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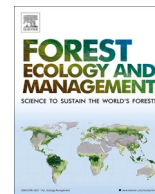
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# Long-term effects of biological sprout control of unwanted hardwoods on conifer sites

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## ABSTRACT

Long-term investigations revealing the effects of a decay fungus, *Chondrostereum purpureum* (Pers. Ex Fr.) Pouzar on competition between deciduous and conifer tree species in young forests are missing. Therefore, the effects of three different sprout control treatments were tested in young Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) stands by evaluating sprouting ability of deciduous tree stumps, and competition level around cultivated conifers five years after the treatments. Sprouting control was performed (i) by cutting only (control), and (ii) by applying low-concentration (dilution 1:400) or (iii) high-concentration (dilution 1:100) *C. purpureum* preparates (mycelial solutions) on stumps immediately after cutting. Deciduous saplings were cut, and fungal inoculum was applied by spreading it onto freshly cut stump surfaces. Following high-concentration fungal treatment, the number of young deciduous trees cut in the treatment was by 25% lower compared to control; moreover, the number of sprouts per stump was also significantly negatively affected by the fungal treatment. As a result, the number of cases when competing deciduous trees occurred within a 1 m sample plot around the investigated conifers was 40% lower following high-concentration fungal treatment than in the control, resulting in better height and diameter development of conifers. Thus, additional sprout control is not necessarily needed after the high-concentration fungal treatment.

## 1. Introduction

In young conifer stands, self-regenerating deciduous tree saplings cause problems for cultivated conifers by competing for resources and causing physical damage (whipping) (Jobidon, 2000; Huuskonen and Hynynen, 2006; Saksa and Miina, 2007; Fahlvik et al., 2011; Huuskonen et al., 2020). The biggest problems caused by self-regenerating deciduous saplings include reduction in height and diameter development of young cultivated conifers such as Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) (Jobidon, 2000; Varmola and Salminen, 2004; Huuskonen and Hynynen, 2006; Saksa and Miina, 2007; Uotila and Saksa, 2014). Therefore, early cleaning is performed in order to give more growing space for cultivated trees, and to ensure their better growth and future timber quality. Traditionally, deciduous trees are being cut with a clearing saw but excessive re-sprouting usually causes a need for subsequent sprout control operations (Uotila et al., 2010, 2012; Thiffault and Roy, 2011; Uotila and Saksa, 2014). Thus, the costs of young stand

management are high: for example, in Finnish forests ca. 56 million euros were used in early pre-commercial and pre-commercial thinnings in 2019 alone (Natural Resources Institute Finland, 2020).

Previously, chemicals (arboricides) have been utilized to reduce the effects of competition caused by deciduous trees in young conifer stands, but their use has raised concerns due to harmful effects on the environment (Thiffault and Roy, 2011; PEFC, 2014). Thus, strict restrictions have requested for new efficient and environmentally friendly alternatives. A decay fungus, *Chondrostereum purpureum* (Pers. Ex Fr.) Pouzar fulfills these requirements (e.g. Jobidon, 1998; Harper et al., 1999; Roy et al., 2010; Lygis et al., 2012; Hamberg et al., 2015; Hamberg and Hantula, 2016, 2018). It can be spread as hyphal inoculum diluted with water or applied as a paste to stump surfaces immediately after a tree has been cut (de Jong, 2000; Bellgard et al., 2014; Hamberg et al., 2015). From stump surfaces the fungus grows within a stump where it decays wood and may finally kill its host, thus preventing sprouting (Dumas et al., 1997; Becker et al., 1999; Hamberg et al., 2017). Since

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*C. purpureum* is common in temperate and boreal vegetation zones, it can be utilized in controlling sprouting of several deciduous tree species (Wall, 1990; Roy et al., 2010; Lygis et al., 2012; Hamberg et al., 2021a). It does not cause harm to healthy deciduous trees or to conifers (Wall, 1990; Gosselin et al., 1999). Fungal inoculum is not sensitive to variation in weather conditions, such as rain showers or high temperatures (Hamberg and Hantula, 2020, Hamberg et al., 2020). However, its efficient use is restricted to growing seasons (Vartiamäki et al., 2009; Laine et al., 2020a; Hamberg, 2021).

Although the biological sprout control method utilizing the ability of *C. purpureum* to kill stump sprouts of deciduous trees has been investigated intensively, it cannot yet be used in forest management in Europe since its commercial use requires permission by authorized European Union institutions (Hamberg et al., 2021a). Furthermore, fully mechanized devices are needed for effective and cost-efficient vegetation management (Laine et al., 2019, 2020a,b), as this can fulfil perhaps the most important task in practical biological sprout control - treating vast numbers of stumps with fungal inoculum immediately after cutting.

A recent study by Laine et al. (2020a) evaluated the efficacy of fully mechanized sprout control methods utilizing *C. purpureum* as a sprout control agent where the effect of cutting only (control treatment) was compared to the treatments with fungal preparates of different dilutions. In the present study, a subset of sites investigated in the above-mentioned study were revisited in order to find out long-term effects of the treatments. The situation five years after the treatments was evaluated in each site by counting viable young deciduous trees cut in treatments, and by assessing the competition level around cultivated conifers. We hypothesized that after five years (1) the density of young deciduous trees cut in treatments and sprouting of deciduous stumps is lower following fungal treatments compared to control (cutting only), and as a consequence, (2) the competition around investigated conifers would be lower in fungal treatment sites compared to the control plots.

## 2. Material and methods

### 2.1. Treatments and investigations in the field

Altogether, five sites located in central Finland were included in the study (Table 1). Three of the sites represented Norway spruce (*Picea abies* (L.) H. Karst.) and two of the sites Scots pine (*Pinus sylvestris* L.)

stands established in 2008 or 2009. Abundant self-regeneration by deciduous trees species was observed on all sites in 2014. Therefore, in order to provide more growing space for conifers, in 2014, young deciduous trees were either (1) cut only (control treatment), or (2) cut and freshly cut stump surfaces treated with a mycelial suspension of *Chondrostereum purpureum* of low (diluted with tap water to 1:400), or (3) high-concentration (1:100). The treatments were carried by Laine et al. (2020a), and at that state the density of conifers decreased from 5000 to 4300, and that of deciduous saplings from 15 500 to 2000 per hectare. All the treatments have been performed using a lightweight mini-harvester Tehojätäkä equipped with a UW40 cleaning head and a spreading device (Usewood Ltd., Finland). The basal suspension of *C. purpureum* was provided by Verdera Ltd., Finland, and it included a fungal strain R5 (Hamberg et al., 2015) at a concentration of at least  $10^6$  colony forming units per gram (González, 1996).

