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The efficacy of the decay fungus *Chondrostereum purpureum* in the biocontrol of downy birch (*Betula pubescens*) sprouting in restored peatlands

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SUMMARY

Ecological restoration of peatlands aims to counteract the negative changes caused by drainage and to restore the natural structure and functions of peatlands. Forestry-drained peatlands are generally restored by filling in the ditches but also by logging the trees that have grown after drainage. As a side-effect, tree logging may cause abundant sprouting of broad-leaved trees which hinders the recovery of peatlands. *Chondrostereum purpureum* is a decay fungus that provides a potential biological control agent for sprout control, but it has not been tested in the context of peatland restoration. We study how effective *C. purpureum* is in the sprout control of downy birch (*Betula pubescens*) in restored peatlands in Western Finland. We conducted a field experiment in ten sites, each having three areas where saplings are either 1) cut and treated with *C. purpureum*, 2) only cut or 3) left uncut. We counted the saplings in the study areas before (2018) and four years after (2022) the treatment. We also recorded the number of sprouts from each cut stump and their diameter in 2022. The relative change in the number of saplings was more negative in *C. purpureum* treatment (-29%) than in the only cut (-14%) or uncut control (-9%). In addition, the percentage of unsprouting stumps was doubled by *C. purpureum* treatment (63%) compared to only cutting (31%). For the sprouting stumps, *C. purpureum* decreased the number of sprouts, especially for large-diameter stumps, compared to stumps that were only cut. Hence, *C. purpureum* treatment is efficient in reducing birch sprouting and moderately efficient in reducing the number of birch saplings on restored peatlands. Yet, we recommend long-term follow-up studies to evaluate how often the treatment should be repeated to reach a favorable result.

Keywords: birch, biological control, Chondrostereum purpureum, cutting, peatland, restoration, sprout

INTRODUCTION

Ecological restoration of boreal peatlands aims to counteract the negative changes due to drainage and restore the natural structure and functions of drained peatlands (Aapala et al. 2013, Kareksela et al. 2021). In their pristine state, boreal peatlands provide a habitat for a wide number of specialist species (Hyvärinen et al. 2019), as well as important ecosystem functions (e.g., carbon sinks that help to mitigate climate change, and water regulation for flooding control). Yet, they have been degraded widely through draining for agriculture, forestry, and peat extraction: in Finland alone, over half of the original peatland area has been drained (Ojanen et al. 2020).

Forestry-drained peatlands are generally restored by blocking and filling the ditches to raise the water table to natural levels (Aapala et al. 2013, Rehell et al. 2013). In addition, the trees grown after drainage are often cut which increases light availability and alters nutrient cycling. This, in turn, may cause accelerated seedling and abundant sprouting of broad-leaved trees (Haapalehto 2013, Rehell et al. 2013). Dense sprouts use resources, evaporate water and shade ground-level vegetation, and thus slow down the recovery of the peatland (Haapalehto 2013) hindering restoration.

Efforts have been made to combat sprouting by chemical and mechanical means. However, the use of chemical pesticides has been reduced due to environmental concerns (Becker et al. 2005, Hamberg et al. 2015), and mechanical cutting alone is ineffective for many tree species as they sprout again from cut stumps (Becker et al. 2005). In addition, mechanical cutting must be repeated at regular intervals, and thus it cannot be considered a cost-effective method of sprout control (Hamberg et al. 2015, Laine et al. 2020).

Chondrostereum purpureum (Pers. ex Fr.) Pouzar is a decay fungus that provides a potential biological control agent for sprout control. *C. purpureum* is an annual lignin-degrading basidiomycete fungus that causes white rot in recently cut deciduous trees (Dye 1974, Vartiamäki et al. 2008). The mycelia of the fungus can prevent the formation of new sprouts and can cause tree mortality (Butler and Jones 1949, Hamberg ym. 2017). *C. purpureum* may also cause pathological symptoms by producing phytotoxins that are translocated to the foliage where they may induce silver-leaf disease (Spiers et al. 1987, Becker et al. 2005).

