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Nitrogen fertilization reduces wild berry production in boreal forests

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ABSTRACT

Nitrogen is the main limiting nutrient in temperate and boreal forests. Large-scale nitrogen fertilization has been suggested as a potential tool to enhance production and meet the increasing demand for wood products and biofuels. Here, we test the effect of N fertilization and thinning on berry (i.e., fruit) production and incidence of fungal pathogens along a latitudinal gradient in Sweden. We used an N fertilization (100–150 kg ha^{-1}) and thinning experiment that was established between 1970 and 1980 in 30 pine forests, covering a latitudinal gradient stretching from southern to northern Sweden. We measured fruit production and disease incidence of fungal pathogens in bilberry and cowberry in the experimental plots (30×30 m), over two years (2014 and 2015), when the stands were between 67 and 85 years old. Nitrogen fertilization reduced fruit production for both species, while thinning had a positive effect. For cowberry, treatment effects on fruit production were mainly associated with changes in plant cover, while direct treatment effects altered fruit production in bilberry. Furthermore, N application increased disease incidence of the parasitic fungus *Valdensia heterodoxa* in bilberry and contributed to the reduced fruit production in the N treatment. In contrast, disease incidence of the main parasitic fungus in cowberry (snow-mold disease) was negatively affected by N. Thinning decreased disease incidence in bilberry, but tended to increase incidence in cowberry. For cowberry, disease incidence increased with latitude. Overall, our results suggest that the N-induced effect on fruit production in bilberry is partly associated with presence of the parasitic fungus, and largely due to unknown direct effects. For cowberry, reduction in fruit production is correlated with N-induced negative effects on plant cover. Large-scale fertilization will have an overall negative impact on fruit production, and given that fruit production is considered highly valuable in the context of ecosystem services and functioning, this reduction should be considered when forest management scenarios that include N fertilization are evaluated. Thinning on the other hand, can promote fruit production and may be used as a management tool to generate berry-rich forests.

1. Introduction

Intense and large-scale forest management practices in the boreal biome aim to maximize wood production and quality; in northern Europe, thinning and nitrogen (N) fertilization are commonly used to achieve this goal. Given the increasing focus on multi-use of forests (Gamfeldt et al., 2013), there is a need to investigate the impact of forest management on other services. Fruit (i.e., berries) production by the dominant boreal dwarf shrubs in the *Vaccinium* genus, such as cowberry (*V. vitis-idaea* L.) and bilberry (*V. myrtillus* L.), is a valuable ecosystem service not only of large monetary value, but also of high recreational and cultural value due to the long tradition of berry picking in many nordic countries (Turtiainen et al., 2011). Moreover, bilberry and cowberry are an important food resource for many herbivores since their plant parts (including fruits) are eaten by, for example, gallinaceous birds, voles and ungulates (e.g. Lakka and Kouki, 2009). Yet, how present forest management practice affect fruit production is not well understood.

Large parts of the boreal zone are to some extent managed for timber production, and in many areas the demand for timber and biomass for use as biofuel has intensified forest management. This is particularly true for Fennoscandia which has a long history of forest management practice including clear-cutting, re-planting and thinning operations. During the last decades, fertilization has also been included to further enhance growth in this N-limited system. Both thinning and fertilization, are known to cause changes in the composition of the forest floor community. Fertilization influences forest ground vegetation by altering competitive interactions, promoting fast-growing graminoids and herbs, while reducing the abundance of slow-growing species, such as berry

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producing dwarf shrubs (Strengbom and Nordin, 2008). Thinning increases light availability (Bartemucci et al., 2006), and often leads to a more productive and species rich forest floor community (Bartemucci et al., 2006; Hedwall et al., 2013). Direct effects of these silvicultural practices are therefore, anticipated to result in negative effects (through fertilizing) and positive (through thinning) on berry production.

Production of wild berries is considered a highly valued service provided by boreal forests. Although only 5–10% of the berries produced are harvested (Turtiainen et al., 2011), estimates suggest that the annual household harvest only in Finland and Sweden corresponds to about 80 million kg of berries (Kardell, 1979; Saastamoinen et al., 2000), which represents a market value in the range of 50–90 million Euro. Despite the high value that berry production represents, it is surprising that quantitative estimates of how modern silvicultural practices affect berry production are largely lacking (Miina et al., 2010).

Fruit production of dwarf shrubs varies in time (between years) and space (within stands and within regions) (Selås, 2000; Ihalainen et al., 2002), and is a result of complex interactions between weather and available resources (carbon, nutrients, water) (Pearse et al., 2016). Still, weather is a good predictor of fruit production of dwarf shrubs and especially colder spring weather or late frost spells, can result in poor flower and fruit formation (Selås, 2000; Krebs et al., 2009). If studied at a per area basis, and not at the plant level, plant abundance becomes a major predictor of fruit production and fruit production strongly correlates with plant cover (Miina et al., 2009; Turtiainen et al., 2013). Furthermore, cover of both cowberry and bilberry are related to light conditions, and these dwarf shrubs generally do not thrive under the dark conditions generated by high tree canopy cover. Fruit production by bilberry is highest in mature, semi-closed forest with intermediate nutrient levels, while fruit production by cowberry is highest in more open and sun exposed stands, often found on drier sites, see further (Ihalainen et al., 2002; Miina et al., 2010).