In each site, within each treatment, 14–15 circular sample plots ( $r = 0.5$  m) were regularly located along the treated area following the layout of the study by Laine et al. (2020a). Thus, in 2019–2020, altogether 208 sample plots were established to investigate the efficacy of the treatments in preventing re-sprouting of the felled deciduous trees (Table 1). Each sample plot was established at a place with a high density of young deciduous trees but without planted conifers. Inventories in the field were performed in late 2019 (21–23 October, after the end of growing season) or early 2020 (19–20 May, before the start of next growing season), i.e., approximately five years after the treatments. Within each sample plot, all deciduous saplings more than 0.5 cm in diameter at a ground level were investigated. The species and origin of each deciduous sapling were recorded and all saplings were divided into two categories: (1) young deciduous trees cut in 2014 and (2) grown from a seed (seedlings, not cut in the treatment), and their total number was counted. Furthermore, all self-regenerated coniferous trees were measured and counted to observe the total number of young conifers in a sample plot. In the present study, the total number of young deciduous trees cut in 2014 was 1011 (this amounts to 89% of all young deciduous trees, treated and seedlings, counted within 208 sample plots established to investigate the effects of the treatments on unwanted young deciduous trees, Tables 1 and 2). The majority of young deciduous trees cut in 2014 belonged to birch (silver and downy birch, *Betula pendula* Roth and *B. pubescens* Ehrh., respectively,  $n = 835$ , i.e. 83%), followed by rowan (*Sorbus aucuparia* L.,  $n = 105$ , 10%) and willow (*Salix* sp.,  $n = 71$ , 7%).

**Table 1**

Sites from the study by Laine et al. (2020a) included in the study, their geographical coordinates, year of plantation establishment, cultivated tree species, timing for the treatment and inventory, and the number of investigated young deciduous trees cut in 2014 (*Betula pendula* and *B. pubescens*, *Sorbus aucuparia* and *Salix* sp.) and planted conifers (Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*)). Number of young deciduous trees cut in 2014 were investigated within circular sample plots 0.5 m in radius and planted conifers from separate sample plots 1 m in radius.

Site	Geographical coordinates	Plantation establishment (year) and tree species <sup>a</sup>	Treated	Inventoried	Number of deciduous trees cut in 2014 within sample plots 0.5 m in radius ( $n = 208$ )			Number of planted conifers investigated within sample plots 1 m in radius ( $n = 208$ )		
					Control <sup>b</sup>	Fungal 1:400 <sup>c</sup>	Fungal 1:100 <sup>d</sup>	Control <sup>b</sup>	Fungal 1:400 <sup>c</sup>	Fungal 1:100 <sup>d</sup>
3.1 Matkala, Keuruu	62°13'47.8"N 24°20'38.4"E	2009 (S)	June 2014	October 2019	109	55	79	15	15	15
4.1 Tuohis, Keuruu	62°18'10.7"N 24°51'02.0"E	2008 (P)	June - July 2014	May 2020	21		32	15		15
5.1 Ilo, Keuruu	62°09'27.7"N 24°45'03.4"E	2008 (P)	July 2014	May 2020	70	76	59	15	14	14
6.1 Limpsi, Keuruu	62°06'43.8"N 24°48'41.9"E	2009 (S)	July 2014	October 2019	75	68	41	15	15	15
8.1 Kälvi, Mänttä-Vilppula	62°05'29.1"N 24°33'15.1"E	2008 (S)	September 2014	October 2019	122	126	78	15	15	15
Altogether					397	325	289	75	59	74

<sup>a</sup> (S): Norway spruces were planted; (P): Scots pines were planted to a site.

<sup>b</sup> Control treatment (cutting only).

<sup>c</sup> *Chondrostereum purpureum* mycelial solution (basal solution diluted with tap water 1:400) was applied on freshly cut stumps.

<sup>d</sup> *Chondrostereum purpureum* mycelial solution (basal solution diluted with tap water 1:100) was applied on freshly cut stumps.

**Table 2**

Number of investigated young silver and downy birch (*Betula pendula* and *B. pubescens*, respectively) trees, rowans (*Sorbus aucuparia*) and willows (*Salix* sp.) following different treatments in Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) sites (for more information see Table 1). Young deciduous trees cut in 2014 and presented in this table were investigated within circular sample plots 0.5 m in radius.

Tree species	Control <sup>a</sup>		Fungal 1:400 <sup>b</sup>		Fungal 1:100 <sup>c</sup>		Total
	Norway spruce	Scots pine	Norway spruce	Scots pine	Norway spruce	Scots pine	
Birches	277	49	228	59	169	53	835
Rowan	16	20	8	9	21	31	105
Willow	24	11	14	7	8	7	71
Altogether	317	80	250	75	198	91	1011

<sup>a</sup> Control treatment (cutting only).

<sup>b</sup> *Chondrostereum purpureum* mycelial solution (basal solution diluted with tap water 1:400) was applied on freshly cut stumps.

<sup>c</sup> *Chondrostereum purpureum* mycelial solution (basal solution diluted with tap water 1:100) was applied on freshly cut stumps.

The diameter (mm) of each stump within each sample plot was measured, and for each stump the total number of living sprouts and height of the tallest living sprout (cm) were recorded. Some young deciduous trees cut in 2014 included more than one stump, possibly because of branching near the soil surface (birches had ca. 1.1, rowans ca. 2.1 and willow ca. 1.4 stumps per a treated deciduous tree). However, only one randomly selected stump was investigated. In some cases, the sprouting stump had decomposed completely but remains of it were still visible (such stumps made about 4% of all young deciduous trees cut in 2014). Because it was not possible to measure the diameter of such stumps it was extrapolated from mean diameter of the same tree species stumps having similar ( $\pm 5$  cm) height of the tallest sprouts within the same site and treatment. Effects of the treatments on birch sprouting three years after setting up the experiments have been reported as a part of the study by Laine et al. (2020a).

To investigate competition between planted conifers and all deciduous saplings in all sites, an additional sample plot ( $r = 1$  m) was established next to each investigated sample plot 0.5 m in radius. In these additional sample plots, a planted conifer – either Norway spruce or Scots pine – was chosen as a center point. Altogether 208 planted conifers (138 Norway spruces and 70 Scots pines) and competition around them were investigated (Table 1). The height (cm) and diameter at breast height (DBH, cm, at the height of 1.3 m) were measured for each planted spruce and pine sapling located in the center point of a sample plot, and the occurrence of browsing was visually evaluated.

Competition from deciduous saplings (both treated and regenerated from seeds) surrounding a selected central conifers was investigated within 1 m radius and assessed using two categories: 0 = no competition, i.e., height of any deciduous saplings is lower than 2/3 of the height of the central conifer, 1 = competition exists, i.e., height of at least one deciduous sapling has reached or exceeded 2/3 of the height of the conifer tree. Competition from conifers within a sample plot was assessed by counting the number of self-regenerated conifers with a height of at least 1/2 of that of the “central” conifer.

