Honor Student Paper:

Palatability of Winter Browse in The Snowshoe Hare (*Lepus americanus*) Herbivore Species Interactions

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ABSTRACT

The major constraint upon winter survival of the snowshoe hare is shortage of food. Ether-extractable resins contained in plants seem to play a prominent role in determining the palatability of a given species. Cafetaria-style experiments conducted revealed a significant difference in that white birch was more readily eaten than trembling aspen (higher resin). In the mammalian herbivory study, the significant difference in percent consumption was due to the lateral sprouts produced following browsing by hare as compared to the differently browsed basal sprouts. Further investigation of these different sprouts offered in terms of resin levels are still in progress. Rhoades (1985) mentions that maybe the evolution of a mechanism to recognize the salivary factors of the particular herbivore by the plant would allocate less to growth and more to defense following an attack. Experiments are in progress to understand better this potential salivary relationship.

INTRODUCTION

In northern latitudes, the availability of food in most habitats is lowest in winter. This lack of food, therefore, presents a crucial barrier for the snowshoe hare (*Lepus americanus*) to obtain high quality winter browse. In the fall, winter and spring, certain plants, by virtue of their specific life form and functions, will influence the movements and ranges of snowshoe hare (Bider, 1961). Moreover, the main abiotic parameters namely, wind, light and snow play independent restrictive roles in the winter movements of the snowshoe hare. For the most part winter movement seems to be determined by necessity.

The most widespread predator deterrent of plants is what might be termed "chemical warfare" (Pianka, 1983). Plants contain a vast array of secondary compounds and have distinct seasonal patterns both with respect to growth and to carbon and nutrient allocation. These are plant characteristics that have important implications for palatability and resistance to herbivores. Forage selection patterns are largely the result of avoidance of plant tissues that contain high concentrations of secondary chemical constituents that are antagonistic to vertebrate herbivore fitness.

Given a choice, hares consistently prefer mature growth forms over intermediate and juvenile growth forms. The preferred food supply of snowshoe hare consists of the early- and mid-successional deciduous trees and shrubs. Some of the trees include: a) *Betula papyrifera* ssp. *humilis* (Alaska paper birch), b) *Populus tremuloides* (quaking aspen), c) *Populus balsamifera L.* ssp. *balsamifera* (balsam poplar), d) *Alnus crispa* ssp. *crispa* (green alder) and e) *Salix alaxensis* ssp. *longistylis* (feltleaf willow) (Bryant, 1981). Snowshoe hare clip twigs (diameter <4mm) and also strip or gnaw the bark which characteristically will have large toothmarks and a shaggy appearance.

Survival of various species of trees and shrubs are differentially influenced by barking pressure. Barking is heavier on species in open-grown places than in dense stands. Browsing takes place over a longer period of the year than barking. The localized distribution of high browsing and barking intensity seems to be governed mainly by the successional stages of the vegetation (de Vos, 1964). Hares switch from a diet of herbaceous vegetation to browsing woody vegetation with the arrival of the first frost. This activity reduces plant vigor and also stimulates increased branching of twigs. Girdling results in death because there is complete removal of the cambial layer and growth of adventitious sprouts.

There is an extreme flexibility with respect to chemical defense in the browse. The advantage of this is that energy rich substances, such as resins, appear to be produced after severe browsing whereas, when there is little browsing, the carbons are allocated to growth of the plant.

The present research project focusses on allelochemics in relation to palatability for the snowshoe hare (*Lepus americanus*). Browsing in relation to timing in the season, use of allelochemics and the effects of other herbivore activities was studied. The main objective of this study then was to assess what balance exist between the damage brought about by hare browsing and the plant's defensive response in relation to palatability. In order to determine this, the following hypotheses were tested:

1. Does the browsing product from different herbivores (beaver, hare, human and forest tent caterpillars) affect the plant in such a way as to affect the browsing activity of the snowshoe hare?
2. Is mechanical clipping of available browse of equal effectiveness to browsing, in terms of how the plant responds?
3. Does the snowshoe hare's browsing timing represent a crucial factor in the timing of plant response?

METHODS

Site selection

The sample area chosen for collection of browse was the Lake Laurentian Conservation Area in Sudbury, Ontario (Lat 46° 27' 30" N; Long 80° 56' 30" W.) Both white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) were selected as they were found to be abundant and the most frequently browsed. The overall experimental feeding site for all these twig collections was located in an area, 12 km west of Sudbury, Ontario, where hares were both abundant and active. Sampling was performed as follows:
a) To study the effects of different herbivores, four sites were selected in the summer of 1988 in order to mark trees defoliated by caterpillars and undefoliated trees. In the winter of 1988-1989, three other sites were selected in the Conservation Area which included browsing by hares, beavers and mechanical clipping by humans.
b) To examine the effects of mechanical clipping versus browsing by hares, another site was chosen at Wanup (34 km SE of Sudbury, Ontario) for a year-long study.

Experimental design

The experimental layout for the cafeteria-style experiment was six individually separated rectangular areas (4X2 m each) that were each sub-divided into eight compartments. Randomly placed bundles of twigs were left to be freely browsed by the snowshoe hares for 7 days.

