allows efficient use of available water quantities and qualities. Overall, however, it is more technically demanding. Regulation of water quantity to avoid oversupply is complicated, which is especially relevant in case of poor water quality.

Other irrigation techniques:

a. *Flow irrigation in deeper basins with thicker substrate:* water can be stored directly below the surface. Reduces irrigation frequency, but more material is needed per propagation unit. Easier on smaller scales, for example for the long-term cultivation of a donor population.
b. *Hose/drip irrigation:* recommended to provide an automated water supply for smaller propagation sites in the field, either above- or below-ground. The distance between, and depth of, the hoses must be adapted to substrate (water storage capacity, capillarity, infiltration loss).
c. *Ditch irrigation:* can be implemented on a larger scale as an alternative to automated irrigation systems. Requires a lot of surface reprofiling to function reliably. The quantity and quality of the water supply as well as the reliable regulation of high and stable water levels are critical.

3.2 Amount and timing of water supply

The water supply should be adjusted to the seasonally fluctuating consumption and rainfall distribution. Sufficiently large storage capacities help to avoid water shortages. This can be achieved, for example, through cistern systems that are fed from larger roof areas.

If an average water consumption of 20 L/m^2/week is assumed for a stable flow irrigation over the summer (April-September), this means a total water supply of 0.5 m^3 per m^2 of propagation area. Assuming that the direct rainwater supply is also captured during this period (0.35 m^3 per m^2, corresponding to an average precipitation of 700 mm per m^2 and year) about 0.5 m^2 of roof area would be sufficient to cover the additional water demand (0.15 m^3) via irrigation for 1 m^2 of propagation area. Accordingly, for a 100 m^2 propagation area, the capacity of a cistern should be at least 35 cubic meters.

Especially in the case of propagation in a spring/early summer with little rain, it is important to ensure that the water reservoir has been filled up early so that a constant water supply can be ensured, especially in the first few months and throughout the entire growing period until autumn. Propagation in autumn usually needs less supplemental irrigation (depending on precipitation distribution), but the falling temperatures also result in lower growth rates.

3.3 Water quality

Since hummock mosses naturally occur in exclusively or predominantly rain-fed raised bogs, water quality is an important factor for successful reproduction. Irrigation should therefore ideally use rainwater, as only rainwater has the necessary low conductivity and low mineral and nutrient content needed by hummock mosses. Interestingly, trials have not found any negative effects of an increased nitrogen content of rainwater, as often observed in regions with intensively farmed livestock.

In exceptional cases, groundwater or surface water can be added temporarily or in small quantities – or even permanently in the case of soft, nutrient-poor water. However, it should be chemically analysed before use (pH, electrical conductivity, if possible ammonium, nitrate, phosphate and dissolved organic carbon). If the amount of groundwater or surface water is too large, severe adverse effects may occur. In particular, large amounts of algae can be introduced to the propagation system through surface water, resulting in algal dominance. In addition, the water can be polluted by increased nutrient concentrations. Groundwater usually contains high levels of carbonates and calcium.

Successful *Sphagnum* moss propagation, requires a constant supply of rainwater, which can be achieved by cistern systems that are filled up over larger roof areas. In addition to ensuring sufficient quantities, the quality of the irrigation water should be checked regularly. The chemical composition of the water should deviate as little as possible, or at least only temporarily, from that of natural bogs to maintain optimal growth conditions for the *Sphagnum* moss.

A substrate mixture consisting of 50 % fine and medium-coarse white peat has proven successful in *Sphagnum* moss propagation. 40-70 L/m^2 corresponds to a substrate thickness of 3-5 cm.

3.4 Propagation substrates

3.4.1 Substrate properties

Weakly decomposed raised bog peat (»white peat«) is a particularly suitable substrate for growing mosses due to its physicochemical properties. It provides consistent substrate moisture to the loose fragments of live moss, which are very sensitive to desiccation. More decomposed peat substrates require greater control of the water supply due to their lower pore volume and resulting low water holding capacity, and carry the risk of nutrient release in polluted sites.

Special care must be taken with the substrate used to ensure that it does not contain any undesirable weeds, either in the form of plant parts or as seeds. This would result in too much competitive pressure from faster growing vegetation, which would reduce

Typical parameters for the assessment of water quality

***pH value*:** rainwater used for irrigation typically has a pH in the slightly acidic range with values around 5.2, whereas groundwater and surface water with higher mineral content usually have a pH around neutral range or slightly above (6.5-8).

Electrical conductivity: values in rainwater are mostly < 100 µS/cm, whereas cistern water usually has higher values due to dust deposition on roof surfaces. The target should be values as low as possible below 120-150 µS cm-1.

Mineral content: low mineral content is even more important than a slightly acidic pH, since hummock mosses naturally gain their nutrient solely from rainwater. The calcium content of the irrigation water should be <15 mg/L, and the overall hardness of the water should be < 3° dH or < 0.55 mmol/L.

Nutrient content: low nutrient levels are desirable, and hummock mosses are particularly sensitive to excessive nitrogen concentrations. Nitrate concentrations of < 3-4 mg/L and ammonium concentrations < 1 mg/L should be aimed for. High phosphate concentrations (>1 mg/L) are not problematic for hummock mosses per se and actually promote growth, but usually result in problematic algal growth in cultivation and should be avoided.

Dissolved organic carbon: high levels of dissolved organic carbon should be avoided, as this usually indicates low water quality (for example, from surface waters). High turbidity significantly decreases the growth of *Sphagnum* mosses.

the propagation success especially if the water and substrate quality is not optimal and would require additional management. A suitable substrate is, for example, weakly decomposed peat from uncontaminated layers of areas of active peat extraction. Peat extracted close to the surface may have to be steam-treated to reduce the diaspore potential, or otherwise discarded.

Propagation areas on peat in the field must be particularly carefully checked to evaluate if topsoil removal is necessary on polluted sites to remove nutrients and undesirable diaspores and roots.

Favourable peat properties

physical properties	**chemical properties**
peat type/degree of decomposition weakly decomposed peat (von Post scale of peat decomposition: H2-H5) *particle size* mixture of 50 % fine (2-7 mm) and 50 % medium-coarse (7-15 mm) fractions + Weed- and pest-free + No further components (such as e.g. Perlite)	*pH [H_2O]* 3.4–3.9 *Mineral content* Total Ca: 0.3-1.0 mass % Total Mg: 0.1-0.2 mass % C/Ca: 49-55 *Nutrient content* Total K: 0.03-0.04 mass % Total P: 0.02-0.3 mass % C/N: 46-50 C/P: 1860-2250 N/P: 38-45 N/K: 25-32

3.4.2 Substrate and site preparation

In order to maintain a constant moisture level through flow irrigation, care must be taken during planting to ensure a homogeneous substrate thickness and density is produced so that the distance to the water level can be adjusted as desired and kept constant. This can be achieved by spreading the substrate with an even thickness and saturating the area completely with water before introducing the moss fragments. This allows uneven surfaces resulting from swelling and subsidence to be eliminated without affecting the fragments. Smaller irregularities can be levelled out by light pressing, larger ones by smoothing. Loose substrate or deep holes should be filled with additional material to prevent hollows forming and poor growth of mosses. Uneven substrate thickness or blocked overflows can cause localised excess water.

Despite the good water storage capacity and conductivity of white peat, if it is spread thinly it can dry out quickly if the water supply stops. Particularly during periods of high evaporation and low rainfall rates, it requires large amounts of additional water and maintaining the supply is crucial for good propagation rates. Sufficiently large storage capacities should be maintained to avoid water shortage situations. The water supply can also be adjusted to seasonal variations in consumption and precipitation.

Methods for propagation on tables and in the field

Propagation on tables	**Propagation in the field**
Propagation in trays - Facilitates the removal and transport of grown sods - Suitable for producing smaller quantities of moss *Propagation on mats* - Improves the water storage capacity of the substrate layer and facilitates larger cultivation areas	*Propagation on peat* - After top soil removal (removal of rooted and potentially nutrient-rich layers) - The surface should be levelled *Propagation on fresh substrate* - For example, on weakly decomposed peat spread out on plastic sheeting or mats

The rewettability of dried peat with water is very limited. The moss fragments should therefore only be applied after intensive watering and substrate swelling. It is important that the substrate is stable enough when saturated to avoid later slumping and poor growth of the mosses. Areas of substrate that are permanently wet at the surface are susceptible to algal growth.

4 Application techniques for propagation

There is no single best way to inoculate the substrate with moss fragments. The choice of technique should be based on the available facilities (dimensions, substrate, irrigation) and the donor material (target species, quantity).

4.1 Fragments or individual plants

The spreading of mosses for regeneration purposes in the form of fragments or individual plants has been practiced successfully for years in Canada. For this purpose, fragments or individual mosses are scattered evenly over the peat-covered area (Quinty & Rochefort, 2003). Favourable hydrological conditions in the form of a uniform, high water table are important here, since the fragments and individual plants are not yet hydrologically connected to the underlying peat. Thus, capillary water rise is severely limited in the initial phase and there is a risk of desiccation if the water table temporarily drops.

As long as there are stable hydrological conditions on planting tables or in suitable propagation facilities in the field, a dense stand of moss can be quickly generated from comparatively little material (30-60 g dry mass/m^2). Depending on the species and starting quantity, the application of whole fragments under optimal conditions leads to complete coverage of the area after 6 to 18 months and maximum biomass growth between 630 and 860 g dry mass/m^2.

Trials with cut fragments (< 1 cm) showed that their multiplication rates are significantly lower than those of whole plants (2-8 cm). Especially species of the section *Sphagnum* were negatively affected by cutting. In contrast, one species from the section Acutifolia (*S. rubellum*) showed a high regeneration capacity even with small plant parts. Cutting the propagation material can therefore introduce a selective bias for certain species and is risky, since many potential target species do not tolerate it. Although studies show that even the smallest fragments of moss are sufficient to develop new plants (Poschlod & Pfadenhauer 1989), this only occurs under optimal conditions and

Hummock mosses and other plant species belonging to typical bog communities after 12 months of propagation on tables with flow irrigation and additional overhead irrigation. The material was spread as single plants. In the picture you can also see the sheeting along the side to reduce evaporation by strong winds.

Propagation trays on an irrigation table containing whole fragments of *Sphagnum papillosum* (initial biomass: 30 g dry matter per m^2) at the beginning of the propagation (left) and 14 months later (right).

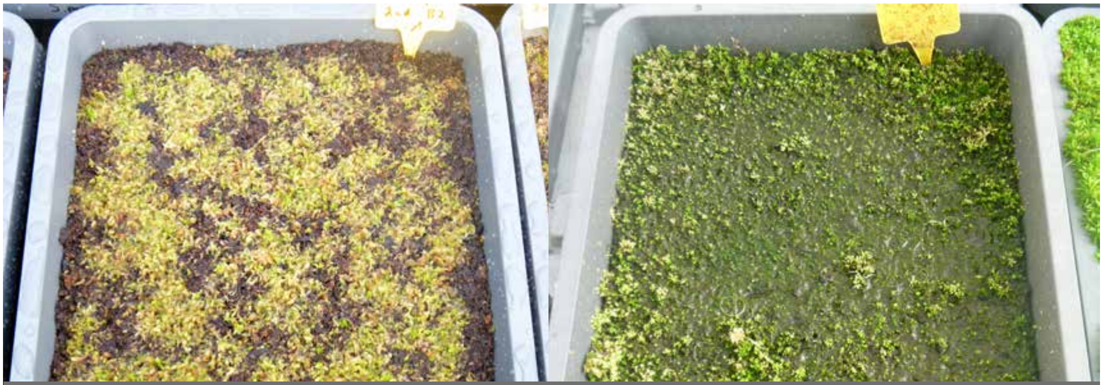
for certain species. Furthermore, the slow initial growth rates of small fragments mean that it is likely that other plants such as algae and grasses will spread faster and threaten the propagation unless conditions are optimal (cf. Beike et al. 2014).