## 2.2. Statistical analyses

All statistical analyses and figure drawings were performed in the statistical program R (R Core Team, 2020). In order to investigate the overall success of each treatment five years after the field experiment has been initiated, we estimated a model for the number of young deciduous trees cut in 2014 per sample plot. As a response we had the number of young deciduous trees cut in 2014 within a sample plot ( $n = 208$ , i.e., the number of observations, each including information on the number of young deciduous trees cut in 2014), and as explanatory variables we had (1) treatment (a factor with three levels: control, low-concentration fungal treatment, and high-concentration fungal treatment) and (2) conifer tree species (a factor with two levels: Norway spruce or Scots pine). A second explanatory variable was included in the model to account for the fact that the number of young deciduous trees cut in 2014 may be lower in drier and nutritionally poorer Scots pine

sites. The numbers of self-regenerated conifers and deciduous tree seedlings within sample plots were not included in the final model since they had effect neither on the response ( $p = 0.670$ ), nor on the coefficients and  $p$ -values of other explanatory variables in the model. Site was included as a random factor in the model since young deciduous trees cut in 2014 within a site may be more similar than single observations from separate sites (one observation only from one site). Generalized linear mixed modeling, GLMM, using package *lme4* and function *glmer* (Bates et al., 2015) was used in the statistical analyses assuming Poisson distribution and using log link.

The number of stump sprouts per stump were compared among the treatments using GLMMs as above. The number of living stump sprouts per stump was as a response ( $n = 1011$ , i.e., the number of observations, each including information on the number of stump sprouts per stump), and as explanatory variables we had (1) treatment (a factor with three levels: control, low-concentration fungal treatment, and high-concentration fungal treatment), (2) deciduous tree species (a factor with three levels: silver and downy birches together, rowan and willow), (3) conifer tree species (a factor with two levels: Norway spruce or Scots pine), (4) stump diameter (mm), and (5) the total number of saplings within a sample plot (young deciduous trees cut in 2014 and self-regenerated deciduous and coniferous trees were included). Silver and downy birches were analyzed together since no difference has been found between their sprouting capacities following the *C. purpureum* treatment (Hamberg et al., 2015). Explanatory variable two was included in the model to account for differences between the investigated deciduous species, and other explanatory variables (numbers 3–5) to account for other variation among young deciduous trees cut in 2014 and sample plots. Site and sample plot were included as nested random factors in the model to account for the fact that sample plots within sites, and saplings within sample plots may be more similar than randomly investigated sample plots and saplings. The model regarding the tallest living stump sprouts ( $n = 1011$ , i.e., the number of observations, each including information on the tallest living stump sprout per stump) among the treatments included the same explanatory variables and random factors as in the number of stump sprouts model. The response, tallest living stump sprout (cm) was log transformed for the analysis. Linear mixed modeling, LMM, in the R package *nlme* and with function *lme* (Pinheiro et al., 2020) was used to estimate the model.

Competition around planted conifers was investigated using generalized linear mixed modeling, GLMM, using package *lme4* and function *glmer*, assuming binomial distribution and using logit link function (Bates et al., 2015). As a response we had the occurrence of competition ( $n = 208$ , a factor with two levels: 0 = no competition, 1 = competition exists). As explanatory variables we had (1) treatment (a factor with three levels: control, low-concentration fungal treatment, and high-concentration fungal treatment), (2) the number of competing conifers (others than the planted central tree) within a sample plot 1 m in radius, and (3) a conifer tree species (a factor with two levels: Norway spruce or Scots pine). The site was used as a random factor in the model to account for the fact that conditions within a selected conifer site may be more

similar than when each observation would have been collected from a separate site.

The effects of different treatments on the height (cm) and the diameter at breast height (DBH, cm) of cultivated Norway spruces or Scots pines were investigated using linear mixed models, LMM, package *nlme*, function *lme*, and assuming normal distribution (Pinheiro et al., 2020,  $n = 208$  for the conifer height and  $n = 207$  for the conifer DBH: one tree was removed from the DBH analysis since it was  $<1.3$  m in height). In both models, explanatory variables were the same as in the competition models, i.e.: (1) treatment (a factor with three levels: control, low-concentration fungal treatment, and high-concentration fungal treatment), (2) the number of competing conifers (other conifers than the planted central tree) within a sample plot 1 m in radius, and (3) tree species (a factor with two levels: Norway spruce or Scots pine). Site was used again as a random factor. All values presented in the result figures are estimated values (predictions) based on the models. Package *AICcmodavg* was used to calculate estimated values based on the linear mixed effect models (Mazerolle, 2020).

### 3. Results

#### 3.1. Effects of treatments on young deciduous trees cut in 2014

All results presented under the section 3.1 relate to the data collected from circular sample plots 0.5 m in radius established for investigations on the effects of the treatments on deciduous trees. The number of young deciduous trees cut in 2014 was ca. by 25% lower in high-concentration fungal treatment sample plots (4.6 in Norway spruce and 2.4 in Scots pine sample plots) than in control treatment (6.1 and 3.2, respectively, GLMM,  $p < 0.001$ ). No significant difference was found between the low-concentration fungal treatment (5.6 and 3.0 young deciduous trees cut in 2014 in the Norway spruce and Scots pine sample plots, respectively) and control ( $p = 0.239$ ). As expected, the number of young deciduous trees cut in 2014 was lower in Scots pine than in Norway spruce sample plots ( $p < 0.001$ ).

The number of stump sprouts per stump was significantly lower ( $p = 0.001$ ) following high-concentration fungal treatment than in control (GLMM, Table 3, Fig. 1). However, statistically significant differences were not found between the low-concentration fungal treatment and the control ( $p = 0.157$ ). The number of stump sprouts per stump was lower for birch than for rowans ( $p < 0.001$ ) and willows ( $p < 0.001$ ), but no difference in the number of sprouts per stump was found between the Norway spruce and Scots pine sites ( $p = 0.456$ ). The number of stump sprouts per stump increased with increasing stump diameter ( $p < 0.001$ ) but decreased with increasing tree density ( $p < 0.001$ ).

The height of tallest stump sprouts did not differ significantly between the control and low-concentration fungal treatment (LMM,  $p = 0.321$ ), or high-concentration fungal treatment ( $p = 0.987$ , Table 3, Fig. 1). Although the tallest sprouts were by 10–20 cm lower in Scots pine sites than in Norway spruce sites (predicted values not shown), no

statistically significant differences ( $p = 0.176$ ) in the height of tallest stump sprouts between the Norway spruce and Scots pine sites were found. Stump sprouts were significantly taller for birch than for rowans ( $p < 0.001$ ) and willows ( $p < 0.001$ ). The height of tallest stump sprouts increased with increasing stump diameter ( $p < 0.001$ ) but the density within a sample plot had no effect on height ( $p = 0.422$ ).

#### 3.2. Inter-tree competition following different treatments

All results presented under the section 3.2 relate to the data collected from circular sample plots 1 m in radius established for investigations on the effects of competition around planted central conifers. Most of the investigated central conifers were visually healthy but ca. 7% of conifers were affected by browsing of wild game. In the Scots pine sites, browsing was more common than in Norway spruce sites. Compared to control, the competition was lower around planted central conifers following high-concentration fungal treatment (GLMM,  $p = 0.052$ , Fig. 2). The difference between control and low-concentration fungal treatment was not statistically significant in this respect ( $p = 0.199$ ). Competition in the control plots was observed around 35%, in low-concentration fungal treatment plots around 25%, and in high-concentration fungal treatment plots around 21% of planted central Norway spruces. The respective values in Scots pine sites were ca. 39, 28 and 23%. The probability of occurrence of competition around Norway spruces did not differ from that around Scots pines ( $p = 0.800$ ). The number of self-regenerated conifers within a sample plot had no effect on the probability of occurrence of competition ( $p = 0.804$ ).

