



Roe deer prefer mixed-sex willow stands over monosexual stands but do not discriminate between male and female plants[☆]

Kim K. Moritz^{a,*}, Amy L. Parachnowitsch^b, Riitta Julkunen-Tiitto^c, Christer Björkman^a,
Matthew P. Ayres^d, Johan A. Stenberg^e

^a Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-75007 Uppsala, Sweden

^b Plant Ecology and Evolution, Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18 D, SE-75236 Uppsala, Sweden

^c Department of Biology, University of Eastern Finland, P.O. Box 111, FIN-80101 Joensuu, Finland

^d Department of Biological Sciences, Dartmouth College, NH 03755 Hanover, USA

^e Department of Plant Protection Biology, Swedish University of Agricultural Sciences, P.O. Box 102, SE-23053 Alnarp, Sweden

ARTICLE INFO

Keywords:

Dioecy
Detoxification limitation hypothesis
Plant secondary metabolites
Herbivory.

ABSTRACT

Male and female plants of dioecious species often experience differential herbivory, possibly due to differences in defences such as secondary metabolite composition or nutritional quality. These plant sex effects on herbivory have been extensively studied for plant individuals, but not for stands/populations. For mobile herbivores, such as deer, stands may be a more relevant scale to study than individual plants. We predicted that male *Salix viminalis* plants should be subject to more extensive roe deer (*Capreolus capreolus*) browsing than female plants due to weaker defence in male plants. Furthermore, we expected that mixed-sex stands should experience more damage than monosexual stands due to positive effects of diet mixing on browsing by generalists. We tested for differences in roe deer browsing in plots that were either monosexual male or female, or a mix of male and female plants in a replicated field experiment. Roe deer browsing was estimated after one growth season with heavy herbivory. We also measured plant secondary metabolite concentrations and nitrogen content in leaves from all experimental clones to test the assumption that the sexes differed in defence or nutrients. Mixed-sex plots were more extensively browsed than monosexual plots. However, there was no difference in browsing between male and female plant individuals within mixed-sex plots or between monosexual plots. Plant secondary metabolite profiles differed between male and female plants, while nitrogen content did not. Our findings suggest that the diversified plant secondary metabolite contents of mixed-sex plots may have led to more extensive herbivory. Higher browsing of plant sex mixes may impact both natural and commercial *S. viminalis* stands with different sex ratios.

1. Introduction

Sex-biased herbivory is common for plants and has long received attention (reviewed by Cornelissen and Stiling, 2005). However, reported studies of sex-biased herbivory have mainly dealt with effects on individual plants while effects over larger spatial scales, such as stands or populations, are not well-understood. Investigating plant sex effects at larger spatial scales is important, because plant sex ratios are often skewed and vary among species, populations, and stands, ranging from strongly female- to strongly male-biased (Barrett et al., 2010). Strong biases can especially be found within vegetatively reproducing species (Alliende and Harper, 1989). Male-biased sex ratios are more common than female-biased sex ratios in dioecious plants but biases in both

directions, and of sex ratios in equilibrium, are common (Field et al., 2012). Sex-biased abundances are at least in part dependent on genetic factors in several dioecious species (Alström-Rapaport et al., 1997; Åhman, 1997; Barrett et al., 2010). However, sex-biased abundances can also be explained partly by a higher mortality among plants of either sex (Lloyd, 1974), possibly due to herbivory (Elmqvist and Gardfjell, 1988).

An important difference between male and female plants of dioecious species can be in how well-defended they are against herbivores. For example, female and male dioecious plants often differ in plant secondary metabolite concentrations (e.g. Nybakken and Julkunen-Tiitto, 2013), and females tend to be better-defended both chemically and structurally (reviewed by Cornelissen and Stiling, 2005). Because

[☆] This article is part of a special issue entitled Sexual dimorphism in response to stress published at the journal Environmental and Experimental Botany 146C.

* Corresponding author.