Because mosses are generally limited in their ability to regulate their water needs, shading can be used to protect individual fragments and plants from desiccation when conditions are temporarily unfavourable. For example, a layer of straw can be placed over the mosses (200-300 g/m^2). Alternatively, fleece can be laid over the surface to improve the microclimate. The necessity of these measures depends on the form of irrigation. However, even with optimal water supply, a thin covering over the summer can provide an advantage by protecting the fragile fragments from strong direct sunlight.

4.2 Sods

The use of intact sods for the propagation of hummock mosses seems promising, since the intact sods offer better capillary connection to water supplies, thus forming more stable units protecting against temporary drought. Since hummock mosses survive shorter periods of drought well, they may be seen as a backup, which can be useful when irrigation is irregular and monitoring is limited.

A major disadvantage of spreading sods is that growth is limited primarily to the edges of the sod and it can take significantly longer to achieve dense moss cover. This is why sods



Propagation trays on an irrigation table containing chopped fragments of *Sphagnum papillosum* (initial biomass: 25 g dry matter per m^2) at the beginning of the propagation (left) and 14 months later with strong algae growth (right).

are generally not used in *Sphagnum* farming, despite appearing to be advantageous. However, for restoration less focused on time and yield, the approach can be quite useful in unstable conditions.

Established propagation site in the field with ebb-flow irrigation after spreading of whole fragments and transplantation of intact sods. Inoculation with sods is useful as they are more resistant to the frequent water level fluctuations often caused by ebb-flow irrigation.

Table 4: Summary of application techniques

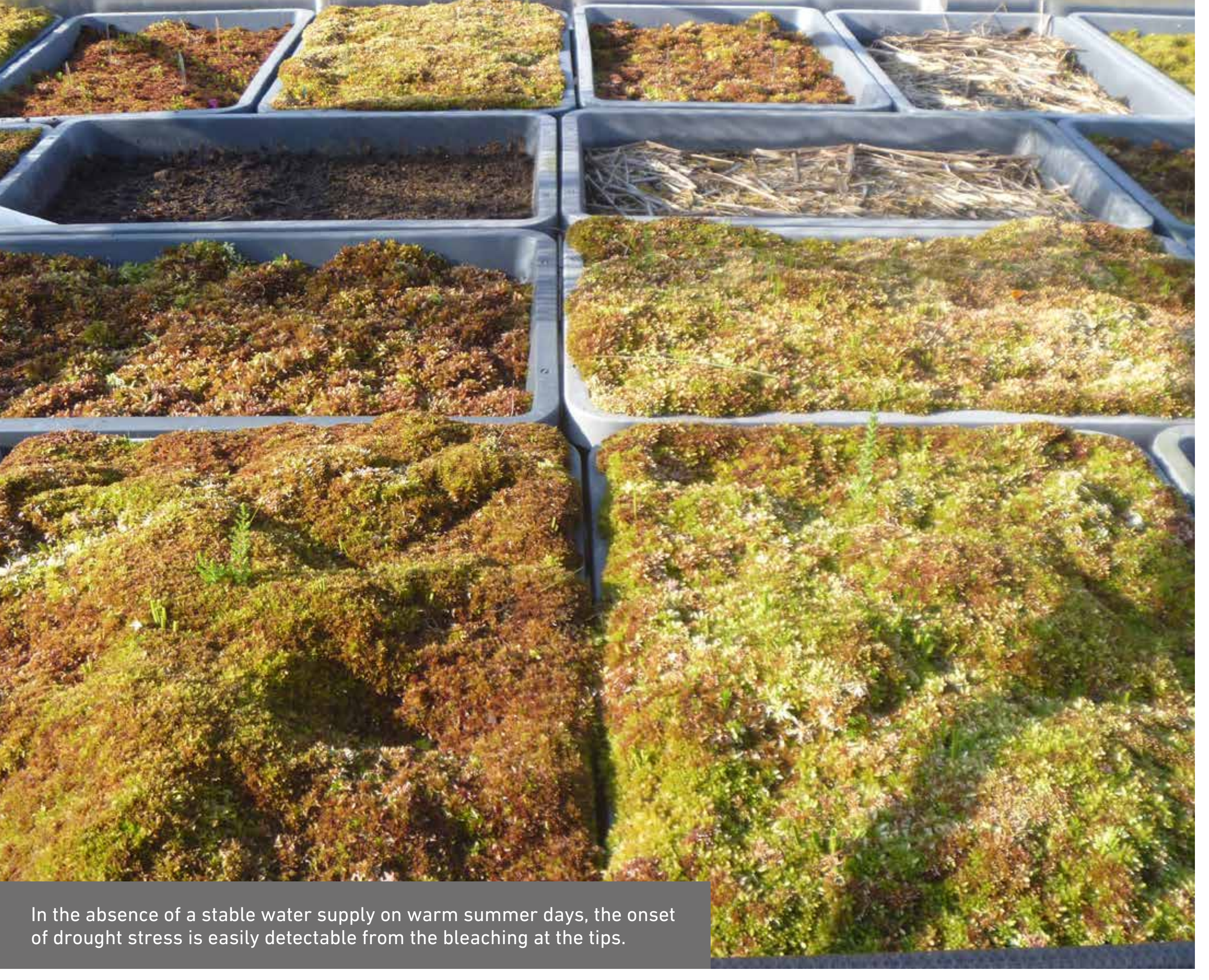
Loose, whole fragments (individual mosses with capitulae)	Chopped fragments	Mixing species (polyculture)
Manual separation of branches of collected mosses	Mechanical chopping. Commonly used in the course of large-scale removal and spreading	Combination of fragments from different species, propagation as a species mixture
Pros Undamaged, healthy plants are important for vegetative regeneration. The more homogeneous the separation of the plants, the more homogeneously they can be portioned and spread. **Cons** Separation by hand is labour-intensive. Fragments that are either too loosely or too densely applied may lack contact to the substrate.	**Pros** No manual separation required Easy spreading of fragments on larger scales by machines **Cons** If the material is chopped too finely (<1 cm) there is a risk that the damage is greater than the benefit or that sensitive species are disadvantaged. The regeneration capacity of the species varies strongly with fragment length and density of capitulae. In case of permanent flooding, slow growth rates allow the spread of algae.	**Pros** A range of different mixtures is possible. Potentially higher adaptability and resilience to strongly fluctuating water availability. In the best case, mutual facilitation between species. **Cons** Despite optimal water supply, species-specific differences in the growth rates can result from unequal application ratios between living capitulae and dead stems

Tips for applying moss fragments to the substrate:

- Gently pressing the fragments or individual plants improves contact with the underlying substrate.
- Loose fragments tend to be more sensitive to fluctuations in water supply and strong direct sunlight.
- Shading of sensitive *Sphagnum* fragments can be beneficial, particularly at the beginning of propagation and during times of high temperatures, to provide protection against desiccation and improve the microclimate.
- Instead of dividing up a moss layer and spreading the material as fragments, donor material can also be cut and transplanted as intact sods. However, since the moss grows only laterally from the edges of the sods, it takes longer to cover larger areas. This technique is particularly suitable for the inoculation of smaller propagation areas with an unstable water supply or for the establishment of a long-term source of propagation material or diaspore bank.

Propagation methods depend on type and quantity of the donor material, the substrate and water quality as well as the objectives of propagation (mono- or polyculture, on tables or in the field)

1. Plant collection (ordered by decreasing naturalness) a. Wild population b. Populations in cultivation for conservation purposes c. Propagation cycles	**2. Fragmentation** The more carefully moss cushions are separated, the better their ability to regenerate. Aim is to keep the largest number of healthy capitulae.	**3. (Potentially) mixing species** When collecting from different populations or cycles, take different water contents and fragment lengths into account.
4. Portioning E.g. 50 g dry mass or 1000 g fresh mass per m^2 (DM:FM ratio 1:20)	**5. Plant spreading** By hand, if no suitable machinery is available for spreading	**6. Additional measures** Lightly press loose fragments onto the substrate. Water from above only with rainwater. If necessary, shade.



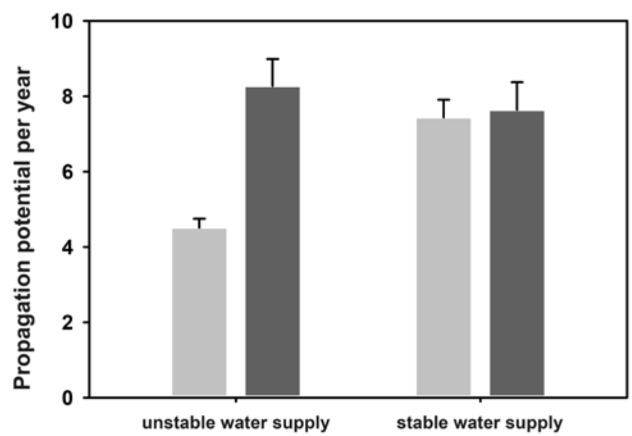
In the absence of a stable water supply on warm summer days, the onset of drought stress is easily detectable from the bleaching at the tips.

5 Effects of species and environmental factors on propagation potential

5.1 Environmental effects

In principle, the extent to which moss growth is controlled by abiotic and biotic factors depends on the physiological optima and tolerances of species as well as on interactions between variables. For example, it is known from many studies conducted in boreal climates that under favourable hydrological conditions, *S. rubellum* shows sufficient growth rates to rapidly recolonise initially bare, degraded peat within approximately 10-20 years (McCarter & Price 2013). The globally highest annual growth rates for *S. papillosum* are reported from more humid climates with long and warm summers (Krebs et al. 2016). However, the average growing season in Central Europe has a limited period of time where growth conditions can be considered optimal. Therefore, to produce sufficient quantities of donor material within reasonable periods of time (2-3 growing seasons), it makes sense to maintain, wherever possible, a constantly high water table level by means of artificial irrigation (e.g. during summer drought periods) - similar to *Sphagnum* farming. Experiments confirm that both a constantly stable water supply from below or a diurnal sprinkling from above in case of unstable water supply produces propagation rates that are on average twice as high as under unstable irrigation systems (see figure below). Continuous growth is only maintained under consistently optimal humid conditions, since high photosynthetic performance cannot be maintained if the water content falls too low. Our field studies show that the rate at which mosses assimilate carbon is considerably slowed if the water content of the capitula falls below 85-80% fresh weight, at which point the mosses start entering a latent resting state.

According to our findings, additional overhead irrigation brings no further advantage if the water supply from below is stable. However, depending on water quality, it can induce unwanted shifts in species composition during propagation.



Propagation potential (multiples of the initial biomass per year with 325 growing days [daily mean temperature > 2 °C]) of hummock mosses (*S. medium*, *S. papillosum* and *S. rubellum* combined) with unstable (left) and stable (right) water supply from below (light) plus seasonal addition of overhead irrigation with collected rainwater (dark). The results clearly show that negative effects of an unstable water supply from below are compensated by targeted overhead irrigation.