For sprout control, a solution containing *C. purpureum* hyphae is applied to a freshly cut stump (Hamberg et al. 2015, Hamberg et al. 2017). Studies have found promising results for the use of *C. purpureum* for sprout control in different deciduous tree species (Becker et al. 2005, Vandenbroucke et al. 2005, Hamberg et al. 2014, Hamberg et al. 2017, Hamberg et al. 2021), especially for birches (*Betula* spp.) (Vandenbroucke et al. 2005, Vartiamäki et al. 2008, Hamberg et al. 2015, Hamberg et al. 2017, Hamberg 2021). Hamberg et al. (2017) found that the high birch mortality results from the ability of *C. purpureum* to penetrate into the roots and to kill them. The physiological condition of the host tree impacts the fungal success: host mortality seems to be higher if the treatment is applied in spring or summer rather than in late autumn (Vartiamäki et al., 2009) but it should also be applied only after the buds have partially opened (Hamberg et al., 2017). In addition, a high density of living untreated saplings of the same species around a *C. purpureum* treated stump can reduce the effectiveness of the treatment (Hamberg et al., 2014). The effectiveness of the treatment also varies between different strains of *C. purpureum*, and crossbreeding has been used to produce more effective strains (Hamberg et al., 2015). Weather conditions and soil properties have only minor or temporary impacts on the efficacy of the treatment (Hamberg & Hantula, 2020).

C. purpureum treatment has been shown to be long-lasting and effective in sprout control (Vandenbroucke et al. 2005). Stump mortality starts about two months after treatment and continues for at least four years after treatment (Lygis et al. 2012, Hamberg et al. 2014, Hamberg et al. 2015, Hamberg et al. 2017). Even if the host is not killed by *C. purpureum*, the fungus can still reduce the number and height of the sprouts, especially in birches (Vartiamäki et al. 2009, Hamberg et al. 2015). The treatment has both direct and indirect benefits, such as maintaining low-growing vegetation, which in turn promotes biodiversity (Vandenbroucke et al. 2005). There seem to be no major risks associated with the use of *C. purpureum*. Becker et al (2005) concluded that *C. purpureum* treatments had no effect on the local population and the strain used in the treatments was not observed in non-treated trees in or near the treatment area.

Effectiveness of *C. purpureum* in sprout control has been studied in field studies on dry land and in laboratory conditions (Hamberg et al., 2021). In the study of Hamberg & Hantula (2020) paludified forest sites did not differ from unpaludified sites in the impact of *C. purpureum* on birch stump mortality. Yet, locally wet soil (stump surrounded by *Sphagnum* mosses or growing in water) increased stump mortality during the first growing season. Thus, *C. purpureum* could be an efficient tool against birch sprouting in peatlands as well. However, data on the effectiveness and usefulness of *C. purpureum* in sprout control in restored peatlands are not yet available.

We study how effective *C. purpureum* is in the sprout control of downy birch (*Betula pubescens* Ehrh.) in restored peatlands, as birch trees are particularly prone to sprouting from the stumps of cut trees (Haapalehto 2013, Rehell et al. 2013). We compare the effect of three treatments: 1) a *C. purpureum* treatment where saplings are cut and inoculated with *C. purpureum*, 2) a cutting treatment where saplings are only cut, and c) a control treatment with no action. Our research questions are:

1. Does *C. purpureum* treatment affect the change in the number of saplings after four years of the treatment?

We hypothesize that the number of saplings has decreased both in cutting treatment and *C. purpureum* treatment when compared to control, but more in *C. purpureum* treatment than in cutting treatment.

2. Does *C. purpureum* treatment affect the ability of a stump to sprout?

We hypothesize that *C. purpureum* treatment decreases the proportion of resprouting stumps compared to cutting treatment.

3. Does the diameter of the stump impact its ability to sprout after *C. purpureum* treatment?

We hypothesize that the larger the diameter of the cut stump, the more effectively *C. purpureum* can penetrate into the stump. This increases stump mortality particularly for larger saplings when compared to only cutting.

