Tree removal as a management strategy for the lady’s slipper orchid, a flagship species for herb-rich forest conservation

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Abstract: In boreal herb-rich forests, the dominance of Norway spruce (*Picea abies*) decreases light availability for understory species, many of which depend on canopy gaps for reproduction. Here, we explored the response of a rare clonal understory herb, the lady’s slipper orchid (*Cypripedium calceolus*), to tree removal. We used demographic data spanning 16 years from ten unharvested control sites and ten harvest sites which were divided into three treatments with differing harvest intensity: (1) dense spruce forests, where half of the total tree basal area (TBA) was cut, (2) sparse spruce forests, where one-fourth of the spruce TBA was cut and (3) sparse broadleaf forests, where one-fourth of the total TBA was cut. The effects of harvesting on different demographic rates (ramet density, reproduction, survival, and dormancy) were studied with generalized linear mixed models with harvest intensity, time since harvest and the starting level of the response variable as explanatory variables. Tree removal sites had 2.2 times higher orchid ramet density, 2.4 times higher odds of survival, and 2.1 – 3.1 times higher odds of flowering and fruiting than the control sites, but these effects were not seen at all treatment levels at all times. Tree removal had no effect on dormancy or seedling or flower density. Orchid flowering and fruiting probabilities increased only at the most intensively harvested sites (both spruce forest sites, and dense spruce forest with 50% TBA removal, respectively), while survival and ramet density increased at the moderately harvested broadleaf forest sites. The effects on flowering and fruiting probabilities and survival disappeared quickly (after three years) when the canopy gaps closed, whereas ramet density responded only with a lag of over three years and was maintained to the end of the study. Our results thus demonstrate that for the lady’s slipper orchid, selective tree harvest might be a suitable management method that increases population size at the ramet level.

Keywords: dormancy, flowering, forest gap, forest overgrowth, reproduction, survival
1. Introduction

The composition of understory vegetation in boreal forests depends on environmental conditions, such as climate, fire, acidification, forest type, and canopy closure (Hart & Chen, 2008; Rydgren, 1996; Økland & Eilertsen, 1996). Understory light conditions and associated changes in e.g. temperature and moisture, are considered to be the major limiting components of forest understory cover and species richness in temperate and boreal forests (Barbier, Gosselin, & Balandier, 2008). In addition to light, canopy closure affects many abiotic and biotic factors of the forest understory, which in turn can modify, both directly and indirectly, the growth, survival, and reproduction of understory plants (Fig. 1). Numerous studies have investigated the effect of woody encroachment on grassland ecosystems (e.g. Alford, Hellgren, Limb, & Engle, 2012; Briggs, Blair, & Mccarron, 2005) as well as tree gap dynamics and their importance for tree recruitment, particularly in tropical rainforests (Brokaw, 1987; Pascarella, 1998; Svenning, 2002). However, the species-specific responses of herbaceous plants to canopy cover in boreal regions have attracted less attention.

In forests, succession is characterized by a transition from an open state dominated by pioneer species to a closed forest with high tree basal area (Clebsch & Busing, 1989; Saldarriaga, West, Tharp, & Uhl, 1988). However, this process may be disrupted by disturbances that change the amount of available resources and affect recruitment. Natural disturbances, such as windthrows or forest fires, are important factors that increase forest biodiversity (Angelstam, 1998; Ulanova, 2000). These disturbances typically increase the amount of light available in the understory, which in turn has been observed to increase the reproduction and growth of understory herbs (Brumback, Cairns, Sperduto, & Fyler, 2011; Gill, 1996; Kirchner, Kammermeier, & Bruelheide, 2009; Valverde & Silvertown, 1998).