Other environmental factors that directly influence the amount of water needed are temperature during dry periods (especially in hot summers), wind speed or high solar radiation during dry weather conditions, and interactions with other species (see next chapter), since they modify the microclimate.

Experimental ***Sphagnum*** propagation on tables with side-mounted windbreaks to reduce desiccation. Trials of growing *Sphagnum* in mono- as well as polyculture can be carried out by using planting trays.

5.2 Interactions and effects of different species

The type of irrigation needed for an optimum growth rate depends on the species of moss. Experiments with monocultures have shown that unstable water supply with additional overhead irrigation is ideal for *S. rubellum* and *S. medium* (Table 5). A stable water supply with overhead irrigation was needed for *S. papillosum* to develop its highest propagation rates, in comparison to *S. rubellum* and *S. medium*, which reduced their productivity. Considering that overhead irrigation is often not technically possible, the next best option for all three species is just to provide a stable water supply from below, producing biomass growth that is only 9-16 % lower than species-specific optima. Moreover, just minor shifts in species composition can be expected if species mixtures are propagated under a stable water supply.

Temporary waterlogging due to additional irrigation (water level < 1 cm below substrate surface) only slightly reduced the growth rates of *S. papillosum* (minus 9 %). In contrast, the same extent of oversupply was more harmful for *S. medium* and *S. rubellum* (average losses of 22-26 %) compared to each species optima (water level 2-4 cm below ground surface). Consequently, the likelihood that significant shifts in species composition occur increases as a result of oversupply of water.

For all tested hummock mosses, by far the most severe growth losses occur during drought stress as a result of temporary water shortage during unstable flow irrigation (losses of 42-70 %). Frequent alternation between wet and dry phases have proven to be particularly unfavourable for the propagation of *S. rubellum* (Raabe et al. 2018). To prevent drought stress, additional measures are recommended to reduce the soil temperatures and reduce desiccation by wind (e.g. temporary shading, straw cover, lateral wind protection).

The ability to form new capitulae, which branch out by length increment of the stem to produce dense moss layers when growing vertically, is an essential characteristic of successful vegetative propagation. The photos show (a) *S. papillosum*, (b) *S. medium* and (c) *S. rubellum*.

Sustainably high rates of growth for species that dry out particularly quickly can be achieved by growing them together with more water-storing species or by promoting accompanying vascular plants. For *S. rubellum*, the presence of other species such as *S. papillosum* and *S. medium* can help to cover water requirements during 1-2 weeks of drought, while monocultures did not show any increase at all. (Raabe et al. 2018). As »nurse plants«, graminoid vascular plants can also positively influence the microclimate to a certain degree by providing shade and also serving as climbing aids (Sliva & Pfadenhauer 1999). In the case of too much shading along with high water availability,

Table 5: Species-specific annual propagation potential of *Sphagnum* monocultures; average multiple of initial biomass after 325 growing days starting with 30-60 g dry matter per m². (a) under optimal water supply: *S. rubellum* & *S. medium* = unstable flow irrigation from below with additional overhead irrigation; *S. papillosum* = stable flow irrigation from below with additional overhead irrigation. (b-d) average relative yield reductions under increasingly less favourable water supply conditions.

	S. rubellum	***S. medium***	***S. papillosum***
a) Optimal supply	9–11	7–8	7–9
b) Stable flow irrigation	< –20–10 %	< –10 %	< –20–10 %
c) Temporary water excess	< –30–20 %	< –30–20 %	< –10 %
d) Temporary water shortage	> –50 %	< –50–40 %	< –50–40 %

however, the moss species preferring full light (e.g. *S. papillosum*, *S. rubellum*) tend to grow long and thin (etiolation) and become more susceptible to drought damage in the absence of water (Clymo 1973).

The rapid development of a compact growth form through healthy and vigorous growth of the scattered fragments allows hummock mosses to better cope with intermittent drought phases. As soon as a compact moss cover (> 95 % cover at a height of approx. > 3 cm) is achieved, the amount of water supplied can be reduced to avoid negative effects caused by highly concentrated solutes (salt and mineral inputs) in the irrigation water and to get more robust plants for transfer to the receptor sites (cf. Hajek, T. & Vicherová, E. W. 2014).

A simple measure of growth rate is the time needed until a moss coverage of > 95 % is achieved. With an inoculation of 60 g dry matter per m², an almost complete ground cover can be achieved with *S. rubellum* after 6 months (May-October). In contrast, *S. papillosum* and *S. medium* achieve this - including winter dormancy - 6 to 9 months later. This is also reflected by differences in height and biomass increment. Starting from the same inoculation density, the growth rates of different sized species are strongly related to the number of individuals present as well as the proportion of photosynthetically active and thus regenerative plant parts. This is related to the ability of existing shoots to divide, which, in the case of more numerous capitulae present, causes them to branch more rapidly and thus to develop an advantage in terms of both lateral cover and vertical height growth (Tuitilla et al. 2003). To determine the relative increase in individual density, the number of capitulae at the beginning and end of the reproductive cycle can be recorded by counting. The most productive species, *S. rubellum*, grows 9-11 times as many capitulae after 18 months, while the rates for *S. medium* can be up to 45 % lower, since this species does not tolerate an over-supply of water.

Although there are differences between the species, previous experiments show that comparably high growth rates can be achieved for all tested target species, even in species mixtures, when uniform irrigation and inoculation techniques are used. The most important prerequisites in the early stage of propagation are constant irrigation with rainwater and the full regenerative capacity of the donor material (Raabe et al. 2018). Species mixtures are also beneficial for the establishment of species-rich receptor sites. Especially with regard to the establishment success on areas with limited water availability, moss mixtures have proven to be advantageous, in that sensitive species (especially *S. rubellum*) benefit from the higher water holding capacity of more robust species (especially *S. papillosum*). It is notable that growth rates for *S. rubellum*, in particular, differ in the early stages of establishment from rates in the preferred drier hummock habitats known from numerous field studies (Gunnarson, 2005). Since the conditions typical of older

Growth rates in propagation trials can be monitored using various parameters. However, uniform methods should be used for comparison (e.g. moss cover change, height increment, change in biomass or capitulum density).

successional stages in established upland bog communities with intact acrotelm are more likely to be niches that the plant has created for itself over a long period, these do not need to have the conditions most favourable for rapid vegetative »juvenile« growth (Rydin & Jeglum, 2006). For the practice of propagation, this means that it is of utmost importance to offer permanently moist growing conditions, especially at the beginning when loose fragments of all species are most vulnerable. In addition, our

Table 6: Species-specific growth rates (multiples of starting biomass) under consistently moist conditions with flow irrigation from below and overhead irrigation using rainwater.

		S. rubellum	***S. medium***	***S. papillosum***
Ratio of species in inoculation material		1:12	1:11	1:9
Initial biomass [g dry matter/m^2]		60	60	60
Initial capitulae density [cap/m^2]		4,400	2,000	2,100
Time needed for > 95 % coverage		6 months	15 months	12 months
Moss height [mm]	6 M	37 ±2	30 ±2	31 ±3
	12 M	45 ±4	37 ±3	41 ±4
	18 M	92 ±9	74 ±13	79 ±11
Reproduction rate (biomass)	18 M	11–15 times	5–12 times	9–13 times
Reproduction rate (capitula density)	18 M	9–11 times	6–10 times	8–9 times

Periods of growth: 6 months = May-October; 12 months = May-April of the following year;
18 months = May-October of the following year

own results indicate that a species that is particularly sensitive to desiccation in the early stages of growth, such as *S. rubellum*, has a much greater potential to successfully re-establish itself in species mixtures on restoration sites with unfavourable water supply, because the combination with other species provides a greater adaptability to different site conditions.

Similar to *Sphagnum* propagation on tables, planting trays can also be used in the field. They not only facilitate the handling of experimental units, but also harvest, transport and transplantation of intact sods at the end of the propagation. Good contact with the underlying water-bearing substrate is crucial also on trays to maintain stable surface moisture by capillary rise to achieve high propagation rates.

6 Examples of successful *Sphagnum* propagation nurseries

To increase and ensure availability of donor material for the restoration of hummock-forming bog vegetation, various *Sphagnum* propagation techniques were tested both on tables and in the field as part of a research project. In general, a well-executed design of the nursery in consideration of local conditions is the first key factor for success in moss propagation. Regular monitoring and maintenance with clear responsibilities as well as possibilities of ongoing optimization were crucial for the smooth functioning of our experimental sites. For this purpose, it is recommended to start with a manageable size of nursery and to experiment on smaller scales in order to learn from initial mistakes and to readjust.

Greenhouse tables have proven to be particularly suitable for rapid and efficient propagation of rare hummock mosses. They allow optimal growth conditions (substrate and irrigation) to be recreated on a small area (10 m^2) and are easy to manage in everyday practice. This approach has been used in practice on an area of 100 m^2 under consideration of available project resources (floor space, moss material, water quantities and personnel). Installing the tables outdoors was beneficial for mosses, as it allowed them to adapt to varying weather conditions. In contrast, propagation trials inside of the greenhouse caused the undesirable side-effects of fungal or algal spread.

Since only thin substrate layers (< 5 cm) can be used on tables, a constant water supply from below or above turned out to be a fundamental factor for success.

If donor material and practical knowledge in *Sphagnum* propagation are limited, cultivation in trays on tables is a good method to test target species composition and irrigation techniques.

This is especially important to keep the moisture content stable, especially during the main growth phases in summer when evaporation is high. Wind can also cause rapid desiccation of *Sphagnum capitulae* and thus significantly reduce growth rates. To minimize the surface wind speed and thus water loss, protective walls (e.g. metal sheets or plexiglass) approximately 20 cm high were installed on the sides of the table. Also, to protect against foraging by birds, a net can be stretched over the tables.

A slight slope and an overflow are necessary on the table to allow excess water to escape after heavy rainfall. The overflow is especially important for thin substrate layers and mosses growing close to the water level, as they are highly sensitive to fluctuations in water levels. Conditions that are permanently too wet slow down growth rates and thus produce lower quantities of donor material. Controlled overhead irrigation is an efficient method for optimizing water supply, especially in the early morning hours. During dry periods, sufficient water supply at the surface should also be maintained during the day. In nurseries with a thicker substrate layer and thus larger water storage capacity and good water conductivity of the substrate, it is in principle possible to adjust the water level deeper in the peat layer (up to 15 cm below the surface).

