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The influence of stand density on bilberry (*Vaccinium myrtillus* L.) cover depends on stand age, solar irradiation, and tree species composition

Katrine Eldegard[a,*], Janneke Scholten[b], Jogeir N. Stokland[b], Aksel Granhus[b], Marit Lie[a,c]

[a] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway
[b] Norwegian Institute of Bioeconomy Research, P.O. Box 115, NO-1431 Ås, Norway
[c] NLA University College, P.O. Box 7153 St. Olavs plass, 0130 Oslo, Norway

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ABSTRACT

The ericaceous shrub bilberry (*Vaccinium myrtillus* L.) is a keystone species of the Eurasian boreal forest. The most optimal light condition for this plant is partial shading. Shade from the forest canopy depends on the stand density, a forest attribute that can be manipulated by forest managers. Most previous studies of the relationship between bilberry abundance and forest density have not explored the potentially modifying impacts of factors like stand age, tree species composition, and the solar irradiation at the site, as determined by location and topography. Using data from the Norwegian National Forest Inventory, we developed a generalized linear model applicable to estimate local bilberry cover across a wide range of environmental conditions in Norway. The explanatory terms in the final model were stand density (basal area per ha), solar irradiation, stand age, percentages of deciduous, pine, and spruce trees, summer (June-August) mean temperature and precipitation sum, mean temperature in January, site index, and soil category, in addition to the two-way interactions between stand density and the following: solar irradiation, stand age, percentage of deciduous trees, and percentage of Norway spruce (*Picea abies*). The final model explained ca. 21% of the total variation in bilberry cover. We conclude that a stand density of c. 30 $m^2\,ha^{-1}$ in general will create favourable conditions for bilberry. If the forest is younger than 80 years old, or dominated by Norway spruce or deciduous trees, the optimal stand density is reduced to around 20 $m^2\,ha^{-1}$. In a forest dominated by Scots pine (*Pinus sylvestris*), basal areas up to 40 $m^2\,ha^{-1}$ would be beneficial to bilberry abundance. Our results demonstrate the importance of considering interactions between stand density and other stand and site characteristics.

1. Introduction

The ericaceous shrub bilberry (*Vaccinium myrtillus*) is a keystone species of the Eurasian boreal forest. Bilberry is an essential food resource for many vertebrate and invertebrate species that feed on the flowers (nectar), berries, leaves, and twigs (e.g. Selås et al., 2011; Dahlgren et al., 2007; Hegland et al., 2010; Hertel et al., 2016; Rasmussen et al., 2016), and it is indirectly important for many animal species that prey on the bilberry consumers (Atlegrim, 1989; Jedrzejewska and Jedrzejewski, 1998). Bilberry also has an economic value through commercial berry picking, especially in Finland and Sweden (Jonsson and Uddstål, 2002; Vaara et al., 2013). Compared to the trees with which they coexist, the standing biomass of bilberry shrubs is small, but their biomass turnover is much higher; > 60% of standing shrub biomass is replaced each year and the aboveground net primary productivity may be comparable to that of the trees (Nilsson and Wardle, 2005). Bilberry also has strong positive effects on litter decomposition as well as soil microbial activity, and can reduce the depletion of soil mineral nitrogen (Nilsson and Wardle, 2005). Consequently, a decreased abundance of bilberry can potentially bring about profound changes in ecosystem function and services in boreal forests.

Previous studies from Sweden and Finland have found that bilberry has declined after the introduction of industrial forestry, probably due to altered management practices and an increased proportion of young, dense forest (see Hedwall et al., 2013; Miina et al., 2009, with references). The forest density is an important determinant of the amount of light that penetrates through the canopy, and thus of the photosynthetically active irradiation available to the ground and field layer vegetation. Partial shading provides the most optimal light conditions for bilberry shrubs (Parlane et al., 2006). Increased shading, due to

* Corresponding author.
E-mail addresses: katrine.eldegard@nmbu.no (K. Eldegard), jogeir.stokland@nibio.no (J.N. Stokland), aksel.granhus@nibio.no (A. Granhus), marithelene.lie@nla.no (M. Lie).

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increased tree density or canopy cover, may thus be expected to reduce bilberry cover (Hedwall et al., 2010; Miina et al., 2009). An intensifying of forest management to increase forest production can therefore result in a decrease in bilberry cover because of increased stand density. Besides stand density, a suite of other characteristics related to site conditions and the developmental stage and structure of the forest, such as site productivity, stand age, and tree species composition, may all affect the understory vegetation (Barbier et al., 2008), including the bilberry cover (Hedwall et al., 2013). Bilberry is typically most abundant on sites of medium productivity (Ihalainen et al., 2005), less abundant on clear-cuts and in young forests than in mature stands (Atlegrim and Sjöberg, 1996; Miina et al., 2009), and is also influenced by tree species composition (Miina et al., 2009; Gamfeldt et al., 2013). Stand age and tree species composition modify the canopy and thus the transmission of light through the canopy. In rugged landscapes, the light conditions in the forest understory also vary with topography (Bonan and Shugart, 1989). Yet, surprisingly little is known about how these factors interact to determine bilberry cover.

