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UNIVERSITY OF ALBERTA

EFFECT OF INHERENT PLANT TRAITS AND TASTE REPELLENTS ON THE PALATABILITY OF CONIFERS TO SNOWSHOE HARES

by

SHEILA A. RANGEN

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE
IN
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DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA

FALL 1991

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Destiny is no matter of chance.

It is a matter of choice:

It is not a thing to be waited for,

It is a thing to be achieved.

William Jennings Bryan

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled EFFECT OF INHERENT PLANT TRAITS AND TASTE REPELLENTS ON THE PALATABILITY OF CONIFERS TO SNOWSHOE HARES (Lepus americanus) submitted by SHEILA A. RANGEN in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in WILDLIFE PRODUCTIVITY AND MANAGEMENT.

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Dr. A.W. Bailey

Date SEPT. 10, 1991.

To Mom and Dad

Abstract

In one part of this study, snowshoe hare feeding preferences for four conifer species, Siberian larch, Norway spruce, white spruce and black spruce, were examined under ad libitum feeding conditions. Final preference measures indicated that two-year-old Siberian larch and Norway spruce were equally selected by hares, though Siberian larch was browsed more than Norway spruce during the first two-thirds of the experiment. White spruce was browsed very little. Overall, plant nutrients and secondary metabolites were not highly correlated with browsing values. However, Siberian larch exhibited significantly high crude protein and calcium and low fiber, while Norway spruce exhibited significantly low condensed tannins and total phenols. The ingestion of large quantities of both Siberian larch and Norway spruce was in agreement with the buffer hypothesis, whereby the ingestion of plant species low in nutritive value or containing toxic substances in small amounts proportional to the total feed intake may produce no ill effects. Four-year-old black spruce was preferentially browsed compared to white spruce of the same age. Black spruce contained significantly high crude protein, calcium and phosphorous and low cellulose and total phenols. As a result of the comparison of only these two species, the evidence suggesting that plant nutrients or plant secondary compounds may control forage selection by snowshoe hares was inconclusive.

In the second part of this study, palatability of white spruce treated with chemical repellents, Anispray®, Anipel® and Bartlett Ropellent®, was assessed in preference and acceptability experiments. Anispray and Bartlett Ropellent were foliar sprays, whereas Anipel was a systemic repellent in two tablet forms. Concentrations of Anispray, ranging from 25% to 100%, did not reduce hare damage to white spruce trees. Neither type of Anipel tablet nor method of application affected forage selection, though one type of tablet gave an indication of attractant rather than repellent properties. During the first and second winters following chemical application, hares under restricted feed conditions preferred untreated trees to those treated with Bartlett Ropellent. Unprotected current annual growth and 89% of apical stems were

clipped by hares the second winter, such that the effectiveness of this repellent may not be significant biologically. Naive and experienced hares consumed similar proportions of white spruce treated with Bartlett Repellent, indicating that a learned food aversion had not been established with experienced animals. The decreased consumption of untreated twigs by naive hares in comparison to experienced hares suggested that a neophobia had developed in naive animals or that experienced animals were more adept at differentiating treatment types.

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Table of Contents

List of Tables

List of Figures

1. General Introduction

1.1 Ecology of the Snowshoe Hare

Snowshoe hare (Lepus americanus) populations cycle every 8-12 years with animal densities ranging from 1.8/ha to 11.3/ha (Keith and Windberg 1978). In Alberta, where the distribution of the snowshoe hare is ubiquitous except for remote southern and southeast areas, differences in density extremes of 40:1 have been exhibited (Tomm 1978). The prolific reproductive capacity of lagomorphs contributes to the periodic fluctuations as hares in central and northern Alberta generally produce 3-4 litters annually (Keith 1972).

Alterations in the behavior of snowshoe hares when population numbers are increasing may help initiate presaturation dispersal, causing the carrying capacity of refugia to be exceeded and hares to move into suboptimal and marginal habitats including cutovers, early successional areas and newly established conifer plantations (Radvanyi 1987; Trapp 1962; Wolff 1980). Sinclair (1986) ascertained that a combination of resource (extrinsic) and behavior (intrinsic) factors serve as regulatory mechanisms for snowshoe hare populations. When food becomes limited, social behavior modifies so that some individuals acquire an adequate amount of food while others, particularly immigrants and immature hares, do not. Juvenile hares are usually the individuals which emigrate as a result of intra-specific competition for resources (Lockley 1961; Meslow and Keith 1968; Myers and Poole 1963; Mykytowycz 1960).

As a consequence, younger animals sustain a higher risk of predation, exposure and starvation in open habitats. Physiological stress also accompanies an increased energy expenditure in searching for browse. Dolbeer and Clark (1975) found survival rates of immature adults averaged 23% in dense cover and 4% in open areas. Juveniles appear to suffer greater mortality than adults (as high as 98%) when high cyclic densities prevail (Keith 1972; Windberg and Keith 1976; Wood and Munroe 1977). Frustrated dispersal or mass migrations associated with peak winter populations may also occur when all acceptable habitats are full and surplus animals have no other alternatives (Lidicker 1973).

Habitat patchiness and interspersion are important factors regulating the distribution of hares. Refugia or optimal habitat are where hares are present at all phases of the population cycle. Suboptimal habitat generally has a greater availability of food, but the degree of cover is significantly less than that of refugia (Wolff 1980). Open habitat may be termed marginal and is the least preferred because cover is virtually non-existent. Substantial foliage densities 1-3 m above ground level provide cover from both avian and terrestrial predators (Wolff 1980; Radvanyi 1987). The presence of low, dense woody cover, particularly coniferous, is essential for winter food, thermal cover and protection from predators. Several studies have documented that hares are not usually found in areas greater than 200-400 m from coniferous stands (Conroy et al. 1979; Keith 1974; Keith et al. 1984). It may be noted, however, that during years of peak populations, the effectiveness of vegetation-free zones up to 400 m may be nullified as a result of forced emigration from intra-specific competition (Radvanyi 1987).

Areas of habitat interspersion are preferred to densely canopied areas as these sites commonly have denser understory vegetation and slash cover. In Alberta, Keith (1972) described prime snowshoe hare habitat as aspen (Populus tremuloides) conversion sites which are products of post-fire succession and logging practices. Similarly, shrubby and immature conifer cover bordering swampy and riparian areas or other natural openings were frequently associated with aspen sites that were densely populated with hares. Litvaitis et al. (1985) correlated spring population levels and overwinter survival with the thermal and escape cover afforded by understory density. Also, understory such as low bush cranberry (Vibernum spp.) only offered concealment, whereas hazel (Corylus spp.), willow (Salix spp.) and alder (Alnus spp.) provided nourishment in addition to cover during the winter (Keith 1972).

The diet of the snowshoe hare consists of forbs, grasses and the leaves of woody plants during the summer and the twigs and bark of woody plants during the winter (De Vos 1964; Klein 1977; Telfer 1972). Bryant and Kuropat (1980) outlined forage preferences of both snowshoe hares and mountain hares as follows: willow ≥ aspen ≥ larch (Larix spp.) ≥ birch (Betula spp.) ≥ jackpine (Pinus banksiana) = lodgepole pine (P. contorta)

- scots pine (P. sylvestris) ≥ white pine (P. strobus) ≥ red pine (P. resinosa) ≥ fir ≥ white spruce (Picea glauca) ≥ black spruce (P. mariana). Despite the general preference for deciduous browse species, conifers appear to be a major diet item for hares throughout North America. Moreover, spruce appears to be an important forage species over a large geographical area, but pine tends to be preferred when available.

1.2 Forage Selection

Forage selection by the snowshoe hare, a generalist herbivore (Vangilder et al. 1982), is affected by numerous factors. The multiplicity of characteristics that affect the palatability of snowshoe hare forage are compounded by the ten-year cyclic fluctuations of hare populations (Keith 1972; Keith et al. 1984; Keith and Windberg 1978; Sinclair and Smith 1984). Palatability may be defined as the selective intake response as determined by the interrelationship between the browsing herbivore, the plants offered the animal and the surrounding environment (Marten 1978). Preference and acceptability are two characteristics upon which the complex phenomenon of palatability is based. Forage preference involves a choice when an animal is confronted with more than one feed type. Forage acceptability comprises a no-choice situation where an animal either finds a single feed acceptable or unacceptable.

A wide array of animal factors affect forage palatability. Palatability may be regulated by basic physiological parameters such as blood sugar level, body temperature, reproductive state, adipose stores (Heady 1964; Young 1948) and morphology of the mouthparts and digestive tract (Bell 1969; Hoffmann 1973; Bunnell and Gillingham 1985). For example, in snowshoe hares, fermentation occurs in the posterior portion of the gut (Demment and Van Soest 1985; Uden and Van Soest 1982). The chemosensory mechanisms of touch, sight, smell and taste elicit various responses to the stimuli afforded by food. Previous experience also may affect food preferences and acceptability of herbivores (Arnold and Maller 1977; Bartmann and Carpenter 1982; Bartmann et al. 1982). The concept of animal instinct applied to forage selection, also known as nutritional wisdom, suggests that an animal can select the diet best suited to its nutritional needs or deficiencies (Marten 1973; Zahorik and Houpt 1977). However, there is evidence which correlates snowshoe hare forage preferences with what are considered to be both nutritionally and unnutritionally wise choices (Bryant and Kuropat 1980; Pease _et_ _al_. 1979; Sinclair _et_ _al_. 1982).

In addition to characteristics of the snowshoe hare, there are various extrinsic and intrinsic plant factors which influence forage palatability. Morphological and physical plant traits as well as age may affect the forage selection process. For example, the mature-growth phase of trees and shrubs are selected by hares prior to juvenile growth phases and apical shoots of conifers are generally selected over lateral branches (Dimock _et_ _al_. 1976; Klein 1977), which may be further related to chemical composition. Inter-specific variation in addition to the frequency and distribution of these species influence feeding preferences. Snowshoe hares generally prefer willow and aspen rather than birch, alder and conifers (Bryant and Kuropat 1980; Klein 1977; Sinclair and Smith 1984). In New Brunswick, Parker (1984) found that hares browsed deciduous twigs at a rate greater than the abundance and twigs of conifers were browsed relative to the availability. However, the availability of diet items varies with locale and season.

The intrinsic chemical composition of plants, including nutrients (Lindlof _et_ _al_. 1974; Miller 1968; Pease _et_ _al_. 1979; Radwan and Campbell 1967; Sinclair _et_ _al_. 1982) and plant secondary compounds such as alkaloids, phenols and terpenoids (Bryant 1981; Bryant and Kuropat 1980) appears to be important in the selection of forage species by hares. Slow-growing species such as gymnosperms may make large investments in plant secondary compounds compared to fast-growing species like many angiosperms because conifers retain their needles and do not grow heavily defended juvenile shoots in response to browsing by herbivores (Coley _et_ _al_. 1985; Sinclair _et_ _al_. 1988). Swain (1978) indicated that gymnosperms rely more heavily on condensed tannins and terpenes than other plant secondary metabolites such as hydrolyzable tannins, alkaloids, cyanogenic glycosides and glucosinolates. Inherent intra-specific plant characteristics also influence feeding strategies. For example, snowshoe hares were reported to preferentially select specific Douglas-fir

(Pseudotsuga menziesii) genotypes (Dimock et al. 1976). Radwan (1972) correlated the resistance of Douglas-fir clones to black-tailed deer (Odocoileus hemionus) browsing with a low digestibility and high concentration of fats and essential oils.

Environmental factors further influence the palatability of forage species including plant disease, animal excrement, synthetic chemical applications, edaphic characteristics and climatic seasonal and diurnal variation (Heady 1964; Marten 1973). For example, soil fertility and shade were shown to affect the terpene concentrations in Alaska paper birch (B. resinifera) and subsequently twig palatability (Bryant et al. 1987). Snow depth in conjunction with tree height is also an important determinant of browse availability. Young or shrubby deciduous plants and conifer seedlings are protected from browsing once covered by snow (Pease et al. 1979; Wolff 1980). However, with adequate snow accumulations, hares may browse at heights ranging from 60-170 cm above ground level (De Vos 1964; Pease et al. 1979; Telfer 1972), enabling hares to clip apical branches otherwise out of reach.

Seasonal variation has a major impact on forage palatability. Snowshoe hares feed on grasses, forbs and the leaves of woody plants during the summer, while the winter diet consists of bark and small diameter lateral and apical twigs of shrubs and deciduous and coniferous trees (De Vos 1964; Telfer 1972). According to De Vos (1964), browsing damage to young conifers occurs primarily from November to May after frosts have destroyed succulent vegetation. In Alaska, the amount of leafy herbaceous plants in the diet increased from 1.5% in winter to 8% and 49% in April and May, respectively, as the intake of spruce and woody browse decreased from 82% to 56% and 25%, respectively (Wolff 1980). Telfer (1972) noted that coniferous species comprised more than half of the available winter browse in New Brunswick, yet conifers still afforded 66% of the hares' diet when the frequency of occurrence of deciduous species was greater relative to conifers.

1.3 Impact of Hares on Forestry

Clipping, identified as smooth, oblique cuts on apical and lateral shoots, and barking on trunks and lower limbs, are the two types of tree injuries caused by hares. In the literature, browsing collectively refers to both damage categories but in the present study it will be used to refer to clipping only. Sustained damage suppresses tree growth (especially height when the apical stem is clipped) and survivorship, and may cause deformities. With successive apical browsing, a tree will develop multiple apical stems and become shrubby in appearance. Complete or partial girdling often causes direct or indirect mortality as the bark and cambium layer are peeled away (Lloyd-Smith and Piene 1981). Removal of bark also increases a plants's susceptibility to fungal infections, insects and disease.

A foresters' knowledge of the proximate and ultimate causes influencing the palatability of forage to snowshoe hares may assist in the development and implementation of reforestation practices to minimize depredation of conifer seedlings. Compared to deciduous species, conifers generally are not highly preferred by hares but the shoots, buds and bark of conifers may be browsed extensively during peaks in hare populations (Aldous and Aldous 1944; Keith 1972; Radvanyi 1987; Tomm and Hudson 1978). As a consequence, concomitant with the peak of the cycle, foresters have documented extensive damage to conifer seedlings in plantations as a result of browsing by hares. Johnson and Walker (1976) documented a 91% seedling mortality from clipping by hares of lodgepole pine as compared to 42% for white spruce in the Peace River region of Alberta. In central and northern British Columbia, 38% of lodgepole pine were girdled (Sullivan and Sullivan 1982) and 24-42% were clipped with an 8% girdling rate (Monts 1980), respectively. In Minnesota, Aldous and Aldous (1944) reported a survival of 43% and 77% in red and white pine seedlings. Of the surviving trees, 85% and 94%, respectively, were damaged. A Douglas-fir plantation in Oregon had an estimated damage from clipping of 94% the first year with 35% mortality (Moore 1940). Also in the Pacific Northwest, hares accounted for 80%, 67% and 34% of deformed Douglas-fir, Port-Orford cedar (Chamaecyparis lawsoniana) and Western hemlock (Tsuga heterophylla), respectively (Staebler et al. 1954).

1.4 Snowshoe Hare Damage Control

Since the early 1900's, when snowshoe hares were identified as a problem wildlife species to forest managers of North America, this lagomorph became the focus of extensive pest management control programs. Several means of population control and silvicultural techniques have coevolved to help alleviate browsing impacts from snowshoe hares (Radvanyi 1987). Types of population control include the provision of alternate food sources, introduction of predators or disease and use of chemosterilants, toxic baits, anticoagulants, traps or snares. Forest management practices encompass habitat manipulation, herbicide application, timing the planting of seedlings to coincide with the low phases of the snowshoe hare cycle and planting larger nursery stock.

1.5 Experimental Objectives

The present study investigated two silvicultural management strategies for the control of snowshoe hare depredation to conifer seedlings, namely, the selection of less preferred plant species for reforestation and the application of chemicals to deter hare browsing.

The first specific objective was to determine snowshoe hare preference ratings of four conifer species and to relate the resulting preference rankings to forage quality. The evaluation of inter-specific genotypes to snowshoe hare browsing would enable foresters to regenerate green areas with the most resistant species. Native and non-native species were selected based on their ability to survive environmental conditions in Alberta and to yield acceptable forestry end-products. The second objective was to examine snowshoe hare feeding preferences for conifers treated with three chemical deterrents. Extensive work has studied both natural and chemical repellents and aversive agents as deterrents for snowshoe hare browsing (Gillingham _et al_. 1987; Hooven 1966; Pepper 1976; Radvanyi 1987; Sullivan and Crump 1984; Sullivan _et al_. 1985; Walter and Soos 1961). In addition to the genotypic variation among conifer species, selected chemical repellents may aid in the protection of existing and newly planted reforestation areas from depredation by snowshoe hares, and thus, reduce the immense monetary losses incurred.

Two major hypotheses were tested:

1) snowshoe hares differentially browse Siberian larch (_L_. _sibericus_), Norway spruce (_P_. _abies_), white spruce and black spruce and a high

plant nutrient and low secondary metabolite content are correlated with high browsing values.

2) snowshoe hares demonstrate a lower intake of conifer seedlings treated with the chemical deterrents Anispray®, Anipel® and Bartlett Ropellent® relative to untreated seedlings.

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2. Snowshoe Hare Preferences for Conifer Species and the Potential Use of Selected Conifers in Reforestation

2.1 Introduction

Three major hypotheses have been examined to explain snowshoe hare forage selection. The first hypothesis suggests that nutrients such as protein or compounds that supply energy form the basis for food preferences (Lindlof et al. 1974, 1978; Sinclair et al. 1982; Wolff 1980). The second theory suggests that hares avoid consuming various plant species or plant parts as a result of the presence of repellent, toxic and digestion-inhibiting plant secondary compounds (Bryant and Kuropat 1980; Bryant 1981a,b; Pehrson 1981, 1983; Bryant et al. 1983; Palo 1984; Palo et al. 1983a,b). The third hypothesis accounts for the potential synergistic effects of both plant nutrients and secondary metabolites, whereby animals may eat quantities of forage with high concentrations of defensive chemicals when buffered by the intake of other less affected feedstuffs (Sinclair and Smith 1984; Klein 1977; Zahorik and Houpt 1977).

Numerous studies have attempted to correlate either total phenols or total resins with feeding preferences of snowshoe hares. In general, findings have been inconsistent and it has been suggested that this incongruity is the result of only a few chemicals or a single chemical producing antifeeding effects rather than an entire class of compounds (Bryant et al. 1985; Cooper et al. 1988; Reichardt et al. 1984; Sinclair and Smith 1984; Tahvanainen et al. 1985). In addition, only a small portion of a class of compounds may have biological consequences and subsequent antifeeding effects. For example, the oxygenated monoterpene camphor in white spruce (Sinclair et al. 1988), the triterpene papyriferic acid in Alaska paper birch (Betula resinifera) (Reichardt et al. 1984), the ß-tannin or stilbene pinosylvin methyl ether in green alder (Alnus crispa) (Bryant et al. 1983; Clausen et al. 1986) and the flavonoid 2,3,6-trihydroxydihydrochalcone in balsam poplar (Populus balsamifera) (Jogia et al. 1989) have been specifically identified as feeding deterrents for snowshoe hares.