The lower competition around planted conifers following high-concentration fungal treatment as compared to the control treatment could also have a positive effect on height and DBH increment in the planted central conifer trees. Following high-concentration fungal treatment, planted conifers were by 8–11% taller than in control plots, and the difference was statistically significant (LMM,  $p = 0.030$ , Table 4, Fig. 3). No statistically significant difference was found between control and the low-concentration fungal treatment ( $p = 0.477$ ). A similar trend was also observed for conifer's DBH growth: it was by 9–14% larger following high-concentration fungal treatment than in the control ( $p = 0.070$ ). No difference was found between the low-concentration fungal treatment and control ( $p = 0.720$ ). The number of self-regenerated conifers did not affect the height or DBH of the planted central conifers in sample plots ( $p = 0.938$  for both the height and DBH models). Scots pines were significantly shorter ( $p = 0.006$ ) and thinner than Norway spruces ( $p = 0.019$ ).

### 4. Discussion

The results of the present study revealed that biological sprout control utilizing high-concentration fungal preparates (dilution 1:100) reduces competition from deciduous saplings around cultivated conifers in young conifer plantations. The density of young deciduous trees cut in 2014 and

**Table 3**

The effects of control treatment (cutting only), low-concentration (dilution 1:400) and high-concentration fungal treatments (dilution 1:100), and the other covariates on the number and height of tallest stump sprouts of silver and downy birch, rowan and willow ( $n = 1011$ ). Statistically significant ( $p < 0.050$ ) coefficients  $\pm$  standard errors are in bold. See Fig. 1 for the predicted values based on the models.

Model	Intercept	Fungal treatment 1:400 <sup>a</sup>	Fungal treatment 1:100 <sup>a</sup>	Effect of Scots pine site <sup>b</sup>	Rowan <sup>c</sup>	Willow <sup>c</sup>	Stump diameter (mm)	Density in a sample plot <sup>d</sup>
Number	<b>0.754 <math>\pm</math> 0.135</b>	$-0.076 \pm 0.054$	<b><math>-0.173 \pm 0.054</math></b>	$0.138 \pm 0.185$	<b>0.608 <math>\pm</math> 0.062</b>	<b>0.595 <math>\pm</math> 0.072</b>	<b>0.014 <math>\pm</math> 0.003</b>	<b><math>-0.029 \pm 0.007</math></b>
Maximum height	<b>4.807 <math>\pm</math> 0.080</b>	$-0.036 \pm 0.036$	$-0.001 \pm 0.036$	$-0.119 \pm 0.088$	<b><math>-0.584 \pm</math> 0.033</b>	<b><math>-0.367 \pm</math> 0.035</b>	<b>0.017 <math>\pm</math> 0.001</b>	$0.004 \pm 0.005$

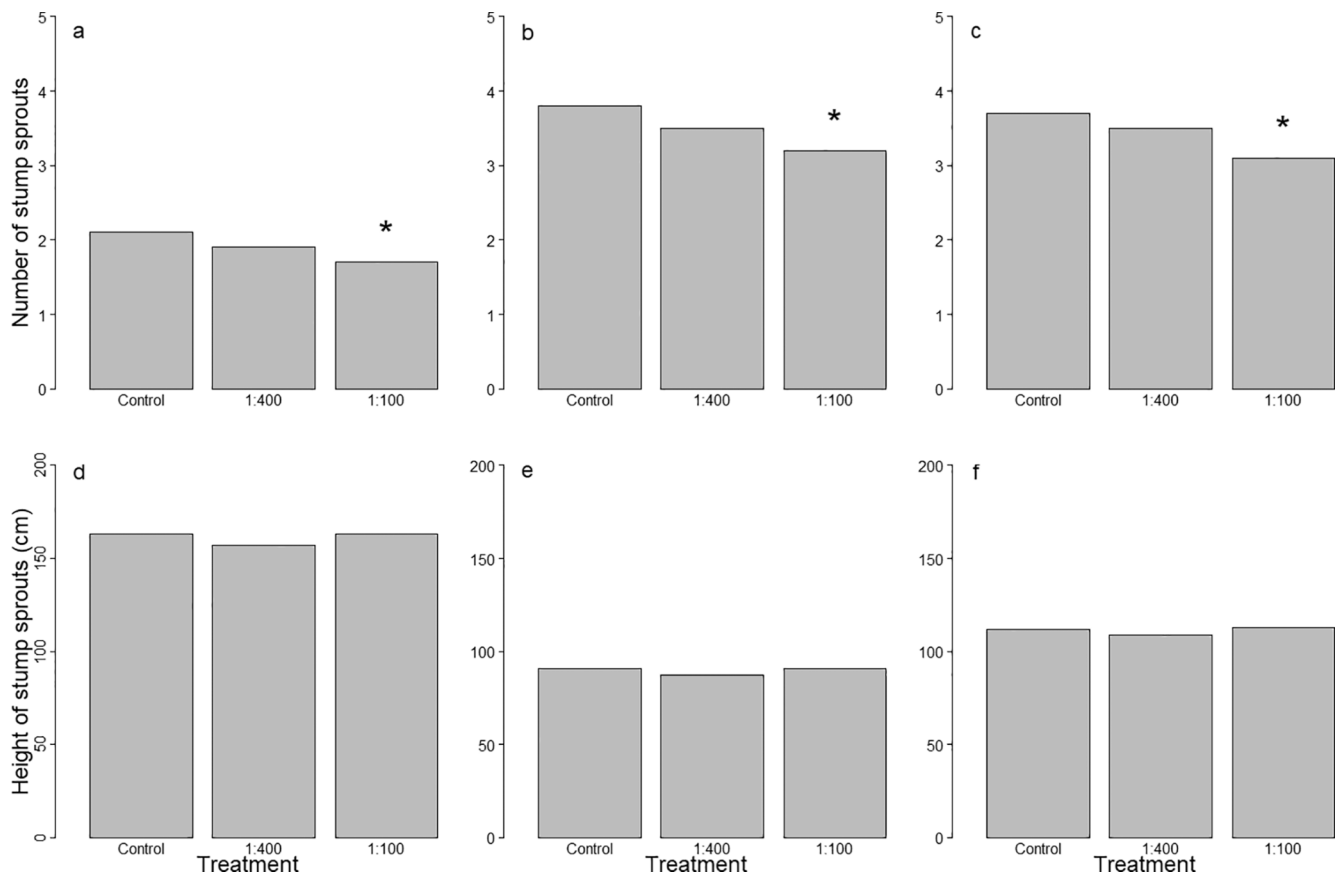
<sup>a</sup> Difference between the control and low-concentration fungal treatment (dilution 1:400), and between the control and high-concentration fungal treatment (dilution 1:100).

<sup>b</sup> Difference between Norway spruce and Scots pine sites.