4. Does *C. purpureum* treatment affect the number of sprouts produced by a cut stump?

We hypothesize that the *C. purpureum* treatment reduces the number of sprouts produced. We also hypothesize that as larger stumps are more likely to produce more sprouts, this effect is stronger for large stumps.

METHODS

Study sites

We performed the study in Seitseminen National Park in Western Finland (Fig. 1). The national park is managed by Metsähallitus Parks & Wildlife Finland that provided ten restored peatlands sites as study sites. The peatland sites had been restored 15-21 years ago by filling in ditches and logging trees, and they had relatively dense downy birch sapling stands (Table 1).

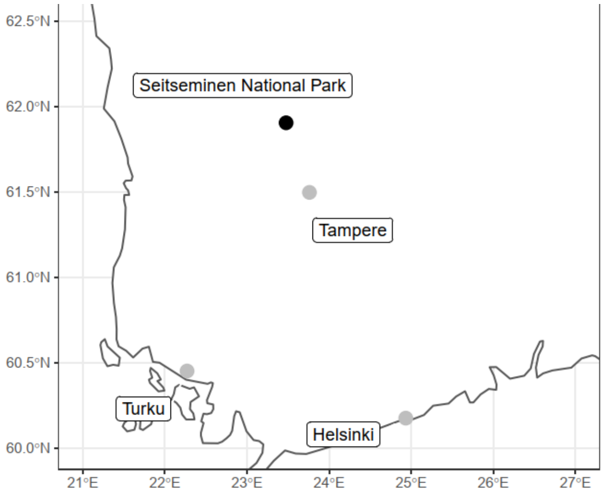

Fig. 1 *Location of Seitseminen National Park (black dot) in Western Finland.*

Table 1 *Information of the study sites: site number, name, coordinates (latitude and longitude, WGS84), year of restoration and the density of downy birch saplings (n/m^2) before the treatments (2018).*

Site number	Site name	Latitude	Longitude	Restoration year	Sapling density
1	N of Pitkäjärvi	61° 56,305'	23° 24,603'	1999	1.92
2	NW of Onkilampi	61° 56,490'	23° 25,114'	1997	1.27
3	NNE of Onkilampi	61° 56,430'	23° 25,518'	1997	1.45
4	NE of Onkilampi	61° 56,411'	23° 25,696'	1997	2.26
5	E of Onkilampi	61° 56,294'	23° 25,821'	2000	7.05
6	W of Isoneva	61° 57,284'	23° 25,330'	2003	3.36
7	S of Isoneva	61° 57,162'	23° 25,681'	2001	2.01
8	E of Löytty	61° 57,061'	23° 25,419'	2003	1.71
9	S of Löytty	61° 56,959'	23° 25,363'	2003	1.85
10	W of Särkivehmas	61° 57,738'	23° 25,783'	2002	3.06

Experimental design

In each of the ten peatland sites, we set up three treatment areas next to the filled ditch. Each treatment area is sized 10×20 m and a distance of at least five meters was left between two treatment areas (Fig. 2). We placed two permanent monitoring circles of five-meter diameter inside each treatment area and the center of the circle was marked with a plastic pipe. One circle was placed near the ex-ditch (adjacent to it) and the other far (10 m) from it (Fig. 2).