Polymeric phenolics generally have greater biological effects than simple phenolics (Levin 1976). Condensed tannins and hydrolyzable tannins are two types of polyphenols which have been attributed with antifeeding effects. Of the total tannins, gymnosperms have no hydrolyzable tannins, approximately 74% condensed tannins and the remaining 26% consists of other tannin groups, primarily ß-tannins (Swain 1976, 1979). Condensed tannins may attach to the cellulose or protein bound to fiber of cell walls, thus inhibiting fermentation of cell wall components by microflora (Zucker 1983). This may be of particular importance to lagomorphs if hindgut fermentation is impaired and nutrient availability is reduced. Hydrolyzable tannins may inactivate digestive enzymes and are 5 to 10-times more astringent and more effective at binding protein than condensed tannins (Swain 1974, 1976; Zucker 1983). Nevertheless, condensed tannins are comparatively stable chemically and are subsequently more difficult to detoxify (Swain 1976, 1979).

Robbins et al. (1987) suggested that soluble phenolics act as defensive chemicals by reducing intake following absorption through toxic effects, altering physiological systems or creating additional energy demands for detoxification rather than through the inhibition of digestion. Substantial evidence implicates the importance of tannins in controlling the feeding of phytophagous insects (Bernays and Chapman 1977; Feeny 1968, 1970; Klocke and Chan 1982). Other findings have also related tannin content with a lowered feed intake or digestibility and toxic effects in herbivores (Cooper and Owen-Smith 1985; Cooper et al. 1988; Jambunathan and Mertz 1973; Lindroth and Batzli 1984; McLeod 1974; Oates et al. 1977; Robbins et al. 1987; Wrangham and Waterman 1981). Swain (1978a) suggested that the threshold limit for vertebrate ingestion of condensed tannins was approximately 0.3%, yet concentrations found in plants often exceed this.

This study investigated snowshoe hare feeding preferences for four coniferous species and the ultimate causes for these food choices based on nutritional and phenolic parameters. The objectives were to:
a) determine snowshoe hare preferences for two-year-old Siberian larch (Larix sibericus), Norway spruce (Picea abies) and white spruce (P. glauca); b) determine snowshoe hare preferences for four-year-old black spruce (P. mariana) and white spruce; c) correlate feeding preferences with nutrient and phenol levels; d) use the results of conifer species

preferences to suggest improvements for reforestation practices. The working hypotheses were that snowshoe hares demonstrate a differential preference for Siberian larch, Norway spruce, white spruce and black spruce and that forage selection was positively correlated with nutrients and negatively correlated with phenols.

2.2 Materials and Methods

2.2.1 Study Area

The study was conducted at the Alberta Horticultural Center and Tree Nursery (AHCTN), Edmonton, Alberta (53°41'N latitude and 113°32'W longitude, elevation approximately 660 m). The geographic region is dominated by a mosaic of grasslands and aspen stands characteristic of the Central Parkland ecoregion (Strong and Leggat 1981). The AHCTN itself is a composite of cultivated fields interspersed by native (18%) and non-native (82%) shelterbelts. Research was conducted in a cultivated field bordered by Basford willow (Salix fragilis Basfordiana), lilac (Syringa villosa), Colorado spruce (P. pungens) and caragana (Caragana arborescens) shelterbelts. A small marsh was located to the northwest of the test pens.

The climate and geology of the site have been described by Bowser et al. (1962). The climate is classified as intermediate between dry and moist sub-humid. Mean temperature for November to March is 8.3°C and for April to October is 11.3°C with approximately 153 frost-free days (values averaged during 1974-1990). Mean annual precipitation is 447.2 mm, of which 80.8% is rainfall. The underlying Upper Cretaceous bedrock is of the Edmonton rock formation. This formation is characterized by bentonitic sandstones, sandy shales, bentonitic clays and coal seams. The Laurentide ice sheet deposited medium-textured alluvial lacustrine material and created level to gently undulating topography in this area. The soils are predominately well drained eluviated black soils of the chernozemic order.

2.2.2 Pen Facilities

Experiments were conducted in outdoor pens used previously for related research (Hawley, unpubl. results). The pens had a perimeter fence 1.5 m high composed of 1x1" poultry wire with a layer of plastic snow fencing 1.2 m high from ground level to protect the animals against inclement weather. Subdivisions within this perimeter were constructed of 1x1" poultry wire only. A roof of 1x1" plastic netting covered the enclosure to exclude avian predators as experimental trials were conducted with conifers planted *in situ* in these pens.

2.2.3 Snowshoe Hares

Snowshoe hares were livetrapped northeast of Vegreville, Alberta. Individual hares were housed in wooden nest boxes (61 cm x 71 cm x 41 cm) and adjoining weldmesh wire cages (90 cm x 60 cm x 46 cm). Animals were maintained on commercial rabbit ration (17.0% crude protein) and willow twigs and/or alfalfa/smooth brome (*Medicago sativa*/*Bromus inermis*) hay fed *ad libitum* between and during experimental trials.

Hares were conditioned to the study site for a minimum of four days, and exposed to the respective conifer species for three days prior to being placed into test pens. Each hare was weighed to the nearest gram prior to and following each experimental trial. Each hare in test pens was supplied with a nestbox or plywood shelter containing straw for bedding. Two or more hares were placed into pens in equal sex ratios on the day an experiment was initiated. Animals were observed daily and sick, injured or dead hares were immediately replaced with one of the same sex preconditioned to the site. The hares were allowed to browse the enclosed trees until approximately one-half of the twigs were browsed or at a point in time when the number of twigs available started to decline relative to the number of twigs browsed unless otherwise specified.

2.2.4 Experimental Design

Snowshoe hare feeding preferences for four conifer species were examined in two randomized block experiments.

2.2.4.1 Experiment 1: Hare Feeding Preferences for Siberian Larch, Norway Spruce and White Spruce

Experiment 1 was conducted during October 9-19, 1990. Hare preferences for two-year-old Siberian larch, Norway spruce and white spruce were tested. For this experiment, each of two pens, approximately 100 m^2, was divided into quarters in order to block tree species because the possibility existed that residual chemicals in the soil (Anispray, Anipel-inserted and Anipel-coplanted) from chemical acceptability experiments conducted one year previously (see Experiment 7 in Chapter 3) may have affected the biochemistry of the planted tree species and, consequently, the palatability of these trees to snowshoe hares. However, no physical barrier segregated pen sections and hare movements were unencumbered throughout a pen.

A total of 112 seedlings per species were planted within each quarter of each pen. Within each quarter, 25 of 112 trees per species were randomly selected and left *in situ* for the preference trial, thus, 100 trees of each conifer species were available for browsing within each pen for a total of 300 trees per pen. The remaining trees were removed for analysis of plant nutrients and plant secondary compounds. For nutritional analyses, three samples were collected, each consisting of eight whole trees of each species within a quarter of a pen. Samples were similarly collected for secondary metabolites with each sample containing seven seedlings. One female and one male hare were present in each pen. Rabbit ration and willow were available to the animals *ad libitum* and feed intake was recorded on a daily basis in both Experiments 1 and 2.

2.2.4.2 Experiment 2: Hare Feeding Preferences for Black Spruce and White Spruce

Experiment 2 was conducted during December 3-11, 1990. This experiment tested hare preferences for four-year-old black spruce and white spruce. Two hundred and two trees of each species were planted at random in each of two pens, approximately 100 m^2. Within each pen, 30 trees of each species were randomly allocated for the preference trial while the remaining seedlings were removed for plant nutrient and secondary compound analyses. For both analyses, five samples of each conifer species were collected from each block. One sample from each of five trees consisted of approximately 10-12 g of lateral branches taken from various heights of a tree and the apical stem. Three male and three female hares were assigned at random to each pen.

2.2.5 Tree Planting

All trees were planted by shovel equidistant from one another and the enclosure boundaries. One-year-old Siberian larch, Norway spruce and white spruce and three-year-old black spruce and white spruce were planted in May 1990. Because a large number of Norway spruce died before the end of the summer, all Norway spruce trees were replaced in August 1990. All trees were grown at the Pineridge Tree Nursery, Smoky Lake, Alberta, with the exception of the second lot of Norway spruce, which were grown at the AHCTN, Edmonton.

At the time of planting, the Siberian larch were container seedlings, whereas the white and Norway spruce were plug + ½ for Experiment 1. White spruce had more twigs (5.3±0.4 twigs, n=400) (all reported values are means ±1SE unless otherwise stated) relative to the other two tree species. Siberian larch, however, had a higher stem height compared to white spruce (6.7±0.5cm, n=200) and Norway spruce (11.2±0.5cm, n=200), respectively. The three-year-old white and black spruce were 1½ + 1½ bareroot, and plug + 2 bareroot, respectively. As a consequence of the different growing conditions, black spruce had a greater average number of twigs (178.9±21.4 twigs, n=60) and stem height (2.7±1.6cm, n=60).

A container seedling or plug denoted that the tree was initially grown in a Spencer-Lemaire tray for a period of one year or one growing season. For the three-year-old white spruce, the first value (ie. 1½) indicated the seedlings were originally planted in a seedbed rather than a container before it was transplanted into the field. The second value (ie. 1½) denoted the number of years in the field. Similarly, the values added to the plugs (ie. ½) indicated the number of years seedlings were in the field following transplanting.

2.2.6 Browse Measurements

All trees were labelled with a numbered aluminum tree tag. All twigs were counted and recorded for individual trees prior to the start of the experiments. A twig was defined as any shoot having a woody stem and its own terminal bud. The numbers of browsed and unbrowsed twigs were counted upon completion of each browsing period. The total number of twigs removed from trees was the final number of unbrowsed twigs subtracted from the initial total. Tree heights were measured to ±0.5 cm before and after each experiment and always on one side of the tree. The difference between these pre- and post-experimental heights was the measure of the tree height removed. I multiple apical stems were present, the height of the highest point was measured.

The total number of twigs and stems browsed was recorded in both experiments at 24 hour intervals. Tree heights were also measured periodically during Experiment 1 to ensure that data were obtained even if the two-year-old seedlings were clipped in a short period of time. Diameter at point of browsing (dpb) of apical stems was measured on trees in both experiments upon termination of the browsing period.

Simulated browsing of tree species used in both experiments estimated the biomass removed by weighing trees prior to and following hand-clipping.

2.2.7 Chemical Analyses

All samples remained frozen at -10°C until laboratory analyses were performed. Nutrient analyses were performed in duplicate and phenol analyses were performed in triplicate. All concentrations were calculated and reported on a dry matter (DM) basis.

For nutritional analyses, tree samples were dried at 60°C and ground through a Wiley Mill equipped with a 30 mm screen. Crude protein (CP) was determined by the Kjeldahl method for nitrogen as described by the Association of Official Analytical Chemists (AOAC 1980). Crude protein was expressed as 6.25-times the concentration of nitrogen. Organic matter was determined by ashing dried samples at 500°C (AOAC 1980). Neutral detergent fiber (NDF), acid detergent fiber (ADF) and acid detergent lignin (ADL) were determined using methods described by Goering and Van Soest (1970). Cellulose and hemicellulose concentrations were estimated by subtraction of ADL from ADF and ADF from NDF, respectively. Gross energy content was estimated by a Parr 1730 adiabatic oxygen bomb calorimeter. Phosphorous and calcium samples were prepared by the methods described in AOAC (1984) and determined using a Perkin-Elmer 4000 atomic absorption spectrophotometer.

For the analysis of phenols, tree samples were lyophilized and ground through a Wiley Mill with a 20 mm screen. Sample extracts were prepared according to Martin and Martin (1982) and stored in a desiccator until analyses were completed. The determination of total phenols and condensed tannins was performed as described by Dawra et al. (1988) with the exception that the chromatography sheets were dipped in BSA solution as opposed to being sprayed to attain an even consistency.

2.2.8 Statistical Analysis

Analysis of variance (ANOVA) was used to compare twig, height and dpb measurements and nutrient and phenol concentrations among species and chemical treatments, followed by a Duncan's multiple range test (Steel and Torrie 1980) if differences between treatments were detected. The main effects were tree species, potential residual chemical in the soil and block for Experiment 1. For Experiment 2, tree species and block constituted the main effects.

For the purpose of statistical analyses of independent variables with non-normal distributions, the Box-Cox procedure (Box et al. 1978) was used to determine the lambda level for the most appropriate transformation. The transformation was selected based on the lambda level possessing the lowest error sum of squares (ie. log transformation for lambda = 0 and squareroot for lambda = 0.5). Prior to transformation, negative values that resulted from a combination of error in twig counting and no browsing were eliminated by adding a constant to each numerical value. Pooling of error was performed based on a probability level of ≥0.1 for the interaction (Weiner 1971).

The number of apical stems browsed was analyzed using a chi-squared goodness-of-fit test or a Fischer exact test (Steel and Torrie 1980). The Kolmogorov-Smirnov two-sample test (Steel and Torrie 1980) was used to compare the total amount of browsing and barking per unit time among treatments. Pearson's correlation (Steel and Torrie 1980) was used to determine the relationship between conifer preference ratings and nutrient and phenol content. Comparisons among condensed tannins and total phenols for the entire tree population were performed using a t-test of difference

(Steel and Torrie 1980). Statistical analyses were performed using SAS (SAS 1989) and Statgraphics (STSC 1986).

2.3 Results

2.3.1 Experiment 1: Hare Feeding Preferences for Siberian Larch, Norway Spruce and White Spruce

Throughout the experiment, the amount of twigs and stems browsed (hereafter, collectively termed twigs browsed) and apical stems browsed was greater for Siberian larch than for either spruce species (Fig. 2.1). Percent height removed for Siberian larch increased steadily over time. The amount of browsing of all types on Norway spruce increased slowly until day five of the experiment when it increased rapidly for two days, after which the amount moderated (Fig. 2.1). At this time, the amounts for height removal and apical browsing approached that of Siberian larch. White spruce was browsed very little until day five of the experiment when, similar to Norway spruce, the amounts of height, twig and apical browsing increased, though only marginally relative to the other two conifer species. The cumulative amounts of height and twig browsing differed among Siberian larch and white spruce ($P \leq 0.001$) as did the amount of apical browsing ($P \leq 0.0001$) (Table 2.1). Norway spruce differed from Siberian larch for the amount of twig browsing ($P \leq 0.01$) and height removal ($P \leq 0.05$) per unit time, though not for percentage of height removal. During the 10 day browsing period, amounts for height removal and percentage of height removal differed significantly ($P \leq 0.05$) between the two spruce species (Table 2.1).

Siberian larch and Norway spruce were browsed significantly more than white spruce (Table 2.2). A lower number of twigs ($P \leq 0.05$) as well as a lower proportion of twigs and stem height ($P \leq 0.05$) were removed on white spruce relative to the other two conifer species. Similarly, the proportions of apicals clipped on Siberian larch and Norway spruce were 82% and 79% greater than those of white spruce, respectively ($P \leq 0.001$).

Significant differences among nutritional parameters occurred more frequently between Siberian larch and Norway spruce than larch and white spruce even though the first two species were highly preferred relative to white spruce (Table 2.3). Siberian larch had the highest CP content

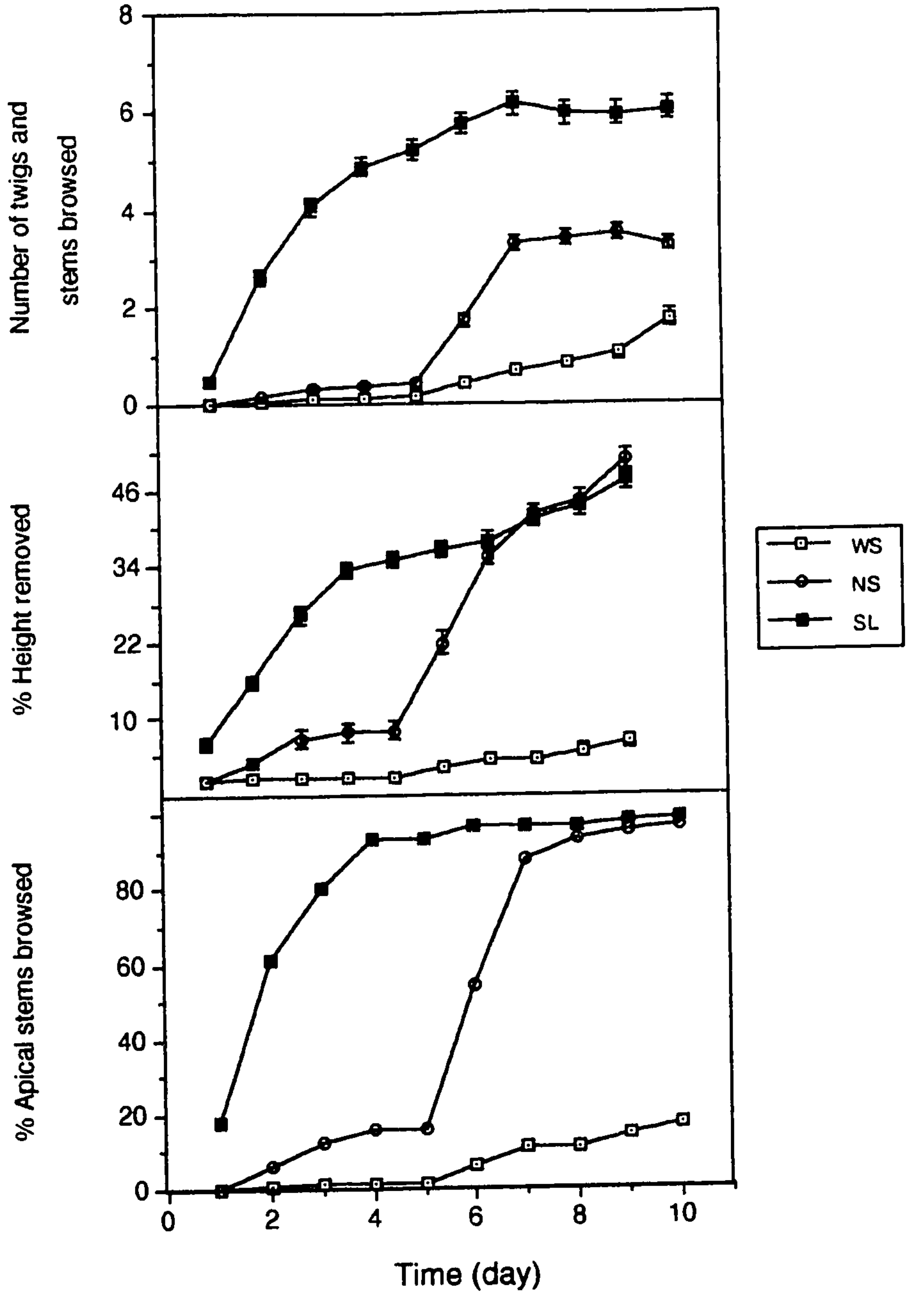

Figure 2.1 Mean number of twigs and stems browsed per tree, percentage of height removed per tree and percentage of apical stems browsed from white spruce, Norway spruce and Siberian larch in Experiment 1 (WS=white spruce, NS=norway spruce, SL=Siberian larch). Vertical bars represent ±1SE.

Table 2.1 Significance of differences of twigs and stems browsed, and tree height and apical stems removed over time from Siberian larch (SL), Norway spruce (NS) and white spruce (WS) in Experiment 1.

Species Comparisons[1]	Tree Browse Measurements			
	Twigs and Stems (no.)	Height (cm)	Height (%)	Apex (%)
SL vs. NS	**	*	NS	NS
SL vs. WS	***	****	***	****
NS vs. WS	NS	*	**	NS

[1] Non-significant differences denoted by NS; significant differences denoted by *($P \leq 0.05$), **($P \leq 0.01$), ***($P \leq 0.001$), ****($P \leq 0.0001$).