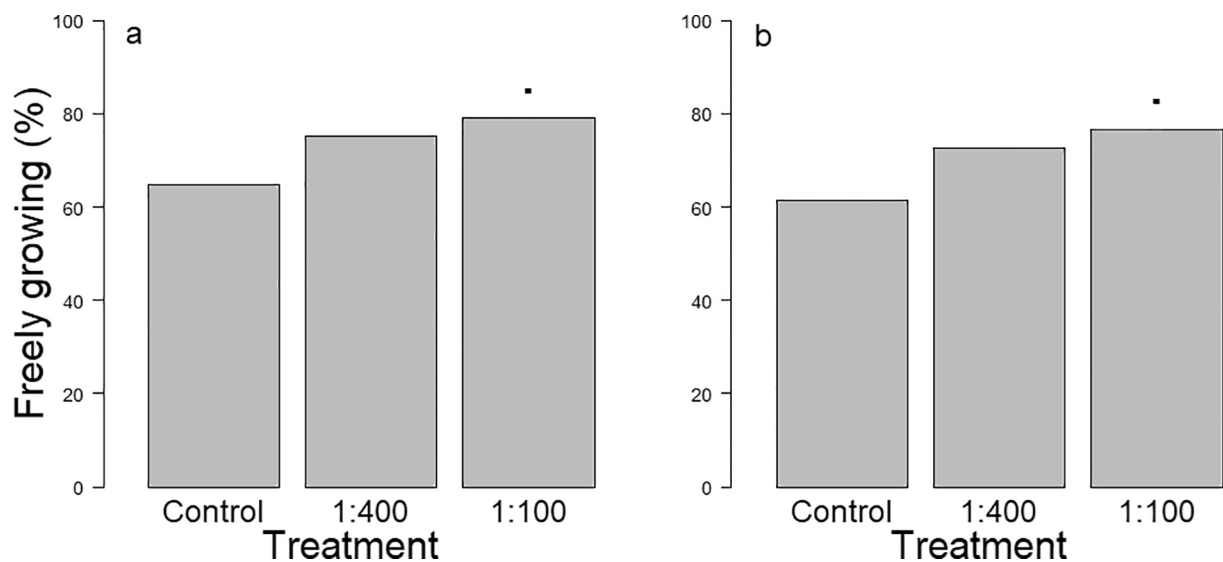
<sup>c</sup> Difference between birches and rowans, and between birches and willows.

<sup>d</sup> Effect of the tree density in a sample plot.





**Fig. 1.** The effects of control treatment (cutting only), low-concentration (dilution 1:400) and high-concentration (dilution 1:100) fungal treatments on the number of stump sprouts and height of the tallest stump sprouts per stump of two birch species (*Betula pendula* and *B. pubescens*) combined (a and d), rowan (*Sorbus aucuparia*) (b and e), and willow, (*Salix* sp.) (c and f). Statistically significant differences ( $p < 0.050$ ) between the control and the other treatments are indicated with an asterisk. The number of investigated young deciduous trees cut in 2014 was 1011. Presented are the predicted values in Norway spruce sample plots with the mean stump diameter and the mean density per sample plot. See the model results in Table 3.



**Fig. 2.** The proportion of freely growing (no competition around) planted central (a) Norway spruces ( $n = 138$ ) and (b) Scots pines ( $n = 70$ ) five years after the control (cutting only), low-concentration (dilution 1:400) and high-concentration (dilution 1:100) treatments with *Chondrostereum purpureum* preparates. Statistically indicative differences ( $0.050 \leq p < 0.100$ ) between the control and the fungal treatments are indicated with a square dot on top of bars. The total number of investigated conifers was 208. Presented are the predicted values with the mean number of self-regenerated conifers per sample plot.

the number of stump sprouts per stump were considerably lower following this treatment compared to cutting only. Consequently, due to reduced competition conifers grew better in high-concentration fungal treatment plots than in control plots (conifers were significantly taller, and their diameters were considerably and significantly larger than that in the control plots five years after the treatments). However, low-concentration fungal treatment did not show good sprout control efficacy and cannot be considered to provide any improvement when compared to cutting only. Yet, high-concentration fungal treatment seems a promising option to achieve better cost-efficiency in sprout control by preventing sprouting of deciduous trees and improving the growth of conifers. Also, consumption of basal fungal solution is ten times lower than in the dilution 1:10 which has also successfully been utilized in previous investigations (Hamberg and Hantula, 2018; Laine et al., 2020b; Hamberg et al., 2021b).

In young Norway spruce stands, young deciduous trees are usually cut at least once and sometimes the clearing operations are carried out several times (Uotila and Saksa, 2014; Uotila 2017). The potential benefit from the fungal treatment is clear if the need to re-visit a young forest stand more than once could be avoided, and consequently costs needed for sprout control can be reduced. Based on our field observations and the proportion of conifers not undergoing any competition in the high-concentration fungal treatment plots (80%), it seems that there is no need for another young stand management operation. In this treatment, the proportion of young deciduous trees cut in 2014 was lower than in the control sites since stumps treated with *C. purpureum* prepate were killed by the fungus. On the other hand, the observed large proportion of planted conifers without competition can be considered to be high enough to ensure formation of conifer (Scots pine or Norway spruce) stands with a sufficient target density (900–1400 stems ha<sup>-1</sup>; Äijälä et al., 2019) after the first thinning. This is promising although only about 34% of the deciduous stumps in high-concentration fungal treatment were dead three years after treatment (Laine et al. 2020a).

We showed for the first time that fungal treatment can reduce competition around young planted coniferous trees and enable their better growth. In young forests, reduced competition increases the height development of conifers but still the effects on stem diameter are more pronounced and reported more often than those on conifer height (Jobidon, 2000; Uotila and Saksa, 2014; Huuskonen et al., 2020). Diameter growth is affected earlier than height growth but if tree growth is inspected for a longer time, similar responses in terms of height and diameter increment are found (Jobidon, 2000; Krasowski and Wang, 2003; Varmola and Salminen, 2004; Zenner, 2008; Hoepting et al., 2011; Uotila and Saksa, 2014; Gauthier and Tremblay, 2018). When competing vegetation is removed, conifer saplings get more space and they start to allocate resources to root growth or to radial growth of a stem, and therefore height growth may be delayed for few years (Zenner, 2008). Increased growing space improves availability of water, nutrients and solar radiation, and conifer saplings start growing more rapidly and therefore suppress the growth of stump sprouts and seedlings of the unwanted deciduous species (Uotila and Saksa, 2014).

Compared to rowan and willow, the number of stump sprouts was lower in birch, although in birch these were taller. Rowan is one of the most preferred species by moose (Andrén and Angelstam, 1993; Motta, 2003), which explains their lower height and higher number of branches compared to birch. In careful manual treatments, *C. purpureum* can prevent sprouting of birch very efficiently: our earlier studies have shown that up to 80–100% of birch stumps may die in a couple of years following fungal treatment (Hamberg et al., 2015; Hamberg and Hantula, 2018). Effects of treatment with *C. purpureum* prepatates on rowan are less pronounced: stump mortality rates rarely exceeded 40–50% (Hamberg et al., 2014; Hamberg, 2021). Some effect of *C. purpureum* treatment has also been observed on sprouting of willow stumps. After the treatment, this fungus has been frequently found on willow stumps (Hamberg et al., 2017), and stump mortality has also been higher among the treated stumps (57%) than in the control (cutting only, 23%, Lygis et al., 2012). In

**Table 4**

Height and diameter at breast height (DBH) of planted central Norway spruces and Scots pines five years after the control (cutting only), low-concentration (dilution 1:400) and high-concentration (dilution 1:100) treatments with *Chondrostereum purpureum* prepatates. Presented are the predicted values (and standard errors) with the mean number of other conifers per sample plot. See Fig. 3.