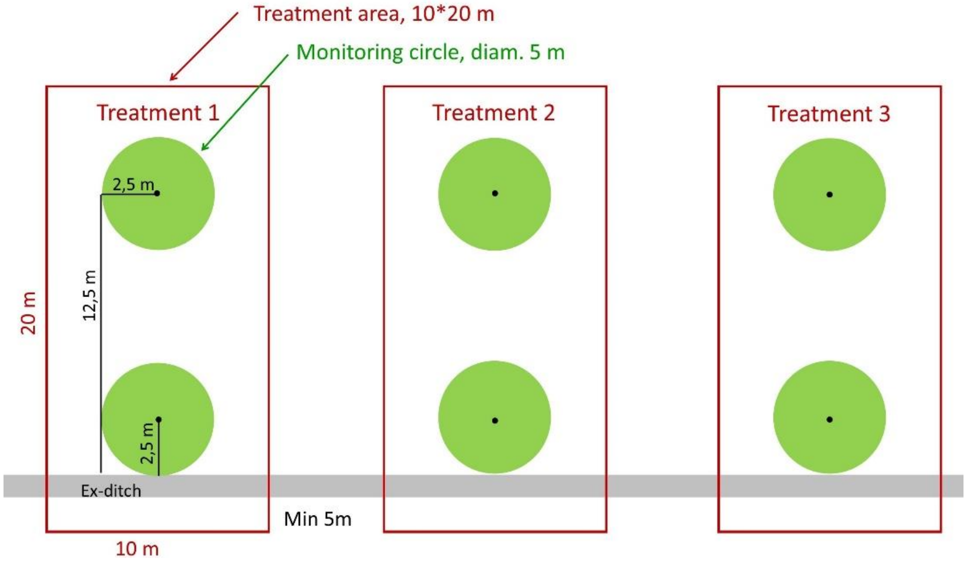

Fig. 2 *The experimental design contains three treatment areas in each study site. Two permanent monitoring circles were placed within the treatment area, one near the ditch and one far from it.*

Treatments

All treatments were made in June 2018. The order of treatments was randomized to each site separately. For the cutting treatment all saplings and young trees (<10 cm diameter at 130 cm height) were cut with a brush cutter at the height of approximately 20 cm. The cut stems were left in place. For the *C. purpureum* treatment, the saplings and young trees were cut at the height of approximately 20 cm, and stumps of deciduous trees were sprayed with a solution containing *C. purpureum* hyphae. The basic solution was produced by Verdera Oy. It contains *C. purpureum* strain $R5_3$ which has been bred for efficient sprout control and has shown a high efficiency for stump mortality: 78% of birch stumps of ca 1- cm diameter had been killed after three growing seasons (Hamberg et al., 2015). The basic solution was diluted with water 1:25 before spraying. The colorful solution was sprayed from a backpack pump on all stumps of deciduous trees following the brush cutter. In the control treatment no actions were performed.

Field work

We visited the sites twice: before the treatments (May 2018) and four years after the treatments (May 2022). On both times, we counted and recorded the species of all trees, saplings and sprouts within the monitoring circles. In 2022, we also recorded cut stumps, and measured their height and diameter at 10 cm height (with an accuracy of 1 cm) and recorded the number of basal sprouts branching from them. The stumps were then classified as either resprouting (at least one sprout) or unsprouting (no sprouts and dead). The late spring of 2022 caused delay in leaf emergence, and we could not evaluate whether the sprouts were dead or alive. Thus, stump mortality could not be recorded for the resprouting stumps. Stumps that had branched at the height of 0-10 cm and multi-stemmed trees were interpreted as the same individual.

Data collected but not used in analyses

In 2018, we measured the height and diameter of saplings. For small saplings (height =< 130 cm), we measured the height with an accuracy of 1 cm, and the diameter with a tape measure at a height of 10 cm with an accuracy of 1 cm. For tall saplings (height > 130 cm), we measured the height to an accuracy of 10 cm using a rod, and diameter with a tape measure at a height of 130 cm to an accuracy of 1 cm. For trees (height > 2 m), we estimated the height to an accuracy of 50 cm, and diameter with a tape measure at a height of 130 cm to an accuracy of 1 cm. In 2022, we only recorded whether the height of saplings was above or below 130 cm due to the limited time and the large number of saplings. Also, we counted the basal sprouts branching from uncut saplings and trees.