An alternative way to produce donor material, especially at larger scales (>100 m^2), is propagation in the field. Also here, cultivation

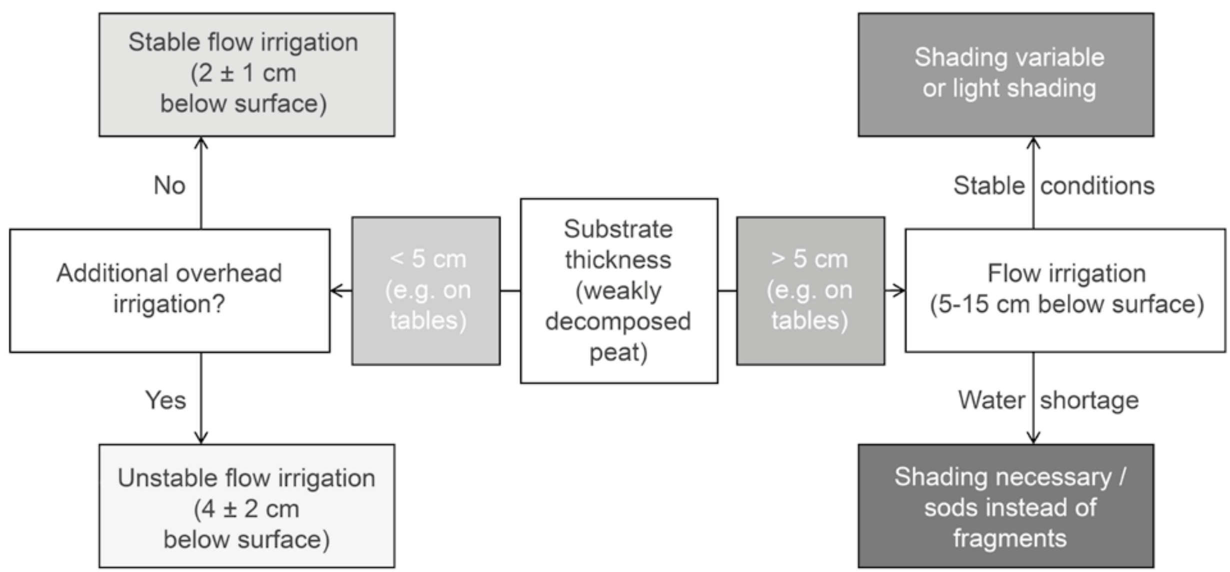
In addition to site preparation (left), the availability of water of sufficient quality (right) is one of the biggest obstacles to *Sphagnum* propagation in the field.

success is dependent on precise water level control. To achieve this, it is important to properly prepare the substrate surface, which will usually require increased technical effort. In the pilot test, an automatic irrigation system (subsurface or surface irrigation controlled via pumps) combined with waterproofing of the propagation beds by foil and overflows proved successful (see chapter 3.1.3). The installation of basins also enables the application of fresh substrate in the field and improves the manageability of water supply. As on the tables, propagation experiments can also be prepared using trays, which also makes transportation easier for the transplantation of intact sods.

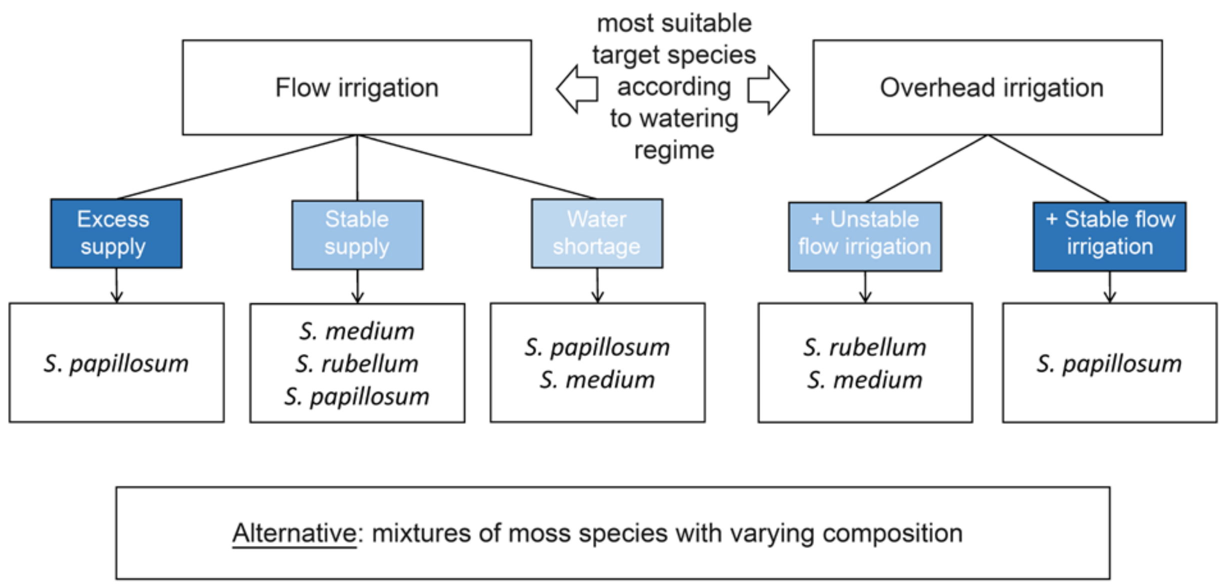
In the site selection process, care should be taken to meet the same requirements for substrate and water quality as they apply on tables, so that successful propagation of target species can also be achieved in the field. Experience has shown that adequate water supply in both quantity and quality is the biggest obstacle to overcome to ensure optimal growth conditions. However, these conditions are, particularly at larger scales, not easily maintained. First, despite favourable residual peat properties (high water holding capacity, low nutrient levels) the amount of water required for constant irrigation can simply be insufficient. Secondly, a water source may provide sufficient amounts, but its use can be limited by its water quality (mineral content, nutrients) and the high decomposition degree of peat. Consequently, it is recommended to first examine the site conditions with regard to the water supply capacities (water reservoir, height differences). This is necessary to adequately prepare the propagation site (topsoil removal, application of fresh substrate layers) and to control the irrigation (manual water supply, installation of an automated irrigation system). In general, the potentially most suitable sites would be located within close proximity to semi-natural or restored areas with good peat and water properties. Despite careful preparation, propagation in the field is still usually less successful than on tables. Therefore, at first only robust species and/or mixtures should be applied as fragments. Depending on the need for further protection or to improve resilience towards desiccation, the mosses should be protected or transplanted as intact sods.

In order to minimize water losses, shallow basins can be waterproofed with plastic sheeting, which are then filled with fresh white peat substrate (~ 10 cm) and irrigation equipment.

7 Decision tree for the establishment of a successful propagation system of hummock-forming mosses



Decision tree for the selection of irrigation and inoculation techniques depending on 1) substrate thickness (thicker/thinner than 5 cm of white peat) followed by either 2A) irrigation possibilities (with or without additional overhead irrigation) or 2B) water supply (excess or shortage of rainwater in a reservoir). Default inoculation as fragments with or without a mulch cover or use of intact sods.



Decision tree for the selection of *Sphagnum* species depending on irrigation technique. Differences in species optima mean that relative growth of different species in both mono- and polyculture can be expected to differ in response to irrigation type, but also in response to water quality due to shifts in the competitive interaction between species.

Harvested hummock-forming mosses on a propagation table in the field. Numerous other typical raised bog plants such as white beak-sedge (*Rhynchospora alba*) and bog cranberry (*Vaccinium oxycoccos*) are also found among the lush *Sphagnum* cushions. Now the question arises, where and in which way the propagated hummock-forming mosses can be spread on regeneration areas.

Part II: Activation of raised bog regeneration through the establishment of *Sphagnum* mosses (AktiMoos)

1 Introduction and establishment of propagated material at the recipient site

After successful propagation, the transfer of *Sphagnum* mosses to degraded raised bog areas is the next essential step in regeneration. While there are already numerous successful examples of this in Canada and the Baltic countries, there is almost no corresponding experience in northwestern Germany or the neighbouring Netherlands. Also, the large-scale methods of the »Moss Layer Transfer Technique« applied in Canada (González & Rochefort, 2014) are not applicable under northwestern German or Dutch conditions, especially because of the almost complete degeneration of the peatlands here and thus the lack of donor areas for the transfer of vegetation. In this guide, we show that a successful establishment of hummock-forming *Sphagnum* mosses (hereafter referred to as hummock mosses) after peat extraction can in principle also be possible and practicable in northwestern Germany. The research on which this guide is based was carried out within two projects funded by the German Environmental Foundation (DBU), as well as an extensive literature review. In the following, the ecohydrological prerequisites for the receptor sites based on stages of restoration, the transplanting techniques as well as the factors controlling the establishment success are presented and discussed. In the concluding chapters, we provide summarizing guidelines for practical application and give a brief outlook on the limitations and perspectives of successful raised bog restoration.

Very young stages with sparse pioneer vegetation growing directly on black peat without an acrotelm are unsuitable for the establishment of hummock-forming mosses due to strongly fluctuating water levels and the lack of nurse plants.

Older rewetted peatlands are characterized by a variety of different successional stages of vegetation depending on age, water and nutrient levels. In the second research project (Part II), their suitability for the establishment of hummock-forming mosses was investigated in detail.

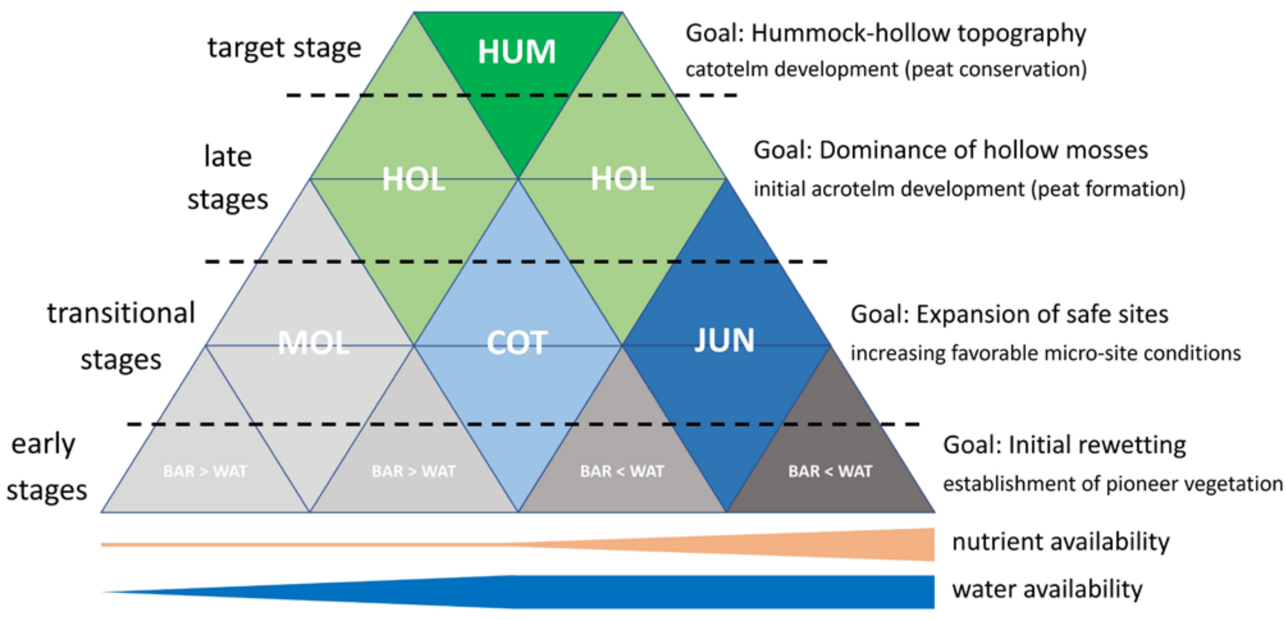
Before we begin, we would like to emphasise three important principles of the transfer of hummock mosses:

I) Whenever possible, propagation material of regional origin should be used, although due to low regional genetic differentiation in the genus *Sphagnum*, material taken from further away can in principle also be used (section 2.3). It is important that, as far as possible, the entire local genetic differentiation, e.g. with regard to water levels, is represented in the propagation material.

II) Due to the scarcity of donor material, only receptor sites with favourable ecological conditions for successful establishment should be considered.

III) During transfer to the receptor site, a clear, planned procedure is absolutely necessary. This can be ensured by a detailed documentation of the transplantation methods and a regular monitoring of the success of the measures. This procedure can also provide essential information for the optimisation of future regeneration measures.