Variable	Control <sup>a</sup>	Fungal 1:400 <sup>b</sup>	Fungal 1:100 <sup>c</sup>
Height (cm)			
Norway spruce	373 ± 37	383 ± 37	401 ± 37
Scots pine	264 ± 42	274 ± 42	292 ± 41
DBH (cm)			
Norway spruce	4.4 ± 0.6	4.5 ± 0.6	4.8 ± 0.6
Scots pine	2.9 ± 0.6	3.0 ± 0.6	3.3 ± 0.6

<sup>a</sup> Control treatment (cutting only).

<sup>b</sup> *Chondrostereum purpureum* mycelial solution (basal solution diluted with tap water 1:400) was applied on freshly cut stumps.

<sup>c</sup> *Chondrostereum purpureum* mycelial solution (basal solution diluted with tap water 1:100) was applied on freshly cut stumps.

studies where fully mechanized stump treatment devices have been used, the mortality of willow stumps was lower (ca. 17–23% following fungal treatment and 6% in the control, Laine et al., 2019).

In general, Scots pine sites are nutritionally poorer and drier than Norway spruce sites (Cajander, 1926). Consequently, the number of young deciduous trees cut in 2014, and the height of stump sprouts were lower in Scots pine sites compared to that in Norway spruce sites. Wild game browsing of planted conifers was observed more frequently in Scots pine than Norway spruce sites (see also Andrén and Angelstam, 1993; Motta, 2003), and this may also have affected the height development of stump sprouts of deciduous trees.

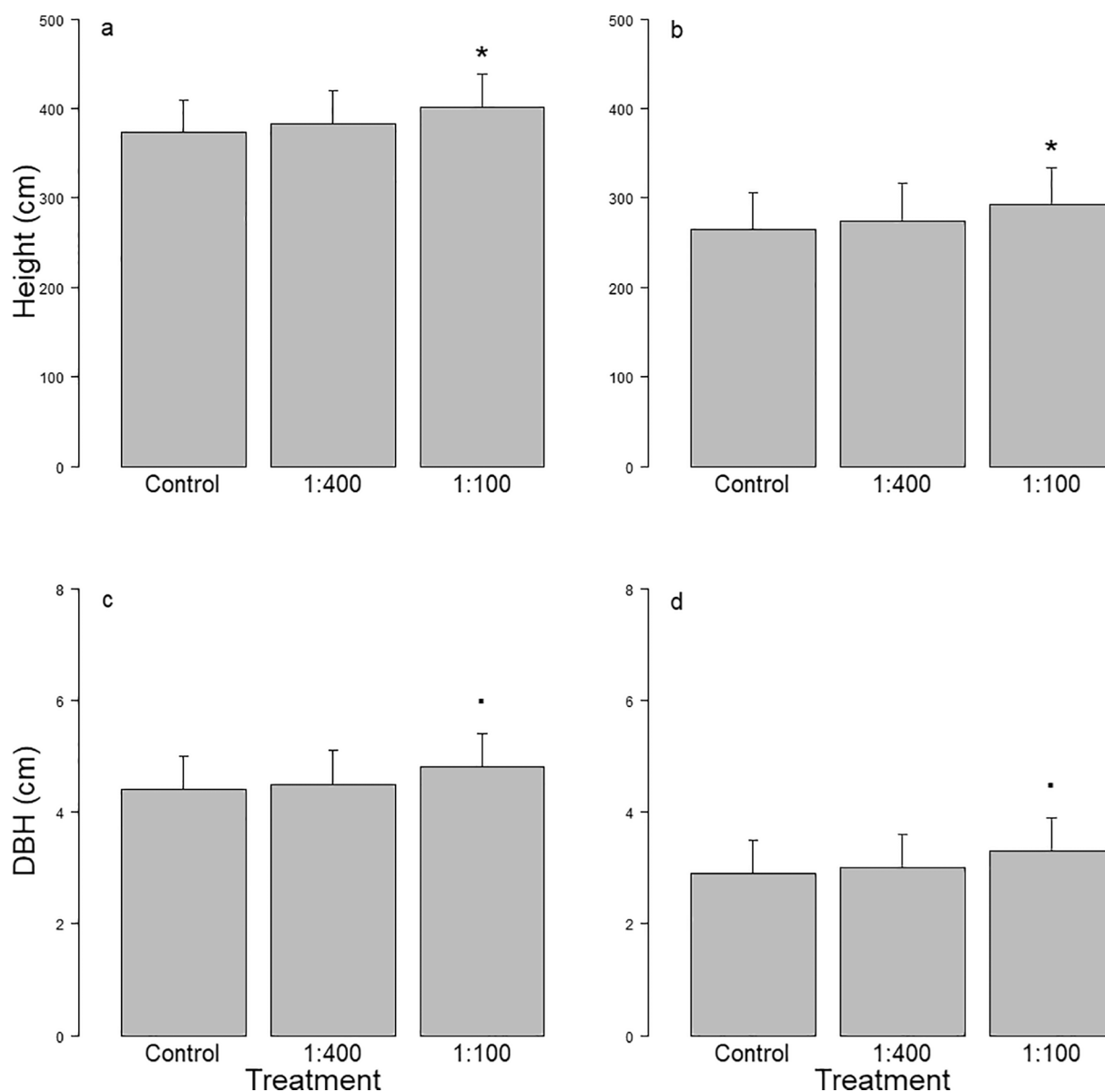
Increase in the stump diameter produced higher number of sprouts and these were generally taller which corresponds to the results of numerous earlier studies (e.g., Uotila and Saksa, 2014; Hamberg et al., 2015, 2020). Also, an increased number (density) of other saplings in sample plots has resulted in lower number of sprouts on treated deciduous tree stumps (see also Hamberg et al., 2015, 2020; Hamberg and Hantula, 2018), yet no effect of the sapling density was found on sprout height.

## 5. Conclusions

We conclude that treatment of deciduous tree stumps with a decay fungus *C. purpureum* provides more growing space for cultivated target tree species (conifers) than cutting only by reducing the number of viable stump sprouts. The high-concentration fungal treatment (dilution 1:100) resulted in better growth of the cultivated conifers as they were taller and larger in diameter at breast height than those in the control plots. Since the proportion of conifers not affected by competition was high enough (80%) following the high-concentration fungal treatment, there is not necessarily need for another young stand management operation before the first thinning. Thus, the results of the present study indicate that high-concentration fungal treatment improves cost-efficiency and could thus be a promising method in young stand management in the future. However, long-lasting studies extending to the first precommercial thinning would be needed to confirm this conclusion.