This increased reproduction and growth may be due to improved nutrient availability. As the canopy cover decreases, soil temperature generally increases (Abd Latif & Blackburn, 2010; Norris,
Blair, & Johnson, 2001; Seastedt & Adams, 2001; Smith & Johnson, 2004), leading to changes in soil respiration (Smith & Johnson, 2004) and rates of decomposition of organic matter (Canham & Marks, 1985; Seastedt & Adams, 2001). Additionally, decomposition rates and, consequently, nutrient availability can change as a result of altered litter composition (Berg et al., 1993; Ovington, 1954). Coniferous forests tend to have slow decomposition rates (D. Zhang, Hui, Luo, & Zhou, 2008), with nitrogen and phosphorus availability decreasing in the late, closed, conifer-dominated successional stage (Bormann & Sidle, 1990). In such forests, canopy gaps provide not only increased light, but also a local reduction in acidic leaf litter, with the potential consequence of improved nutrient availability.

Canopy cover also affects the soil water balance. On one hand, soil moisture is expected to increase with decreasing canopy cover as plant transpiration decreases and more precipitation reaches the ground (Abd Latif & Blackburn, 2010; Alanen, Leivo, Lindgren, & Piri, 1995; Canham & Marks, 1985). On the other hand, though, decreasing canopy cover may increase evaporation as a result of elevated temperatures, thus reducing soil moisture levels. These effects are probably partially dependent on prevailing climatic conditions. In boreal forests that are typically cold and moist, canopy cover has been observed to be negatively correlated with soil moisture and species richness (Rydgren, 1996), while in arid grasslands the opposite is true and soil moisture is highest under tree canopies (D’Odorico, Caylor, Okin, & Scanlon, 2007; De Boever, Gabriels, Ouessar, & Cornelis, 2016).

The overall net effect of canopy gaps on understory plant performance often depends on gap size and age. For example, slow-growing understory herbs may suffer when canopy gaps are too large because of increased competition from vigorously growing grasses (Sjöberg & Ericson, 1992). Large gaps might also have unfavorable microclimates as wind speed and temperature variations increase (Abd Latif & Blackburn, 2010; Runkle, 1985), which may result in a greater risk of frost.
Figure 1. A flow-chart depicting the effects of canopy closure and abiotic factors (dashed line) on different demographic rates (solid lines) of forest understory herbs. Variables in bold circles are measured in the current study.
Langvall & Ottosson Löfvenius, 2002; Norris et al., 2001) and fruiting failure (Abeli, Jäkälnäkki, Wannas, Mutikainen, & Tuomi, 2013). In general, the effects of canopy gaps on light conditions and vegetation are most pronounced immediately after disturbances and then weaken over time (Beaudet & Messier, 2002), as the gaps close with the lateral growth of surrounding trees and height growth of saplings (Runkle, 1985).

The lady's slipper orchid (Cypripedium calceolus) is a rare understory herb which prefers half-shaded lime-rich habitats (Rankou & Bilz, 2014). It has intrinsically slow population dynamics, with the long-term population growth rate being close to 1 and very slow convergence to the equilibrium state (Nicolè, Brzosko, & Till-Bottraud, 2005). This suggests that the recent population declines reported in many European countries (Rankou & Bilz, 2014) are due to extrinsic factors. Indeed, previous studies have shown that the viability of lady’s slipper orchid populations decreases with increasing canopy closure in boreal and nemoral forests (Bjørndalen, 2015; Brzosko, 2002; but see García, Goñi, & Guzmán, 2010). As noted in extensive field observations of this species, flowering probability, seed set, and seedling establishment are limited under closed-canopy conditions in boreal forests in northern Finland (Laitinen, 2006). Moreover, in a shading experiment, Shefferson et al. (2012) observed that the flower production and survival of shaded plants were lower than those of unshaded plants. These authors also noticed that orchids were able to escape the negative effects of shading through vegetative dormancy (hereafter ‘dormancy’), a state in which a plant produces no above-ground shoots for one year or more, and only the below-ground rhizome survives (Shefferson et al., 2012). Dormancy is widely assumed to be a way to escape stress by avoiding unfavorable conditions (Davison, Nicole, Jacquemyn, & Tuljapurkar, 2013; Shefferson et al., 2012; Shefferson, Warren, & Pulliam, 2014). In addition, the rate of photosynthesis of understory species in shaded habitats has been observed to be low (Lett & Knapp, 2003; S.-B. Zhang, Hu, Xu, Li, & Yang, 2007), suggesting that the benefits of sprouting
would be small and the costs of dormancy would be low. Therefore, we can expect dormancy to be more common in shaded environments than in habitats with more light.