In this study, we used a nationwide dataset, the Norwegian National Forest Inventory, to investigate the relationship between bilberry cover and stand density. Similar nationwide forest inventory (NFI) data from Sweden (Hedwall et al., 2013) and Finland (Miina et al., 2009) have been used previously to analyse relationships between bilberry cover and biotic and abiotic explanatory variables. Most of the forested area in Sweden is within the boreal zone, but a substantial part is in the boreonemoral zone (Hagen et al., 2013). In contrast, almost all forest in Finland is of southern, middle, or northern boreal types. Neither Hedwall et al., (2013) nor Miina et al., (2009) conducted a sub-selection of NFI plots, based on e.g., site or vegetation types, before analysing factors influencing bilberry cover. Both studies found that productivity was an important predictor of bilberry cover. In vegetation science, it is well known that bilberry occurs at its highest abundance in forests of low to intermediate productivity (Ritchie, 1956; Arnborg, 1990; Hill et al., 1999). We argue that including data from all forest types, including very poor and rich habitats, in which average bilberry cover is known to be (close to) zero, will overemphasise the productivity gradient and may not capture more subtle patterns of variation in the influence of forest structure. To increase our understanding of how forest structure variables may influence bilberry cover, we restricted our analyses to typical bilberry habitats.

The main aim of this study was to improve our understanding of how stand density influences bilberry abundance and how the influence of stand density is modified by other factors. Stand density is a factor that is manipulated by forest management and it is important to provide useful quantitative information for managers about the impact of stand density on bilberry cover. We hypothesized that bilberry cover would peak at intermediate stand densities. Furthermore, we expected the influence of stand density to be modified by factors such as available light, forest age, and tree species composition.

In open forests, increased amounts of light should have a negative impact on bilberry cover, whereas in denser forest, high levels of available light should have a positive influence on bilberry cover. Due to the differences in forest structure, we expected bilberry cover to be higher in old forests than in young forests with the same stand densities. Likewise, we expected the relationship between stand density and bilberry cover to differ between forests dominated by pine, spruce, or deciduous trees, due to the differences in forest structure. We expected bilberry cover to peak at higher stand densities in pine forests than in deciduous or spruce forests. We also expected the influence of stand density on bilberry cover to be less pronounced in deciduous forest. We therefore included interactions between stand density and these three factors, light availability, forest age, and tree species composition, in our analyses. Both Hedwall et al. (2013) and Miina et al. (2009) included measures of forest density, stand age, and tree species composition as predictors of bilberry cover, but did not consider interactions with stand density (Hedwall et al. 2013) or concluded that they were insignificant (Miina et al., 2009). To our knowledge, our study is the first to assess whether light availability (solar irradiation) influences the relationship between stand density and bilberry cover.

2. Material and methods

2.1. Forest inventory data

We used data from the permanent plots of the Norwegian National Forest Inventory (NNFI) collected during 2007–2011. One fifth of the NNFI plots are measured per year, resulting in a complete coverage of Norway in five years. The plots are located on a 3×3 km grid on all forested land below the altitudinal coniferous forest limit, and on a 3×9 km grid elsewhere, except for the birch forest in the northernmost county Finnmark, where a 9×9 km grid is used (Viken, 2017).

At each plot, variables are measured at either the stand level (circular plot sized $1000\,m^2$), or within a core plot sized $250\,m^2$ (radius 8.92 m). Within the core plot, all trees exceeding 5 cm in diameter at breast height are identified to species and callipered, and a subset of the trees are sampled for height measurement. The heights of the remaining trees are estimated based on diameter – height curves derived from the sampled trees, for use in subsequent volume calculations using standard volume functions. The plot is divided into two parts if at least 15% of the plot belongs to a different area type than forest, or if conditions differ with respect to stand age, site productivity or standing volume. If so, each part is recorded separately.

Variables recorded at the stand level include the site index and maturity class, as well as a terrain description including slope (percent) and aspect (degrees). The site index classification follows the Norwegian H_{40} system, where site productivity is grouped into classes (Table 1) according to the expected average height of the 100 largest (by diameter at breast height) trees per hectare at a reference age of 40 years (Tveite, 1977). Maturity class shows how close a stand is to maturity in five different classes, where 1 is a clear cut and 5 is a mature forest, with upper and lower age boundaries for the different maturity classes depending on site productivity. The lower age boundary for mature forest (class 5) varies from 60 years on the most productive sites to 120 years on sites with lowest productivity. The stand type is defined by the share of total volume (maturity class 3–5) or crown cover (maturity class 1–2) of the different tree species.

The soil type is classified as either mineral soil or peat (depth of organic layer at least 40 cm), and soil depth is recorded in four classes (1: < 25 cm; 2: 25–50 cm; 3: 50–100 cm; 4: > 100 cm). The percentage of bilberry cover is quantified by visual estimation on four $0.25\,m^2$ sample squares ($0.5\,m \times 0.5\,m$), located within the core plot at 5 m from the plot centre in each of the four cardinal directions (north, east, south and west). The bilberry cover per plot (or plot part) was calculated by taking the average of the individual sample squares.

2.2. Data preparation

The whole dataset consisted of 12,499 NNFI plots. Before carrying out exploratory and statistical analyses, we extracted a subset of these data through a stepwise exclusion of plots: (1) to avoid confounding edge effects, divided plots were excluded; (2) we excluded data from plots located on unproductive forest land (i.e., with a yield capacity less than $1\,m^3\,ha^{-1}\,year^{-1}$), because such forest land is not used for commercial timber harvesting in Norway; (3) to avoid problems with zero inflation during modelling, we excluded plots located on forested mires, plots in vegetation types reflecting very fertile site types on mineral soil with an expected absence of bilberry, and plots in stands dominated by alder (*Alnus* spp.) or noble broadleaves (oak *Quercus* spp., beech *Fagus sylvatica*, elm *Ulmus glabra*, ash *Fraxinus excelsior*, or linden *Tilia cordata*). The final dataset consisted of 6870 plots (Fig. 1) dominated by boreal tree species, and where the ground and field layer vegetation corresponded to the following plant association types (Kielland-Lund, 1981): *Cladonio*