We measured peat depth using a metal stick in 2018, but 75% of the circles had deeper peat than the length of the measuring stick (100 cm), so this data was not useful. In addition, we measured water table dept by blowing air into a flexible tube that was set into a thicker plastic tube placed in the peat in 2018 and 2022. However, we excluded the water table level from the analyses because one point measurement from the center of the circle does not describe the water table level of the whole circle well enough as there is likely to be a reasonably large variation in water level height within the circles.

Statistical analysis

For all the analyses, we considered only birch saplings, and excluded saplings of other trees. For the first study question, we analyzed whether the treatments affect the relative change of the number of saplings (either uncut or cut by resprouting). We calculated this ‘sapling number change’ as a percentage

$$\frac{n_{2022} - n_{2018}}{n_{2018}} * 100$$

where n_{2022} is the number of saplings in 2022, n_{2018} is the number of saplings in 2018. We used a linear mixed-effects model [function ‘lme’ from the R package nlme (Pinheiro et al. 2022)]. We set sapling number change as a response variable, site as a random factor, and treatment (Control/Cutting/Cutting + *C. purpureum*) and circle (near the ditch/far from the ditch) as fixed factors.

For the following analyses, we used only data from the year 2022. For the second study question, we analyzed whether *C. purpureum* treatment affected stump sprouting ability. We calculated the percentage of unsprouting stumps from all stumps. Again, we used a linear mixed-effects model, and set percentage of unsprouting stumps as a response variable, site as a random factor, and treatment (Cutting/Cutting + *C. purpureum*) and circle (near the ditch/far from the ditch) as fixed factors.

For the third study question, we analyzed whether the sprouting ability of a stump depended on the diameter of the stump. We used a generalized linear mixed-effect model [function ‘glmer’ from R package lme4 (Bates et al. 2015)] with a binomial model and logit link. We set the status of a stump (unsprouting/resprouting) as a response variable, site as a random factor, and stump diameter (cm), treatment (Cutting/Cutting + *C. purpureum*) and their interaction as fixed factors.

For the fourth study question, we analyzed whether *C. purpureum* treatment affected the number of sprouts produced by a resprouting stump. We used a linear mixed-effect model and set the number of sprouts from a stump as a response variable, site as a random factor, and stump diameter (cm), treatment (Cutting/Cutting + *C. purpureum*) and their interaction as fixed factors.

We inferred the assumptions of the models visually from the model residuals. The analyses were conducted with R version 4.2.1 (R Core Team 2022).

RESULTS

The sapling number change (%) from 2018 to 2022 was on average negative in all three treatments, including controls: -9.2±10.6 (mean±SD) in control, -14.3±29.1 in cutting treatment, and -29.0±28.3 in *C. purpureum* treatment (Fig. 3a). The sapling number change was more negative in *C. purpureum* treatment than in control (Table S1, Fig. 3a) but we did not find a statistical difference between control and cutting (Table S1, Fig. 3a). There was considerable variation in the sapling number change, particularly in cutting treatment, and the change was even positive in some sites.

The percentage of unsprouting stumps from all stumps was higher in *C. purpureum* treatment (62.7±20.2) compared to cutting (31.1±18.4) (Fib. 3b, Table S2). The location of the circle (whether near or far away from the ditch) did not affect the sapling number change or percentage of unsprouting stumps (Tables S1&S2).

