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Borrowed plant defences: Deterring browsers using a forestry by-product

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ABSTRACT

Mammalian browsers can cause ecologically and economically significant damage to important tree species, particularly at the vulnerable seedling stage. Some tree species or particular parts of trees are less preferred as a result of chemical defences – harnessing such defences could reduce the appeal of more preferred trees and thus their loss to browsing. We tested the potential of birch bark extract, a forestry by-product, to protect seedlings of Scots pine *Pinus sylvestris* from two globally significant browsers: moose *Alces alces* and red deer *Cervus elaphus*. We quantified the responses by captive animals to extract application as a function of both the distance between seedlings and whether the extract was applied to all or alternate seedlings. Both moose and red deer consumed pine seedlings less frequently when seedlings were treated with birch bark extract, but their responses differed when only alternate seedlings were treated. At inter-seedling distances equivalent to those used in forestry, red deer browsed untreated seedlings more frequently when alternate seedlings were treated than when none were treated (associational susceptibility), whereas moose browsed untreated seedlings less frequently with treated than untreated neighbours (associational refuge). These neighbourhood effects were not evident at inter-seedling distances three times larger or smaller than those used in forestry. There was also no significant difference in the frequency of browsing on treated seedlings in alternate compared to completely treated arrangements at any inter-seedling distance. Red deer removed significantly less foliage from treated than untreated seedlings once browsed. Browsing by moose followed a similar but non-significant trend. The relative number of untreated to treated seedlings browsed was 2:1 for red deer and 4:1 for moose. Red deer used a finer scale of selection than moose for choosing between seedlings, consistent with their smaller body mass. However, the coarser-scale of selection used by moose resulted in consumption of more untreated relative to treated seedlings. Our study highlights the potential of existing plant defensive chemistry, harvested from forestry by-products, to reduce herbivore damage to tree seedlings. We also demonstrate the need to consider both plant associational effects and the foraging strategies of the dominant herbivores in applying repellents.

1. Introduction

Browsing of trees, particularly at the vulnerable juvenile stage, has significant effects on plant community structure and composition in many parts of the world (Côté et al., 2004; Moles and Westoby, 2004). Not only does it influence the natural regeneration of trees in forests, with cascading effects for ecosystems, it can hamper revegetation efforts and damage stocks in forestry plantations (Bulinski and McArthur, 1999; Meers and Adams, 2003; Nuttle et al., 2011). Although exclusion fencing and hunting are sometimes employed to manage browsing by herbivorous mammals, such practices are often undesirable because they can be difficult to implement (e.g. due to terrain and safety concerns), prohibitively expensive over large areas, interfere with conservation measures, elicit negative public perceptions, and conflict with the needs of game hunters (Mattsson, 1990; Di Stefano, 2004; Miller et al., 2009). One alternative is to manipulate the foraging choices of herbivores by using repellents to reduce the appeal of otherwise preferred plants (Nolte, 1999).

Many commercial repellents exist, only some of which have been tested experimentally, with variable results (e.g. Harris et al., 1983; Arnould and Signoret, 1993; Woolhouse and Morgan, 1995; El Hani and Conover, 1998; Nolte, 1998). Some repellents have shown promise as browsing deterrents but they often require valuable raw materials to produce, involve introduction of novel

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materials into an environment with unknown secondary effects, and reduce in effectiveness over time (Engle and Shimmel, 1984; Murray et al., 2006). An opportunity that has been largely overlooked is to take advantage of existing plant defensive chemistry, particularly from forestry by-products. Over their long history of co-existence with herbivores, plants have evolved a gamut of physical and chemical characteristics that deter consumption (Ehrlich and Raven, 1964). The latter include compounds that are either toxins (e.g. terpenes) or digestibility reducers (e.g. tannins, phenolic compounds) (Belovsky and Schmitz, 1994; Foley and McArthur, 1994). These defences result in some plants or parts of plants being less preferred or even avoided by herbivores either by conferring some negative consequences on handling and/or consumption, or by being associated with cues indicating such consequences (Provenza et al., 1992). It is therefore plausible that harnessing these chemical plant defences could help defend preferred plants from consumption.

We tested the potential of one such deterrent, birch bark extract (*Betula pubescens* and *B. pendula*), to protect commercially valuable Scots pine seedlings (*Pinus sylvestris*) from browsing by two large ungulates, red deer *Cervus elaphus* and European moose *Alces alces*. Birch bark contains tannins, phenols and terpenes (Palo, 1984; Vainiotalo et al., 1991), with several compounds implicated in reducing digestibility (Palo, 1985; Sunnerheim et al., 1988). The addition of birch bark extract to food pellets reduced consumption by another ungulate, the fallow deer (*Dama dama*; Bergvall et al., 2013). We extended this study to test the extract on a commercially important tree and its susceptibility to browsing by two globally significant ungulates.