Collection of samples

For every collection, twigs utilized had a diameter of < 4 mm which is usually considered to be the preferred size by snowshoe hare (Reichardt, *et al.*, 1984).

Samples collected for the forest tent caterpillar study consisted of 12 trembling aspen and 12 white birch trees. Six trees of each species had suffered severe defoliation whereas the remainder had not been attacked and were used as controls. A twig (<4mm) bundle and a control bundle (to determine the degree of dessication) for each tree was fastened together and presented to the hares, upright, to mimic a shrub. Selection of twigs was done in such a way as to achieve optimal similiarity between the bundles.

Samples collected from beaver, hare and human activity consisted of white birch, which were either cut by beavers, mechanically clipped by pruning shears, or browsed upon by snowshoe hares. Every collection consisted of basal sprouts except for the lateral sprouts that had grown in response to browsing by snowshoe hare.

At the Wanup site, three different areas of white birch (diameter up to about 6cm) were chosen and enclosed using chicken wire fence. The fenced-in areas had been previously either severely browsed by snowshoe hare, or, as far as could be determined, had never been browsed at all by hares. The latter trees were fenced either following mechanical clipping with pruning shears or left untouched to be used as a control. Lastly, one area of heavy hare activity was left unfenced. The following winter, 1989-1990, bundles of twigs from each of the three fenced-in area and the unfenced area were prepared using the regrowth of each of the trees.

Chemical analysis

All samples were analysed for the extractable resin content following the method of Chapin *et al.* (1985). This ether-extractable fraction is a complex of waxes and secondary metabolites that have been shown to be repellent to mammalian herbivores (Bryant, 1981).

RESULTS AND DISCUSSION

Effect of insect herbivory

In the present study on insect herbivory, there was no significant difference ($P<0.05$) in consumption by snowshoe hare of the bundles of twigs prepared from trees that had been defoliated by forest tent caterpillar the previous summer, from the undefoliated controls (Fig 1). There was a significant ($P<0.05$) species difference, however with white birch being selected over trembling aspen irrespective of insect defoliation (Fig 1). It is assumed, therefore, that damage brought about by the forest tent caterpillar was confined to the tree foliage and not to the twigs. Other studies, however, seem to indicate that larvae grew poorly on foliage from trees defoliated in the previous year (Haukioja and Neuvonen, 1985). Samples of the twig bundles that remained following browsing were analyzed for resin content. The levels of resin were higher in the trembling aspen as compared to the white birch (Fig 1). There was no significant difference ($P<0.05$) between resin levels of the

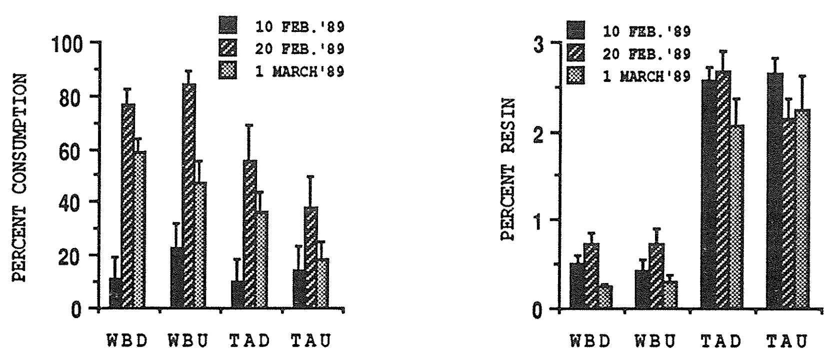


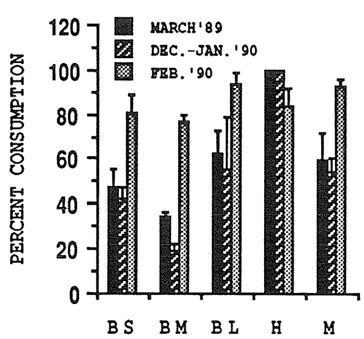
Fig. 1 Percent consumption (n=6) of, and percent resin (n=18) in, twig bundles of white birch and trembling aspen, whose leaves had been attacked by forest tent caterpillar. WBD=white birch defoliated; WBU=white birch undefoliated; TAD=trembling aspen defoliated; TAU=trembling aspen undefoliated

undefoliated and defoliated twigs of each respective study species. The weight loss of the control bundles owing to dessication was negligible. Levels of resin and the percentage of twigs eaten seem to indicate that as the level of resin rises, the degree of browsing decreases (Fig 1).