Because of its large, showy flowers, the lady’s slipper orchid is an ideal flagship species to attract public interest in conservation. Moreover, due to its stable population dynamics, occurrence on rare habitat types, and tendency to co-occur with several other rare orchids, herbs, and mosses, it has been suggested that the lady’s slipper orchid could be used as an umbrella species (Bjørndalen, 2015; Laitinen, 2006; Nicolè et al., 2005). In other words, the decline of the lady’s slipper orchid indicates the degradation of the habitat, and therefore, an improvement in conditions for this orchid might ensure the survival of other species that are dependent on similar habitats (Simberloff, 1998). For example, studies from Sweden and Norway indicate that management favoring half-open forests instead of dense vegetation is recommended to promote the viability of orchid populations (Antonelli, Dahlberg, Carlgren, & Appelqvist, 2009; Bjørndalen, 2015). In this study, we use long-term demographic data from northern Finland to examine whether selective tree harvest could be used as a management method for rare orchids in over-grown herb-rich forests. More specifically, we explored the effects of tree removal treatments of differing intensities on the ramet density, reproduction, survival, and dormancy of the lady’s slipper orchid. We hypothesized that the survival and reproduction of the lady’s slipper orchid individuals would be highest in the most intensive tree removal treatment, while the proportion of dormant plants would be lowest at the harvested sites. We further predicted that the effects of tree removal treatments would be the most pronounced immediately or shortly after the harvest, and would then slowly decrease over the 16 years of the study as the canopy gaps closed.

2. Methods

2.1 The species and study areas
The lady’s slipper orchid (*Cypripedium calceolus*) is a nectarless, clonal, long-lived herb with a horizontal rhizome. Ramets form clumps consisting of several clones, in which vegetative propagation dominates over sexual reproduction (Brzosko, 2002; Kull, 1999). Some clones and ramets can remain dormant for several years, although one year is more typical (Brzosko, 2002; Shefferson, Sandercock, Proper, & Beissinger, 2001). One stalk supports one to two, rarely three, yellow slipper-shaped flowers. The average number of minute seeds per capsule is about 6 000–20 000 (Brzosko, 2002; Kull, 1998; Laitinen, 2006). The seedlings live in symbiosis with fungi and spend their first three years as underground protocorms (Kull, 1999). This orchid is mainly boreal, and is widely distributed from Europe to Asia. It grows in moist, half-shaded, herb-rich forests and wooded peatlands with calcium-rich bedrock (Kull, 1999). The species has been declining in several countries, but many populations are now stable or increasing due to the implementation of successful conservation actions (Rankou & Bilz, 2014).

As part of the EU Life project in 2001 (details in Laitinen, 2006), all known populations of the lady’s slipper orchid in northern Finland were mapped. From these populations, ten sites were chosen for active forest management and ten sites as controls (Table A.1). Three managed and three control sites were located in Oulanka National Park in Kuusamo, northeastern Finland, and the rest of the sites were situated in the municipalities of Tervola and Ylitornio in southwestern Finnish Lapland (Fig. A.1). The habitats consisted of herb-rich forest and were mostly dominated by the Norway spruce (*Picea abies*). In Finland, spruce-dominated old-growth forest represents a natural part of the succession cycle of herb-rich forests. *P. abies* offers shelter and substrate for certain birds and decomposing fungi (Alanen et al., 1995), but also effectively shades the understory and produces acidic litter that decomposes slowly (Alanen et al., 1995; D. Zhang et al., 2008), and the subsequent resource limitation can be detrimental for herbaceous understory species.
2.2 Field methods and assessment of canopy cover