Table 2.2 Means and standard errors (SEM) of final tree browse measurements for Siberian larch (SL), Norway spruce (NS) and white spruce (WS) in Experiment 1.

	Conifer Species			
Measurement (per tree)	SL	NS	WS	SEM
twigs removed (log)	8.2 (0.9)^{a}[1]	8.0 (0.9)^{a}	2.0 (0.3)^{b}	0.07
twigs removed (%)	81.0^{a}	84.5^{a}	14.6^{b}	4.4
height removed (cm)	11.6^{a}	6.8^{ab}	0.9^{b}	1.1
height removed (%)	47.1^{a}	50.7^{a}	5.7^{b}	5.6
twigs and stems browsed (log)	6.0 (0.8)	3.3 (0.6)	1.9 (0.3)	0.08
apical stems browsed (no. trees)[2]	198	192	34*[3]	

[1] Means within measurements that do not share a common letter were significantly different ($P \leq 0.05$).

[2] $n=200$ trees/species.

[3] Asterisk indicates significant differences among conifer species ($P \leq 0.001$).

Table 2.3 Nutritional composition of Siberian larch (SL), Norway spruce (NS) and white spruce (WS) in Experiment 1.

Chemical Constituent[1]	Conifer Species			SEM
	SL	NS	WS	
dry matter	94.0^{b}[2]	94.7^{a}	94.2^{b}	0.1
organic matter	87.6^{a}	86.6^{b}	86.0^{b}	0.3
crude protein	13.4^{a}	10.2^{c}	12.1^{b}	0.2
neutral detergent fiber	40.6^{b}	45.8^{a}	43.7^{a}	0.8
acid detergent fiber	32.4^{a}	34.3^{b}	32.7^{a}	0.5
acid detergent lignin	15.8	15.6	15.6	0.5
hemicellulose	8.1	11.6	11.0	0.9
cellulose	14.8^{b}	15.8^{a}	14.1^{b}	0.3
calcium	0.6	0.3	0.3	0.02
phosphorous	0.2	0.2	0.2	0.01
gross energy (kJ/g)	21.2^{a}	20.2^{b}	21.5^{a}	0.1

[1] All chemical constituents are given on a percent dry matter basis.

[2] Means within measurements that do not share a common letter were significantly different ($P \le 0.05$).

followed by Norway spruce and white spruce ($P \leq 0.0001$). Norway spruce and white spruce had higher NDF than Siberian larch ($P \leq 0.0001$), whereas Siberian larch and white spruce had lower ADF ($P \leq 0.05$). Acid detergent lignin content and phosphorous and calcium levels were similar among tree species. Hemicellulose values did not differ significantly among species. Norway spruce had lower gross energy content relative to Siberian larch and white spruce ($P \leq 0.001$)

All correlations between feed preference measurements and nutrient values were not significant (Table 2.4) with the exception of twigs browsed and organic matter ($P \leq 0.05$). Gross energy and phosphorous tended to show a negative relationship with all browse measurements. Cellulose content was the only value which showed a positive trend relative to the percentage of twigs and height removed.

Neither total phenols nor condensed tannins were correlated with feeding preferences (Table 2.4). Siberian larch had a condensed tannin content which exceeded that of Norway spruce and white spruce by a factor of 1.4 and 1.1, respectively ($P \leq 0.0001$) (Table 2.5). Total phenol levels were almost identical for Siberian larch and white spruce, which were 1.3-fold higher than Norway spruce ($P \leq 0.01$). Total phenol levels (16.4±0.6%, n=72) were 1.2-fold greater than those of condensed tannins (13.4±0.4%, n=72) for all three conifer species ($P \leq 0.0001$).

Siberian larch had a higher dpb (3.1±0.3mm, n=20) compared to Norway spruce (2.4±0.3mm, n=20) and white spruce (1.8±0.3mm, n=20) ($P \leq 0.001$). Norway spruce had the greatest estimated biomass consumed per tree (1.6±0.2g, n=10) while white spruce had the lowest (0.69±0.22g, n=10). The mean estimated weight hares removed from Siberian larch was 0.97±0.10g (n=10).

Hares gained 36.0±13.2g (n=4 hares) during the experiment. The mean daily intake of rabbit ration and willow was 69.2±5.3g (n=11) and 54.0±3.9g (n=11), respectively.

2.3.2 Experiment 2: Hare Feeding Preferences for Black Spruce and White Spruce

Amounts of browsing over time did not differ significantly between black and white spruce (Fig. 2.2), but snowshoe hares preferentially

Table 2.4 Correlation coefficients between browse measurements and chemical composition of Siberian larch, Norway spruce and white spruce.

Chemical Constituent[1]	Browse Measurement twigs removed (log)	twigs removed (%)	height removed (cm)	height removed (%)	twigs browsed (no.)
dry matter	0.223	0.324	-0.181	0.350	-0.411
organic matter	0.827	0.763	0.982	0.745	0.999*[2]
crude protein	-0.026	-0.131	0.372	-0.158	0.583
neutral detergent fiber	-0.173	-0.068	-0.549	-0.041	-0.733
acid detergent fiber	0.307	0.406	-0.094	0.431	-0.329
lignin	0.384	0.285	0.718	0.258	0.864
hemicellulose	-0.419	-0.321	-0.744	-0.296	-0.883
cellulose	0.754	0.819	0.432	0.834	0.204
calcium	0.736	0.660	0.944	0.640	0.995
phosphorous	-0.923	-0.959	-0.696	-0.966	-0.504
gross energy (kJ/g)	-0.786	-0.847	-0.477	-0.861	-0.253
condensed tannins	0.036	-0.069	0.429	-0.097	0.632
total phenols	-0.361	-0.458	0.037	-0.482	0.275

[1] All chemical constituents are given on a percent dry matter basis, (N=3).

[2] Asterisk indicates significant correlation between browse measurements and chemical constituent ($P \leq 0.05$).

Table 2.5 Condensed tannin and total phenol composition of Siberian larch (SL), Norway spruce (NS) and white spruce (WS) in Experiment 1.

	Conifer Species			
Chemical Constituent[1]	SL	NS	WS	SEM
condensed tannins	15.4^{a}[2]	11.3^{c}	13.4^{b}	0.6
total phenols	17.9^{a}	13.8^{c}	17.5^{b}	0.9

[1] All chemical constituents are given on a percent dry matter basis.

[2] Means within chemical constituent that do not share a common letter were significantly different ($P \leq 0.05$).

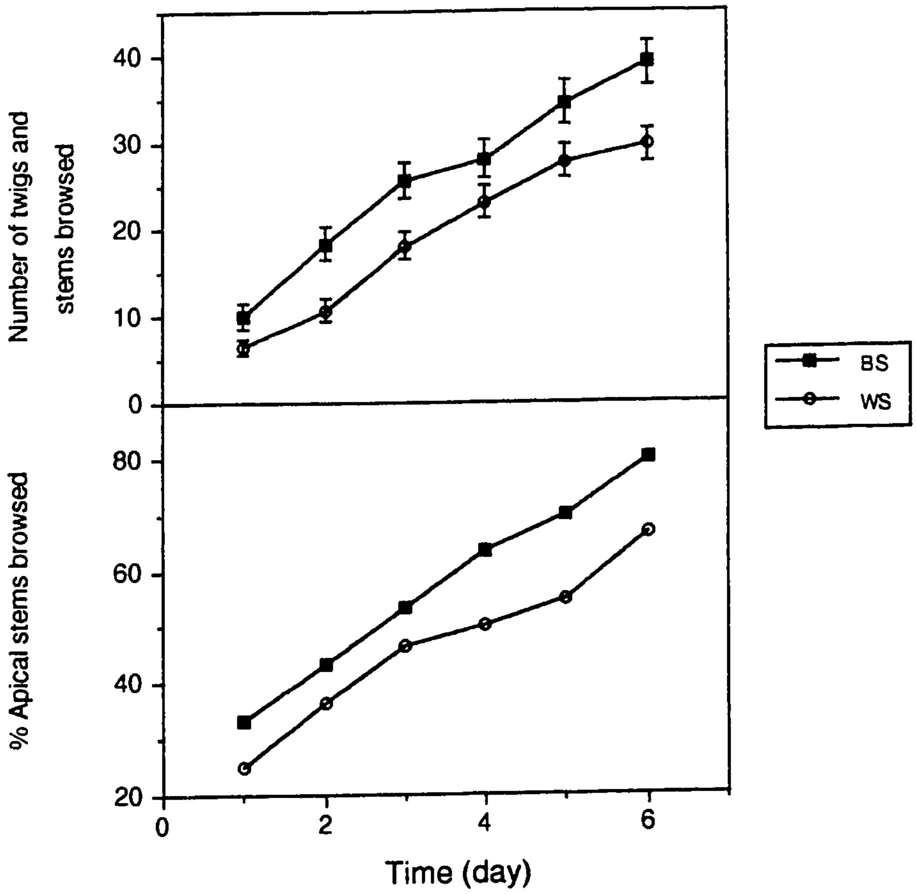

Figure 2.2 Mean number of twigs and stems browsed per tree and percentage of apical stems browsed from black and white spruce in Experiment 2 (BS=black spruce, WS=white spruce). Vertical bars represent ±1SE.

browsed black spruce in terms of final browsing values. The number of twigs removed was significantly higher for black spruce than white spruce (Table 2.6). Overall, white spruce had a high, though not significant, proportion of twigs removed($P \geq 0.05$). The proportions of height removed and the number of twigs browsed were 1.3 and 1.1-times greater for black spruce ($P \leq 0.01$).

Crude protein, calcium and phosphorous content were high in black spruce (Table 2.7). Forage quality of black and white spruce were similar for values other than cellulose, which was significantly lower in black spruce ($P \leq 0.01$).

White spruce contained 1.3-fold more total phenols than black spruce ($P \leq 0.01$) (Table 2.8). Overall, condensed tannins were 1.4-fold greater in white spruce, though this difference was not significant. For all species collectively, the amounts of condensed tannins (11.9±1.1%, n=20) and total phenols (12.0±0.6%, n=20) were almost identical.

The dpb for white spruce (3.4±0.3mm, n=20) and black spruce (3.0±0.2mm, n=20) were not significantly different. The estimated biomass consumed by hares was marginally higher for white spruce (19.6±2.6g, n=10) than black spruce (14.8±2.3g, n=10).

Throughout the browsing period, hares gained 44.0±36.7g (n=11). The mean daily intake of rabbit ration and willow was 45.8±1.8g (n=7) and 44.6±3.6g (n=7), respectively.

2.4 Discussion

2.4.1 Preferences for Conifers

The high amounts of browsing on Siberian larch and Norway spruce in comparison to white spruce in Experiment 1 suggested that these two species were equal in preference and both were preferred to white spruce. Estimates of consumed biomass obtained by the simulated browsing of these species further supported this preference ranking. These findings agree with those of other studies. Cafeteria-style experiments by Bookhout (1963) reported that larch (L. laricina) was browsed more than white spruce, black spruce and balsam fir (Abies balsamea), but had a lower preference value on average than pine (Pinus spp.), cedar (Thuja spp.) and hemlock (Tsuga spp.). Similar feeding trials in Alaska indicated that the

Table 2.6 Means and standard errors (SEM) of final tree browse measurements for black spruce (BS) and white spruce (WS) in Experiment 2.

	Conifer Species		
Measurement (per tree)	BS	WS	SEM
twigs removed	132.2**[1]	51.6	10.0
twigs removed (%)	44.0	49.1	2.4
height removed (cm) (squareroot)	9.3 (2.8)	6.1 (2.1)	0.2
height removed (%) (squareroot)	24.8 (4.6)*	17.8 (3.5)	0.3
twigs and stems browsed (log)	53.2 (1.7)**	33.8 (1.5)	0.02
apical stems browsed (no. trees)[2]	52	43	

[1] Asterisks indicate significant differences between conifer species *($P \leq 0.01$), **($P \leq 0.0001$).

[2] $n=60$ trees/species.

Table 2.7 Nutritional composition of black spruce (BS) and white spruce (WS) in Experiment 2.

	Conifer Species		
Chemical Constituent[1]	BS	WS	SEM
dry matter	95.1	94.2	0.8
organic matter	89.7	90.1	0.9
crude protein	11.4**[2]	9.5	0.2
neutral detergent fiber	43.7	44.2	0.4
acid detergent fiber	32.4	32.4	0.6
acid detergent lignin	17.4	16.3	0.5
hemicellulose	11.3	11.8	0.3
cellulose	14.0*	15.2	0.2
calcium	0.81***	0.55	0.02
phosphorous	0.18**	0.16	0.01
gross energy (kJ/g)	21.9	22.1	0.1

[1] All chemical constituents are given on a percent dry matter basis.

[2] Asterisks indicate significant differences between conifer species *($P \leq 0.01$), **($P \leq 0.001$), ***($P \leq 0.0001$).

Table 2.8 Condensed tannin and total phenol composition of black spruce (BS) and white spruce (WS) in Experiment 2.

	Conifer Species		
Chemical Constituent[1]	BS	WS	SEM
condensed tannins	9.8	13.9	1.6
total phenols	10.3*[2]	13.8	0.7

[1] All chemical constituents are given on a percent dry matter basis.

[2] Asterisk indicates significant differences between conifer species *($P \leq 0.01$).

mean weight of tree material consumed by hares was 1.2-fold greater for larch than for white spruce (Klein 1977), whereas a 5.6-fold difference was found in the present study. Larch was highly preferred in New York (Cook and Robeson 1945) and other states (Anonymous 1936) compared to white spruce. In Ontario, qualitative data indicated light barking and browsing on both larch and white spruce (De Vos 1964). Quantitative data in the same study showed 50% browsing of low intensity on larch trees, while a 16% browsing on white spruce consisted of light, moderate and heavy intensities. Dodds (1960) found similar trends for snowshoe hare browsing in Newfoundland with larch having a palatability factor 2-fold higher than white spruce. In Alberta, Tomm and Hudson (1978) reported that larch was a highly preferred species in terms of twig numbers, but the consumption of twig length and mean dpb suggested a lower browsing intensity than for pines. Collectively, all indices used by these researchers characterized larch as more palatable than white and black spruce and balsam fir. In interior Alaska, white spruce constituted a large proportion of the winter diet but this was likely a consequence of the limited distribution of larch and the absence of pines (Wolff 1978).

The extensive use of white and black spruce in Experiment 2 supports the fact that despite their generally low palatability, the ubiquitous distribution of these native spruces warrants them as important browse species for hares. Black and white spruce were reportedly main constituents of the snowshoe hare diet in the Maritimes (Telfer 1972) and Ontario (De Vos 1964), though they did not appear to be a preferred species. In interior Alaska, white and black spruce comprised 56% of the diet during the winter and 33% during the fall (Wolff 1978). In Minnesota, white spruce had a mortality of 44% as a result of clipping by hares, with signs of damage on 86% of the surviving trees (Aldous and Aldous 1944). Kittredge (1929) similarly reported hare injuries to 78% of white spruce in Minnesota. Hare damage documented in the Peace River region of Alberta was responsible for a 42% mortality of white spruce seedlings (Johnson and Walker 1976). White spruce was heavily fed upon in New York, preceded by white and red pine and followed by white cedar and balsam fir, in terms of snowshoe hare feeding preferences (Cook and Robeson 1945). Snowshoe hare damage to black spruce is not as well documented since this species is not typically used for reforestation.

In Experiment 2, preference measures indicated that black spruce was either selected prior to white spruce or that there were no differences in forage selection. Feeding trials in Alberta (Tomm and Hudson 1978) and Michigan (Bookhout 1963) corroborated that black spruce was preferred to white spruce with hares exhibiting an increased use of black spruce as preferred foods were depleted over time in Alberta. Tomm and Hudson (1978) reported that white spruce was browsed 1.9-fold and 7.3-fold less than black spruce for percent of twigs and twig length browsed, respectively.

In contrast, a higher palatability of 1.5-fold was reported for white spruce relative to black spruce in Alaska (Klein 1977) and De Vos (1964) noted the same preferences in Michigan. Pease et al. (1979) noted a low browsing impact on black spruce under field conditions in Alberta, but no comparisons with white spruce were made. No comparative work was done to differentiate white and black spruce palatabilities in interior Alaska; however, the feed intake of black spruce needles approximated 40% with 95% frequency of occurrence in the winter months (Wolff 1978).

Norway spruce, a non-native species, appeared to be one of the most preferred spruce species in the present study. As a result of the similar proportions of twigs and height removed for both black and white spruce in Experiment 2, it may be postulated that Norway spruce would be highly preferred to black spruce as well as white spruce. In Quebec, Norway spruce was a highly preferred species relative to red pine (P. resinosa), white pine (P. strobus) and white spruce (Bergeron and Tardif 1988). Norway spruce sustained 44% severe browsing of the stem above the lowest whorl of lateral branches and 38% severe browsing or girdling of the trunk. Forty-one percent of white spruce, however, suffered no damage. These researchers further suggested that Norway spruce may have a browse index as high as some pines, though jack pine (P. divaricata) in Quebec (Bergeron and Tardif 1988) and scots pine (P. sylvestris) in Sweden (Lindlof et al. 1978) were preferred to Norway spruce.

There are a number of factors that could affect the browsing preferences displayed by snowshoe hares, which include plant nutritional and secondary metabolite composition. The following sections describe the contribution of each of these parameters to the feeding preferences demonstrated by hares.

2.4.2 Nutritional Quality of Twigs

Crude protein, though relatively different for each species, showed no clear relationship with preference measures. However, crude protein, in addition to other nutrients, were not likely limiting due to the availability of rabbit ration and willow. Klein (1977) reported no consistent trends for protein levels and eight browse species. However, protein correlated positively with feeding preferences for larch, white spruce and black spruce, whereas the present study did not find this trend for Siberian larch, white spruce and Norway spruce. The lack of significant correlations may easily have been attributable to the small sample size, but those correlation coefficients which were extremely high may still exist biologically.

Gross energy showed a negative trend in relation to all browse measurements. Bryant and Kuropat (1980) reported that the gross energy of highly palatable browse species was much lower than that of less palatable browse species such as conifers. Gross energy, however, was likely a poor indicator of forage quality as digestible energy and metabolizable energy provide a more meaningful measurement of the nutritional value of a feedstuff. Furthermore, the gross energy of conifers may be elevated compared to other species as a result of the fats and essential oils containing terpenes, waxes and phenols, which in turn, may act as feeding deterrents. Concentrations of soluble carbohydrates in addition to nutrients were also negatively correlated with hare forage preferences (Bryant and Kuropat 1980).

Lindlof *et al*. (1974) found preference measures of the mountain hare in Sweden to be correlated with nutrient content, particularly protein and phosphorous. Despite the general trends indicated, deviations did occur, however, with some highly preferred species having low protein and phosphorous and the reverse (Lindlof *et al*. 1974). Other researchers also reported a positive relationship between food choices and phosphorous (Lindlof *et al*. 1974; Miller 1968; Radwan and Campbell 1967). This is opposite to the relationship of phosphorous to forage selection in this study, as phosphorous was negatively correlated with feeding preferences. Similar results were reported in Scotland where selection of heather (Calluna vulgaris) by mountain hares was not correlated with phosphorous content (Hewson 1973).

Other than cellulose, which showed an unexpected positive correlation, fiber and lignin showed no pattern of relationship to hare feeding preferences. Similarly, Klein (1977) reported no correlations of fiber and lignin content with selection of forage species. Bookhout (1963) classed white and black spruce as having a good palatability rating relative to larch, which had a fair rating. Nevertheless, no-choice feeding trials which attempted to examine nutritive value of browse species, demonstrated that black spruce had a poor nutritive rating, yet this was not substantiated by chemical analyses.