2 Successional stages in bog regeneration as the basis for planning *Sphagnum* reintroduction



Succession model of typical stages of vegetation development on raised bog sites after peat extraction and rewetting. The greatest potential for successful re-establishment of hummock mosses/activation of raised bog regeneration is in later stages. Abbreviations: HUM = hummock-forming moss dominance, HOL = hollow-inhabiting moss dominance, MOL = *Molinia caerulea* dominance, COT = *Eriophorum* dominance, JUN = *Juncus effusus* dominance, BAR = bare peat, WAT = open water

Recommendations to establish hummock mosses are best described using model scenarios, knowing full well that there are numerous overlaps between the stages and states shown here (Fig. 1, Table. 1). The differentiations made for this purpose are based on the generally accepted successional stages in raised bog restoration (Eigner & Schmatzler 1991, Drachenfels 2011). In addition to the factor of time, these are based primarily on gradients of the mean water level and its fluctuation as well as the nutrient levels. In the field, these successional stages can be recognized at an age of 5-15 years by the dominant vegetation. In detail, the following stages can be distinguished:

a) Stages dominated by common heather (*Calluna vulgaris*). These are established in the medium term on strongly oligotrophic sites without nutrient residues, but are characterized by a low mean water table of about 30-60 cm below ground level. In these mostly very species-poor dwarf shrub communities, purple moor-grass (*Molinia caerulea*) often occurs as the co-dominant species.

b) Stages dominated by purple moor-grass (*Molinia caerulea*). These stages are characterized by a higher mean water level with simultaneous strong fluctuations, with almost consistently no water-saturated conditions in the root zone of the grasses, especially during the growing season.

Stages with larger proportions of *Molinia caerulea* together with *Eriophorum* characterize sites with phases of very low water levels (< 25 cm below ground level) and strong differences in water level between winter and summer.

c) Stages dominated by tussock cottongrass (*Eriophorum vaginatum*) and purple moor-grass (*Molinia caerulea*). This vegetation indicates that higher mean water levels and weaker fluctuations already prevail here during the growing season. Under the influence of more mineral-rich groundwater, *Eriophorum vaginatum* may be partially or completely replaced by *Eriophorum angustifolium*.

d) Cottongrass stage with dominance of *Eriophorum vaginatum* and hollow inhabiting *Sphagnum* mosses. This stage is characterized by predominantly high water levels, which are just below or above the soil surface almost all year round and show only comparatively small seasonal fluctuations. *Eriophorum angustifolium* may also become dominant initially under the influence of more mineral-rich groundwater.

Pure *Eriophorum* stages with co-dominance of hollow mosses are found on sites with year-round high water levels near the soil surface (> 25 cm below ground level), such as on floating mats. These stages usually provide very good conditions for successful hummock moss establishment.

e) Stage dominated by common rush (*Juncus effusus*). This increasingly common stage is hydrologically very similar to the cottongrass stage described above, but differs significantly from the latter in trophic terms due to markedly elevated Ca, N and P levels in the peat substrate, mostly resulting from prolonged agricultural use of the sites prior to peat extraction. Accordingly, the dominance of *Juncus effusus* is caused by competitive advantages over the cottongrasses due to a significantly increased nutrient level.

Stages a and b are not (a) or only under certain conditions (b) suitable for re-establishment of hummock mosses.

In the following, we will therefore focus on stages (c), (d) and (e), while for (a) and (b) hydrological improvement measures must first be carried out before attempts are made to establish hummock mosses.

The succession model used here assumes that the necessary conditions (water level stabilisation, acrotelm formation and corresponding soil hydrological conditions) must first be created by the dominance of

Stages with tall-growing and often very biomass-rich stands of *Juncus effusus* also characterize sites with quite high water levels throughout the year, but which also have a noticeably higher nutrient level, mostly being areas of former arable land use. In recent years, increasing areas formerly used for arable farming have been used for peat extraction, meaning that areas dominated by *Juncus effusus* are becoming more common.

typical species of the early and transitional stages (Timmermann et al. 2009). Only then, through the targeted introduction of hummock mosses as functional key species of subsequent stages, can succession proceed towards the complete regeneration of raised bogs.

Stages with *Eriophorum angustifolium* are easily recognizable by the rust-red discoloration of the leaves, even later in summer, and are typical for sites with a stronger influence of mineral-rich groundwater. These are often sites with a very thin or partially ruptured base of black peat, which means that hydrological conditions are often rather unstable, especially in summer when groundwater levels generally drop.

Collection of *Sphagnum* fragments by hand

3 *Sphagnum* harvesting and introduction

3.1. Sphagnum harvesting

Sphagnum material for restoration purposes can either be collected from semi-natural sites, e.g., old areas where peat was cut by hand, or pristine sites that have never been cut. Alternatively, it can be sourced from propagation cultures specifically established for the purpose of producing larger quantities of donor material, such as irrigated greenhouse tables or *Sphagnum* cultivation fields (Graf et al. 2017, Raabe et al. 2019). In many regions, e.g., northwestern Germany or the Netherlands, populations of hummock mosses in many semi-natural sites are already too small to remove further material. Here, targeted *Sphagnum* propagation for restoration purposes is usually the only feasible way to produce material for reintroduction. The concepts and methods necessary for this are presented in Part I of this guide. Specific aspects to be considered when removing *Sphagnum* material from semi-natural areas and from propagation facilities are compared in Table 1. In general, nature conservation law requires permits be obtained in advance both for removal from the donor site and for introduction to the regeneration site.

Table 1: Comparison of the harvest of *Sphagnum* from semi-natural areas or propagation facilities (see Part 1 of this guide)

Harvest from semi-natural sites	Harvest from propagation facilities
- Harvest of moss species typical of hummocks and hollows. - Collection of hummock mosses mostly limited by the small size of the few remaining populations. - Collection points difficult to reach. - Permit required.	- Usually only hummock mosses are harvested, but accompanying propagation of hollow moss species is also possible. - Harvesting is easier. - After initial approval and continuous propagation, material can be harvested almost as often as desired. - Reproduction of always the same individuals (genetic restriction). - When new material is introduced to the propagation stage, the origin must be documented.

3.1.1 Hollow-inhabiting *Sphagnum* mosses

Hollow mosses can usually be removed quite easily from a natural bog or from surrounding regeneration sites where these species have already established themselves in larger populations. Removal of these mostly floating or loosely structured species can be done with a bucket or by hand. The most common species, *Sphagnum cuspidatum* and *S. fallax*, should be distinguished, if possible, as *S. fallax* prefers noticeably more nutrient- and mineral-rich sites (Hölzer 2010). This characteristic should match the target site as much as possible (Fig. 1, Tab. 1).

3.1.2 Hummock-forming *Sphagnum* mosses

Hummock *Sphagnum* mosses can be harvested in the form of single plants and small cushions as well as in the form of larger compact sods. Semi-natural sites should be harvested particularly carefully, usually by hand, where groups of individual plants to small cushions are collected from *Sphagnum* lawns or hummocks. Since the collected material will be scattered later as individual plants or fragments, it is sufficient to remove the living upper 10 cm. Material should be collected evenly throughout the stand at intervals of at least 50 cm. A person experienced in identification of *Sphagnum* species should coordinate the collection,


Collection of *Sphagnum* sods with the aid of a coring cylinder

give advice on species characteristics and microhabitats, and check the material during the collection. Collection from semi-natural or natural sites should always be carried out with as little disturbance as possible and in a way that does not damage the stand (Zoch et al. 2022).

Due to their compact growth form in mature stands, hummock mosses can also be harvested as sods, thus maintaining synergistic relationships between the plants with regard to microclimate, water balance and competitive strength. The transfer of intact sods to restoration sites provides advantages over the spreading of plant fragments, especially on sites with fluctuating water levels, because the sods have increased resilience to drought and waterlogging (Granath et al. 2010, Taylor & Price 2015) and increased competitive vigour against vascular plants. Material is harvested by pulling clumps of approximately 10 cm^3 by hand from the hummock, or by cutting out larger sods of about 30 cm x 30 cm to a height of about 15 cm with a sharp tool. The extraction site should be pressed together and/or re-inoculated with fragments to promote the »closing« of the hummock. Even though sods are generally more resilient than loose fragments, they should nevertheless be collected carefully and transferred rapidly to the receptor site.

Due to the lack of semi-natural donor areas, the removal of hummock sods on a large scale is often problematic. Therefore, in many regions, intermediate propagation in specially designed facilities is often the only option to


Greenhouse table with *S. papillosum* after removal of sods

enable hummock moss establishment via sod transfer (Caporn et al. 2017, Raabe et al. 2018; 2019). For reintroducing mosses propagated on tables outdoor, the most successful method was to cut sods by hand to a height of about 4-10 cm and with a diameter or edge length of about 20 cm as round or square transplantation units, using coring cylinders or a knife. The sods are usually propagated on a thin layer of white peat and planted out with it.

With regard to sod size, there are currently few reference values for assessing the ideal dimensions (basal area, height and the relationship between these factors) and characteristics (species composition, plant density, water capacity) under different site conditions. The information in this guide is therefore indicative, based on experience to date, without claiming completeness or representativeness. In general, however, our experience has shown that a minimum size of 10-15 cm diameter and a sod structure that is as compact as possible have proven advantageous for successful establishment on the receptor sites. Furthermore, less demanding species such as *S. papillosum* should initially be targeted. The presence of other, also more demanding species in the sod may also prove beneficial, as the introduced sods can respond to different site conditions by shifting dominance when a broader species spectrum is present (see below).

Sod removed, ready for transport to the receptor site

3.2 Introduction of *Sphagnum* to the regeneration site

Transfer of *Sphagnum* is usually accomplished either by spreading whole plants or their fragments over a larger area, or by a more selective transplantation of *Sphagnum* sods (Quinty & Rochefort 2003, Cagampan & Waddington 2008, Breeuwer et al. 2010, Chimner et al. 2017, Karofeld et al. 2017, Zoch et al. 2022).

In principle, *Sphagnum* material can be transplanted in autumn or spring. Both options have advantages and disadvantages, mainly determined by the weather. Most authors, weighing the factors, recommend transplanting in the autumn. If carried out in spring, the water supply is usually very good due to the stored water from the winter, and together with rising temperatures in spring, this provides good conditions for moss growth. However, due to the high degree of water saturation, the areas are sometimes very difficult to access. In addition, the risk of a dry spring can jeopardize the establishment success. In the event of rapid drying, establishment may be severely delayed or fail altogether. In contrast, transplanting in the autumn offers the advantages that the areas are drier at the end of the summer and thus more accessible, and subsequent precipitation provides a good water supply. In addition, suitable accompanying measures can optimise water management in winter so that sufficient water reserves are available in the following spring, which can be a factor that prevents regime shifts in the event of drought (Laine et al. 2019). In Canada and the Baltic countries, large-scale vegetation transfer with accompanying measures to improve the hydrological conditions (blocking drainage ditches, levelling the surface, parcelling, etc.) is therefore carried out most successfully in the autumn (McCarter & Price 2013, Purre et al. 2020). Furthermore, transplanting in autumn complements the propagation procedure described in Part I of this guide. Due to the optimal growing conditions for the mosses in propagation facilities (especially irrigation), propagation should be started in spring. Usually after only about 18 months, sufficient donor biomass can be harvested at the end of the following summer and this can then be transferred to the receptor site directly in the autumn.