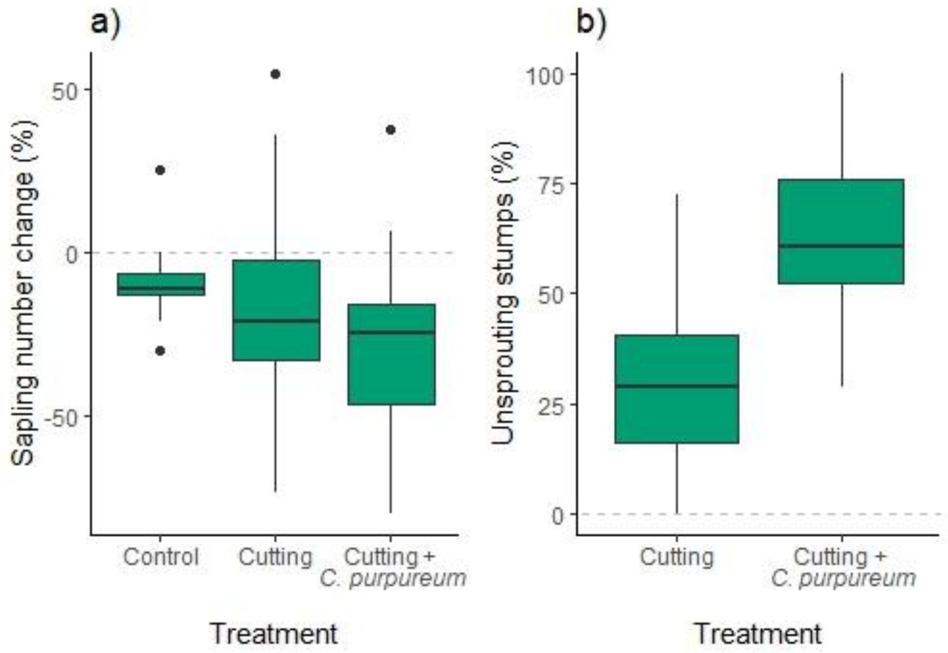

***Fig. 3** Sapling number change from 2018 to 2022 in Control, Cutting and Cutting + C. purpureum (a) and percentage of unsprouting stumps out of all stumps in Cutting and Cutting + C. purpureum 2022 (b). The thick black line shows the median, the hinges show the 25th and 75th percentiles, the upper/lower*

*whisker extends to the largest/smallest value no further than 1.5 * inter-quartile range, and data points further away are shown individually.*

The chance of stump sprouting decreased with increasing stump diameter in both cutting and *C. purpureum* treatments (Fig. 4a,b, Table S3). In *C. purpureum* treatment, more than half of the stumps with a diameter larger than 1 cm did not sprout (Fig. 4b). If a stump sprouted, a larger diameter caused a larger number of sprouts in cutting treatment but not in *C. purpureum* treatment (Fig. 4c, Table S4). In other words, a large stump produced fewer sprouts in *C. purpureum* treatment than in cutting treatment.