Inter- and intra-specific comparisons are difficult for both plant nutritional and secondary compound parameters because of differences in the age and parts of trees sampled. Feeding trials in Alaska found that protein, ADF and lignin values collectively averaged for larch, white spruce and black spruce were 6.58%, 33.8%, and 19.7% (Klein 1977), compared to values in this study of 11.6%, 32.5% and 16.3%, respectively. The seedlings used in these experiments were very young, which probably accounted for the high protein and low lignin. Moreover, cellulose values of 40.4%, 41.5%, 44.8% and 51.1% have been reported in the wood of Norway spruce, Siberian larch, white spruce and black spruce (Fengel and Wegener 1984), respectively, which were considerably higher than the values of the combination of wood, bark and needles of whole seedlings in this study. Similarly, the same authors found levels of lignin about 1.7-fold higher for Siberian larch, Norway spruce and white spruce compared to the present study.

Lindlof et al. (1978) reported a crude protein level in Norway spruce very similar to that found in Experiment 1, though phosphorous and calcium contents were 1.6-fold higher and 2.5-fold lower, respectively. As indicated by the two age groups of white spruce in Experiments 1 and 2, the mature-growth form had lower protein and higher fiber and lignin. However, the older trees had a high level of calcium and gross energy content.

Mature-growth phases of trees and shrubs are selected by hares in preference to juvenile-growth phases (Bryant 1981a,b; Klein 1977; Sinclair and Smith 1984). Some researchers report that the apical shoots of conifers are selected over lateral branches (Aldous and Aldous 1944; Bookhout 1963; Dodds 1960; Klein 1977), while others found that conifer tops were less preferred than the side branches of mature trees (Sinclair and Smith 1984). In deciduous browse species, small diameter twigs of the mature-growth form contain lower levels of nutrients than comparable twigs of the juvenile-growth form (Bryant and Kuropat 1980; Bryant et al. 1985). Nevertheless, younger twigs generally have lower dry matter and protein digestibilities (Bryant et al. 1985).

Siberian larch were browsed almost exclusively the first five days of Experiment 1, at which time hares began to heavily browse Norway spruce. This alteration in feeding preference may be related to twig diameter as hares generally prefer twigs 2-3 mm in diameter and do not eat twigs larger than 6 mm in diameter unless under conditions of reduced forage quality and quantity (Sinclair and Smith 1984; Pease et al. 1979; Bryant 1981b; Bookhout 1963; Wolff 1980). Larch was a fast-growing conifer relative to spruce and, consequently, was 2 to 3-times the height of Norway spruce with much larger twig diameters at the time of the experiment. The dpb of Siberian larch apical stems was approximately 0.7 mm and 1.3 mm greater than Norway spruce and white spruce, respectively, at the end of the browsing period. Therefore, by day five of the trial, the dpb of larch may have exceeded the twig size preferred by hares, which initiated the change in diet to Norway spruce. Tomm and Hudson (1978) reported that the rate of consumption of larch decreased after a threshold dpb (≥3 mm) was exceeded. Despite the effect of twig diameter on feeding preferences, hares continued to browse larch during the increased consumption of Norway spruce. Consequently, other factors, such as plant secondary compounds were likely affecting forage selection.

Numerous studies have related the preference of hares for smaller twigs with nutritional value (Pease et al. 1979; Sinclair et al. 1982; Wolff 1980) and digestibility (Pehrson 1981). Wolff (1980) observed a greater concentration of zinc, calcium, magnesium, potassium and nitrogen in willow and alder (Alnus spp.) twigs 3 mm in diameter relative to those

≥6 mm in diameter. Bailey (1967) also reported high protein in the terminal portion of twigs. However, on average, Siberian larch trees had significantly higher protein and gross energy and significantly lower NDF, ADF and cellulose than Norway spruce. The high lignin content associated with the larger twig diameter in Siberian larch may have contributed to the change in choice of species.

In Experiment 2, black spruce was browsed more than white spruce in terms of twigs removed and percent height removed, with a dpb of 0.45 mm less than white spruce. Therefore, black spruce may have been preferred to white spruce as a result of twig size, though the preference ranking may have been different if the white spruce had twigs of comparable diameter. Consequently, the nutritional parameters associated with smaller diameter twigs may have played a large role in the selection of white and black spruce. For example the calcium, crude protein and phosphorous content of black spruce was 1.5, 1.2 and 1.1-fold greater than white spruce, respectively. In addition, cellulose was 1.1-times less in the preferred spruce species. However, Tomm and Hudson (1978) reported the dpb of black spruce to exceed that of white spruce by 0.62 mm with a similar preference rating. Therefore, the relationship between nutritional composition and twig diameter may not be constant among tree species. Unfortunately, the different growing conditions of these two spruce species contributed to the high number of twigs of smaller diameter on the black spruce.

The amount of biomass estimated to be removed from white spruce trees was more than for black spruce trees by a factor of 1.3. If preference ratings were determined on a weight basis, white spruce may have been preferred to black spruce, though this is difficult to prove relying only on simulated browsing. Nevertheless, the differences in biomass removed may have been related to twig diameters, since white spruce had twigs of larger diameter which subsequently weighed more than the twigs of black spruce. This was assuming, however, that equal proportions of twig length were removed per species.

According to Sinclair _et_ _al_. (1982), a diet of 9% and 20% crude protein produced an apparent dry matter digestibility of 45% and 67%, respectively, and that for each increase in 5% dietary crude protein in this range, a corresponding increase of 3% crude protein in the feces occurred. Crude extrapolations based on these figures estimated the dry matter digestibility of two-year-old Siberian larch, white spruce and Norway spruce to be 51%, 48% and 46%, respectively. Because white spruce was the least preferred species, this suggested that the palatability of white spruce was not exclusively controlled by its ease of digestibility, in addition to nutrients, relative to other conifer species. The estimated dry matter digestibilities were 45% for four-year-old white spruce and 47% for four-year-old black spruce, which may have influenced the increased use of black spruce compared to white spruce.

2.2.3 Phenolic Content of Twigs

All of the estimated digestibilities, based on the findings of Sinclair et al. (1982), were very similar. However, the effects of plant secondary compounds specific to a particular tree species may not be adequately accounted for. For example, rabbit ration treated with phenols of a deciduous browse species did not affect the amount of feed eaten, but significantly lowered dry matter digestibility and doubled the fecal protein content in snowshoe hares (Sinclair et al. 1982). Similarly, the phenolic content of coniferous species significantly reduced the apparent digestibility of protein in mule deer and white-tailed deer (Robbins et al. 1987).

Although the least preferred species tended to have the highest content of condensed tannins and total phenols in Experiment 2, no correlations were demonstrated in Experiment 1. In fact, Siberian larch, which was browsed almost exclusively the first five days of the browsing period, had the highest concentration of both phenol types. Siberian larch was preferred to white spruce even though its condensed tannin content was 1.2-fold higher. Norway spruce was selected equally to Siberian larch but had a significantly lower content of both condensed tannins and total phenols. These observations do not support the theory (Bryant and Kuropat 1980; Sinclair and Smith 1984) that high levels of phenols have antifeeding effects.

Lack of correlations for both secondary compounds and nutrients with preference measures may be related to the low number of tree species tested, since several studies have examined these relationships with a minimum of eight species (Cooper and Owen-Smith 1985; Klein 1977; Lindlof and Pehrson 1978; Sinclair and Smith 1984). Moreover, the particular trees or, perhaps, the individual conifer species tested may have contained low levels of the measured phenols. However, condensed tannin values obtained in this study appeared to be consistent with the reported contents of 5-18% and 5-25% water-soluble condensed tannins in Norway spruce and larch species, respectively (Hathway 1962). Despite the rather wide range, these values indicate that Norway spruce may, on average, have lower levels of condensed tannins. This corroborates the results of the current study whereby the condensed tannins and total phenols of Siberian larch exceeded those of Norway spruce by a factor of 1.4 and 1.3, respectively.

The failure of measured phenols to deter feeding in this study may be attributed to herbivore-specificity of these compounds. For example, snowshoe hares may have a higher tolerance for phenols and tannins and, subsequently, sophisticated detoxification systems to metabolize these plant secondary compounds relative to other herbivores. Furthermore, soluble phenolics may not defend plants from herbivory simply by lowering nutrient digestibility (Bryant _et_ _al_. 1985); tannins which precipitate proteins may only represent a small proportion of the total soluble phenolics in a particular forage (Robbins _et_ _al_. 1987).

Contrary to the present study, numerous findings have reported the negative effects of tannins on forage palatability for monogastrics and ruminants. Mountain gorillas of the African Congo fed on plant species which had low levels of condensed tannins (Bate-Smith 1972; Schaller 1963). Colobus monkeys (_Colobus_ spp.) generally preferred plant species and plant parts that were 3 to 4-fold lower in tannins than other potential feedstuffs and generally contained ≤0.2% tannins (McKey _et_ _al_. 1978; Oates _et_ _al_. 1977). Arnold and Hill (1972) reported a 70% decrease in voluntary intake in cattle feeding on the legume _Lespedeza_ _cuneata_ when tannin content rose from 4.8% to 12%. However, several studies fail to comment on feeding preferences relative to the individual proportions of hydrolyzable and condensed tannins. A threshold level of 5% tannins caused the rejection of 14 plant species by goats, kudus (_Tragelaphus_ strepsiceros) and impalas (Aepyceros melampus) in South Africa (Cooper and Owen-Smith 1985) as well as the rejection of bracken fronds (Pteridium aquilinum) by cattle and deer (Cooper-Driver et al. 1977).

Though some studies have found clear negative relationships between tannins and forage selection, other findings, in addition to this study, have been inconsistent with these expected trends. Sinclair and Smith (1984) reported that total phenol content was not correlated with snowshoe hare preferences for plant species or growth stage, and in only one out of eight experiments was protein-complexing phenol content negatively correlated with plant species preference. Forage palatability was also not affected by concentrations of protein-precipitating polyphenols for browsing ruminants in South Africa (Cooper and Owen-Smith 1985). Cooper and Owen-Smith (1985) have also suggested that increases in condensed tannins following leaf damage may have evolved as a defense against microbial attack rather than as an antiherbivore defense.

In the present study, concentrations of condensed tannins and total phenols ranged from 12.8% and 14.6%, respectively, similar to values reported in other hare studies. Bryant (1981a) reported that plant material was not ingested by hares if the terpenoid and phenolic resin content was ≥8%. Snowshoe hares were found to use plant species in the Yukon with up to 15% resin and phenols, suggesting that some undefined compound may have been responsible for plant species avoidance (Sinclair and Smith 1984). However, these studies combined two major plant secondary metabolite classes which may have very different threshold levels when examined independently. A similar value of 10% total phenol concentration was found to deter mountain hares feeding on Scots pine (P. sylvestris) bark (Rousi and Haggman 1984). Therefore, it appears that snowshoe hares have much higher threshold levels for condensed tannins and total phenols than other herbivores.

The theory of plant secondary metabolites controlling forage intake cannot, however, be discounted as feeding preferences may be attributable to terpenoids or to other specific chemicals within the various classes and subclasses of the wide array of plant secondary metabolites. For example, camphor in white spruce has been identified as a feeding deterrent for snowshoe hares (Sinclair et al. 1988). Even though this oxygenated monoterpene caused a decreased consumption of rabbit ration in cafeteria-style feeding trials, it may not have the same effect when it is an integral part of a natural feedstuff under natural environmental conditions. In the wild, an animal is exposed to a plethora of confounding factors affecting forage palatability not only within one particular feedstuff, but among the numerous forage species ingested as well.

Contrary to the theory that snowshoe hare feeding behavior is controlled by plant antiherbivore chemistry, the buffer hypothesis suggests that hares may consume feedstuffs with a high content of defensive chemicals if they are buffered by the intake of other foods with little or no defensive chemicals (Sinclair and Smith 1984; Zahorik and Houpt 1977). Though the buffer hypothesis may not be wholly supported, the results of this study gave a strong indication of the potential for synergistic effects of plant nutrients and secondary compounds. Siberian larch was one of the most highly preferred species and possessed a significantly high crude protein and low NDF. However, it also had the highest content of total phenols and condensed tannins. Norway spruce exhibited the lowest crude protein and gross energy contents and highest ADF and cellulose content, though the phenol levels were the lowest. Therefore, in the strictest sense of the buffer theory, the ingestion of Norway spruce, a species with low phenols, may have buffered the high concentrations of defensive compounds in Siberian larch. Intermediate levels of phenols, crude protein and fiber predominated in the white spruce, yet this species was consumed the least. Nevertheless, the absolute amounts of condensed tannins or total phenols may not be important if the effectiveness of one type of phenol or other plant secondary compound is higher than another.

According to Swain (1978b, 1979), gymnosperms have the highest concentration of tannins (up to 40%) in the heartwood or bark, while much lower amounts, ranging from 0.5-10%, are contained within the leaf tissue, both of which protect trees against fungal and bacterial attack. This may account, in part, for the higher tannin content in Siberian larch. The experiment was conducted at a time when the needles of this species were beginning to be shed. As a result, white spruce and Norway spruce may have experienced a dilution effect from the greater amount of foliage remaining on the trees.

Tannin content increases in leaf tissue with age (Swain 1979). However, this relationship was not apparent between the two-year-old and four-year-old white spruce. Little difference occurred in the concentration of condensed tannins, though levels in the older trees were marginally higher, while total phenols were higher in the younger trees. These comparisons may not be entirely valid as the entire tree was sampled for the two-year-old white spruce and only the lateral and apical branches of the four-year-old were sampled. Twig diameters of the older branches were equivalent to, or slightly larger than, the main trunk of the younger tree; yet, this may not ensure similar results when factors such as genotype and location on a tree were also having an influence.

The different growing conditions of the conifer species may have contributed to the nutritional and phenol variability among the spruces and larch. Environmental factors such as fertilizers and shading can reduce the concentrations of carbon-based secondary metabolites including tannins and phenolic glycosides (Bryant and Chapin 1986; Hanley et al. 1987; Larsson et al. 1986; Warin et al. 1985; Waterman et al. 1984) as well as terpenes (Bryant et al. 1987; Mihaliak and Lincoln 1985) and these decreases in defensive chemistry have been implicated in the increased palatability of woody browse to herbivores (Bryant et al. 1987; Waterman et al. 1984).

The methodology used for tannin analysis was reputedly selective for both condensed and hydrolyzable tannins only (Dawra et al. 1988). Several alternative methods for the determination of tannins are rather insensitive and often measure flavonoids other than tannins (Makkar 1989), which in turn, makes comparisons with other studies difficult. According to Dawra et al. (1988), the sum of the total condensed tannins and hydrolyzable tannins yield total phenols. Initially, total phenols appeared to be an inappropriate term since only tannins were examined.

Because conifers do not contain hydrolyzable tannins, theoretically the value for total phenols should have been equivalent to condensed tannins. In Experiment 2, these two values were similar; however, in Experiment 1, total phenols exceeded condensed tannins by a factor of 1.2.

This indicated that either the technique for tannin analysis successfully measured condensed tannins only, as in Experiment 2, or that it also measured monomeric flavonoids. In addition, the degree of precision may have increased as the analysis progressed. The differences between condensed tannins and total phenols for the three tree species in Experiment 1 may not have been an artifact of measurement precision. This would suggest that a higher proportion of monomeric flavonoids were in the two-year-old Siberian larch, Norway spruce and white spruce than in the four-year-old black spruce and white spruce.

Harborne (1979) suggested that low molecular weight flavonoids have greater antiherbivore effects than polymeric flavonoids, whereas McLeod (1974) and Levin (1976) suggested that polymeric flavonoids generally have greater biological effects. The ability of monomeric flavonoids to bind with proteins and produce digestive-inhibiting effects is not well known, but these compounds are potent enzyme inhibitors (Harborne 1979). If indeed monomeric flavonoids have antifeeding properties, the high levels of monomeric flavonoids in two-year-old conifers would be consistent with evidence that indicated juvenile-growth forms were more heavily defended than the mature-growth forms (Bryant 1981b; Bryant _et al_. 1985; Bryant and Kuropat 1980; Reichardt _et al_. 1984; Rousi _et al_. 1987; Sinclair and Smith 1984).

2.4.4 Determinants of Preferences: Summary

The nutritional and secondary metabolite composition of conifer species may have influenced the preference values. Siberian larch and Norway spruce were highly preferred species to white spruce. Siberian larch exhibited high crude protein and calcium and low fiber, but also high condensed tannins and total phenols. Norway spruce, however, showed trends reverse to those of Siberian larch with lower nutrient and higher phenol levels. Smaller twig diameters, and the associated higher nutritional value, probably contributed to the increased consumption of Norway spruce part way through the experimental trial, once Siberian larch had been clipped beyond a threshold dpb as well as the higher amounts of black spruce consumed. Preferences for Siberian larch and Norway spruce suggested that plant nutrients and secondary compounds may have synergistic effects which control feeding preferences in concert either within one or among several browse species. Hare preferences for black spruce, however, intimated that high nutrient and low secondary compound levels may have a positive influence on forage selection. The ingestion of rabbit ration and willow may have buffered nutrient or secondary metabolite concentrations in the conifer species, thus, confounding browse preferences and subsequently, the determinants of these preferences.

2.4.5 Future Research

The consumption of essential oils may inhibit microbial activity in the caecum of snowshoe hares (Radvanyi 1987; Radwan 1972; Radwan and Crouch 1974), thereby retarding nitrogen assimilation, fatty acid production and vitamin B synthesis (McBee 1971). Future research should more closely address the effects of specific terpenes or terpene groups on the forage selection of snowshoe hares. The oxygenated terpenes of forage species, particularly alcohols, inhibited rumen microbial activity in sheep and deer (Oh et al. 1968). Within the oxygenated monoterpenes, borneol was found to be more inhibitory than camphor in rumen digestion trials (Schwartz et al. 1980). Bell and Harestad (1987) found that pine oil, containing terpene alcohols and monoterpenes, decreased the feed consumption of snowshoe hares and voles. Essential oils and the level of volatile terpenes within the oils have been attributed with causing the differential browsing of damage-resistant clones and susceptible clones of Douglas-fir by black-tailed deer (Odocoileus hemionus) (Radwan 1978; Radwan and Ellis 1975). Radwan and Crouch (1974) found no relationship between amounts of essential oil and feeding preferences of black-tailed deer, but this was likely because comparisons were made between the same amounts of oil rather than actual concentrations.

The essential oil content of Larix species may be as much as 4.2-fold lower than various Picea species (Makovkina and Moshanova 1977). The amount of oxygenated monoterpenes in Siberian larch was reportedly 8% of the total essential oil content (Kolesnikova et al. 1977), whereas in white and black spruce it was approximately 50-60% (von Rudloff 1967). Preliminary work performed with the species examined in the present study similarly indicated that Siberian larch not only had fewer terpenes within the oxygenated category, but that the concentrations of those present were much lower relative to the three spruce species. (Seedling samples from both Experiments 1 and 2 were frozen (-20°C) in preparation for related future research.)

As previously discussed, Sinclair et al. (1988) attributed camphor with antifeeding properties in white spruce. Of the oxygenated monoterpenes in this species, camphor had the highest concentration, which was approximately 3.5-fold greater than bornyl acetate (von Rudloff 1967). The low palatability of black spruce, however, may be a result of the high concentrations of bornyl acetate, which were 235-fold greater than camphor, according to earlier work by von Rudloff (1967). Consequently, future efforts should emphasize specific compounds rather than all-encompassing categories such as total phenols and total resins.