In the summer of 2001, a randomly located 1 × 10 m plot was established at each study site. At sites with under 100 ramets, an extra square (up to 8 m²) was included to obtain a sufficient sample size. The plot size thus varied from 10 m² to 18 m² (Table A.1). Each isolated ramet or ramet clump was marked using a steel stick with a numbered plastic label, with the number of observed living clumps per plot per year varying from 1 to 299 (mean = 92 clumps). We use a clump as a proxy for a clone, as the ramets grow so closely together that we could not reliably follow them individually, and the identification of actual genetic clones would have required genetic tests or excavation of the plants. Therefore, some clumps may have actually contained multiple overlapping clones and some genetic clones may have been dispersed across several clumps. However, as our analyses primarily focused on population-level variables, we are confident that this did not qualitatively affect our results.

In years 2001–2004, 2008–2010, and 2014–2016, we visited all sites once a year during the fruiting time in July and recorded the state of each ramet clump as dormant, vegetative, or flowering. The numbers of flowers and capsules were counted, and newly emerged clumps and seedlings were marked every year. Tree removal was conducted in the winter of 2001 (i.e. after the first summer survey). Three types of forest were represented in the management areas, and each differed in the intensity of selective tree harvest: (1) dense spruce forests, where half of the total tree basal area (TBA) was cut (mean of 48.9% (SD 8.4%)), (2) sparse spruce forests, where one-fourth of the spruce TBA was cut (mean reduction in TBA mean of 26.4% (SD 7.4%)), and (3) sparse broadleaf forests, where one-fourth of the total TBA was cut (mean reduction in TBA mean of 25.7% (SD 0.7%)) (Table A.1). Control sites, in which no trees were cut, included the same forest types as the treated sites. Note that due to different initial tree densities, differences in the proportions of removed trees are not directly translatable to differences in the reduction in total amount of wood between habitat types; for example, the total amount of wood removed was smallest in the sparse broadleaf forests because these sites had the lowest initial tree density. The size of the managed...
areas varied from 600 m$^2$ to 1700 m$^2$, with the demography plot in the middle. Tree removal was conducted without heavy machinery and all logs and branches were removed from the sites. A thick snow cover protected the plants and ground from mechanical disturbance during cutting.

To assess how tree removal affected the light regime, we took photographs during the pre-harvest period and then again in the middle and late post-harvest periods. A camera with a standard zoom lens was oriented straight up toward the sky at 1-m intervals along each plot (10 in total per plot) and from each extra square. The camera was placed at the height of the top of the herbaceous vegetation layer in order to capture the level of canopy openness for trees and shrubs, but not for herbs. Photographs were edited in Adobe Photoshop by filling the open sky with white and canopy with black. We then calculated the canopy cover as the percentage of black in the photographs. The canopy cover percentages calculated from the photographs revealed that the average canopy cover had increased in nearly all sites by the middle post-harvest period, indicating ongoing canopy closure at the control sites and the rapid closure of canopy gaps at the harvest sites (Fig. B.1). The only treatment that resulted in a longer-lasting canopy gap in terms of increased light availability was the most intensive treatment (spruce forest 50% removal). However, none of the statistically tested changes in canopy cover (i.e. differences between treatments or time periods during the pre-harvest and middle and late post-harvest periods) were significant (Fig. B.1, Table B.1).

Unfortunately, no comparable photographs were available from the immediate post-harvest period, but according to Laitinen (2006), the tree removal treatments substantially increased light availability during this period, especially the most intensive treatment (spruce forest 50% removal).