3.2.1 Hollow-inhabiting *Sphagnum* mosses

The transfer of hollow mosses is comparatively simple and can be carried out with little effort. The mostly floating species can be collected and transported in buckets and then spread in waterlogged areas. Since wave action is detrimental to *Sphagnum* dispersal, banks should be shallow and some vascular plants or peat structures should reduce water movement (Smolders et al. 2003). In early successional stages, the introduction of hollow mosses can mitigate water level fluctuations and accelerate acrotelm development (Tomassen et al. 2004). Little is known about the minimum amount of material required to initiate or accelerate large-scale acrotelm development. However, it can be assumed that the earlier the hollow

Planting of hollow-inhabiting mosses and cotton grass (Josef Gramann)

mosses are introduced and the larger their quantity, the greater their promotion of the reestablishment of hummock mosses by creating suitable conditions such as uniform water availability, ideal pH, etc. If species can be selected, preference should be given to transferring *S. cuspidatum*, as *S. fallax* can outcompete other *Sphagnum* species, which may affect subsequent restoration efforts (Limpens et al. 2003, Bu et al. 2013).

3.2.2 Fragments of hummock-forming *Sphagnum* mosses

Under favourable conditions, especially water levels that are high with little fluctuation and only short periods of oversupply with good quality water, hummock mosses can establish successfully from fragments even in early and transitional stages. However, their sensitivity to waterlogging and desiccation mean that under suboptimal conditions, the growth of hummock mosses in these stages is often not sufficient to allow them to establish successfully alongside the hollow mosses (Tab. 1, scenarios 1 and 2) (Tuittila et al. 2003, Hájek & Vicherová 2014). When hydrological conditions are favourable, such as in optimally prepared peatland areas, hummock moss material can also be introduced to areas free of vegetation. The decisive factor here is the contact with open and water-saturated substrate, e.g. by pressing or rolling.

Transfer of *Sphagnum* fragments is usually carried out on large areas of unvegetated peat to accelerate the formation of a closed stand. In principle, *Sphagnum* fragments

Large-scale transfer of *Sphagnum* fragments with a straw layer after peat extraction, levelling and blocking of drains (Ruhingu, Estonia)

If fragments of hummock mosses are spread too thinly, they are very unlikely to succeed in asserting themselves against the competition of hollow mosses.

can also be planted in unvegetated gaps or rarely-flooded stands of hollow mosses. Denser vascular plant vegetation can also be selectively disturbed to create gaps for planting. The layer thickness of the spread fragments should not exceed a few centimetres (Campeau & Rochefort 1996). On a *Sphagnum* cultivation site in northwestern Germany, the application of about 90 m^3/ha resulted in a dense lawn of moss cover after 36 months (Gaudig et al. 2014). Quinty & Rochefort (2003) recommend a 1:10 ratio of donor to receptor area. Transfer of whole moss stems without chopping usually results in faster stand closure and faster height growth of mosses (Hölzel et al. 2019).

In order to protect the sensitive hummock moss fragments from excessive drying or silting during heavy rainfall in the establishment phase on open peat areas, a covering with straw has proven to be effective, which should be applied at about 300 g/m^2 (Quinty & Rochefort 2003). In (temporarily) flooded areas, moss fragments can also be protected from drifting by a net made of decomposable material, e. g. coconut fibres.

Fragments can also be used for the large-scale spreading of hummock mosses in areas dominated by hollow mosses (Tab. 1, scenario 3). Larger species from the *Sphagnum* section such as *S. papillosum* (Smolders et al. 2003, Robroek et al. 2009) are most suitable for this purpose, which are spread as particularly long and highly branched plants (5-10 cm) in clumps flat over the existing hollow moss vegetation and pressed down well. In small-scale experiments, successful establishment was observed within three growing seasons (Raabe et al. 2019). It is especially important for fragments to have a stable water supply (Brown et al. 2017). However, fragments should not be placed at too low level in closed stand. Depending on the weather, they may then be exposed to excessively wet conditions and, consequently, quickly become overgrown by hollow mosses. However, in many cases it is not necessary to improve the competitiveness of introduced hummock mosses by disturbing the existing hollow mosses (Gunnarsson & Söderström 2007).

Instead, to reduce competition between *Sphagnum* species, cuttings of raised bog dwarf shrubs such as bog rosemary (*Andromeda polifolia*) or bog cranberry (*Vaccinium oxycoccos*) can be planted, which serve as climbing scaffolds for the hummock mosses (Malmer et al. 1994) and can also positively influence the microclimate during dry periods (Farrick et al. 2009). If, on the other hand, fast-growing and competitive hollow moss species such as *S. fallax* are dominant at sites rich in nutrients and/or minerals, the creation of disturbance sites or transplantation of the hummock mosses by means of sods may be useful.

3.2.3 Transplants of hummock-forming *Sphagnum* mosses

In contrast to moss fragments, transplanting whole sods or clumps of vegetation does not usually cover the entire area (Raabe et al. 2019, Thom et al. 2019). The use of the latter, however, offers the advantage over fragments that hummock mosses can be introduced more successfully in transitional and late stages of succession with stronger competition from vascular plants (see also Part I of this action guide). In areas with strong water level fluctuations, it is recommended to transplant sods as deep as possible (> 10-15 cm) into the edges of vascular plant stands that are covered with hollow mosses. While water availability is usually optimal in later stages of floating mat development, transplanting sods can be problematic on younger, less stable stages. Particularly in the absence of root penetration, sods generally sink deeper once they reach water saturation and, like fragments, they can become completely overgrown, also known as the »overtopping« effect (Vanderpoorten & Goffinet 2009). In contrast, even in thin sods (3-10 cm), as long as the substrate is firm and water-saturated, hummock mosses can hold their own against surrounding hollow mosses until they concentrically overgrow their neighbours. Positive feedbacks with vascular plants can give hummock mosses an advantage over

Concentrated planting of fragments by hand. It is important to establish direct contact with the substrate by pressing firmly. With this form of planting, there is a risk that the fragments will drift in the event of flooding.

Sod transport and equipment for transplantation on an *Eriophorum-Molinia* site. The transfer of hummock moss sods requires thorough planning and preparation.

hollow mosses, therefore it is recommended to combine hummock mosses with vascular plants from the beginning (cf. Rydin 2009). This is relatively easy to achieve in propagation facilities (see Part I of this guide) or during the collection from donor areas.

In order to achieve the self-regulating effects intended by transplanting sods, it is recommended that the following points be observed:

- Sods should remain compact after their removal. Depending on the moss species and growth form, a favourable area-to-height ratio should be observed to prevent it from falling apart and thus drying out more quickly (undesirable transplantation effects).

- It is advantageous if the sods contain a root network or include substrate with roots.

- Sods should be planted neither too high nor too deep. It is advisable to prepare suitable planting holes. This more important the smaller and taller a sod is.

- To determine the depth of planting, the long-term mean water level and fluctuation amplitude should be used as a guide.

- Sods should have contact with water-saturated peat layers for as long as possible.

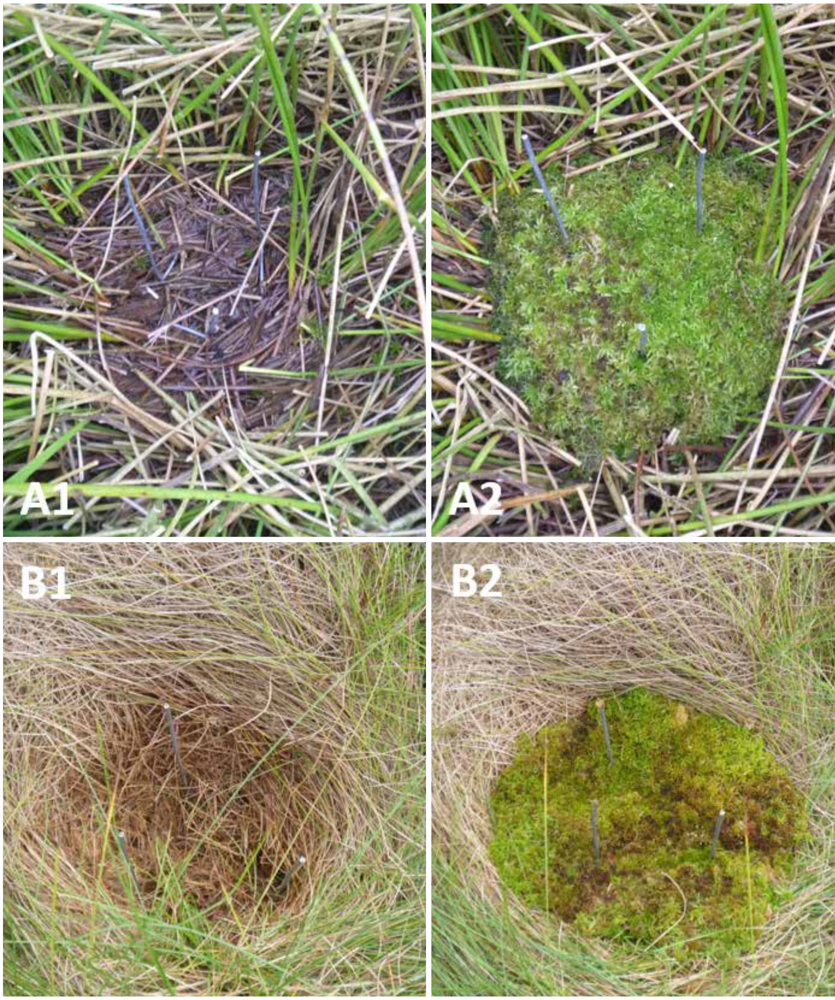
- Litter and above- and below-ground plant parts should be removed from below the sod if possible.

- After planting and pressing in the sod, the capitulae should be slightly above the surface of the ground. This reduces the likelihood of them being covered by silt after heavy rain on open peat and the risk of »overtopping« in later stages due to differences between hummock and hollow species in floating or sinking on soft, waterlogged substrates.

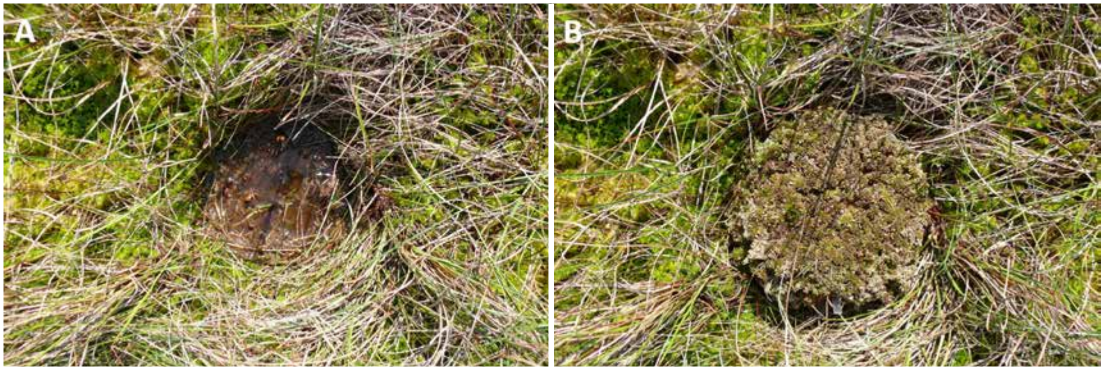
- Generally, sods as well as fragments are not transplanted at full water content. The initial moisture content may therefore not be sufficient for the plants to survive a long dry phase immediately after transplantation without damage. Surface structures that provide wind protection and collect rainwater can help here.