The effects of stilbenes or ß-tannins in conifers on hare browsing should also be addressed further. Pinosylvin and pinosylvin methyl ether in green alder deterred feeding by snowshoe hares (Bryant et al. 1983; Clausen et al. 1986). These two stilbenes are present in over 60 Pinus species and resveratrol and piceatannol are common in Picea species (Gorham 1980; Swain 1979). Several stilbene glycosides are also widely distributed within conifers (Gorham 1980).

2.4.6 Forestry Implications

The non-native species, Siberian larch and Norway spruce, were preferred by snowshoe hares relative to native species, which suggested that they would not be wise choices for reforestation, at least during the peak of the hare cycle. Of course, factors in addition to seedling type influence the selection of conifer species for reforestation.

Nova Scotia Department of Lands and Forests (NSDLF 1989, 1990) reported Siberian larch as a fast-growing species relative to spruces and similarly, Norway spruce as fast-growing compared to native spruces. The greater growth rates of larch and Norway spruce could potentially increase forest productivity by 50% and reduce rotation period to 30 years or less (NSDLF 1989, 1990). Even though these conifers are highly palatable to hares, the rapid height growth may enable these species to outgrow the reach of snowshoe hares in a shorter time span than other species. This rapid growth could be exploited if seedlings are planted at the low of the snowshoe hare cycle to allow for maximum growth prior to the peak of the cycle. Nevertheless, adequate snowfall in early fall or winter may protect slower growing spruces from depredation, while the apical portions of Siberian larch or Norway spruce may still be exposed to browsing herbivores.

Higher growth rates are also important for successful competition with deciduous growth. If non-native species, particularly Siberian larch, can compete comparatively well against aspen (P. tremuloides) regrowth, larch may be less susceptible to browsing in cut blocks than other conifer species. The vulnerability of larch to depredation may not be substantially reduced at the peak of the snowshoe hare cycle, however, when the early successional regeneration of cut blocks provides both cover and an abundance of food sources. Furthermore, the longer growing season of larch relative to other conifers, makes it more susceptible to herbicide application (NSDLF 1989). The practice of mechanical brushing to remove aspen regeneration from conifer plantations decreases the habitat available to snowshoe hares and depending on the effectiveness of this population control strategy, the particular conifer species planted may be of little consequence.

The native spruces, especially white spruce, appear to be the most appropriate choices for reforestation programs in Alberta, due to their inherent characteristics that deter snowshoe hare depredation. To date, white spruce (85%) and lodgepole pine (14%) form the largest proportion of seedlings planted in Alberta, whereas other species, including black spruce, form the remaining 1% (B. Court, pers. comm.). Black spruce may be used more extensively in the future. However, environmental conditions in much of northern Alberta are not as conducive to the growth of black spruce as they are to other reforestation species. The reverse occurs in areas of Manitoba and Ontario where the percentage of black spruce planted is similar to that of white spruce in Alberta (B. Court, pers. comm.).

Siberian larch and Norway spruce have not been planted operationally in Alberta, though the Alberta Forest Service is currently testing the potential of these species for reforestation. Norway spruce has been planted extensively in other provinces, particularly Quebec (Bergeron and

Tardif 1988) and Nova Scotia (NSDLF 1990). However, non-native species may have an increased susceptibility to disease or pests. For example, Norway spruce is more vulnerable to spruce budworm (*Choristoneura fumiferana*) and white pine weevil (*Pissodes strobi*) than native spruces (NSDLF 1990) and larch is damaged by porcupine (*Erithizon dorsatum*) (NSDLF 1989). Moreover, larch has a water-soluble extractive content 3 to 4-fold higher than other coniferous species, a condition which is not conducive to mechanical pulping but is suitable for kraft pulping (NSDLF 1989).

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3. Effect of Chemical Repellents on Diet Selection of Snowshoe Hares and the Implications for Forestry Practices

3.1 Introduction

In herbivores, the special senses of sight, hearing, touch, smell and taste are involved in searching for food and food selection (Harborne 1972). Arnold (1966) reported that sheep with impaired senses displayed alterations in ingestive behavior, either through diet selection or food intake. Forage selection is primarily influenced by the chemical stimuli which affect taste (Reidinger and Mason 1983), since smell basically serves to reinforce taste (Marten 1978). For example, rats (Rattus norvegicus) do not use olfactory stimuli until a taste aversion is established (Hankins et al. 1973). Guinea pigs (Cavis porcellus), however, use gustatory and visual cues during initial forage selection (Braveman 1974). As a result of inter-specific differences in taste responses, extrapolation to other species is difficult.

Taste thresholds are determined by variables affecting the taste medium and by internal factors of an organism (Coatcher and Church 1970; Howard and Marsh 1970). Physiological conditions such as hunger or low blood glucose may raise the rejection threshold of various gustatory or olfactory stimuli (Goatcher and Church 1970). Furthermore, preconditioning or learned behavior may either increase or decrease the palatability of a particular forage species (Arnold and Maller 1977; Bartmann and Carpenter 1982; Bartmann et al. 1982). Also, gustatory experiences are associated through learning with odors and, conversely, olfactory experiences are associated with taste (Howard and Marsh 1970).

Chemical taste repellents affect the sensory systems of herbivores and create the potential for aversive conditioning. A taste repellent deters an animal from feeding on a certain object or plant species simply by the distasteful gustatory sensations it elicits. Conversely, a learned food aversion results when an illness or other negative reinforcement is paired with a particular food, space or event, such that the item is avoided in the future (Dorrance and Gilbert 1977). The strength of the aversion is directly related to the intensity of the flavor and illness, and inversely related to the time between consumption of the flavor and onset of illness (Gustavson 1977). Furthermore, the physical presence of ingested substances are not necessary to cause aversions, due to an animal's ability to retroactively associate various tastes with an illness (Garcia and Hankins 1977).

Taste and olfactory cues may signal the properties of foods and, therefore, warn herbivores of repellent or toxic substances. The investigation of taste properties of repellents, baits and rodenticides, and the behavioral responses of small herbivores to these substances, may lead to improved formulations and techniques in the control of pest species (Reidinger and Mason 1983).

Numerous repellents, both natural and chemical, have been used to protect tree seedlings against damage by wildlife. Thompson (1953) and Pepper (1976) investigated the ability of N-butylmercaptan, a compound in skunk (Mephitis mephitis) and mink (Mustela vison) odor, to deter hare browsing. Predator odors, originating from scent glands or urine, have also been studied to create and maintain feeding suppression (Sullivan and Crump 1984; Sullivan et al. 1985). Systemic chemical repellents, including selenium (Gillingham et al. 1987; Rediske and Lawrence 1962) and octamethylpyrophosphoramide (OMPA) (Rediske and Lawrence 1962) as well as foliar sprays such as trinitrobenzene analine (TNBA), zinc dimethyl-dithiocarbamate cyclohexylamine (ZAC) and tetra-dimethyl thiuram disulphide (thiram) have also been examined (Radvanyi 1987). Systemic repellents, as opposed to foliar repellents, afford protection to an entire plant, including current annual growth, over an extended period of time.

Thiram has an extensive history as use as a chemical taste repellent for deterring animal depredation of plant species (Hooven 1966; Radvanyi 1987; Swihart 1990; Walter and Soos 1961), though it was originally developed for its fungicidal properties (Radwan 1969; Tisdale and Flenner 1942). However, the mode of action of thiram has not been fully examined, so this chemical may either have repellent or aversive properties or both.

Anipel® and Anispray® are currently unpatented chemical formulations in tablet and spray form, respectively, to deter animal damage to browse species. At present, these chemicals are classified as taste repellents based on their bitter qualities. However, there are no experimental data indicating whether Anipel and Anispray function as taste repellents or aversive agents.

In theory, the active ingredients in Anipel tablets are absorbed by tree roots and act as a systemic repellent (Anipel Silviculture, n.d.). Chemical absorption rates are dependent upon the rate of tablet deterioration and leaching; consequently, degradation is closely related to soil moisture. Foliar sprays, such as Anispray and thiram are susceptible to rain washoff and other weathering which often necessitate reapplication.

This study was initiated to document forage preferences and acceptability displayed by snowshoe hares for white spruce (Picea glauca) trees treated with three commercial chemical repellents namely, Anispray, Anipel and Bartlett Ropellent® (active ingredient was thiram). The objectives were to: a) determine snowshoe hare preferences for, and acceptability of, trees treated with Anispray and Anipel; b) assess snowshoe hare acceptability of white spruce treated with Bartlett Ropellent with animals subjected to feed deprivation; c) investigate learned feeding aversions of snowshoe hares to Bartlett Ropellent; d) use results of snowshoe hare forage preferences to suggest improvements for forestry practices. The working hypotheses were that snowshoe hares prefer untreated seedlings to treated seedlings and snowshoe hares previously exposed to Bartlett Ropellent demonstrate learned behavior through avoidance or decreased consumption of trees treated with the chemical.

3.2 Materials and Methods

3.2.1 Treatments

Details of the study area, pen facilities as well as capture and maintenance of snowshoe hares were as described in Chapter 2.

Experiments with chemical repellents compared forage preferences or forage acceptability displayed by hares between treated and untreated specimens of white spruce. Preference trials examined the diet selection displayed by hares when numerous treatments were offered. Acceptability trials compared the feeding response of hares to each chemical treatment in the absence of other treatments.

The chemical treatments involved Bartlett Ropellent (N.M. Bartlett Inc., Beamsville, Ontario), Anispray (AS) and Anipel (T.S. Research, Ltd., Surrey, British Columbia) all of which were commercially available as wildlife repellents. Barlett Ropellent contained 13% thiram, a dithiocarbamate fungicide; hence, Bartlett Ropellent will hereafter be termed thiram. The active ingredients in Anispray and Anipel were complex ammonium salts, N-(2-((2,6-dimethylphenyl-amino)-2-oxoethyl)-NN-diethylbenzenemethaminium benzoate and N-(2-((2,6-dimethylphenyl) amino)-2-0-oxoethyl)-NN-diethyl-benzoate, respectively.

Two methods of Anipel application were compared. In the first, tablets were inserted adjacent to the root system of existing trees, hereafter termed Anipel-inserted (AI). This simulated the method foresters might use to treat existing trees in plantations. In the second, tablets were coplanted with seedlings, hereafter termed Anipel-coplanted (AC). This method simulated the simultaneous planting of repellent tablets and nursery seedlings or older trees under field conditions. Two types of Anipel tablets were also tested. Type 1 tablets had a higher concentration and slower rate of release of the active ingredient than those of type 2. Type 1 and type 2 were both coplanted with seedlings (AC1, AC2), while only type 1 was inserted into the root system of established trees (AI1).

A number of trees were randomly selected at the start of each pen trial for the determination of chemical concentrations in or on white spruce needles. A foliage sample consisted of an apical stem and a number of lateral branches. One sample of lateral branches pooled among trees was used for a cafeteria-style experiment. The branches remained frozen at -10°C until analyses were performed. The concentrations of thiram were determined by the commercial laboratory Envirotest. Envirotest was unable to determine the concentration of the active ingredient of Anispray and Anipel because of the structural and chemical properties of the chemicals. Therefore, doses were estimated from the amount of material sprayed on the trees.

3.2.2 Experimental Design

Nine experiments were conducted (Table 3.1). Eight comprised pen

Table 3.1 Summary of preference and acceptability experiments.

Experiment				Date				
No.	Type[1]	Chemical[2]	Dose (%)	Chemical Application (mo. yr.)	Browsing Period[3]	No. Trees	Tree Age (yrs.)	No. Hares[4]
1	P	AI1 AS	 20	08 89 11 89	Nov. 4-15 89	33	6	4
2	P	AI1 AS	 20*[5]	08 89 11-12 89	Jan. 19-30 90	33	6	4
3	P	AS	0 25 25* 33 50 100	06 90	July 1-3 90	120	2	2
4	P	AC1 AC2		07 90 07 90	Aug. 6-12 90	75	2	2
5	P	Thiram	50	06 90	June 15-16 90		7	20
6	A	AC1		08 89	Nov. 4-6 89	60	1	12
7	A	AI1 AC1 AS	 20*	08 89 08 89 11-12 89	Jan. 2-15 90	144	6	24
8	A	Thiram	50	11-12 89	Mar. 13-22 90	144	6	24
9	A	Thiram	50	11-12 89	Nov. 17-26 90	132	7	24

[1] P=Preference, A=Acceptability.

[2] AS=Anispray, AI1=Anipel-inserted type 1, AC1=Anipel-coplanted type 1, AC2=Anipel-coplanted type 2.

[3] Experimental period during which hares were allowed to browse on trees.

[4] Total number of hares in each experimental pen at any given time during a browsing period.

[5] *=dual application as described in the chemical application section.

trials conducted from November 1989-December 1990. Experiments 3 and 4 were conducted during the frost-free period and were of completely randomized designs while Experiments 1, 2 and 6-9 were conducted between November and January, when snowshoe hares seasonally forage on conifer species, and were randomized block designs. The ninth experiment examined forage preferences in the context of learned behavior using a split-plot design with individually-housed animals during the frost-free period.

3.2.2.1 **Experiment 1: Hare Feeding Preferences for AS and AI1 Trees.**

Hare preferences for AS, AI1 and untreated six-year-old white spruce were tested during November 4-15, 1989. Fifteen trees in each of two pens, each approximately 50 m^2, were randomly assigned one of three treatments. Three trees of each treatment were removed at random for chemical analysis. Two male and two female hares were randomly allocated to each pen. Rabbit ration and alfalfa were available ad libitum. In all experiments, hares were naive to the particular chemicals tested.

3.2.2.2 **Experiment 2: Hare Feeding Preferences for AS and AI1 Trees**

Experiment 2 was conducted during January 19-30, 1990. This experiment was identical to Experiment 1 with the exception that AS trees were sprayed twice as described in the chemical application section below.

3.2.2.3 **Experiment 3: Hare Feeding Preferences for AS Trees**

Hare preferences for one-year-old white spruce seedlings treated with one of five concentrations of AS were tested during July 1-3, 1990. The concentrations of treatment solutions were 0%, 100%, 50%, 33% or 25% of commercial solution. All AS dosages were applied only once. In a sixth treatment, a 25% solution was applied twice as described in the chemical application section. Within one pen of approximately 50 m^2, 20 trees per treatment were offered to two hares, one female and one male. Rabbit ration and Basford willow were available ad libitum.

3.2.2.4 **Experiment 4: Hare Feeding Preferences for AC1 and AC2 Trees**

Experiment 4, conducted during August 6-12, 1990, tested hare preferences for type 1 and type 2 Anipel tablets coplanted with one-year-old white spruce seedlings. A total of 75 trees, 25 trees per treatment, were available to one female and one male hare in a single pen. Rabbit ration was available ad libitum.

3.2.2.5 Experiment 5: Effect of Learning on Hare Feeding Preferences for Thiram-Treated Trees

This experiment tested whether naive hares or those previously exposed to thiram demonstrated differential feeding behavior when offered thiram-treated and untreated twigs from six-year-old white spruce twigs in a cafeteria-style split-plot design during June 15-16, 1990. Experienced hares were animals that had been previously exposed to thiram in an acceptability pen trial (see Experiment 8). All animals had been exposed to white spruce in previous pen trials. Five female and five male individually housed naive hares and the same number of experienced hares were offered 5-10 g of each of treated and untreated white spruce. The material was left in the cages for one hour after which it was removed and reweighed. This was repeated 14 times during one day so that the food material was available to hares for a total of 14 hours from dusk to dawn. However, each hour of the total fourteen hours were not consecutive since a 20 minute interval was required between one hour increments to allow the exchange of old and fresh spruce twigs. Rabbit ration was available ad libitum at all times.

3.2.2.6 Experiment 6: Hare Feeding Acceptability of ACl Trees

Experiment 6, conducted during November 4-6, 1989, tested the acceptability of one-year-old white spruce seedlings coplanted with Anipel. Four pens, each approximately 28 m^2, and each containing 21 equally spaced trees, were randomly assigned to either a treatment of Anipel or untreated control. Six trees per pen were removed for a pre-trial chemical analysis, leaving 15 trees per pen. Two female and one male hares were present in each pen. Rabbit ration and alfalfa were available ad libitum.

3.2.2.7 Experiment 7: Hare Feeding Acceptability of AS, AI1 and ACl Trees

In this experiment, the acceptability of six-year-old white spruce trees that were treated with AS, AI1 or were left as untreated controls were tested during January [illegible]-15, 1990. Both methods of Anipel insertion were tested. Five-year-old trees were used for the AC1 treatment because six-year-old trees were unattainable. Treatments were randomly assigned to each of eight pens, approximately 28 m^2, in a randomized block design. Upon removal of three trees per pen for chemical analyses, 18 trees of each treatment were available for browsing by hares. Two female and one male hares were present in each pen. Rabbit ration and willow were available <u>ad</u> <u>libitum</u>.

3.2.2.8 Experiment 8: Hare Feeding Acceptability of Thiram-Treated Trees in the Spring

Experiment 8, conducted during March 13-22, 1990, tested the acceptability of thiram-treated six-year-old white spruce under two joint constraints. Firstly, thiram was allowed to deteriorate over the winter. Secondly, the snowshoe hares were placed on a restricted diet prior to and during the experiment, in order to approximate more closely the hunger stress that is likely to occur under natural winter conditions at the peak of the hare cycle. All hares used in this experiment and additional replacement hares were placed on a restricted feeding regime thirteen days prior to the experiment in order to attain approximately a 10% loss of initial body weight immediately prior to their introduction into test pens. All hares were weighed daily during this time. The animals were fed a diet of about 50% willow (2-8 mm diameter) and 50% commercial rabbit ration during the pre-trial feeding period and during the experimental trial. All feed rations were determined as a percentage of a hare's initial body weight.

The experiment was a randomized block design with four pens, approximately 50 m^2, randomly assigned to either thiram treatment or a non-treatment. Thirty-six trees per pen were available for browsing after four trees were removed for chemical analysis. The experiment was terminated when twigs were almost depleted on one treatment. Three males and three females were present in each pen.

During the browsing component of the experiment, hares were weighed every 2-3 days to monitor weight loss. The feeding regime was altered based on the mean weight changes of all animals in all pens in order to maintain a 10% weight loss on average. Six hares were used in each pen throughout the trial. Six feed rations were placed throughout the pen to help ensure equal access by all animals. Weight loss was greatest for hares exposed to thiram-treated white spruce. Thus, these hares became the basis for which the feed ration was regulated. Hares in all treatments were fed the same percentage of their collective initial body weight.

3.2.2.9 Experiment 9: Hare Feeding Acceptability of Thiram-Treated Trees in the Fall

The acceptability of six-year-old white spruce trees treated with thiram following one season of growth was tested during November 17-26, 1990. The same thiram-treated trees were used as for Experiment 8 because of the minimal amount of damage they sustained. These trees were not retreated with the chemical, leaving current annual growth unprotected by thiram in Experiment 9. New, untreated control trees of equivalent age and from similar stock were planted to replace those consumed in Experiment 8. The design and conditions of this trial were identical to Experiment 8 except that 33 trees were available for browsing after three trees were removed for chemical analysis.