### 2.3 Statistical analyses

Clonal growth and sexual reproduction of the lady’s slipper orchid were assessed using the following five variables: the densities of ramets (excluding seedlings), flowers, and seedlings (per
m²), flowering probability (the proportion of flowering ramets out of mature ramets), and fruiting probability (the proportion of flowers that produced capsules). Moreover, we measured clone-level dormancy as the proportion of dormant clumps out of all clumps known to be alive in a given year. Clone-level survival was measured as the number of clumps that survived to the next year divided by the number of clumps with known fates in the next year. Clumps were assumed dead if they had not been seen aboveground for three or more consecutive visits. Dead plants were further assumed to have died instantly after the last observation. Therefore, final time period (2014 – 2016) had to be excluded from survival analyses due to its spurious perfect survival (i.e. no deaths could be observed). Similarly, we excluded the last year of the study period (2016) from the dormancy analyses because dormancy was inherently defined by observations in subsequent years. Some of the plastic labels were lost during the study, and the fate of these clumps after the last observation of the label is unknown. For these clumps, only the years before the disappearance of the label were used in the analyses. In order to estimate dormancy and survival, knowledge of individual demographic history was needed. Therefore, clumps clearly consisting of more than one clone (e.g., seedlings and mature plants in the same clump) were either removed from the dataset (91 clumps out of 2304 clumps) or, when possible, were divided into two or more clumps (270 clumps out of 2304 clumps) for analytical purposes.

We tested differences in demographic rates between managed and control sites using generalized linear mixed models. All models included the starting level (the value of a given response variable in 2001 before treatment), time period (four levels), and treatment (four levels) as fixed explanatory variables. The four levels for time period were: pre-harvest period before logging (summer 2001), immediate post-harvest period (2002 – 2004), middle post-harvest period (2008 – 2010), and late post-harvest period (2014 – 2016). The starting level was used as a covariate to account for initial differences in the response variables among sites. Moreover, the models included geographic region (Kuusamo or SW Lapland) and all possible two-way interactions with time as fixed explanatory
variables when these terms were determined to be significant by likelihood-ratio tests. Note that it
was not possible to examine other interactions among main factors due to the unbalanced study
design. Study site (nested within region) and year were included as random factors in order to take
into account the fact that repeated measurements were conducted from the same sites, and that each
time period contained three years. Density responses were modeled using a negative binomial
distribution with log link, based on the counts and with plot area as an offset, and proportional
responses were modeled with a binomial distribution and logit link (function glmmadmb from
package glmmADMB, Fournier et al., 2012). Negative binomial distribution was used instead of
Poisson distribution because of its better fit with our overdispersed density data. We assessed model
fit based on residual plots (Figure C.1), and evaluated the statistical significance of the fixed factors
by comparing the full model to a model without a given factor using likelihood-ratio tests. As the
models of dormancy and survival both used different reduced data sets, the original p-values from
the likelihood-ratio tests were Bonferroni-corrected only for the models of growth and reproduction.
If the treatment term was significant according to the likelihood-ratio tests, each treatment was
compared to the control treatment using Dunnet-style contrasts with the exact Dunnett adjustment
of the p-values (package lsmeans, Lenth 2016). If the treatment × time interaction was significant,
contrasts were calculated separately for each time period. All statistical tests were performed using
the statistical program R (Team, 2015).

3. Results

Based on the likelihood-ratio tests, there were differences between the four tree removal intensities
in all the studied demographic rates, except seedling density (Table 1). However, contrasts
comparing the treated and control showed significant differences only for the ramet density, clump
survival, flowering probability, and fruiting probability of the lady’s slipper orchid (Table D.1,
Ramet density was higher in the broadleaf forest 25% removal treatment compared to the control treatment, but this difference was significant only during the middle and late post-harvest periods, with the ramet density being 2.2 times higher at the harvested sites than at the control sites (Fig. 2A, Table D.1). Additionally, the lady’s slipper orchid clumps had 2.4 times higher odds of surviving in the broadleaf forest 25% removal treatment in the immediate post-harvest period compared to control (Fig. 2B, Table D.1). Compared to the control sites, flowering probability was higher at both types of treated spruce forest sites (2.2 higher odds in dense spruce forest with 50% total TBA removal and 3.1 higher odds in sparse spruce forest with 25% spruce TBA removal; Fig. 2C, Table D.1), while the fruiting probability was higher only in the spruce forest 50% removal treatment sites (2.1 times higher odds of fruiting, Fig. 2D, Table D.1). However, these increases in the probabilities of flowering and fruiting were seen only during the immediate post-harvest period (up to 3 years after the harvest; Fig. 2). There were no regional differences in the overall means of most of the measured demographic variables (Table 1). A posteriori contrasts revealed statistically significant differences between regions for ramet density and survival only (Table D.1). Both these variables were higher in the Kuusamo region than in SW Lapland, with ramet density being 1.8 fold during the middle harvest period and 2.0 fold for the late post-harvest period, and with survival being 2.5 fold in the immediate post-harvest period (Table D.1).