In many areas of Scandinavia, red deer and moose co-exist and are major contributors to the mammalian browsing pressure on conifers (Nichols and Spong, 2014). Intense browsing by these herbivores has affected other components of ecosystems (Pastor et al., 1993; Pedersen et al., 2007) and reduced the profitability of the forestry industry (Heikkilä and Härkönen, 1996). Deterring red deer and moose from browsing Scots pine is particularly important as even very low levels of damage significantly reduce its production value (Nilsson et al., 2016).

Our study moved beyond the traditional tests of repellent effectiveness by considering both the distance between plants and the plant neighbourhood created by the application scheme. Foraging by large herbivores involves decisions made at a hierarchy of spatial scales from landscapes to parts of plants (Senft et al., 1987; Kotliar and Wiens, 1990); to understand how a repellent operates, it is therefore critical to consider the spatial context in which it is applied. We tested the effectiveness of birch bark extract at inter-seedling distances equivalent to those used in commercial forestry operations, and one larger and one smaller distance. There is a cost to foraging ungulates of greater distances between food items, manifested in faster movement between patches, larger and increased number of bites, and more time spent in patches (Shipley and Spalinger, 1995). These behaviours likely account for the pattern of moose browsing observed in Sweden, with greater damage at lower densities of Scots pine (Andrén and Angelstam, 1993). However, the plant neighbourhood can also affect herbivory, either by creating refuge for neighbours or by increasing their susceptibility to herbivory (Tahvanainen and Root, 1972; Atsatt and O'Dowd, 1976). Associational plant effects have been demonstrated across many taxa including large mammalian herbivores (Callaway et al., 2005; Bergvall et al., 2008; Stutz et al., 2015). For herbivores with movement capacities comparable to deer, the magnitude of associational effects decreases with greater distance between plants (Champagne et al., 2016); we therefore explored these effects as a function of inter-seedling distance.

Associational effects are influenced not only by relative plant palatability (based on nutritional content and plant defences), but also by the scale at which herbivores predominantly make foraging decisions (Tahvanainen and Root, 1972; Atsatt and O'Dowd, 1976). By applying a repellent to a plant, the plant's appeal to the herbivore should be reduced. Repellent-treated plants may protect their untreated neighbours from herbivory by reducing the appeal of the plant patch. This outcome is contingent on the herbivore making decisions based primarily on the palatability of the whole patch relative to other patches, rather than between plants within a patch (i.e. the between-patch scale). This is the classic case of associational refuge via the repellent plant mechanism (Atsatt and O'Dowd, 1976). In this way, not all seedlings may need to be treated to be effectively protected from herbivory, substantially reducing the amount of repellent needed in commercial operations. However, the inverse effect may be observed if herbivores choose primarily between plants within a patch (i.e. the between-plant scale). Untreated plants may then be more vulnerable to herbivores because they are of higher palatability relative to their treated neighbours, leading to associational susceptibility via the neighbour contrast mechanism (Bergvall et al., 2006). Being in a mixed palatability neighbourhood can also have consequences for repellent-treated plants: between-patch selection would result in greater consumption of treated plants due to the presence of the more palatable untreated plants (susceptibility via shared doom; Wahl and Hay, 1995), whereas between-plant selection would result in reduced consumption due to lower relative palatability (refuge via attractant-decoy or neighbour contrast; Atsatt and O'Dowd, 1976; Bergvall et al., 2006). In this study, we explored the potential for any associational plant effects that could result from different inter-seedling distances and repellent application schemes.

The effectiveness of a chemical plant defence may vary by herbivore species: they may differ in the physiological and behavioural mechanisms they have evolved for dealing with plant secondary compounds, and exhibit differing foraging strategies based on the quantity and quality of food they require for self-maintenance. Moose are both larger than red deer and consume a greater proportion of browse plants, such as trees and shrubs, as part of their diet (Hofmann, 1989). This may influence the relative foraging behaviours of these two ungulates, and we thus we expected that they could respond differently to seedlings in different neighbourhoods and at different inter-seedling distances. For both red deer and moose, we tested whether: (1) birch bark extract reduced the probability that a pine seedling was browsed; (2) inter-seedling distance affected browse probability overall; and (3) associational plant effects existed at any of the inter-seedling distances. We therefore not only determined whether birch bark extract could deter browsing of pines by red deer and moose, but tested associational plant effect theory in an applied context, with implications for repellent application in multi-ungulate systems.

2. Material and methods

2.1. Herbivores

We conducted our experiments with captive red deer and moose held in large enclosures (12 ha and 6 ha, respectively) in Södermanland, south-central Sweden. The red deer herd was kept at Tovetorp Research Station (Zoology Department, Stockholm University) and consisted of 11 individuals including one adult male, five adult females, and their five offspring from the previous season (all male). The moose were located approximately 1 km away at the Öster Malma Hunting Association's Wildlife Park; the group included one adult male and one adult female, with