3.2.3 Tree Planting

All white spruce trees were planted equidistant from one another and the enclosure boundaries. White spruce trees six years of age, five years of age and seven years of age were bareroot planted in May 1989, August 1989 and August 1990, respectively. One-year-old Spencer Lemaire (65 cc) container seedlings were planted in August 1989 as well as in May and July 1990.

3.2.4 Chemical Application

Trees were treated with Anipel tablets (17 mm diameter) in August 1989 and July 1990 using one of two methods specified by the manufacturer. In the first method, a metal pipe, 1.5 cm in diameter, was used to remove a soil core in vertical line with the outer branches of established six-year old trees (range of 2.6-20.5 cm from the base of the stem) to a depth estimated to be approximately one-half of the way down the root system (range of 5.1-15.4 cm from the soil surface). Tablet placement within the root system was based on the ability to estimate root depth from tree-planting experience. The tablet was dropped into the hole which was then back-filled. In the second method, five-year old white spruce were bareroot planted with the Anipel tablet situated about 10.2 cm from the soil surface and 15.4 cm from the base of the trunk. Similarly, Anipel tablets were coplanted with one-year-old white spruce, such that the tablet was placed beside the root plug approximately 3.8 cm from the soil surface.

It was necessary to apply the Anipel treatment prior to September to allow sufficient time for the root systems to take up the chemical before the roots entered the dormant season. Also, at least three weeks were allowed for root uptake of the chemical prior to testing.

Solutions of AS were applied to six-year-old trees in experiments 1, 2 and 7 using a backpack hand-sprayer with an LF 67 nozzle. Thiram was similarly applied to trees in Experiments 5,8 and 9 using an 8002 nozzle. All trees not being sprayed were covered with plastic pails or bags to prevent cross-contamination among treatments.

Rates of application for both chemicals followed manufacturers' specifications. A total of 25 ml of a 20% AS solution was applied in November 1989 to each tree. Within 48 hours of spraying, 6.4 mm of rain fell on the treated trees. This may have washed the AS off of the trees before it had dried adequately. The concentration of the chemical on the tree could not be quantified to determine if the chemical had been washed off. Therefore, these trees were resprayed in December 1989 at temperatures above 0°C. Anispray was applied to one-year-old white spruce trees in Experiment 5 using a hand-spray bottle in June 1990 at concentrations ranging from 25% to 100% to find the concentration at which hares may be deterred from browsing trees. A concentration of 25% applied twice was also tested upon the manufacturer's recommendations. The second application occurred 48 hours after the first application to allow for drying.

A total of 40 ml of a 50% solution of thiram was applied to six-year-old white spruce in November 1989 in Experiments 8 and 9 and in June 1990 in Experiment 5. As a result of difficulties with thiram solidifying in the spray nozzle and hose, thiram was reapplied to the trees in Experiments 8 and 9 in December to ensure adequate concentrations on the trees.

3.2.5 Browse Measurements

Browse measurements taken were as described in chapter 2, with the exception of the following. When only a portion of the terminal bud was eaten, it was recorded as browsing of a bud as opposed to a twig. The number and area (cm^2) of bark wounds were determined upon trial completion. A dot grid of 0.04 cm squares was used to estimate the areas of bark removed.

At 24 hour intervals, the number of twigs, stems and buds browsed and the number of bark wounds were recorded in Experiments 1,2,6,7,8 and 9, to give estimates of the amounts of browsing over time. Similarly, the number of twigs and stems browsed and tree height were recorded every two hours for Experiment 3 and every four hours for Experiment 4. The number of twigs, stems and buds browsed and bark wounds were summed to yield the total number of browse points. Periodic height measurements were only recorded for Experiments 3 and 4 to ensure the required data collection in the event that the two-year-old seedlings were completely consumed in a very short period of time. As a result of the small size of the one and two-year-old trees, no browsing of buds or bark wounds were observed. The weight (grams) of tree material consumed was measured as the dependent variable in Experiment 9 by determining the difference in twig weights before and after feeding.

The apical stem and lateral branches of seven-year-old white spruce were clipped by hand to estimate the biomass consumed by snowshoe hares. Browsing intensities were simulated at three levels: light, moderate and heavy. For the light intensity, about 50% of apical stems and 25% of lateral twigs were clipped. About 75% of apical stems and 50% of lateral twigs were clipped for the moderate category. Trees sampled for the heavy intensity had all apical stems and lateral branches removed leaving only the main trunk.

3.2.6 Statistical Analysis

Statistical analyses were similar to those in chapter 2. Analysis of variance was used to compare twig and height variables among chemical treatments, followed by a Student-Newman-Keuls multiple range test (Steel and Torrie 1980) if differences between chemicals were detected. Pooling of error was performed based on a probability level of ≥0.2 for the interaction (Weiner 1971) The main effects were chemical treatment for pen trials with a completely randomized design, while chemical treatment and block were the main effects for experiments with a randomized block design. Chemical treatment and type of hare experience constituted the main effects for the cafeteria-style experiment with a split-plot design. The simple effects of this experiment were tested using a t-test (Steel and Torrie 1980).

The number of buds browsed as well as the number of bark wounds were analyzed using a chi-squared goodness-of-fit test or a Fischer exact test (Steel and Torrie 1980). Bark wound area data were analyzed using Kruskal-Wallis or Wilcoxon tests (Steel and Torrie 1980). A homogeneity of regression coefficients test, using time as a covariate, analyzed weight of twigs consumed within each level of experience and chemical group in Experiment 5.

3.3 Results

3.3.1 Experiments 1 and 2: Hare Feeding Preferences for AS and AI1 Trees

There were no differences in the amounts of browsing per time increment in Experiment 1 (Fig. 3.1) or in final browsing values in Experiments 1 and 2 (Tables 3.2 and 3.3). Throughout the duration of the experiment, twig and stem browsing (hereafter, collectively termed twig browsing) was greater for Anispray than Anipel-inserted trees (P≤0.05) and bark wounding was greater for Anispray than untreated trees (P≤0.001) in Experiment 2 (Fig. 3.2).

Simulated browsing of moderate intensity estimated that the biomass consumed of all treatments in Experiments 1, 2 and 7 as well as thiram-treated trees in Experiment 9 was 63.2±12.1g (n=10). Hares gained 13.3±20.9g (n=8 hares) and 21.0±15.3g (n=8), in Experiments 1 and 2, respectively. The mean daily intake of rabbit ration was 74.1±4.6g (n=10)

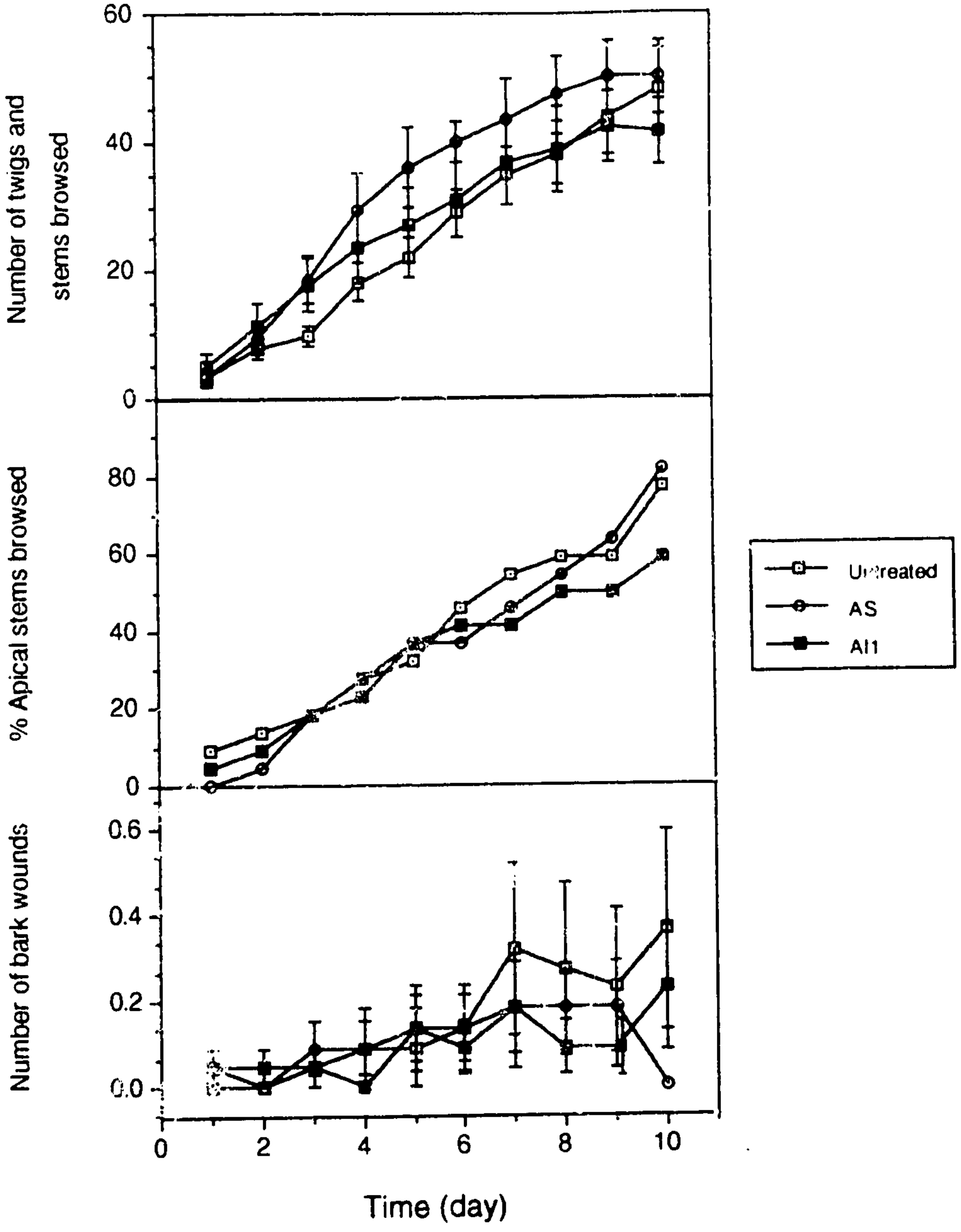

Figure 3.1 Effect of chemical treatment on the mean number of twigs and stems browsed per tree, percentage of apical stems browsed and mean number of bark wounds per tree in Experiment 1 (AS=Anispray, AI1=Anipel-inserted type 1). Vertical bars represent ±1SE.

Table 3.2 Means and standard errors (SEM) of final tree browse measurements for Anispray (AS) and Anipel-inserted (AI1) trees in Experiment 1.

Measurement (per tree)	Untreated	Chemical		SEM
		AS	AI1	
twigs removed (log)	128.8 (2.0)	164.6 (2.1)	141.4 (2.0)	0.1
twigs removed (%)	60.0	63.1	57.6	4.9
height removed (cm) (square root)	4.9 (1.8)	7.8 (2.4)	5.6 (2.0)	0.3
height removed (%)	17.1	26.4	18.7	4.1
twigs and stems browsed (log)	55.2 (1.7)	58.6 (1.7)	51.2 (1.2)	0.1
total browsed[1] (log)	56.5 (1.7)	59.7 (1.7)	52.8 (1.7)	0.1
buds browsed	1.0	0.8	1.2	
bark wounds	0.3	0.3	0.4	
bark wounds (cm^2)	0.2	0.3	0.1	
apical stems browsed (no. trees)[2]	17	19	15	

[1] Total browsed is the aggregate of twigs and stems browsed, buds browsed and bark wounds.

[2] n=22 trees/chemical treatment.

Table 3.3 Means and standard errors (SEM) of final tree browse measurements for Anispray (AS) and Anipel-inserted (AI1) trees in Experiment 2.

		Chemical		
Measurement (per tree)	Untreated	AS	AI1	SEM
twigs removed	122.8	141.7	159.2	
(log)	(2.0)	(2.1)	(2.1)	0.1
twigs removed (%)	58.0	72.3	64.0	4.7
height removed (cm)	10.4	10.3	10.2	0.02
height removed (%)	34.4	35.0	35.8	3.4
twigs and stems browsed	45.3	54.1	46.0	
(log)	(1.6)	(1.7)	(1.6)	0.1
total browsed[1]	45.6	54.6	46.4	
(log)	(1.5)	(1.6)	(1.6)	0.1
buds browsed	0.05	0.05	0.05	
bark wounds	0.3	0.5	0.3	
bark wounds (cm^2)	0.1	0.1	0.1	
apical stems browsed (no. trees)[2]	22	22	22	

[1] Total browsed is the aggregate of twigs and stems browsed, buds browsed and bark wounds.

[2] n=22 trees/chemical treatment.

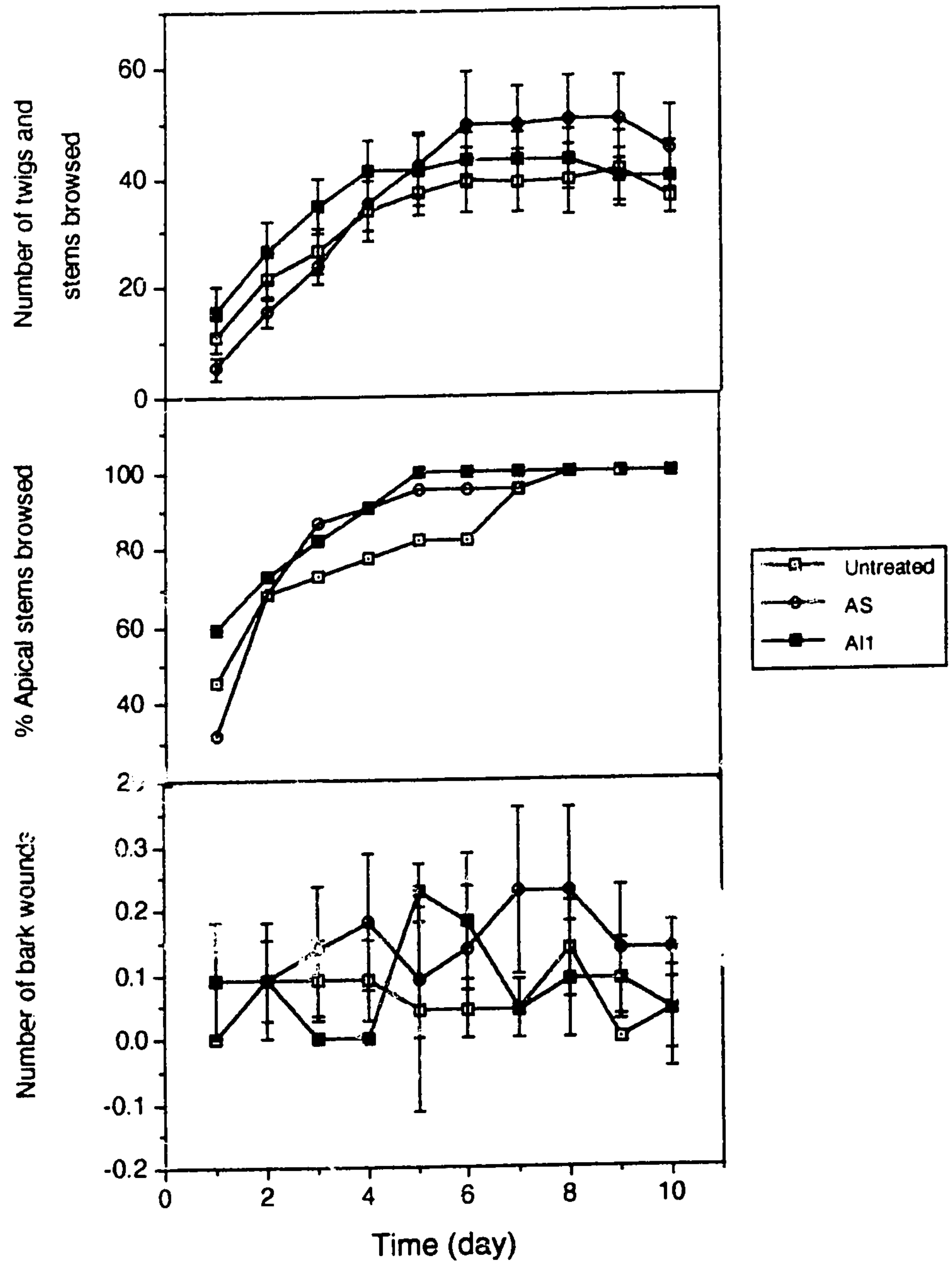

Figure 3.2 Effect of chemical treatment on the mean number of twigs and stems browsed per tree, percentage of apical stems browsed and mean number of bark wounds per tree in Experiment 2 (AS=Anispray, Al1=Anipel-inserted type 1). Vertical bars represent ±1SE.

in Experiment 1 and 64 8±8.9g (n=10) in Experiment 2.

3.3.2 Experiment 3: Hare Feeding Preferences for AS Trees

Percentages of tree height removal and apical browsing throughout the browsing period were consistently lower for undiluted compared to all other concentrations ($P \leq 0.01$) (Fig. 3.3, Table 3.4). Untreated trees had a lower amount of twig browsing and percent height removal per time increment relative to AS concentrations of 50% and 25% applied twice, respectively ($P \leq 0.05$). The stepwise progression of the curves indicated periods of browsing activity and inactivity. Periods of feeding generally coincided with nocturnal hours. No variables differed significantly among AS concentrations between 0% and 100% (Table 3.5).

Hares gained weight during the trial (5.5±2.5g n=2). The mean daily intake of rabbit ration was 81.7±4.4g (n=2).

3.3.3 Experiment 4: Hare Feeding Preferences for AC1 and AC2 Trees

Over time, height removal and apical browsing differed among all treatments ($P \leq 0.05$), while amounts of twig browsing differed among the two tablet types and among untreated and type 2 tablets ($P \leq 0.05$) (Fig. 3.4). At the end of the experiment, hares removed 23.3% and 32.7% more twigs on type 2 Anipel trees than type 1 Anipel and untreated trees, respectively ($P \leq 0.05$) (Table 3.6).

Upon the termination of the trial, hares had gained 42.0±69.0g (n=2). The mean daily intake of rabbit ration was 92.8±24.5g (n=3).