E-mail address: kim.moritz@hotmail.com (K.K. Moritz).

female plants have higher reproductive costs (reviewed by Obeso, 2002), they are expected to grow more slowly (Lloyd and Webb, 1977). This can at least partly be explained by the Resource Availability Hypothesis, predicting that defence, growth and reproduction are traded off against each other (Coley et al., 1985). Meanwhile, a higher reproductive effort is often associated with a higher resource allocation to defence at further cost of growth, leading to the expectation that females are better-defended than males. Differences in defences has in turn been suggested as an explanation for why female plants often experience less herbivory than males (e.g. Cornelissen and Stiling, 2005).

Foraging choices by herbivores should balance intake of plants in a way that provides necessary nutrients while minimizing ingestion of harmful compounds (Marsh et al., 2006). Freeland and Janzen (1974) proposed that generalist herbivores diversify their diets in terms of toxin contents through consuming a diversity of plant species because they have a limited capacity to process high amounts of any particular plant secondary metabolite (the Detoxification Limitation Hypothesis). Studies of generalist herbivore diet choices and physiological effects of mixed diets across plant species have provided some support for the Detoxification Limitation Hypothesis (e.g. Dearing and Cork, 1999; Miura and Ohsaki, 2004; Unsicker et al., 2008; Pankoke et al., 2012; Sotka and Gantz, 2013). Thus, one may hypothesize that intersexual differences in defensive plant secondary metabolite content may lead to differences in browsing patterns across stands of different sex ratios. If total plant secondary metabolite concentration is important for herbivores, and female plants contain higher levels of secondary metabolites, monosexual female populations or stands should be subject to less herbivory than mixed or male ones. If, on the other hand, avoiding accumulation of single compounds is more important for herbivores, mixed-sex stands should experience more herbivory than monosexual stands.

We investigated how plant sex composition affects roe deer (*Capreolus capreolus* L.) browsing patterns in stands of a dioecious shrub used for bioenergy production, the common osier (*Salix viminalis* L.). Commercial plantations of *Salix* are often monoclonal and thus monosexual. Roe deer is a generalist that can cause serious damage to both wild *Salix* spp. plants as well as *Salix* short rotation coppice in Europe (Bergström and Guillet, 2002). We hypothesized that roe deer prefer male plants to female plants, and that a sexually mixed diet would be preferred to a monosexual diet. We expected male and female *S. viminalis* to differ in defence because it belongs to a genus where intersexual quantitative differences in plant secondary metabolites are well-documented (Nybakken et al., 2012; Ruuhola and Nybakken, 2013; Nybakken and Julkunen-Tiitto, 2013). We recorded natural browsing intensity in experimental *S. viminalis* field plots either with only males, only females or a balanced sex ratio and related herbivory patterns to intersexual variation in plant secondary metabolites. In addition, we measured leaf nitrogen (N) content as a proxy for nutritional quality. We tested the predictions that (i) female *S. viminalis* contain higher total plant secondary metabolite concentrations and (ii) individual male plants in mixed-sex stands are browsed to a higher extent. We also predicted (iii) that plant secondary metabolite profiles differ between sexes and (iv) that secondary metabolite diversity is higher in sex mixes. Finally, we tested the Detoxification Limitation Hypothesis-based prediction (v) that plant sex mixes are more extensively browsed than monosexual stands.

2. Materials and methods

The common osier (*S. viminalis* L.) is a dioecious shrub-like tree species that is naturalized in large parts of Europe and used in short rotation coppice forestry for bioenergy production. Natural populations and commercial plantations are often subject to herbivory from insects and mammals, and the first year is a critical phase because biomass removal, especially during summer, can reduce biomass production substantially (Guillet and Bergström, 2006). Previous studies have