## CRedit authorship contribution statement

**Leena Hamberg:** Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - review & editing, Writing - original draft. **Tiina Laine:** Conceptualization, Investigation, Methodology, Validation, Writing - review & editing. **Jarkko Hantula:** Writing - review & editing. **Timo Saksa:** Conceptualization, Funding acquisition, Methodology, Project administration,



**Fig. 3.** Height and diameter at breast height (DBH) of planted central Norway spruces (a and c) and Scots pines (b and d) five years after the control (cutting only), low-concentration (dilution 1:400) and high-concentration (dilution 1:100) treatments with *Chondrostereum purpureum* preps. Statistically significant differences between control and different fungal treatments are indicated with an asterisk ( $p < 0.050$ ) and indicative differences ( $0.050 \leq p < 0.100$ ) with a square dot. Presented are the predicted values (and standard errors) with the mean number of other conifers per sample plot. See Table 4 for values used in the figure.

Resources, Supervision, Validation, Writing - review & editing.

for publication.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### References

- Äijälä, O., Koistinen, A., Sved, J., Vanhatalo, K., Väisänen, P. (Eds.), 2019. Metsänhoidon suositukset. Tapion julkaisu. ISBN 978-952-5632-75-0. (In Finnish).
- Andrén, H., Angelstam, P., 1993. Moose browsing on Scots pine in relation to stand size and distance to forest edge. J. Appl. Ecol. 30, 133–142. <https://doi.org/10.2307/2404277>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Becker, E.M., Ball, L.A., Hintz, W.E., 1999. PCR-based genetic markers for detection and infection frequency analysis of the biocontrol fungus *Chondrostereum purpureum* on Sitka alder and trembling aspen. Biol. Control 15, 71–80. <https://doi.org/10.1006/bcon.1999.0693>.
- Bellgard, S.E., Johnson, V.W., Than, D.J., Anand, N., Winks, C.J., Ezeta, G., Dodd, S.L., 2014. Use of the silverleaf fungus *Chondrostereum purpureum* for biological control of stump sprouting, riparian weedy tree species in New Zealand. Aust. Plant. Pathol. 43, 321–326. <https://doi.org/10.1007/s13313-014-0273-z>.
- Cajander, A.K., 1926. The theory of forest types. Acta For. Fenn. 29 (3), 1–108.