3.3.4 Experiment 5: Effect of Learning on Hare Feeding Preferences for Thiram-Treated Trees

Naive and experienced hares, collectively, ate 7-times more untreated spruce twigs than thiram-treated twigs ($P \leq 0.001$) (Table 3.7). Experienced hares had a total spruce intake, consisting of both thiram-treated and untreated white spruce, 1.8-fold higher than naive hares ($P \leq 0.05$). Further examination of the significant interaction of chemical treatment and type of experience ($P \leq 0.05$) (Fig. 3.5), indicated that hares previously exposed to thiram-treated spruce consumed 2-times the total weight of untreated twigs than did naive hares ($P \leq 0.05$). Weights of

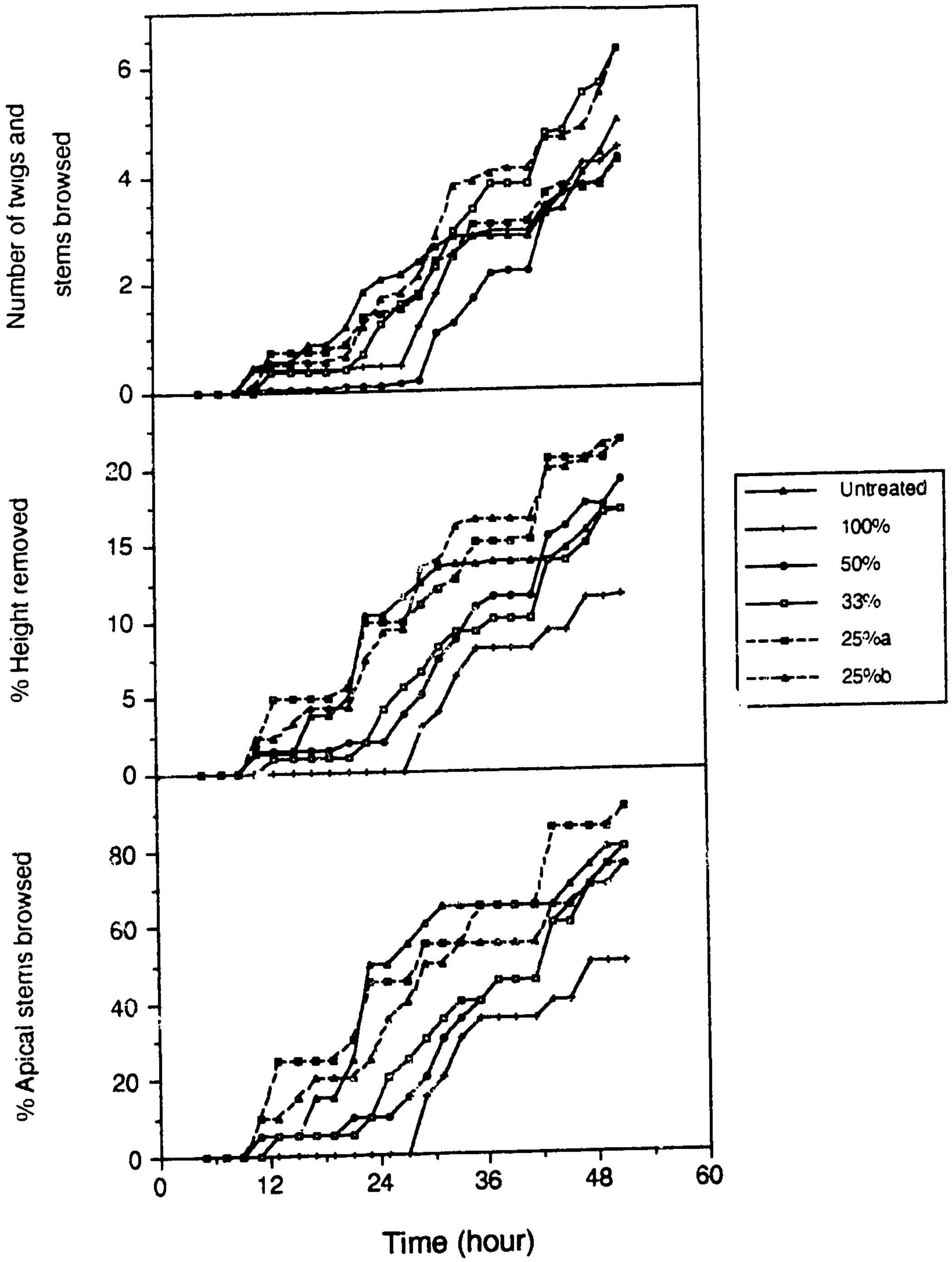

Figure 3.3 Effect of concentrations of Anispray on the mean number of twigs and stems browsed per tree, percentage of height removed per tree and percentage of apical stems browsed in Experiment 3 (25%a= single application, 25%b=dual application).

Table 3.4 Comparative effects of Anispray concentrations on twigs and stems browsed and tree height and apical stems removed over time in Experiment 3.

Concentration (%) Comparisons[1]		Tree Browse Measurements			
		Twigs and Stems (no.)	Height (cm)	Height (%)	Apex (%)
Untreated	vs. 100	NS	*	NS	NS
	vs. 50	*	NS	NS	NS
	vs. 33	NS	NS	NS	NS
	vs. 25	NS	NS	NS	NS
	vs. 25[2]	NS	*	*	NS
100	vs. 50	*	**	**	**
	vs. 33	NS	**	**	**
	vs. 25	NS	***	***	***
	vs. 25[2]	*	**	**	**
50	vs. 33	NS	NS	NS	NS
	vs. 25	NS	NS	NS	*
	vs. 25[2]	*	NS	NS	NS
33	vs. 25	NS	*	NS	*
	vs. 25[2]	NS	*	NS	NS
25	vs. 25[2]	NS	NS	NS	NS

[1] Non-significant comparisons denoted by NS; significant comparisons denoted by *($P \leq 0.05$), **($P \leq 0.01$), ***($P \leq 0.001$).

[2] Dual application of Anispray.

Table 3.5 Means and standard errors (SEM) of final tree browse measurements for concentrations of Anispray in Experiment 3.

	Chemical Concentration (%)						
Measurement (per tree)	0	100	50	33	25	25[1]	SEM
twigs removed	5.6	4.9	5.3	7.3	5.4	7.2	1.0
twigs removed (%)	32.5	25.0	27.8	35.1	28.8	35.1	4.3
height removed (cm) (squareroot)	1.9 (1.2)	1.5 (0.9)	2.2 (1.3)	1.9 (1.2)	2.6 (1.5)	2.6 (1.4)	0.2
height removed (%) (arcsin)	1.3 (981.7)	0.9 (695.5)	1.3 (1146.0)	1.2 (987.6)	1.5 (1276.7)	1.4 (1258.3)	160.8
twigs and stems browsed	5.6	4.8	4.8	6.8	4.6	6.8	[illegible]
apical stems browsed (no.trees)[2]	16	11	16	16	18	15	

[1] Dual application of Anispray.
[2] n=30 trees/chemical treatment.

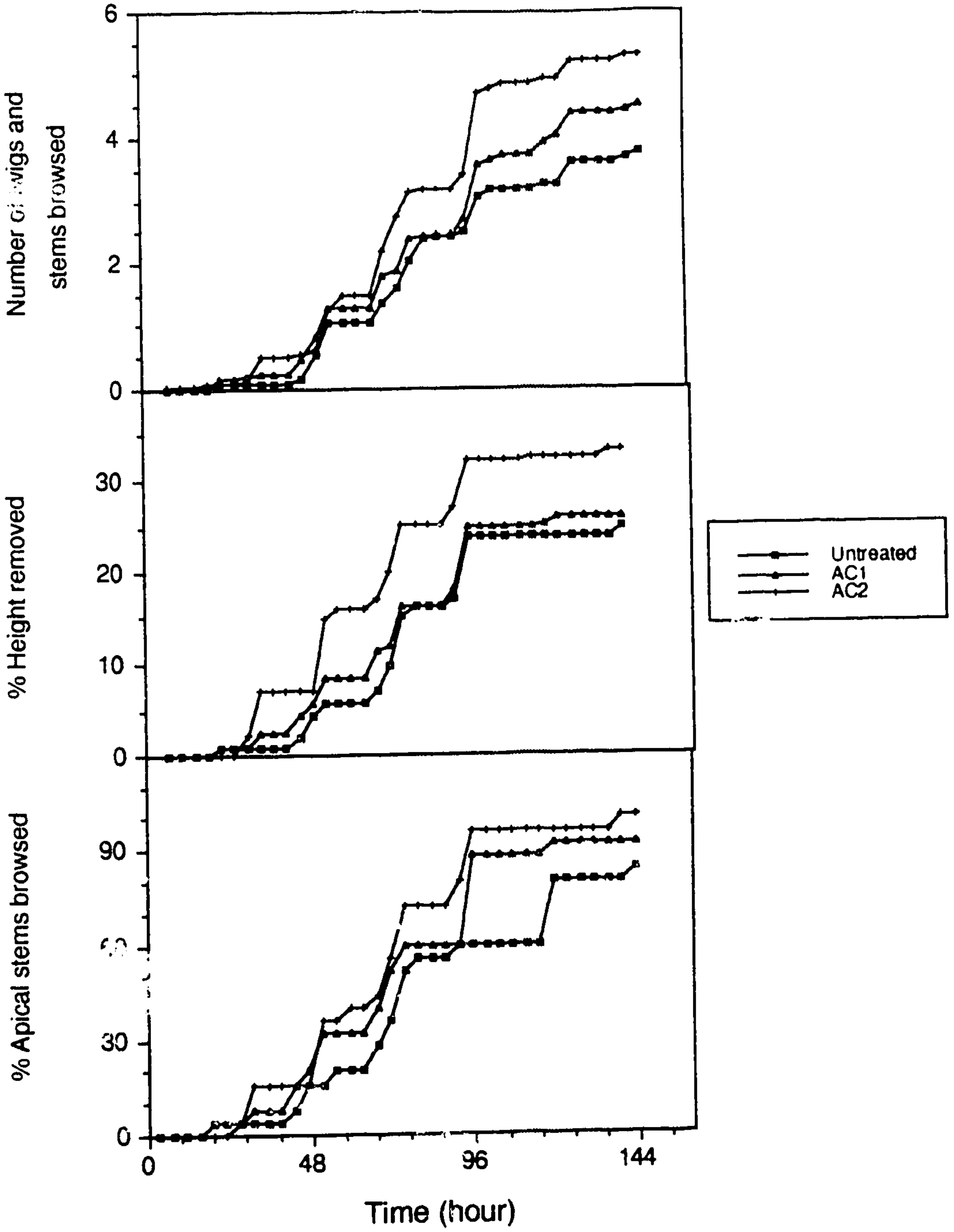

Figure 3.4 Effect of Anipel tablet type on the mean number of twigs and stems browsed per tree, percentage of height removed per tree and percentage of apical stems browsed in Experiment 4 (AC1=Anipel-coplanted type 1, AC2=Anipel-coplanted type 2).

Table 3.6 Means and standard errors (SEM) of final tree browse measurements for Anipel tablet types in Experiment 4.

Measurement (per tree)	Untreated	Tablet Type Type 1	 Type 2	SEM
twigs removed	4.3^{b}[1]	4.9^{b}	6.4^{a}	0.5
twigs removed (%) (arcsin)	30.4 (1807.3)	35.9 (2131.3)	42.5 (25[illegible].6)	 (227.6)
height removed (cm)	3.7	3.6	4.5	0.4
height removed (%)	27.6	26.6	33.2	2.6
twigs and stems browsed	4.0	4.8	5.3	0.5
apical stems browsed (no.trees)[2]	22	23	25	

[1] Means within measurement that do not share a common letter were significantly different ($P \leq 0.05$).

[2] n=25 trees/tablet treatment.

Table 3.7 Means of weight (g [illegible]e/hour) of thiram-treated white spruce consumed by na[illegible] experienced [illegible]res in Experiment 5.

Treatment[4]	Type of Experience[4] Naive[2]	 Experienced[2]	Overall Mean[1]
Untreated[3]	0.76	1.47	1.11
Thiram	0.15	0.16	0.16
Overall Mean[1]	0.45	0.82	

[1] Overall means were significantly different between treatments ($P \leq 0.001$) and types of experience ($P \leq 0.05$).

[2] Individual cell means for naive ($P \leq 0.01$) and experienced hares ($P \leq 0.0001$) were significantly different between treatments.

[3] Individual cell means within treatment were significantly different between type of experience ($P \leq 0.05$).

[4] Standard errors for means were 0.11 for type of experience, [illegible] for treatment and 0.16 for type of experience by treatment.

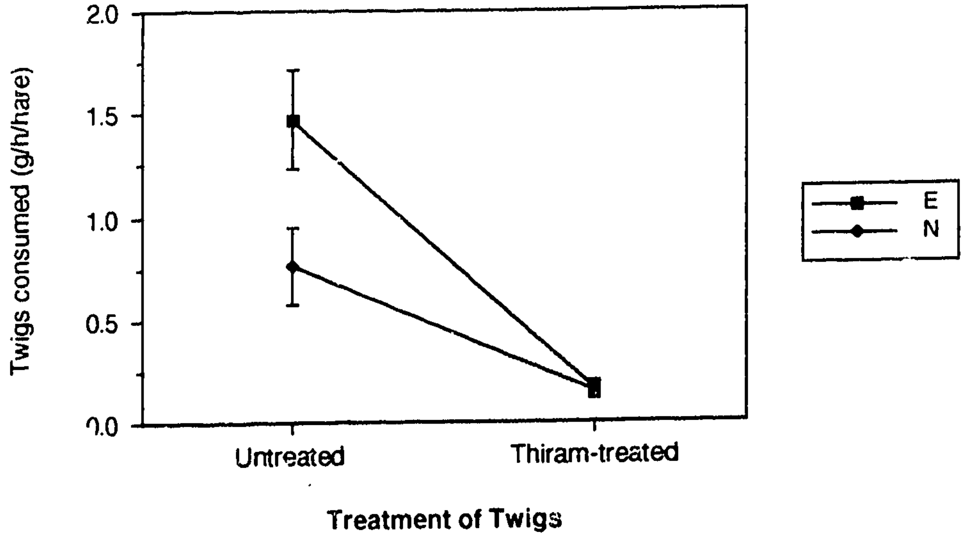

Figure 3.5. Interaction between type of experience of hares (E=experienced, N=naive) and chemical treatment of twigs for twig consumption in Experiment 5. Vertical bars represent ±1 SE.

thiram twigs eaten by both naive and previously exposed hares were similar. Within type of experience, naive hares ($P \leq 0.01$) and experienced hares ($P \leq 0.0001$) consumed a higher amount of untreated twigs than treated twigs.

Comparisons of slope for each type of experience (naive or experienced) by chemical (thiram or untreated) group were significant ($P \leq 0.001$) (Fig. 3.6). Experienced animals consumed a greater cumulative quantity of untreated spruce relative to the other three experience by chemical groupings. Though the naive hares consumed smaller quantities of untreated controls compared to experienced hares, they ate more than either naive or experienced hares did of thiram-treated spruce. The cumulative amounts of thiram-treated spruce eaten by naive and experienced hares were almost identical.

The concentration of thiram in the pooled sample of white spruce twigs was approximately 384.00 ppm.

3.3.5 Experiment 6: Hare Feeding Acceptability of ACl Trees

Anipel-coplanted trees suffered heavier browsing by hares than did untreated control trees. Hares removed approximately 12% more twigs ($P \leq 0.05$) and stem height ($P \leq 0.01$) from ACl trees than from untreated trees. (Table 3.8). There was no difference ($P \geq 0.05$) in the number of apical stems or twigs browsed. Most trees were clipped flush to ground level, with the exception of one untreated tree standing immediately adjacent to a shelter. Treatments were not tested with the Kolmogorov-Smirnov two-sample test because the amount of browsing was recorded over only two days.

The mean daily intake of rabbit ration for hares exposed to untreated controls and ACl trees was 91.1±3.1g (n=2) and 64.8±8.9g (n=2), respectively.

3.3.6 Experiment 7: Hare Feeding Acceptability of AS, AI1 and ACl Trees

Throughout the 12 day browsing period, clipping and barking differed among treatments (Fig. 3.7). The amount of bark removal was significantly greater and significantly lower for ACl and AS treatments, respectively,

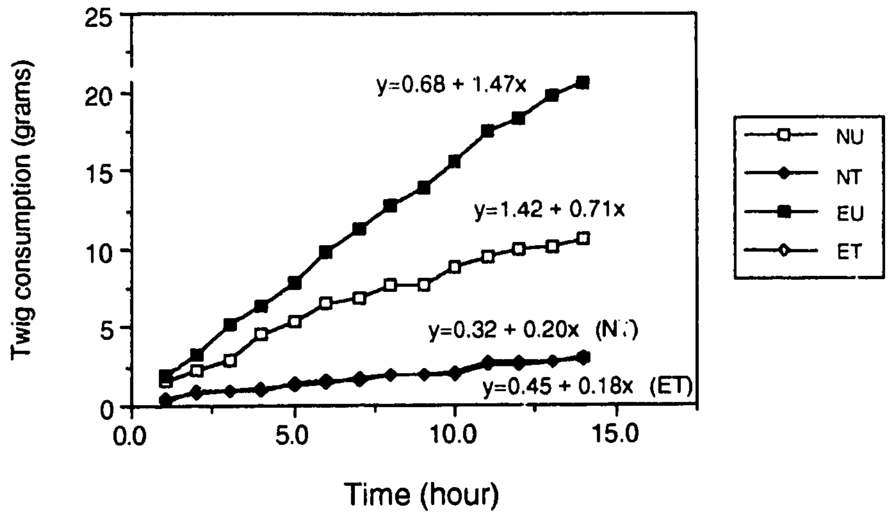

Figure 3.6 Effect of type of experience of hares on the cumulative consumption of thiram-treated white spruce in Experiment 5 (NU=naive-untreated twigs, NT=naive-treated twigs, EU=experienced-untreated twigs, ET= experienced-treated twigs).

Table 3.8 Means and standard errors (SEM) of final tree browse measurements for Anipel-coplanted (AC1) trees in Experiment 6.

Measurement (per tree)	Untreated	Chemical AC1	SEM
twigs removed	6.8	8.3	0.6
twigs removed (%)	65.5^{b1}	77.3^{a}	4.0
height removed (cm) (lambda = 1.5)	10.4 (9.4)	12.1 (7.7)	0.9
height removed (%)	76.7^{b}	88.4^{a}	2.8
twigs and stems browsed (log)	0.4 (0.5)	0.5 (0.5)	0.03
apical stems browsed (no.trees)[2]	29	30	

[1] Means within measurement that do not share a common letter were significantly different ($P \leq 0.05$).

[2] n=30 trees/chemical treatment.