4. Discussion

4.1 Effect of tree removal on the lady’s slipper orchid

Ramet density, survival, and probabilities of flowering and fruiting of the lady’s slipper orchid responded positively to the tree removal treatments, though not at all sites during all time periods. Our results are consistent with previous studies that have reported the positive effect of light on forest understory herbs (Brumback et al., 2011; Gill, 1996; Kirchner et al., 2009; Valverde &
Figure 2. a) Ramet density, b) survival, c) flowering probability, and d) fruiting probability of *Cypripedium calceolus* by treatment and time period. Bar heights represent the model prediction, and error bars denote standard errors. Asterisks indicate a significant difference between the treatment and the control of the same time period. Predictions are averaged over geographic regions and starting level covariates. Count responses are on a logarithmic scale and proportional responses are back-transformed to the original proportion scale.
Table 1. Results of likelihood-ratio tests of explanatory factors in linear mixed models used to examine the effect of tree removal on the demographic rates of ramet clumps of the lady’s slipper orchid over time (significant results in bolded).

<table>
<thead>
<tr>
<th></th>
<th>Ramet density</th>
<th>Proportion of dormant ramets</th>
<th>Clump survival</th>
<th>Flower density</th>
<th>Seedling density</th>
<th>Flowering probability</th>
<th>Fruiting probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Starting level</td>
<td>NT</td>
<td>NT</td>
<td>NT</td>
<td>20.81, &lt;0.001</td>
<td>13.01, 0.002</td>
<td>NT</td>
<td>6.701, 0.048</td>
</tr>
<tr>
<td>Treatment</td>
<td>NT</td>
<td>NT</td>
<td>NT</td>
<td>NT</td>
<td>7.193, 1.000</td>
<td>NT</td>
<td>NT</td>
</tr>
<tr>
<td>Time</td>
<td>NT</td>
<td>NT</td>
<td>NT</td>
<td>NT</td>
<td>8.642,0.067</td>
<td>NT</td>
<td>NT</td>
</tr>
<tr>
<td>Region</td>
<td>NT</td>
<td>0.991,0.320</td>
<td>NT</td>
<td>NT</td>
<td>0.5581,0.331</td>
<td>6.141, 0.066</td>
<td>0.0681, 1.000</td>
</tr>
<tr>
<td>Starting level × Time</td>
<td>10.42, 0.027</td>
<td>34.42, &lt;0.001</td>
<td>4.021, 0.045</td>
<td>2.432, 1.000</td>
<td>2.612,1.000</td>
<td>25.02, &lt;0.001</td>
<td>3.752, 0.766</td>
</tr>
<tr>
<td>Treatment × Time</td>
<td>25.56, 0.001</td>
<td>48.46, &lt;0.001</td>
<td>9.203, 0.003</td>
<td>19.46, 0.018</td>
<td>0.8566,1.000</td>
<td>77.26, &lt;0.001</td>
<td>18.96, 0.022</td>
</tr>
<tr>
<td>Region × Time</td>
<td>47.12, &lt;0.001</td>
<td>1.122, 0.571</td>
<td>13.71, 0.002</td>
<td>13.22, 0.007</td>
<td>3.632,0.815</td>
<td>4.882, 0.436</td>
<td>1.462, 1.000</td>
</tr>
</tbody>
</table>