- de Jong, M.D., 2000. The BioChon story: deployment of *Chondrostereum purpureum* to suppress stump sprouting in hardwoods. *Mycologist* 14, 58–62. [https://doi.org/10.1016/S0269-915X\(00\)80005-1](https://doi.org/10.1016/S0269-915X(00)80005-1).
- Dumas, M.T., Wood, J.E., Mitchell, E.G., Boyonoski, N.W., 1997. Control of stump sprouting of *Populus tremuloides* and *P. grandidentata* by inoculation with *Chondrostereum purpureum*. *Biol. Control* 10, 37–41. <https://doi.org/10.1006/bcon.1997.0507>.
- Fahlvik, N., Agestam, E., Eko, P.M., Linden, M., 2011. Development of single-storied mixtures of Norway spruce and birch in Southern Sweden. *Scand. J. For. Res.* 26, 36–45. <https://doi.org/10.1080/02827581.2011.564388>.
- Gauthier, M.-M., Tremblay, S., 2018. Precommercial thinning as a silvicultural option for treating very dense conifer stands. *Scand. J. For. Res.* 33 (5), 446–454. <https://doi.org/10.1080/02827581.2017.1418422>.
- González, J.M., 1996. A general purpose program for obtaining most probable number tables. *J. Microbiol. Methods* 26, 215–218. [https://doi.org/10.1016/0167-7012\(96\)00818-4](https://doi.org/10.1016/0167-7012(96)00818-4).
- Gosselin, L., Jobidon, R., Bernier, L., 1999. Biological control of stump sprouting of broadleaf species in rights-of-way with *Chondrostereum purpureum*: Incidence of the disease on nontarget hosts. *Biol. Control* 16, 60–67. <https://doi.org/10.1006/bcon.1999.0736>.
- Hamberg, L., 2021. The effect of a biocontrol fungus *Chondrostereum purpureum* on sprouting of rowan (*Sorbus aucuparia*) at different application times. *Biol. Control* 154, 104520. <https://doi.org/10.1016/j.biocontrol.2020.104520>.
- Hamberg, L., Hantula, J., 2016. The efficacy of six elite isolates of the fungus *Chondrostereum purpureum* against the sprouting of European aspen. *J. Environ. Manage.* 171, 217–224. <https://doi.org/10.1016/j.jenvman.2016.02.016>.
- Hamberg, L., Hantula, J., 2018. Tree size as a determinant of recovery of birch (*Betula pendula* and *B. pubescens*) and grey alder (*Alnus incana*) trees after cutting and inoculation with *Chondrostereum purpureum*. *Biol. Control* 126, 83–89. <https://doi.org/10.1016/j.biocontrol.2018.07.015>.
- Hamberg, L., Hantula, J., 2020. The biocontrol efficacy of *Chondrostereum purpureum* is not sensitive to prevailing environmental conditions in boreal forests. *For. Ecol. Manage.* 456, 117646. <https://doi.org/10.1016/j.foreco.2019.117646>.
- Hamberg, L., Vartiamaäki, H., Hantula, J., 2015. Breeding increases the efficacy of *Chondrostereum purpureum* in the sprout control of birch. *PLoS ONE* 10 (2), e0117381. <https://doi.org/10.1371/journal.pone.0117381>.
- Hamberg, L., Lemola, J., Hantula, J., 2017. The potential of the decay fungus *Chondrostereum purpureum* in the biocontrol of broadleaved tree species. *Fungal Ecol.* 30, 67–75. <https://doi.org/10.1016/j.funeco.2017.09.001>.
- Hamberg, L., Malmivaara-Lämsä, M., Löfström, I., Hantula, J., 2014. Effects of a biocontrol agent *Chondrostereum purpureum* on sprouting of *Sorbus aucuparia* and *Populus tremula* after four growing seasons. *Biocontrol* 59, 125–137. <https://doi.org/10.1007/s10526-013-9550-y>.
- Hamberg, L., Saarinen, V.-M., Rantala, M., Hantula, J., Seiskari, P., Saksa, T., 2020. Rainstorm effects on the biocontrol efficacy of the decay fungus *Chondrostereum purpureum* against birch sprouting in boreal forests. *Appl. Microbiol. Biot.* 104, 5107–5117. <https://doi.org/10.1007/s00253-020-10574-3>.
- Hamberg, L., Saksa, T., Hantula, J., 2021a. Role and function of *Chondrostereum purpureum* in biocontrol of trees. A mini-review. *Appl. Microbiol. Biot.* 105, 431–440. <https://doi.org/10.1007/s00253-020-11053-5>.
- Hamberg, L., Strandström, M., Saksa, T., 2021b. Cutlink cleaning head with a spreading feature for biological sprout control. *Croat. J. For. Eng.* (in press).
- Harper, G.J., Comeau, P.G., Hintz, R.E., Wall, R.E., Prasad, R., Becker, E.M., 1999. *Chondrostereum purpureum* as a biological control agent in forest vegetation management. II. Efficacy on Sitka alder and aspen in western Canada. *Can. J. For. Res.* 29, 852–858. <https://doi.org/10.1139/x99-121>.
- Hoepfing, M.K., Wagner, R.G., McLaughlin, J., Pitt, D.G., 2011. Timing and duration of herbaceous vegetation control in northern conifer plantations: 15th-year tree growth and soil nutrient effects. *Forest. Chron.* 87 (3), 398–413. <https://doi.org/10.5558/frc2011-030>.
- Huuskonen, S., Hynynen, J., 2006. Timing and intensity of precommercial thinning and their effects on the first commercial thinning in Scots pine stands. *Silva Fenn.* 40 (4), 645–662.
- Huuskonen, S., Haikarainen, S., Sauvola-Seppälä, T., Salminen, H., Lehtonen, M., Siipilehto, J., Ahtikoski, A., Korhonen, K.T., Hynynen, J., 2020. Benefits of juvenile stand management in Finland – impacts on wood production based on scenario analysis. *Forestry* 93, 458–470. <https://doi.org/10.1093/forestry/cp2075>.
- Jobidon, R., 1998. Comparative efficacy of biological and chemical control of the vegetative reproduction in *Betula papyrifera* and *Prunus pensylvanica*. *Biol. Control* 11, 22–28. <https://doi.org/10.1006/bcon.1997.0573>.
- Jobidon, R., 2000. Density-dependent effects of northern hardwood competition on selected environmental resources and young white spruce (*Picea glauca*) plantation growth, mineral nutrition, and stand structural development – a 5-year study. *For. Ecol. Manage.* 130, 77–97. [https://doi.org/10.1016/S0378-1127\(99\)00176-0](https://doi.org/10.1016/S0378-1127(99)00176-0).
- Krasowski, M.J., Wang, J.R., 2003. Aboveground growth responses of understory *Abies lasiocarpa* saplings to different release cuts. *Can. J. For. Res.* 33, 1593–1601. <https://doi.org/10.1139/x03-074>.
- Laine, T., Hamberg, L., Saarinen, V.-M., Saksa, T., 2019. The efficacy of *Chondrostereum purpureum* against sprouting of deciduous species after mechanized pre-commercial thinning. *Silva Fenn.* 53 (3), 10195. <https://doi.org/10.14214/sf.10195>.
- Laine, T., Hamberg, L., Saarinen, V.-M., Saksa, T., 2020a. The efficacy of *Chondrostereum purpureum* in the sprout control of birch during mechanized pre-commercial thinning. *Biocontrol* 65 (1), 13–24. <https://doi.org/10.1007/s10526-019-09971-z>.
- Laine, T., Saarinen, V.-M., Hantula, J., Saksa, T., Hamberg, L., 2020b. Efficacy of different clearing saw methods in biological sprout control in birch (*Betula pendula* [Roth] and *B. pubescens* [Ehrh.]) compared to manual and mechanized application. *For. Ecol. Manage.* 475, 118429. <https://doi.org/10.1016/j.foreco.2020.118429>.
- Lygis, V., Bakys, R., Burokienė, D., Vasiliauskaitė, I., 2012. *Chondrostereum purpureum* based control of stump sprouting of seven hardwood species in Lithuania. *Baltic For.* 18, 41–55.
- Mazerolle, M.J., 2020. AICcmadv: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. <https://cran.r-project.org/package=AICcmadv>.
- Motta, R., 2003. Ungulate impact on rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* (L.) Karst.) height structure in mountain forests in the eastern Italian Alps. *For. Ecol. Manage.* 181, 139–150. [https://doi.org/10.1016/S0378-1127\(03\)00128-2](https://doi.org/10.1016/S0378-1127(03)00128-2).
- Natural Resources Institute Finland, 2020. Silvicultural and forest improvement work 2019. [https://stat.luke.fi/en/silvicultural-and-forest-improvement-work-2019\\_en](https://stat.luke.fi/en/silvicultural-and-forest-improvement-work-2019_en). Statistics. Cited 21 January 2021.
- PEFC, 2014. PEFC-metsäsertifiointin kriteerit, PEFC FI 1002:2014. <http://pefc.fi/wp-content/uploads/2016/09/>. 41 p. (in Finnish) Cited 21 January 2021.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2020. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-150, URL: <https://CRAN.R-project.org/package=nlme>.
- Roy, V., Dubeau, D., Auger, I., 2010. Biological control of intolerant hardwood competition: Silvicultural efficacy of *Chondrostereum purpureum* and worker productivity in conifer plantations. *For. Ecol. Manage.* 259, 1571–1579. <https://doi.org/10.1016/j.foreco.2010.01.033>.
- Saksa, T., Miina, J., 2007. Cleaning methods in planted Scots pine stands in southern Finland: 4-year results on survival, growth and whipping damage of pines. *Silva Fenn.* 41 (4), 661–670.
- Thiffault, N., Roy, V., 2011. Living without herbicides in Québec (Canada): historical context, current strategy, research and challenges in forest vegetation management. *Eur. J. For. Res.* 130, 117–133. <https://doi.org/10.1007/s10342-010-0373-4>.
- Uotila, K., 2017. Optimization of early cleaning and precommercial thinning methods in juvenile stand management of Norway spruce stands. *Dissertationes Forestales* 231: 42 p. University of Helsinki. <https://dissertationesforestales.fi/pdf/article2014.pdf>.
- Uotila, K., Saksa, T., 2014. Effects of early cleaning on young *Picea abies* stands. *Scand. J. For. Res.* 29 (2), 111–119. <https://doi.org/10.1080/02827581.2013.869349>.
- Uotila, K., Rantala, J., Harstela, P., Saksa, T., 2010. Effect of soil preparation method on economic result of Norway spruce regeneration chain. *Silva Fenn.* 44, 511–524.
- Uotila, K., Rantala, J., Saksa, T., 2012. Estimating the need for early cleaning in Norway spruce plantations in Finland. *Silva Fenn.* 46, 683–693.
- Varmola, M., Salminen, H., 2004. Timing and intensity of precommercial thinning in *Pinus sylvestris* stands. *Scand. J. For. Res.* 19, 142–151. <https://doi.org/10.1080/02827580310019545>.
- Vartiamaäki, H., Hantula, J., Uotila, A., 2009. Effect of application time on the efficacy of *Chondrostereum purpureum* treatment against the sprouting of birch in Finland. *Can. J. For. Res.* 39, 731–739. <https://doi.org/10.1139/X09-009>.
- Wall, R.E., 1990. The fungus *Chondrostereum purpureum* as a silvicide to control stump sprouting in hardwoods. *North. J. Appl. For.* 7 (1), 17–19. <https://doi.org/10.1093/njaf/7.1.17>.
- Zenner, E.K., 2008. Short-term changes in *Pinus strobus* sapling height/diameter ratios following partial release: testing the acclimative stem-form development hypothesis. *Can. J. For. Res.* 38, 181–189. <https://doi.org/10.1139/X07-153>.