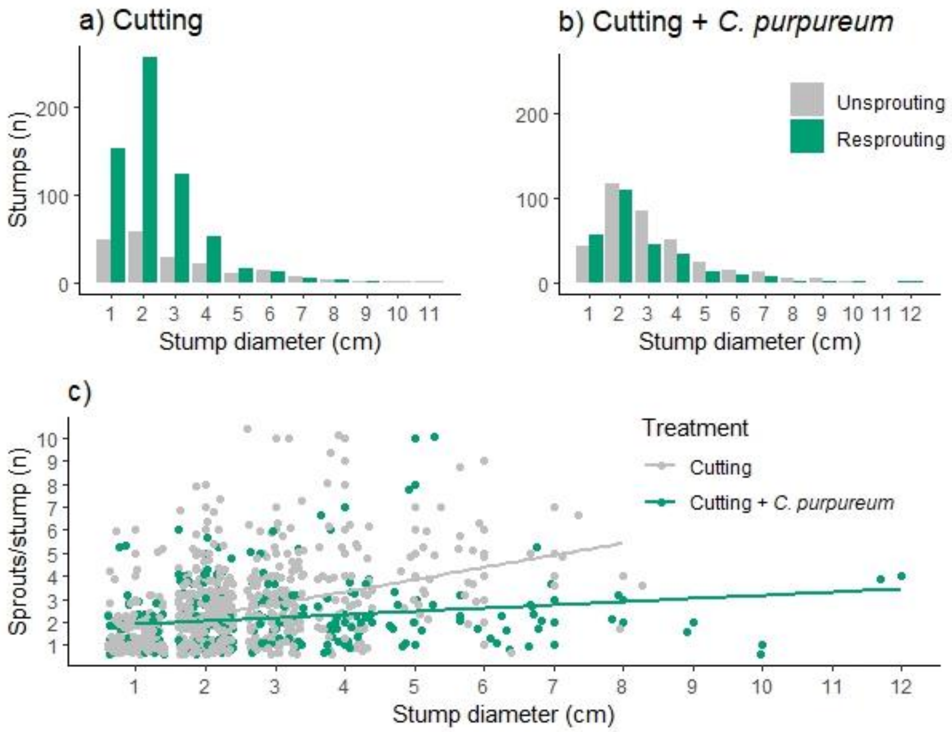

Fig. 4 *Number of unsprouting and resprouting stumps in a) cutting treatment and b) cutting + C. purpureum treatment, and number of sprouts from a stump in relation to diameter of the stumps in the two treatments (c; please note that the points are jittered to increase the readability of the figure).*

DISCUSSION

We conducted a field experiment to test how effective *C. purpureum* is in the sprout control of downy birch in restored peatlands. We found that the number of birch saplings decreased more in the *C. purpureum* treatment than in the control of no action. The measured sapling number change of -29% in the *C. purpureum* circles is rather modest but this count of saplings contains both newly established individuals and stumps that had resprouted. After the treatment, the reduced competition for light and growing space encourages the growth of new individuals, although the established vegetation should limit seed germination (see Atkinson, 1992). The control of surviving stumps and newly established seedlings would thus require repeated treatment after several years. Therefore, it seems that *C. purpureum* treatment is moderately efficient in reducing birch saplings on restored peatlands.

C. purpureum treatment decreased the proportion of stumps that were able to sprout when compared to only cutting. On average, the proportion of unsprouting stumps was doubled by *C. purpureum* (62.7%) compared to cutting (31.1%). Therefore, *C. purpureum* very efficiently kills the birch stumps soon after inoculation. Birches have low tolerance against *C. purpureum* which often penetrates the roots and kills the individual in three months (Hamberg et al., 2017). Earlier studies on dry land have reported mortalities between 33 and 83% after the first growing season (Hamberg & Hantula, 2018, 2020; Vartiamäki et al., 2008). On paludified spruce plantations the mortality was highest for those birch individuals that grew on wet soil (surrounded by *Sphagnum* mosses or in water). After the first growing season, 53.2% of these individuals were dead (Hamberg & Hantula, 2020). This percentage is similar to the percentage of unsprouting stumps in our study. The mortality caused by *C. purpureum* also increases from the first growing season after the treatment, varying between 59 and 97% in two to four growing seasons after the treatment (Hamberg & Hantula, 2018, 2020; Vartiamäki et al., 2008, 2009). We were not able to record whether the sprouts from the stumps were dead or alive (due to late leaf emergence during the spring of our follow-up data collection), and it is likely that some stumps have died during the following years due to *C. purpureum.* Thus, the percentage of dead stumps four years after the treatment is likely to be larger than the percentage of unsprouting stumps recorded here. Repeating the data collection after leaf emergence is recommended to confirm long-term mortality.

In general, large-diameter stumps were less likely to survive the treatment and sprout than smaller stumps. If a stump sprouted, *C. purpureum* decreased the number of sprouts on larger stumps, thus causing stumps of all sizes to have as few sprouts. The *C. purpureum* treatment is therefore more efficient on slightly larger stumps (basal diameter around 3 cm or more). The bigger area exposed on a large stump provides space for more fungal hyphae to colonize and decay the wood, which causes mortality faster than in smaller stumps (Hamberg et al., 2021; Hamberg & Hantula, 2020). Previous studies have also found that large diameter increases birch stump mortality after *C. purpureum* treatment (Hamberg et al., 2015; Hamberg & Hantula, 2020), although Hamberg & Hantula (2018) found that mortality was high for small stumps and lowest for medium-sized stumps (around 13 cm in diameter) after the first growing season.

