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Ungulate browsing affects subsequent insect feeding on a shared food plant, bilberry (*Vaccinium myrtillus*)

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Abstract

Browsing by ungulates may induce plant responses and affect subsequent plant food quality for other animals. Populations of many deer species have increased to unprecedented levels in Europe and North America. In Norway, population densities of red deer (*Cervus elaphus*) have increased over the past decades, but little is known about how increased deer browsing pressure may change the palatability of key food plants for other taxa in the boreal ecosystem. We conducted a cafeteria experiment to assess if long-term deer-browsing intensity affected the palatability of bilberry (*Vaccinium myrtillus*) leaves for leaf-eating larvae (mainly Lepidoptera). We found that leaf-eating insect larvae preferred bilberry leaves from the lightly browsed bilberry plants; the larvae consumed twice as much leaf biomass from the lightly browsed plants than from the unbrowsed and moderately browsed ones, and four times more than from highly browsed plants. Larvae never selected leaves from highly browsed plants as their first choice. Our study suggests that browsing-induced changes in the quality of shared food plants may be important in mediating indirect interactions between browsers of widely separated taxa. Whereas low levels of long-term red deer browsing increases the palatability of bilberry leaves for leaf-eating larvae, high browsing pressure reduces food consumption. Whether changes in palatability lead to changes in population densities of leaf-eating larvae remains to be studied, but any such adverse effects could have cascading ecological consequences for insectivorous birds and mammals.

Keywords: Browsing; Competition; Facilitation; Induced defense; Lepidoptera; Red deer

Introduction

Many herbivore species, often from widely separated taxa, may defoliate the same plant species and – directly or indirectly – compete for food resources. Plants can respond to herbivory by producing chemical (War et al. 2012) or physical (Gómez & Zamora 2002) resistance, or compensate by increased growth (McNaughton 1983). In addition to production of chemical defense substances, changes in plant stress levels can lead to changes in the content of plant nutrients like nitrogen, protein and simple sugars, which are important to herbivores (English-Loeb, Stout, & Duffy 1997; Nykänen & Koricheva 2004). Consequently, the quality of a food plant

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for herbivores is determined by a complex interplay between nutrient content and chemical and physical defence substances and structures. The plant stress hypothesis predicts that stressed plants become a better food source for invertebrates because of mobilization of soluble nitrogen (White 1984), but the hypothesis has received variable support. This is likely due to the wide variety of both plant stressors and plant and herbivore species (Larsson 1989). Indeed, in a meta-study, Nykänen and Koricheva (2004) documented that both plant and damage type, the time between damage and subsequent feeding, as well as the timing of damage, affected insect responses to damage-induced changes in woody plants.

Many studies on plant stress response have focused on abiotic stressors like limitations in water and nutrient supply. However, we do also know that biotic stress, for example ungulate herbivory, can affect plant chemistry and subsequent herbivory by ungulates (Mathisen, Milner & Skarpe 2017) as well as other taxa like insects (Danell & Huss-Danell 1985; Nykänen & Koricheva 2004; Hrabar & Du Toit 2014). In boreal forests, some studies have shown that browsing by moose (*Alces alces*) can have a positive influence on subsequent feeding by insects and mountain hares (*Lupus timidus*) on birch (*Betula pendula* and *Betula pubescens*; Danell & Huss-Danell 1985), wheras red deer browsing negatively affected the amount of invertebrate feeding on bilberry, *Vaccinium myrtillus* (Hegland, Rydgren, & Seldal 2005). Winter browsing by mammals on feltleaf willow (*Salix alaxensis*) increased levels of digestible nutrients in the new emerging biomass, subsequently increasing summer herbivory by snowshoe hares (*Lepus americanus*) (Bryant 2003). Productivity may also be important in driving the effect of ungulate browsing on insect food choice and abundance (Tuomi, Niemelä, Haukioja, Siren, & Neuvonen 1984). For example, it has been shown that browsing reduces the number of grey pine aphids (*Schizolachnus pineti*) only at productive sites (Vesterlund, Suominen, Bergström, Danell, & Persson 2012). Furthermore, Pato and Obeso (2013a) found that repeated damage to bilberry facilitated insect herbivory under N-fertilization.