- On open peat, it is advisable to surround the inoculation sites with straw, especially when spreading before summer, while the sods are only partially covered or lightly shaded.

To plant smaller clumps of *Sphagnum*, it is useful to prepare a hole with a stick or with your hands, insert the *Sphagnum* material and press it down. This ensures immediate contact with the surrounding substrate. Ideal locations are the edges of polders with hollow mosses and/or *Eriophorum*. The good anchoring in the substrate and the protection against weather extremes provided by the vascular plants ensures a high establishment success. The ideal time for planting is in autumn, when the otherwise very wet edges of the polders can be walked on.



Sod planting in graminoid-dominated areas, above in *Juncus effusus*, below in *Eriophorum vaginatum* stands. The sods are placed in a hand-dug depression. Here, too, it is important to establish direct contact with the substrate below by pressing down carefully.



Sod planting in areas dominated by hollow mosses with few grasses. In such a situation, the sod should still protrude about 2-3 cm from the hollow moss vegetation. Accordingly, the planting hole must not be too deep to prevent overgrowth by the hollow mosses.

»Safe Sites« with favourable micro-site conditions for establishment can be found both in the centre of a hummock (top) and between two hummocks (bottom).

Comprehensive establishment experiments were set up and scientifically monitored as part of this project. The main purpose of these experiments was to obtain information on the factors that significantly influence the success of establishment. In the foreground, artificially created black peat banks; in the background, vegetation-rich older succession stages.

4 Factors affecting the establishment success

In the following, the factors determining the establishment success of introduced hummock mosses are presented and discussed to derive important conclusions for the restoration practice. The underlying findings originate from a series of establishment experiments, which were monitored over several years. The results are discussed with other findings from the literature.

4.1 Water level

Optimal for the establishment of hummock mosses are water levels that are predominantly a few to a maximum of 25 cm below the soil surface (Granath et al. 2010, Gaudig et al. 2020). In general, the greater the fluctuation in water levels, the lower the establishment success. This applies both to water levels that are too low in summer and too high in winter. Even with comparatively high and stable summer water levels, prolonged winter flooding has an extremely negative effect and can lead to the almost complete death of the introduced hummock mosses. This pronounced sensitivity of the introduced mosses to flooding was altogether very surprising and has far-reaching consequences for restoration practice, which will be discussed later. Regarding the sensitivity to water levels and their fluctuation, clear species-specific differences were also found. For example, in an establishment experiment with sods, *S. rubellum* was only able to establish successfully after 6 years at a mean water level of 7 cm below ground level and a mean fluctuation between summer and winter of 10 cm.

The tall tussocks of purple moor-grass (*Molinia caerulea*) and tussock cottongrass (*Eriophorum vaginatum*) are signs of pronounced water level fluctuations, which have a very negative effect on the establishment success of hummock mosses.

Months of winter flooding of up to several decimetres in height also have an extremely negative effect on hummock moss establishment.

In contrast, in the same experiment, establishment of *S. papillosum* was still very successful even at a mean water level of 21 cm below ground level and a mean annual amplitude of 20 cm, while *S. medium* occupied an intermediate position in this respect. Areas with particularly high establishment success and clear lateral and height growth of the introduced sods are often older floating

After a prolonged summer dry period in a transplanted sod, the moisture-demanding *S. rubellum* (thin branches) is already completely bleached, while the more robust *S. papillosum* (thick branches) is still green.

mat-like stands with surface oscillation (i.e., surfaces that vary in elevation along with water table levels), which means that there is always an optimal water supply for hummock mosses (Howie & Hebda 2018). If water levels can be kept as constant as possible, very good establishment of sod transfers with straw cover can be achieved, even on bare peat. This again applies especially to *S. medium* and *S. papillosum*, while *S. rubellum* is particularly sensitive to desiccation. However, even under optimal water level conditions, *S. rubellum* showed significantly lower lateral growth compared to *S. medium* and *S. papillosum*, which contrasts with its clearly superior growth rates in artificial propagation (Part I, Table 6).

In addition to direct effects, water levels and their fluctuations also have other indirect effects on establishment success via vegetation composition, water chemistry and nutrient ratios. However, their relative importance and interactions are sometimes difficult to separate. Overall, water conditions are undoubtedly by far the most important factor in the establishment success of introduced hummock moss species. If the hydrology of a site is inappropriate, it must first be improved before establishment experiments can be conducted.

A floating mat with oscillating surface offers optimal conditions for the establishment of hummock mosses. Even *S. rubellum*, which is so sensitive to desiccation, thrives here. The picture shows the development of a pyramid-like hummock seven years after the sod transfer.

Propagated *Sphagnum* on a table with white peat substrate. The white peat layer transferred with the sod did not lead to better establishment success.

4.2 Substrate

Weakly decomposed, or white peat is particularly suitable for the establishment of hummock mosses due to its greater porosity and thus its greater water conductivity and water storage capacity. In contrast, black peat is much less suitable as it is much denser and does not hold water in the range favourable for hummock-forming *Sphagnum* species (Smolders et al. 2003). However, in an establishment experiment in which hummock moss sods were transferred with and without a layer of white peat approx. 4 cm thick, no significant positive effects of the white peat substrate were shown. On the contrary, the white peat seems to act as a capillary barrier on sites with lower water levels after drying out due to its coarse pores, which prevent capillary transport of water from below (cf. Taylor & Price 2015). This is probably the reason why worse establishment results were sometimes achieved on white peat substrates. Here, too, however, the water level ultimately proved to be the dominant factor. Based on our limited investigations, we do not recommend the addition of white peat when transplanting sods. Nevertheless, we also observed obvious positive effects of existing white peat layers in raised bog restoration, for example for the formation of floating mats. In addition, in the case of strongly degenerated black peat, there is a risk of poor rehydration after temporary drying and/or easy erodibility of loose material.

Freshly formed organic substrate (acrotelm) in a floating mat of hollow mosses and *Eriophorum*. The formation of a loose acrotelm improves the hydrological self-regulation of the sites and has a very positive influence on the establishment of hummock mosses.

In contrast, the thickness of the new acrotelm layer formed since the beginning of the rewetting measures appears to be very significant for the establishment success in older, vegetation-rich stages. The thicker the layer of dead plant parts, the more successful the establishment. The main reason for this is presumably that from a layer thickness of approx. 10-15 cm, there is a significantly improved water storage and water replenishment capacity during summer dry phases and/or improved self-regulation during rainfall due to the coarse porosity and oscillation capacity (cf. Lucchese et al. 2010, McCarter & Price 2013).

Atmospheric nitrogen deposition, often in combination with summer drought, can lead to severe grass encroachment (*Eriophorum vaginatum* in the picture) and the formation of thick litter layers. If vascular plant cover is too dense, the establishment success of hummock mosses decreases, with lateral spread in particular being impaired.

4.3 Water chemistry and nutrients

The establishment of hummock mosses was most successful on oligotrophic sites, while nutrient-richer sites (often as a result of previous agricultural use) usually showed lower establishment success. Trophic differences are particularly evident in the nutrient ratios in the freshly formed acrotelm. Nutrient-rich sites have calcium contents > 0.15 wt%, C/N ratios < 40 and N/P ratios < 20 in the fresh peat substrate as well as narrow N/P ratios of < 15 in the vascular plant biomass. These are particularly stages dominated by *Juncus effusus*, but in some cases also those dominated by *Eriophorum angustifolium* or *Molinia caerulea*, which are more tolerant of high mineral levels. The negative influence of higher nutrient levels on the establishment of hummock mosses is likely to occur indirectly via competition from vascular plants and hollow mosses adapted to nutrient-rich conditions, such as *S. fallax*.

4.4 Surrounding vegetation

The greatest establishment successes were almost universally achieved on sites with low vascular plant height, cover and biomass (around 100 g/m^2). These are mostly oligotrophic sites with high mean water levels dominated by *Eriophorum vaginatum* and *S. cuspidatum*. This contrasts with stages dominated by the nutrient-affine Juncus effusus, which are characterized by three times the vascular plant biomass (approximately 300 g/m^2) and nearly double the vegetation height. Even under relatively favourable water levels, less competitive species such as *S. rubellum* and *S. medium* experience a marked decline in establishment success, while the more competitive *S. papillosum* is largely able to hold its own. However, when higher vascular plant biomass of > 250 g/m^2 and vascular plant cover of > 60 % occur in conjunction with less favourable mean water levels, establishment success also decreases significantly for *S. papillosum*, and *S. medium* and *S. rubellum* fail completely due to competitive pressure.

Compared to fragments, hummock mosses transplanted as sods are able to assert themselves better against both hollow mosses and vascular plants and are less sensitive to desiccation.

4.5 Transplanting methods

In the transplantation trials conducted as part of this project, sods were clearly superior when compared to fragments. The superiority of sods increases the less favourable the site is in terms of water balance, nutrient levels, and vascular plant competition. Our results are thus largely consistent with findings in the literature. Convincing and sometimes spectacular successes with large-scale fragment application have so far been achieved primarily under climatic conditions generally more favourable for *Sphagnum* in the boreal or subboreal zone (Quinty & Rochefort 2003). Examples of successful application in nemoral lowland raised bogs have so far remained limited to a few experiments with optimal, strongly controlled water levels and open substrate surfaces (Gaudig et al. 2014). Under the suboptimal conditions that prevail today in many places, including northwestern Central Europe, and which are currently being exacerbated by recent climate change, transfer of hummock mosses in sod form is probably preferable in the future.

The introduction of hummock mosses to peat sites specially created for this purpose showed surprisingly positive establishment results when water levels were kept constant. In practice, however, this method is unlikely to be of any significance due to the extensive preparatory work required and the constant water levels needed. Instead, we recommend introduction to more advanced stages of vegetation development, such as the *Eriophorum vaginatum* stage shown here. The vascular plants provide the hummock mosses with structural support and protection from weather extremes, and the initial acrotelm formation significantly mitigates the effect of dry phases.

5 Synthesis

In the following synopsis, the main findings on the establishment of hummock mosses for regeneration purposes are summarised into practice-relevant key statements:

1. *Sphagnum* mosses grow mainly in spring and autumn and often suffer from drought in summer, while vascular plants grow mainly in summer. Therefore, transfer of material should preferably be carried out in autumn, or if necessary in early spring, in order not to expose the initially sensitive mosses or moss fragments to drought and increased competition with vascular plants too soon after application.

2. Establishment should focus on sites with water levels that are high throughout the

year (a few to 25 cm below ground level) and that fluctuate comparatively little. Prolonged waterlogging (several weeks) can lead to rapid death of the hummock mosses and should therefore be avoided at all costs. Floating mats with oscillating surfaces, which ensure an optimal water level near the soil surface all year round, proved to be particularly favourable.

3. As a rule, establishment is particularly successful on oligotrophic sites with low nutrient loads. Unfavourable nutrient-rich sites are easily identifiable by clearly elevated Ca contents and lower C/N and N/P ratios, both in the vascular plant biomass and in the fresh peat substrate. These are often stands dominated by *Juncus effusus* or *Eriophorum vaginatum*/*E. angustifolium*, and their transitional forms to *Molinia caerulea*, which are characterized by particularly luxuriant growth of the dominant grasses (often > 300 g dry biomass per m^2) and at the same time tend to form dense litter layers.

4. Establishment is most successful when the competitive pressure is as low as possible from vascular plants (optimal approx. 100 g dry biomass per m^2) or hollow mosses (especially *S. fallax*). With increasing vascular plant and litter cover, the establishment conditions deteriorate rapidly, especially with regard to the lateral spreading of the introduced hummock mosses.