Flowering probability is estimated as the proportion of flowering ramets out of mature ramets, and fruiting probability is the proportion of flowers that produced capsules. Starting level was used as a continuous covariate, and treatment, time, and region were used as fixed factors. All models included site-nested-within-region and year as random factors. Presented are the deviances, their degrees of freedom and p-values (degrees of freedom and p-values in subscript). p-values are Bonferroni-corrected when applicable (see the methods for details). NT = not tested due to significant interactions.
Silvertown, 1998). For the lady’s slipper orchid, the positive effect of forest harvest on flowering and fruiting probabilities during the immediate post-harvest period was probably due to increased nutrient availability and increased pollinator density and activity which resulted in improved pollination success (Fig. 1) as the species is mostly pollinated by solitary bees of the genus *Andrena* that prefer open or half-open habitats (Antonelli et al., 2009; Erneberg & Holm, 1999; Kull, 1999). A similar increase in pollination success due to improved light conditions has also been observed for other forest understory species (Gill, 1996; Pascarella, 1998). However, the positive effects on flowering and fruiting observed here were seen only in the most intensive treatments, where the amounts of removed trees were the highest and only during the first few years after tree removal, before the canopy gaps quickly closed.

In general, as flowering and fruiting probabilities increase, seedling production can also be expected to increase (Fig. 1). However, even though the density of seedlings was higher in the treatment sites, these differences were not statistically significant. In other words, the increased capsule production observed at the treated dense spruce forest sites did not translate into a significant increase in seedling production nor did tree removal release the sprouting potential of a potentially preexisting seedling bank. While it is possible that some seedlings may have established during the years the sites were not visited, we can assume that these seedlings would have been observed during some of the subsequent visits. Because the lady’s slipper orchid has a long protocorm period (Kull, 1999), the effect of seed input (if any) on recruitment will be seen with a time lag, but a study period of 16 years should have been long enough to detect such lagged responses. Assuming that tree removal did not significantly affect the number of seeds per capsule or their quality, the lack of response in seedling numbers suggests that seedling production of the lady’s slipper orchid is constrained by the number of favorable microsites rather than by the number of seeds (Fig. 1), as was observed by Kull (1998) in Estonia. It is possible that tree removal enhanced the growth of other forest herbs that had a stifling effect on the seedlings of the lady’s slipper orchid. The fact that
increased flowering and capsule-formation probabilities due to selective tree removal did not affect
the population size of the lady’s slipper orchid calls into question the usefulness of tree harvest as a
management method. However, we did observe an increase in the survival of established
individuals, which is likely to increase population size at the harvested sites in the long run.
Elasticity analyses on both animals and plants have shown that in long-lived species, such as the
lady’s slipper orchid, the most important demographic component for population growth rate is
survival (Franco & Silvertown, 2004; Heppell, Hal, Crowder, Caswell, & Crowder, 2000), making
it an ideal target for management efforts. Nevertheless, there may be practical limitations to such an
approach: survival is often high in long-lived species and thus difficult to increase sufficiently to
halt the population decline. For example, the high clump survival observed in this study (83-99% of
clumps survived from year to year) is in line with values reported previously for terrestrial orchids
(Gill, 1996; Kéry & Gregg, 2004; Shefferson, 2006; Sletvold & Ågren, 2015). The practical
constraints related to high survival values may make demographic rates with lower elasticities (e.g.,
fecundity) more feasible targets for conservation (see e.g. Lehtilä, Syrjänen, Leimu, Begona Garcia,
& Ehrlen, 2006).

It should be noted, though, that in this study we only compared treated sites to the control sites and
did not test changes in reproduction, dormancy, and survival between pre-harvest and post-harvest
periods. Furthermore, we could not confidently estimate population sizes at the clone level, as many
clones could have been intermingled or were lost during the study and possibly marked with
another label later on. However, at the ramet level, population size was significantly higher at the
broadleaf 25% removal treatment sites than at the control sites during the later years. This higher
ramet density seems to be due to increased clonal growth (greater number of ramets per clone)
resulting from improved light and nutrient availabilities, and not, instead, the consequence of
increased clump sprouting, as the treatments had no effects on the proportion of dormant clumps.
Alternatively, the higher ramet density could also potentially be explained by the improved survival of existing clones immediately after the harvest (Fig. 1).