Although previously browsed plants can be preferentially re-browsed (Danell, Huss-Danell, & Bergstöm 1985; Dahlgren, Oksanen, Sjödin, & Olofsson 2007), browsed plants can also be avoided (Gibberd, Edwards, & Wratten 1988). In Finland, the growth of the autumnal moth *Oporinia autumnata* was reduced when the moths were feeding on previously defoliated leaves of birch (*B. pubescens*) (Haukioja & Niemelä 1977; Haukioja 1980). Adverse effects on herbivores resulting from feeding on particular plants are often attributed to induced plant defense (Karban 2011). A large body of research has documented that induced plant defense is important in mediating interactions between herbivores – mainly insects – and their food plants (e.g. Anderson, Inouye, & Underwood 2015). Acacia thorn lengths increase following ungulate browsing (Young, Stanton, & Christian 2003), but there have been few studies documenting chemically induced defense resulting from ungulate browsing (but see Ohse et al. 2017).

During the past century, large areas of Europe and North America have experienced considerable increase in population sizes of many deer species (Milner et al. 2006). Norway currently has unprecedented population densities of deer (Statistics Norway 2017). In particular, there has been a fourfold increase in the harvest of red deer during the past 30 years (*Cervus elaphus*) (Statistics Norway 2017). The boreal forest is strongly seasonal and red deer often congregate in areas of favorable snow conditions during winter, resulting in local high population densities and high browsing pressure in the winter ranges. Red deer winter diet comprises mainly low shrubs (Mysterud 2000) and the biomass of food plants may be considerably affected (Hegland et al. 2005). High densities of deer with repeated defoliation of food plants may affect not only the long-term food quality for deer, but also plant quality for other species with overlapping diets (Pedersen, Andreassen, Julkunen-Titto, Danell, & Skarpe 2011).

Bilberry (*V. myrtillus*) is a common deciduous dwarf shrub and in many areas a dominant species in the understory of Scandinavian boreal forests. Although plant performance can be negatively affected already at low browsing intensities (Hegland et al. 2005), bilberry is commonly assumed to be relatively herbivore-tolerant (Dahlgren et al. 2007; Hegland, Jongejans, & Rydgren 2010). Bilberry is a key resource for many invertebrate and vertebrate species. It is one of the main winter food resources for red deer in Norway (Melis et al. 2006), but also an important food plant for leaf-eating insects larvae, such as many Lepidoptera species (Selås, Kobro, & Sonerud 2013). Consequently, changes in the quantity and quality of bilberry could have cascading multi-trophic effects in the boreal ecosystem. Den Herder, Helle, Niemelä, Henttonen, and Helle (2016) found that semi-domesticated reindeer feeding on bilberry reduced densities of bilberry with concomitant reduction of voles and insectivorous shrews, as well as affecting several other bilberry-dependent organisms across trophic levels. Also, it has been suggested that the variation in the food quality of bilberry might be an underlying cause behind the cyclic fluctuations of some small mammal species (Selås 2006).

Given that bilberry is a key food plant for many vertebrates and invertebrates, it is important to assess whether increasing browsing pressure by red deer affects the food quality of bilberry for other herbivores, like leaf-eating insect larvae. We conducted a cafeteria experiments to explore whether leaf-eating larvae (mainly Lepidoptera) discriminated between bilberry leaves from plants sampled at sites with different population densities – and thus different browsing intensities – of red deer. We used leaves from bilberry plants subjected to four different red deer long-term browsing intensity categories to test the contrasting hypotheses that (i) larvae prefer bilberry leaves from plants which have been browsed by red deer, or (ii) that leaves from plants which have been browsed by red deer are avoided by leaf-eating larvae.