Besides abiotic conditions and plant-plant competition, fruit production may also be directly or indirectly affected by biotic interactions with herbivores or pathogens. For example, increased N input can lead to increased insect herbivory with subsequent reductions in plant cover (Strengbom et al., 2002, 2005). In addition, *Valdensia heterodoxa* Peyronel, a generalist parasitic fungus that infects *Vaccinium* species, particularly *V. myrtillus*, can cause severe leaf damage (Norvell and Redhead, 1994), and its disease incidence in bilberry is also positively correlated with N addition (Strengbom et al., 2002). For cowberry, snow-mold disease (*Eupropolella vaccinii* (Rehm) Höhn. may have similar effects. This parasitic fungus is dependent on a continuous snow cover, as its asexual stages spread by mycelia growing in the snowpack from one diseased plant to neighboring plants. Diseased cowberry shoots eventually die and spores (sexual dispersal) are produced from infected plants during the snow-free period of the fall or early winter. How this fungus is affected by nitrogen addition or thinning is currently unknown, but it is likely to be affected since thinning may influence snowpack thickness, and thereby alter disease incidence. Moreover, as disease incidence is often influenced by altered changes in nutritional status of the host plant following N addition (Schoeneweiss, 1975; Strengbom et al., 2002; Strengbom and Reich, 2006), altered disease incidence by snow-mold disease can be anticipated after both thinning and N fertilization.

The aim of our study was to investigate the impact of thinning and N application on fruit production of cowberry and bilberry. Specifically, we tested if the effects on fruit production are associated with changes in plant cover (i.e., living biomass), or other factors such as disease incidence by parasitic fungi or herbivory. We predicted that fruit production would decrease with N fertilization, but would increase with thinning. We also expected differences in fruit production to be primarily explained by changes in plant cover.

2. Methods

2.1. Experimental design

We used a a thinning and fertilization experiment that was set up between 1966 and 1981 at 30 sites in Scots pine (*Pinus sylvestris* L.) stands, along a 1400 km south-north gradient within Sweden (Fig. 1). The treatments applied at these sites were: control (no nitrogen, no thinning, no phosphorous), N fertilization (N), thinning (Th), thinning in combination with N fertilization (Th + N), and thinning in combination with N and P fertilization (Th + N + P). The (N) treatment (i.e., N added but no thinning performed) was applied at 9 of these 30 sites, and were distributed along the gradient. Thinning was performed according to standard practices in Swedish forestry and took place three times during the experimental period. On average, thinning reduced the basal area between 17 m^2 ha^{-1} and 24 m^2 ha^{-1} (c. 30%). All stands were originally established in the late 40 s by sowing and the treatments were initiated when the stands were in the same successional stage, i.e., when they were due for the first thinning which occurs when the canopy is closed (tree height about 12 m). Depending on location along the gradient, this stage was reached when the trees were between 32 and 54 years old. Nitrogen was applied every fifth year the first 30 years and thereafter every seventh year. At the northern sites (above latitude 61), 100 kg N ha^{-1} was applied, and at the southern sites (below latitude 61) 150 kg N ha^{-1} was applied. The phosphorus treatment, which was in combination with N and thinning, corresponded to 100 kg P ha^{-1} and was applied on two occasions, at the start of the experiment and after 21–22 years. Nitrogen was added as ammonium nitrate (NH_4NO_3) and phosphorus as superphosphate ($CaSO_4 + Ca(H_2PO_4)^3$). For general information and more detail on each of these sites see (Nilsson et al., 2010; Bergh et al., 2014).

2.2. Sampling

To investigate the impact of thinning and N application on fruit production, fruit production of bilberry and cowberry was recorded in two consecutive years, 2014 and 2015. Two sites were only recorded in 2014 due to a clear-felling and logistical reasons. Compared to the long-term averages for May-July (1970–2015: temp = 12.6 C, precipitation = 188 mm), 2015 was colder (1.6 C) and wetter (81 mm more precipitation) than average, while 2014 was warmer (0.9 C) and drier (13 mm less rain) than average (data from SMHI weather stations along the latitudinal gradient, www.smhi.se).

Sampling, in both years, began in July and started at the southern sites, gradually continuing to north, in order to track fruit formation phenology. In each treatment plot, the total number of fruits were counted in 14 0.25 m^2 quadrats placed randomly along two 30 m diagonal transects (7 quadrats per transect). Within each 0.25 m^2 quadrat we used a 10×10 grid (i.e. 100 5×5 cm cells in the sampled quadrat) to record vegetation cover. Cover was estimated as the number of cells with the presence of bilberry and cowberry, respectively. Fungal incidence of *Eupropolella vaccinii* in cowberry was recorded as the total number of blackened/whitened dead shoots, while for bilberry the fungus (*Valdensia heterodoxa*) was recorded as the number of cells with observed diseased leaves. Herbivory was quantified as the number of cells with clear signs of herbivory (leaf, flower or branch herbivory).