In contrast to using *C. purpureum*, mechanical cutting alone does not seem to be efficient in reducing birch saplings and sprouts in restored peatlands: the number of saplings was not significantly decreased compared to control, only 31% of cut stumps did not sprout, and although larger stumps were more likely to die, they also sprouted more vigorously if they survived. Indeed, in some sites the number of saplings had even increased after cutting. Even though cutting decreases the biomass of saplings temporarily, the treatment needs to be repeated frequently, which increases costs (Hamberg et al., 2021; Laine et al., 2020). In addition, it does not seem likely that performing no sapling removal would result in a favorable restoration result. In our study, the number of saplings decreased slightly on the control plots, which is probably due to competition for light (Atkinson, 1992; Hamberg & Hantula, 2018). However, the uncut saplings have grown during the study, and therefore their total biomass has most probably increased. This, in turn, increases shadowing and water evaporation which counteracts restoration.

Conclusions

Using *C. purpureum* to control birch sprouting on restored peatlands is efficient compared to only cutting the saplings. The fungus halves the percentage of stumps that are able to sprout, and thus reduces the impact of the birches on the recovering peatland ecosystem. However, new seedlings and saplings appear and thus the number of saplings is only moderately reduced. Repeated treatment is therefore needed, but it could be postponed by several years due to the long impact of the fungus on stump mortality, and because the treatment is most efficient when used on larger saplings. We recommend long-term follow-up studies on both these study sites and on others to confirm how *C. purpureum* impacts mortality during several years, and to see how the density of saplings develops after treating with *C. purpureum*, or only cutting. This would allow the evaluation of how often the treatments should be repeated to reach a favorable result, and hence the evaluation of the cost-efficiency of the methods.

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SUPPORTING INFORMATION

Table S1 *Results from the general linear mixed model having the change of the sapling number as the response variable, and treatment and circle as fixed factors. Site was used as a random factor. Control treatment and circle near the ditch were used as reference levels. The table presents parameter estimates, standard errors (SE), degrees of freedom (df), t-values and associated p-values.*

Variable	Estimate	SE	df	t	p
(Intercept)	-7.02	6.63	47	-1.06	0.295
Treatment Cutting	-5.11	6.87	47	-0.74	0.461
Treatment C. purpureum	-19.79	6.87	47	-2.88	0.006
Circle Far from ditch	-4.29	5.61	47	-0.77	0.448

Table S2 *Results from the general linear mixed model having the percentage of unsprouting stumps as the response variable, and treatment and circle as fixed factors. Site was used as a random factor. Cutting treatment and circle near the ditch were used as reference levels. Column headings as in Table S1.*

Variable	Estimate	SE	df	t	p
(Intercept)	28.40	5.51	28	5.15	<0.001
Treatment C. purpureum	31.67	5.44	28	5.83	<0.001
Circle Far from ditch	5.30	5.44	28	0.98	0.338

Table S3 *Results from the generalized linear mixed model having the status of the stump (unsprouting/resprouting) as a response variable, and stump diameter (cm), treatment and their interaction as fixed factors. Site was used as a random factor. Treatment Cutting was used as a reference level. The table presents parameter estimates, standard errors (SE), degrees of freedom (df), z-values and associated p-values.*

Variable	Estimate	SE	z	p
(Intercept)	1.71	0.22	7.75	<0.001
Stump diameter	-0.22	0.06	-3.84	<0.001
Treatment C. purpureum	-1.79	0.24	-7.36	<0.001
Stump diameter:Treatment	0.13	0.07	1.74	0.081

Table S4 *Results from the general linear mixed model having the number of sprouts on a resprouting stump as a response variable, and stump diameter (cm), treatment and their interaction as fixed factors. Site was used as a random factor. Treatment Cutting was used as a reference level. Column headings as in Table S1.*

Variable	Estimate	SE	df	t	p
(Intercept)	1.34	0.18	884	7.53	<0.001
Stump diameter	0.51	0.05	884	10.82	<0.001
Treatment C. purpureum	0.56	0.2	884	2.81	0.005
Stump diameter:Treatment	-0.39	0.07	884	-5.85	<0.001