established variation between sexes in terms of plant secondary metabolites in other *Salix* spp.; female leaves of *S. lasiolepis* (Boecklen et al., 1990) and *S. pentandra* (Hjältén, 1992) have been reported to have higher concentrations of total phenolic substances than males. However, there are also examples of the opposite pattern within the genus: Nybakken and Julkunen-Tiitto (2013) found that total phenolic acid concentrations were higher in male than in female *S. myrsinifolia*. The latter study also found that leaves from females contain higher total concentrations of salicin and SaOH-diglucoside than leaves from males. In addition to leaf chemistry, shoot tissue plant secondary metabolite concentrations often vary between sexes of *Salix* spp.; total phenol concentration is higher in female *S. lasiolepis* (Price et al., 1989) and salicortin concentrations have been found to be highest in stems of females of both *S. rigida* (Elmqvist et al., 1991) and *S. myrsinifolia* (Nybakken and Julkunen-Tiitto, 2013). For the present study we used cuttings of 20 female genotypes and 19 male genotypes (20 males collected, but one was later excluded – see explanation below) collected in March 2013 from clone archives holding clones originally collected in other locations in Sweden, outside Uppsala, Sweden (Latitude: 59°80', Longitude: 17°66'). The cuttings were stored in –5 °C dark rooms until planted in fields and a greenhouse.

Roe deer (*Capreolus capreolus* L.) is a common herbivore in large parts of the natural and naturalized range of *S. viminalis* and causes extensive biomass losses in *Salix* short rotation coppice plantations (Dimitriou et al., 2011). Fencing commercial *Salix* short rotation coppice plantations is an expensive management option and it is therefore important to find a method to reduce the negative impact of roe deer on the economic sustainability of bioenergy production. Roe deer avoids high total tannin concentrations and it has been suggested that they actively avoid high concentrations of single toxins by diversifying their diet (Verheyden-Tixier and Duncan, 2000), which would imply detoxification limitations.

The study area (Latitude: 58°83'N, Longitude: 17°78'E), is located east of Uppsala, Sweden. It is an open agricultural landscape surrounded by mixed coniferous and deciduous forests. Adjacent to the experimental area were agricultural fields with crops that included *Hordeum vulgare*, *Brassica napus*, and *Trifolium* spp. We frequently observed roe deer in, and in the proximity of, the experimental plots throughout the growing season. The other herbivores, which caused much less of the visible damage, included the European hare (*Lepus europaeus*) and various insect herbivores, most of which were coleopterans and lepidopterans. Hare browsing is easily distinguished from roe deer browsing by the former leaving cleaner, angled, cuts on lower parts of stems (Åhman and Bertholdsson, 2001). We observed this on plants that had died during the course of the field experiment and on few surviving plants.

To quantify plant secondary metabolite concentrations, and investigate potential differences between plant sexes and clones, we analysed leaf chemistry of greenhouse grown *S. viminalis* clones. We planted cuttings collected and stored as for the field experiment in January 2014. Five cuttings per genotype were planted in individual plastic pots (11 × 11 × 12 cm, Göttinger) with planting soil (Hasselfors™). Prior to planting, the soil-filled pots were heated in groups of six in a microwave oven at 900 W for 6 min to prevent soil contamination by microorganisms or plant seedlings from affecting secondary metabolite production or growth of *S. viminalis* plants, thus equalizing initial growth conditions. We grew plants randomly placed on trays in a greenhouse at 20 °C with 18 h of light per day and collected fully expanded single leaves from each plant after 6 weeks. The leaves were dried for two days in 18 °C, and milled using a ball mill (CryoMill, Retsch) with three 12 mm diameter steel balls for 2 min. We divided milling time over two rounds, with a one minute pause in between rounds, to avoid high temperatures that could potentially alter chemical composition. We stored the leaf material in transparent plastic vials in a cardboard box until extraction. 29 plants were not large enough after six weeks; these were either grown for an additional four

Download English Version:

<https://daneshyari.com/en/article/8887136>

Download Persian Version:

<https://daneshyari.com/article/8887136>

[Daneshyari.com](https://daneshyari.com)