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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.

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 and Chen, 2008; Rydgren, 1996; Økland and 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 et al., 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 et al., 2012; Briggs et al., 2005), as well as tree gap dynamics and their importance for tree recruitment, particularly in tropical rainforests (e.g. 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 and Busing, 1989; Saldarriaga et al., 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 et al., 2011; Gill, 1996; Kirchner et al., 2009; Valverde and Silvertown, 1998).

This increased reproduction and growth may be due to improved nutrient availability. As the canopy cover decreases, soil temperature

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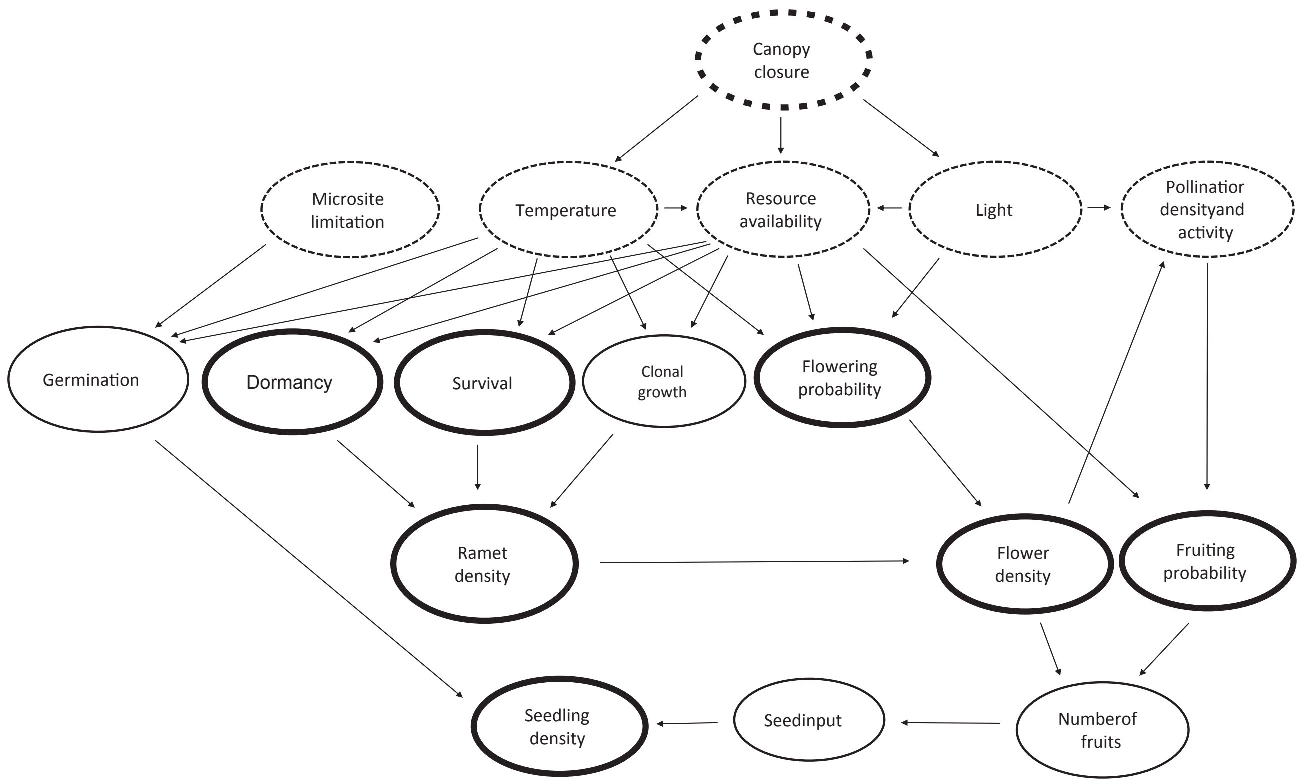

Fig. 1. A flow-chart depicting the effects of canopy closure and abiotic factors (dashed line) on different demographic rates (solid lines) of forest understory herbs. Variables in bold circles are measured in the current study.

generally increases (Abd Latif and Blackburn, 2010; Norris et al., 2001; Seastedt and Adams, 2001; Smith and Johnson, 2004), leading to changes in soil respiration (Smith and Johnson, 2004) and rates of decomposition of organic matter (Canham and Marks, 1985; Seastedt and Adams, 2001). Additionally, decomposition rates and, consequently, nutrient availability can change as a result of altered litter composition (Ovington 1954; Berg et al., 1993). Coniferous forests tend to have slow decomposition rates (Zhang et al., 2008), with nitrogen and phosphorus availability decreasing in the late, closed, conifer-dominated successional stage (Bormann and 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 and Blackburn, 2010; Alanen et al., 1995; Canham and 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 et al., 2007; De Boever et al., 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 and Ericson, 1992). Large gaps might also have unfavorable microclimates as wind speed and temperature variations increase (Abd Latif and Blackburn, 2010; Runkle, 1985), which may result in a greater risk of frost (Langvall and Ottosson Löfvenius, 2002; Norris et al., 2001) and fruiting failure (Abeli et al., 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 and 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 and 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 et al., 2005). This suggests that the recent population declines reported in many European countries (Rankou and 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; Kull, 1999; but see García et al., 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 et al., 2013; Shefferson et al., 2012, 2014). In addition, the rate of photosynthesis of understory species in shaded habitats has been observed to be low (Lett and Knapp, 2003; Zhang et al., 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.