4.2 Management implications and conclusions

As has been found with many other rare orchids, the main threats to the lady’s slipper orchid include increased shading due to succession, the abandonment of traditional grazing activities and the replacement of natural forests with spruce plantations (Bjørndalen, 2015; Rankou & Bilz, 2014). Therefore, ensuring sufficient light conditions on the forest floor is important for maintaining lady’s slipper orchid populations (Antonelli et al., 2009; Bjørndalen, 2015; Rankou & Bilz, 2014) and species richness in herb-rich forests, even if it requires interfering with natural succession through management actions (Alanen et al., 1995).

Previous observations from Scandinavia (Antonelli et al., 2009; Bjørndalen, 2015) and our findings show that selective tree harvest might be a suitable management method for the rare lady’s slipper orchid. In our study, a 25 – 50% reduction in tree basal area increased population size at the ramet-level by enhancing survival and clonal growth at sparse broadleaf forest sites, and increased the probabilities of flowering and fruiting at spruce forest sites, although these positive effects were not seen during all years. While we can expect responses to change in canopy cover to be species- and habitat-specific, it is likely that tree removal could be used as a management method for other understory species whose reproduction benefits from canopy gaps. For example, Kirchner et al. (2009) observed that the forest herb *Trientalis europaea* produced a higher number of flowers and fruits in canopy gaps than in the shade, and that ramet density increased with increasing light availability, and in primrose (*Primula vulgaris*) populations, brighter patches have been observed to have higher reproduction and lower mortality (Valverde & Silvertown, 1998). Moreover, in the orchid *Isotria medeoloides*, selective removal of 25% TBA more than doubled the number of stems
during a ten-year study period (Brumback et al., 2011), showing that tree removal has indeed the potential to increase shoot density also in other orchid species.

None of the tree removal treatments considered here significantly increased seedling production, even though there were large differences between the years and study sites in seedling density. The differences between treatments were, however, inconsistent, meaning that rather than being affected by the tree removal treatments, seedling density was dependent on site-specific factors such as microsite limitation (Kull, 1998). Kull (1998) also observed that in Estonia the germination of the lady’s slipper orchid was highest at sites with high amounts of light, small total herb coverage, and a thick moss layer that provided stable and moist conditions. Therefore, the germination of the lady’s slipper orchid could possibly be enhanced by sowing seeds to small plots where herbs have also been removed. Furthermore, our treatments resulted in only a transient increase in light availability, so it is possible that a repeated or more intensive treatment (e.g., 75% TBA removal) would have resulted in larger and longer-lasting responses. While the positive effects of forest management on survival and flowering probability were seen only for a maximum of three years after tree removal, suggesting a need for repeated treatments, ramet density responded with a lag of several years and lasted until the end of the study period (15 years after harvest). More experiments are needed to determine the optimal intensity and frequency of tree removal to maximize benefits for the orchid populations. Although clear-cuts have been observed to significantly increase the number of plant species in spruce dominated herb-rich forests in Finland, this increase is accompanied by a considerable shift in species composition benefitting early-successional species (Pykälä, 2004). Further, in Sweden (Sjöberg & Ericson, 1992) and Norway (Bjørndalen, 2015) clear-cuts have been observed to have negative effects on lady’s slipper orchid populations, presumably due to the increased risk of frost and competition with graminoids and other herbs (Sjöberg & Ericson, 1992). Irrespective of the extent of tree removal, intensive disturbance of the soil surface should be avoided because the rhizomes of the lady’s slipper orchid grow near the
ground surface (Kull, 1999; Laitinen, 2006) and are thus easily damaged. Moreover, when
removing spruce, the highly acidic logging waste (e.g., twigs and needles) must also be removed
from the site to avoid negative effect on soil quality (Alanen et al., 1995) and, consequently, on the
lady’s slipper orchid. Overall, we recommend selective tree removal, together with sowing seeds in
plots where the herbaceous layer has been removed, to manage this rare flagship species in
overgrown forests.

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