Effect of mammalian herbivory

Percent consumption was significantly different (P<0.05) for all categories of mammalian herbivory for the first two runs (March '89; Dec-Jan '90)(Fig 2). The difference was due to the hare browsed lateral sprouts which were totally consumed as compared to the other choices. The last run (Feb '90) showed no significant difference (P<0.05) for all categories (Fig 2). Resin levels for the first run was not significantly different (P<0.05) for basal sprouts produced from large beaver-cut stumps, lateral sprouts following hare browsing and the mechanically-clipped basal sprouts, but was different for the basal sprouts that initiated from small and medium sized beaver-cut stumps (Fig 2). Again, the percent consumption and the level of resin are in agreement with the experiment on insect herbivory in that twigs with elevated resin levels were less browsed. Control bundle weight loss owing to dessication was also negligible. Data for the second (Dec-Jan '90) and third (Feb '90) runs are as yet unavailable owing to analytical equipment failure.

In the mammalian herbivore study, beavers seem to react to palatability in a similar fashion to that of the snowshoe hare. Basey *et al.* (1988) state that when the juvenile form of aspen is uncommon in an area (ie. low levels of previous beaver activity) the beavers choose aspen by size following what is known as the optimal foraging model. On the other hand, when beavers are abundant they select large diameter trees that are more likely to have a low concentration of a specific phenolic compound. Thus in conducting this experiment, the sprouts presented to the hares had previously been rejected by beaver as being of low palatability (Fig 2). The data seem to indicate that there is a difference in taste preference because the hares browsed these twigs. The lateral sprouts from a hare-browsed tree were preferred by the hare and contained little resin (Fig 2). This finding indicates that the lateral sprouts do not have the same chemical defense strategy as the adventitious shoots which deter hares readily. The resin content determination of this same series of twigs is incomplete.



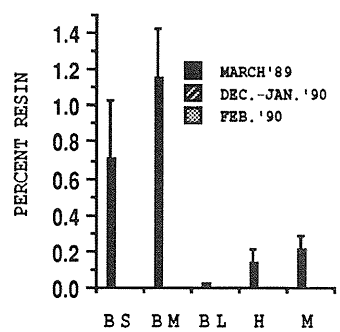


Fig. 2 Percent consumption (n=3) of, and percent resin (n=9) in, twig bundles of white birch previously browsed by beavers or hare or subjected to mechanical clipping. Basal sprouts from: BS=small, beaver browsed stump (<3cm); BM=medium, beaver browsed stump (3-5cm); BL=large, beaver browsed stump (>5-6cm); M=mechanically clipped trees; and Lateral sprouts from: H=hare browsed trees

Effect of browsing technique

Percent consumption differences were only detected between the unfenced trees (Hare) and the fenced control, and between the unfenced trees and the mechanically clipped trees (Fig 3). Mechanical clipping does not affect palatability to the same extent as browsing by hares which indicates an allelochemic response in trees that have been naturally browsed. If this is true, the effect is long-lived because hare-browsed trees that were fenced in the spring of 1989 showed no difference in palatability from trees which hares had been able to browse as they wished (Fig 3). Further analysis of twig resin levels will be investigated to support the second and third hypotheses.

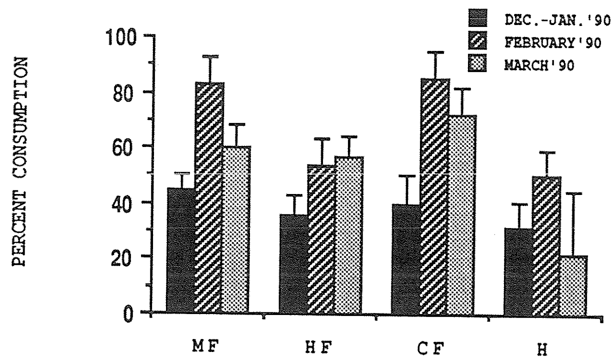


Fig. 3 Percent consumption by snowshoe hare of twig bundles of white birch (n=3). Fenced off: MF=mechanically clipped; HF=hare browsed; CF=control; Unfenced: H=hare browsed

CONCLUSIONS

Over the years the strong selection pressures imposed by populations of herbivores have affected the vegetation that forms part of their environment through many different mechanisms. Important factors include seasonal climatic conditions, the location of herbivore and plant, both spatially and temporally, and changes in the respective population densities. Plant species with their inherent genetic potential are subject to predictable, systematic and directional pressures from herbivores which participate with them "in a continual evolutionary dance" (Levin, 1976).

It is recognized that juvenile-form woody plants express traits associated with low palatability to browsing mammals (Schaffalitzky de Muckadell, 1962). It is also observed that herbivores such as the snowshoe hare do not feed on all different parts of a plant but only specific ones (Bryant *et al.*, 1983).

Hares clearly are able to select preferentially the browse that they eat both in terms of species and degree of palatability. The resin content in a given food species seems to play a critical role in the selection of browse by hares. Data collected support other reports in the literature; namely, that species that contain low levels of resin are preferred over those with high resin contents. Other mammalian and insect herbivores do not seem to affect hares directly but actually contribute (in the case of beaver) to an increase in browse availability. The effects of hare saliva on browsed twigs will be confirmed further after more resin analyses have been performed.

Snowshoe hares definitely play a vital role in the adaptive history of plant species and, in return, allelochemics allow for palatability levels to change. To ensure the survival of both snowshoe hares and the plants that they eat, this evolution is continuous.

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