5. Generally, hummock mosses should be established on areas where, after rewetting and colonisation by cottongrasses (especially *Eriophorum vaginatum*) and hollow mosses (especially *S. cuspidatum*), the formation of an acrotelm (loose, spongy and coarse-pored layer of dead plant material) at least 10 cm thick has already taken place above the usually existing dense black peat. The acrotelm ensures that the water supply of the hummock mosses is maintained during periods of low precipitation, due to its optimal water retention properties and oscillatory capacity of the surface. In contrast, hummock moss establishment on bare black peat is only recommended if a consistently high and stable water level can be ensured even in dry periods, for example by pumping water from neighbouring areas or reservoirs, since the black peat lacks the ability for hydrological self-regulation.

6. Transplanting hummock moss sods has significant advantages, especially under unfavourable hydrological and competition conditions. Spreading of fragments is only recommended under optimal moisture conditions, on well prepared flat surfaces, and under low competitive pressure from vascular plants and/or nutrient-affine hollow mosses (*S. fallax*).

7. During propagation as well as establishment experiments, *S. papillosum* proved to be a particularly robust and

Mixtures with a high proportion of broad-leaved *Sphagnum* species are usually characterized by a greater water storage capacity or desiccation tolerance and therefore remain moist even if the water level falls below a certain threshold above which capillary water supply is usually no longer available. The formation of spores is not uncommon under these conditions.

resilient species, capable of successful establishment and lateral spread even under less favourable hydrological conditions, higher nutrient levels, and stronger competitive pressure from vascular plants. This species showed by far the least sensitivity both to temporary flooding and to desiccation, due to its very compact and robust structure. In contrast, successful establishment of *S. rubellum* was only possible under optimal water, nutrient and competition conditions, while *S. medium* is intermediate in this respect.

8. For regeneration practice under the hydrological conditions of northwestern Germany, which are often suboptimal for hummock moss establishment, we therefore recommend focussing on *S. papillosum*. The other two species should be included in the transfer material only in small proportions to ensure a later succession and niche differentiation after the formation of a closed moss layer. In contrast, mixtures dominated by *S. rubellum* or *S. medium* should only be used in the establishment phase under

optimal water, nutrient and competitive conditions. In general, it can be assumed that different species have different growth and survival optima. Therefore, instead of single species, moss mixtures generally offer advantages and allow natural selection and niche differentiation based on the prevailing site conditions.

Overflow pipe to prevent prolonged winter flooding of a restoration area, which in extreme cases can lead to the almost complete loss of introduced hummock mosses. In the course of climate change, accompanying regulatory measures to control water levels on restoration areas will continue to gain in importance.

6 Risks of non-establishment and accompanying measures

As already described in sections 4 and 5, a wide variety of factors affect the success of establishment. The risk of establishment failure should be minimised as far as possible before starting revegetation measures. This is particularly true if hummock mosses are removed from natural areas, damaging these without clear prospects for successful establishment in receptor areas. Even the usefulness of artificial propagation must be fundamentally questioned in the absence of realistic prospects of establishment success.

When hummock mosses are transplanted as sods, they often already contain typically associated species, both from propagation facilities and from natural donor sites. Thus, in this project, the transfer and secondary spread of typical vascular plants of upland bogs such as white beak-sedge (*Rhynchospora alba*), round-leaved sundew (*Drosera rotundifolia*), bog cranberry (*Vaccinium oxycoccos*), bog rosemary (*Andromeda polifolia*) and cross-leaved heath (*Erica tetralix*) were regularly observed. If these species are still partially or completely absent after hummock moss establishment, they can be established comparatively easily by the selective introduction of individual plants, cuttings or rhizomes, which subsequently usually leads to their rapid vegetative reproduction and spread.

The greatest risk factor in the various stages of raised bog regeneration is undoubtedly the temporary lack of water, usually in summer.

After transplanting hummock peat moss sods in the spring on bare peat (A), it is advisable to additionally apply straw (B), otherwise far more water will evaporate than normally falls through precipitation, especially in the summer.

This often affects sites in northwestern Germany, whether due to problematic topography (often in hand-cut peat bogs) caused by differences in depths of peat extraction, or due to water loss through the base of the bog or from ditches. Hydrological buffer zones may become increasingly important in the future, especially with

Even at high water levels, sods remain in place (while moss fragments easily drift away). Nevertheless, they can be overtopped by floating hollow mosses, especially in the event of prolonged flooding (> 4 weeks). The risk that hummock mosses will therefore not establish can be reduced by inoculating nurse plants or stable floating mats.

extended dry periods in spring and summer due to climate change. Water should be kept in the area as much as possible, even if the quality is not optimal. In addition to the lack of precipitation, there are many reasons for water shortages and droughts and they usually require a larger-scale hydrological consideration. Land use in the surrounding areas means that the groundwater levels outside of the peat bogs are usually lower, and large amounts of water are lost via inadequately sealed ditches, or when the base of the bog has been damaged (e.g. in the case of only thin fen peat layers under raised bog peat). In problematic cases, only major interventions can help, such as the creation of large, deep dams, waterproof layers/trenches or walls, or the creation of larger buffer zones with high groundwater levels and water retention capacity.

Within the regeneration area, small-scale variability in moisture can be positive, as drier areas provide protection from excessive winter flooding and wetter depressions provide refuges for bog vegetation during dry periods. Drier structures may be embankments or dams, while wetter depressions are created, for example, when material is removed to seal ditches. Conditions that are too dry can usually already be inferred from the vegetation. A dominance of common heather (*Calluna vulgaris*) and/or purple moor-grass (*Molinia caerulea*) clearly indicates that the hydrology must be improved before or at least during the establishment of hummock mosses (see above). Birch growth is also an important contributor to high water losses through transpiration. Regular mechanical removal can remedy this situation.

Too much water can also affect the establishment success. Flooding for too long in the winter months is usually not tolerated by hummock mosses. Therefore, when water levels are high, it is important to have accompanying vegetation that the hummock mosses can support themselves on and maintain the necessary height above the water level. At high water levels and without accompanying vegetation, wave action also occurs, which makes it difficult or even impossible for *Sphagnum* to spread. In such cases, vegetation spreads only slowly from the edge of raised structures. Nevertheless, because of the increasing risk of water shortage in spring and summer, as much water as possible should be kept in the area.

This can be accomplished by intelligent design of the site, such as dividing the area into parcels, creating water storage in existing structures, targeted and controllable overflows, and small-scale, cascading drainage impoundments with only small differences in elevation.

High nutrient levels is another major factor that can prevent successful establishment. High nutrient availability usually implies high competition from undesirable vegetation (such as *Juncus effusus*, see descriptions of successional stages above), especially also when bare peat is exposed. Extensive topsoil removal experiments have been conducted in the past for this purpose, especially in the case of previous agricultural use. Topsoil removal is a considerable labour and cost factor. However, it can be used to significantly and sustainably reduce the nutrient load of the area and the pressure from vegetation untypical of raised bogs. It should be noted that the removed material also exerts an influence on the area if, for example, it is deposited around the area as an embankment. However, since this influence is only at the edge, it is much less of a problem, and the relatively strongly decomposed peat can hold water well in the area due to its low conductivity. While topsoil removal down to 30 cm depth has become established as a guideline in practice, the exact depth of peat degradation and nutrient enrichment should be determined, if possible, to keep the depth of removal effective but still as shallow as possible.

Excessive nutrient influx can also occur in cutover peatland if inputs from neighbouring areas still in agricultural use are not taken into account. Separating structures, ideally made of peat, and adapted water management on the still drained areas can be used to avoid this. However, such situations usually bring about lasting problems in hydrology due to the small-scale nature of the restoration sites.

In the medium to long term, the chances of restoration can also be significantly improved by reducing atmospheric nitrogen deposition from agriculture. Together with hydrological changes in the course of recent climate change, atmospheric nitrogen deposition is undoubtedly the greatest current obstacle to the restoration of functionally intact raised bog ecosystems.

Older large-scale rewetting with much open water and gradually progressing floating mat development. The challenge of the following decades will be to transform these areas into hydrologically self-regulating greenhouse gas sinks under climate change. In addition to flexible and technically sound planning of measures, this will also require further basic scientific research.

7 Outlook

Efforts to activate the regeneration of self-regulating peatland ecosystems will become increasingly important in the future for the reasons mentioned above - hydrological disturbances, lack of source populations of target vegetation, eutrophication, atmospheric nitrogen deposition and others. The status and development of the largest possible regeneration areas also requires long-term monitoring, which should only be carried out with professional expertise and scientific support. Research and educational institutions such as universities can play a vital role in such tasks. In some countries, detailed knowledge about bog restoration has been gained through such cooperations (e.g. Netherlands, Canada, Baltic countries). New restoration and management concepts are needed, as they can make a valuable contribution to better understanding and maintaining raised bog ecosystems. There are many examples of current approaches to regeneration not achieving their goals, for a variety of reasons that cannot be fully addressed here. Appropriate accompanying measures and establishment approaches, such as those outlined in this guide, can significantly increase success and thus also initiate regeneration following peat extraction in a better and more comprehensible way. In well-developed regeneration areas, additional measures should, of course, be implemented only when necessary and in a targeted manner. It should be decided on a case-by-case basis which measures are actually necessary. In many cases, further investigations are certainly necessary first, often with regard to hydrology, in order to determine where larger-scale hummock moss introduction is promising. The most tolerant species are *S. papillosum* and *S. medium*, although even these generally achieve their greatest establishment rates only at consistently high water levels. However, they tolerate winter flooding best. In cases of insufficient knowledge of the species and/or problematic conditions, it may be prudent to rely on species mixtures to

Measures for the establishment of hummock mosses require not only careful planning but also regular monitoring of the success of the measures in order to counteract undesirable developments and to gain important insights for future restoration measures.

In the long-term experiment (after 6 years), the reintroduction of the tested hummock mosses in a remote, later successional stage with a stable stand of floating hollow mosses that was already closed but still species-poor at the time of planting proved to be most successful. Further studies will show to what extent the actively introduced target vegetation continues to spread and whether biodiversity and climatic potential also approach natural reference values on a larger scale.

avoid losing all the material used. Although areas dominated by hollow mosses and dense stands of *E. vaginatum* without an acrotelm at intermittent high water levels already resemble semi-natural bogs (such images are often disseminated in the media), an at first glance seemingly less suitable patchy stand of *E. angustifolium* or *Juncus effusus* with minerotrophic *Sphagnum* species such as *S. fallax* or *S. squarrosum* may sometimes equally or even better ensure the regeneration of an ombrotrophic bog with corresponding hollow species, even if this may temporarily lead to increased methane emissions by the vascular plant vegetation at high water levels.

The selection and implementation of a regeneration concept and its success depend not least on its objectives and budget. To assess whether a site is suitable for *Sphagnum* establishment, a number of indicators can be used, such as the predominant vegetation, above-ground biomass and nutrient content, water levels and water-holding capacity of the topsoil, etc. Monitoring of soil, water and plant chemistry is strongly recommended, but in practice will probably have to be limited to a few key variables.

This compact guide for the propagation and establishment of hummock mosses aims to highlight the considerable challenges and risks, but above all the great opportunities of raised bog regeneration. The prerequisite in each case is the consideration of the prevailing environmental factors, comprehensive and forward-looking planning, and long-term monitoring of the areas in order to be able to take corrective action at an early stage if necessary.

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