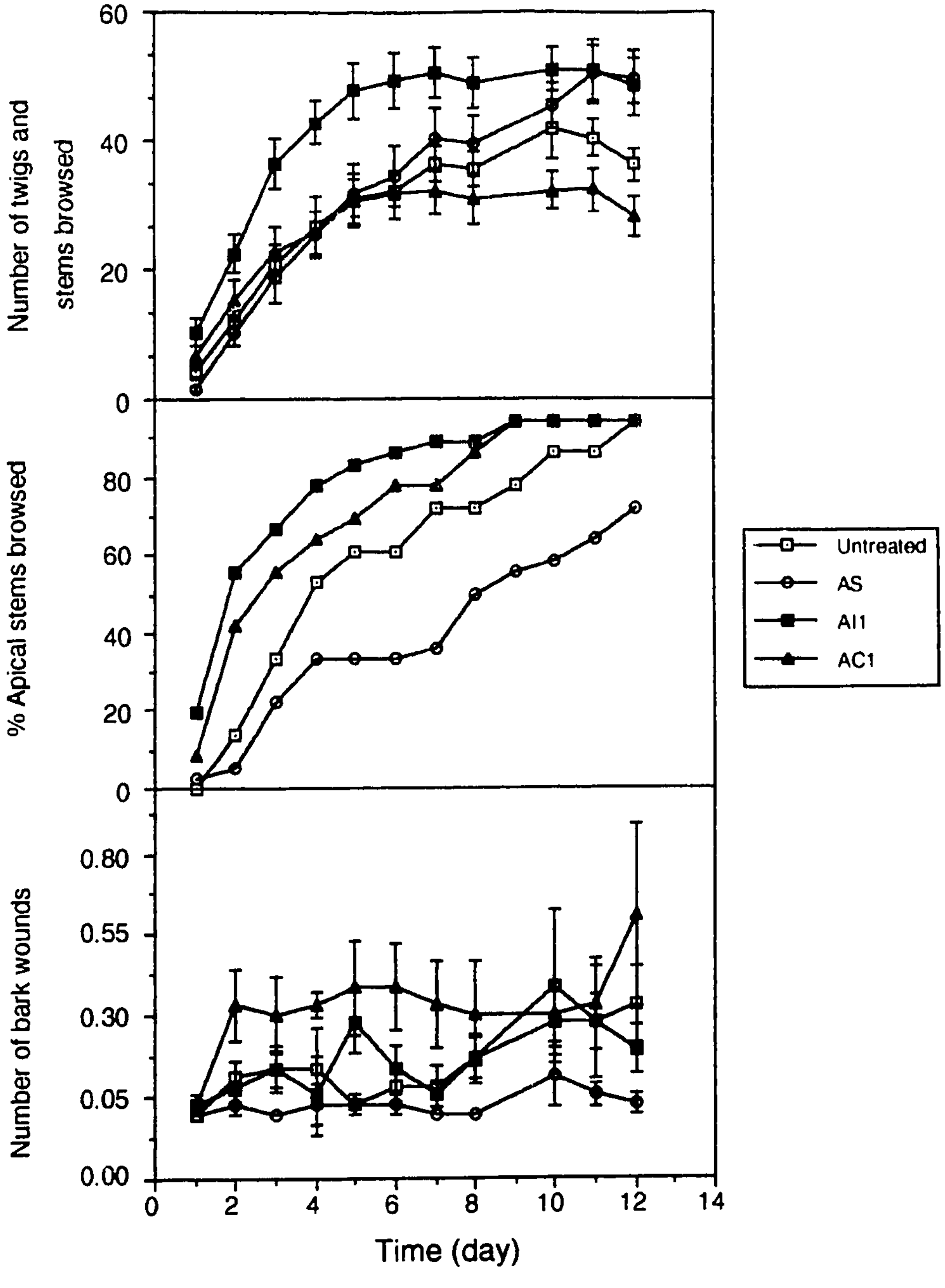

Figure 3.7 Effect of chemical treatment on the mean number of twigs and stems browsed per tree, percentage of apical stems browsed and mean number of bark wounds per tree in Experiment 7 (AS=Anispray, AI1=Anipel-inserted type 1, AC1= Anipel-coplanted type 1). Vertical bars represent ±1SE.

relative to other chemical treatments. Anipel-inserted trees had higher amounts of twig browsing than untreated and ACl trees ($P \geq 0.05$) (Table 3.9). The amount of apical browsing was lower for AS relative to both Anipel treatments ($P \leq 0.01$).

At the end of the experiment, Anipel-coplanted trees had a lower number of twigs browsed and total browse points than other chemical treatments ($P \leq 0.0001$) (Table 3.10). However, these trees were almost completely denuded of available twigs. For AS trees, 72% of apicals were browsed as opposed to 94% for other chemicals ($P \leq 0.01$). All other variables did not significantly differ among treatments.

During the trial, hares gained 15.3±10.0g (n=24). The mean daily intake of rabbit ration for hares (n=12) exposed to untreated, AS, ACl and AIl trees was 64.8±2.2g, 82.3±3.1g, 81.2±4.1g and 80.6±3.3g, respectively.

3.2.2.8 Experiment 8: Hare Feeding Acceptability of Thiram-Treated Trees in the Spring

The amounts of browsing of twigs, bark, apicals and totals of twigs, buds and bark browsed were higher for untreated seedlings ($P \leq 0.001$) throughout the eight day browsing period. Hares frequently stripped foliage from thiram-treated trees and left it uneaten on the ground. For an extremely small proportion of the tree population (≤6%), this feeding behavior subsequently facilitated extensive barking, girdling and consumption of whole seedling trunks. For example, a single tree was barked near the base of the trunk on the first day of the experiment. By the end of the trial, the remaining foliage was stripped from the seedling stem and left uneaten on the ground, whereas the trunk was completely consumed. Bark removal tended to increase at a higher rate than that of twig consumption on thiram trees. Amounts of browsing over time for the number of bark wounds, number of twigs and stems browsed and percent of apical stems browsed are shown in Fig. 3.8.

Hares preferentially browsed untreated trees, completely denuding these trees of twigs and causing heavy barking damage (Table 3.11). Hares browsed treated trees only lightly even when food sources were limiting. At the end of the experiment, hares removed 6.5-times more untreated than

Table 3.9 Comparative effects of Anispray (AS), Anipel-inserted (AI1) and Anipel-coplanted (AC1) on twigs and stems browsed and tree height and apical stems removed over time in Experiment 7.

	Tree Browse Measurements				
Chemical Comparisons[1]	Twigs and Stems (no.)	Buds (no.)	Bark (no.)	Total[2] (no.)	Apex (%)
Untreated vs. AS	NS	NS	**	NS	NS
Untreated vs. AI1	**	NS	NS	**	NS
Untreated vs. AC1	NS	*	**	NS	NS
AS vs. AI1	NS	**	***	NS	**
AS vs. AC1	NS	**	***	NS	**
AI1 vs. AC1	**	**	***	**	NS

[1] Non-significant comparisons denoted by NS; significant comparisons denoted by *($P \leq 0.05$), **($P \leq 0.01$), ***($P \leq 0.001$).

[2] Total is the aggregate total of twigs and stems, buds and bark.

Table 3.10 Means and standard errors (SEM) of final tree browse measurements for Anispray (AS), Anipel-inserted (AI1) and Anipel-coplanted (AC1) trees in Experiment 7.

		Chemical			
Measurement (per tree)	Untreated	AS	AI1	AC1	SEM
twigs removed	194.7	184.5	218.1	153.1	34.5
twigs removed (%) (arcsin)	71.3 (4892.4)	61.9 (4105.9)	75.6 (5177.7)	71.6 (5140.0)	1092.2
height removed (cm) (square root)	11.1 (3.0)	5.4 (1.8)	9.1 (2.8)	14.6 (3.5)	0.7
height removed (%) (square root)	29.5 (4.9)	14.9 (3.0)	25.6 (4.8)	40.4 (6.0)	1.2
twigs and stems browsed (log)	47.4 (1.6)^{a}[1]	69.4 (1.8)^{a}	61.7 (1.7)^{a}	36.0 (1.5)^{b}	0.04
total browsed[2] (log)	48.1 (1.7)^{a}	69.7 (1.8)^{a}	62.7 (1.7)^{a}	36.8 (1.5)^{b}	0.04
buds browsed	0.2	0.2	0.6	0.2	
bark wounds	0.5	0.1	0.4	0.8	
bark wounds (cm^2)	0.4	0.1	0.6	3.1	
apical stems browsed (no. trees)[3]	34	26*[4]	34	34	

[1] Means within chemical that do not share a common letter were significantly different ($P \leq 0.0001$)

[2] Total browse is the aggregate of twigs and stems browsed, bud browsed and bark wounds.

[3] $n=36$ trees/chemical treatment.

[4] Asterisk indicates significant differences among treatments ($P \leq 0.01$).

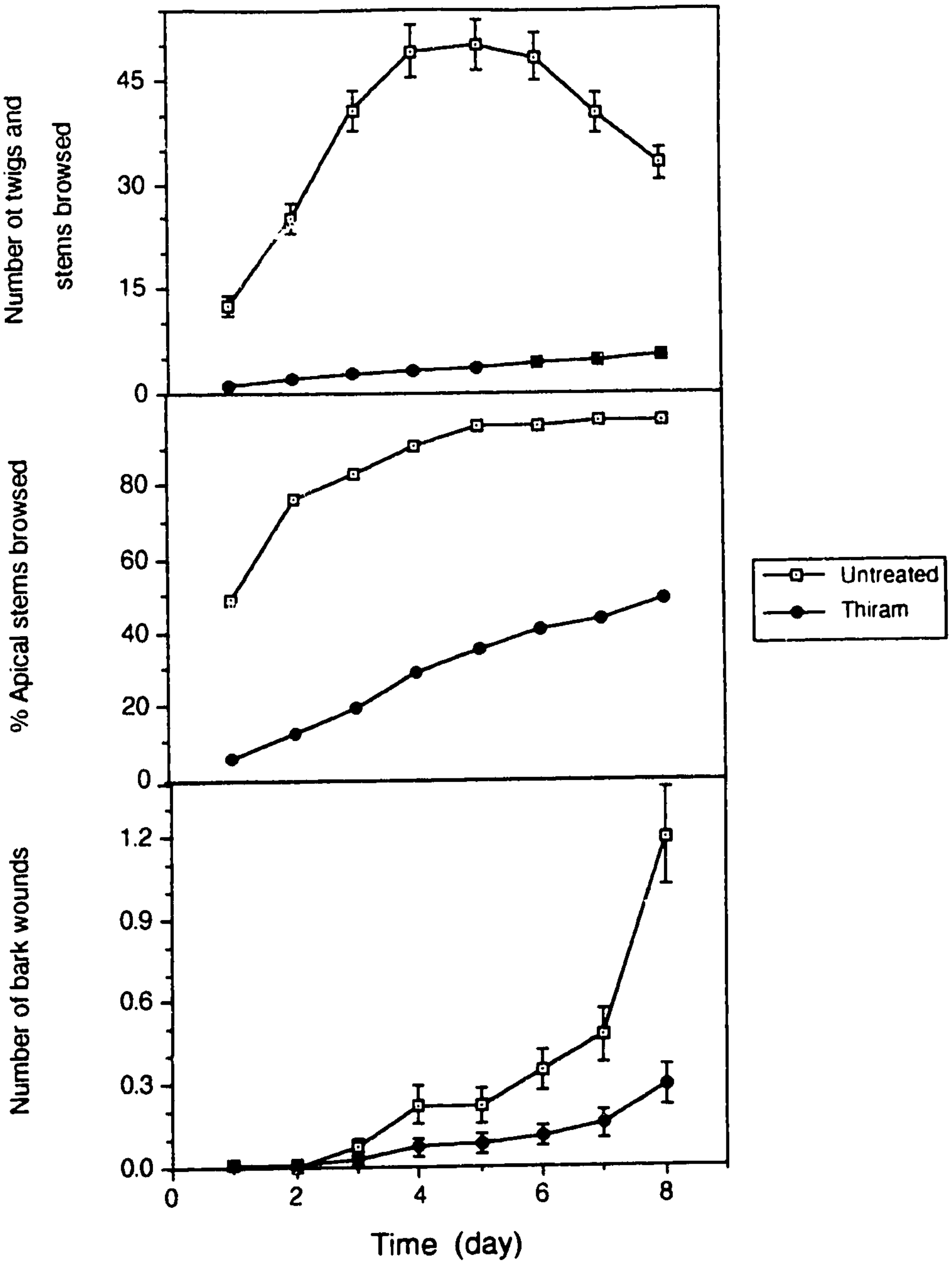

Figure 3.8 Effect of thiram treatment on the mean number of twigs and stems browsed per tree, percentage of apical stems browsed and mean number of bark wounds per tree during the spring in Experiment 8. Vertical bars represent ±1SE.

Table 3.11 Means and standard errors (SEM) of final tree browse measurements for thiram acceptability experiments in spring and fall (Experiments 8 and 9).

	March			November		
Measurement (per tree)	Untreated	Thiram	SEM	Untreated	Thiram	SEM
twigs removed (log)	279.1 (2.3)***[1]	41.9 (1.1)	0.1	440.1 (20.6)***	268.6 (15.6)	0.6
twigs removed (%) (squareroot) (lambda = 1.5)	87.9 (9.3)	14.1 (2.9)	0.4	98.4 (71.8)***	72.8 (47.5)	0.5
height removed (cm) (squareroot)	18.1 (4.1)	5.4 (1.5)	0.3	21.5 (4.6)***	9.6 (2.6)	0.2
height removed (%) (squareroot)	42.6 (6.3)	13.0 (2.4)	0.4	50.7 (7.0)***	28.2 (4.5)	0.3
twigs and stems browsed (squareroot)	33.8 (5.6)***	7.9 (2.5)	0.2	23.2 (5.2)***	57.4 (7.1)	0.3
total browsed[2] (squareroot)	37.0 (5.8)***	8.4 (2.6)	0.2	31.6 (5.5)***	59.3 (7.3)	0.3
buds browsed	1.2**	0.1		0.2*	0.3	
bark wounds	2.1**	0.4		2.2	1.6	
bark wounds (cm^2)	6.5***	0.5		10.0*	5.5	
apical stems browsed (no. trees)[3]	71***	40		64	59	

[1] Asterisks indicate significant differences between treatments *($P \leq 0.05$), **($P \leq 0.001$), ***($P \leq 0.0001$).

[2] Total browse is the aggregate of twigs and stems browsed, buds browsed and bark wounds.

[3] n=36 trees/chemical treatment.

thiram-treated twigs ($P \leq 0.0001$). Twigs browsed and apicals browsed on thiram trees were about 4-times and 2-times less, respectively, than those of untreated trees ($P \leq 0.0001$). Hares sampled most thiram-treated trees; foliage was often clipped on the lower or underparts of the tree. The number of buds browsed and bark wounds were greater for untreated trees ($P \leq 0.01$). Similarly, the area of bark removed was 13-fold greater for untreated trees compared to treated trees ($P \leq 0.0001$). The percentage of twigs removed as well as amount and percentage of height removed did not differ significantly. Yet, browsing of untreated trees exceeded that of thiram-treated trees by a factor of about 3 ($P \geq 0.052$), 2.5 ($P \geq 0.12$) and 2.5 ($P \geq 0.08$) for each variable, respectively.

Simulated browsing of light and heavy intensities estimated the biomass consumed for thiram-treated trees in Experiment 8 (32.8±7.2g n=10) and untreated controls in Experiments 8 and 9 (142.4±16.8g n=10), respectively. The thiram concentration on tree twigs was 411.6 ±10.5ppm (n=8).

Hares placed in the two control pens had an a priori weight loss of 11.1±0.3% (n=12), while the hares assigned to thiram pens lost 11.0±0.5% (n=12) of their initial body weight. During the trial, hares exposed to thiram-treated trees lost 24.6±19.9g (n=12) compared to animals exposed to untreated trees which gained 23.7±11.4g (n=12). The mean daily intake of rabbit ration and willow for hares in pens with thiram-treated trees was 21.6±0.5g (n=9) and 21.7±0.5g (n=9), respectively. Similarly, hares exposed to untreated controls consumed 21.1±0.4g (n=9) of rabbit ration and 20.9±0.5g (n=9) of willow.

3.3.8 Experiment 9: Hare Feeding Acceptability of Thiram-Treated Trees in the Fall

Throughout the browsing period, the amount of twig browsing did not differ significantly between untreated and thiram-treated trees. Upon termination of the experiment, the number of twigs browsed on treated trees was commencing a downward trend toward twig depletion as already exhibited by untreated twigs (Fig. 3.9). Contrary to the spring trial (Experiment 8), where the number of bark wounds increased exponentially on untreated trees throughout the experiment, a greater number of bark wounds

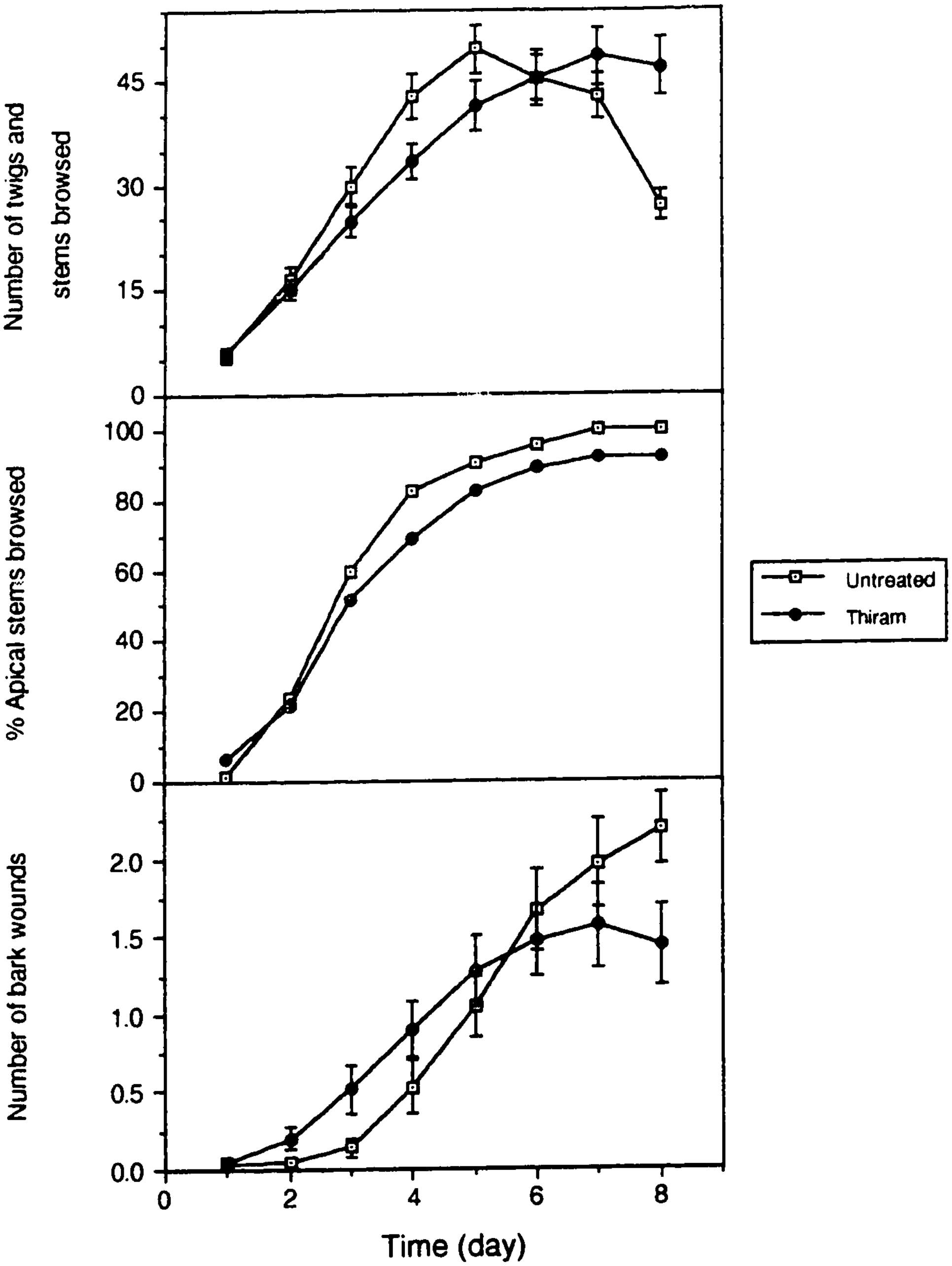

Figure 3.9 Effect of thiram treatment on the mean number of twigs and stems browsed per tree, percentage of apical stems browsed and mean number of bark wounds per tree during the fall in Experiment 9. Vertical bars represent ±1SE.

were incurred initially for treated trees in the fall, but these were later surpassed by that of untreated trees two-thirds of the way through the experiment. Both treatments showed similar trends for the percentage of apicals browsed.

Almost all untreated trees were completely denuded of foliage and sustained moderate barking damage, whereas the bulk of twigs on treated trees remained on the trees, even though 73% of twigs suffered some browsing (Table 3.11). The percentage of tree height and the percentage of twigs removed were 1.5 -times greater for untreated trees than treated trees ($P \leq 0.0001$). The number of apicals browsed did not differ significantly between treated (100%) and untreated (92%) trees ($P \geq 0.05$). Thiram-treated trees had 1.4-times the number of twigs browsed relative to untreated trees ($P \leq 0.0001$). Untreated trees sustained almost 2-fold more bark (cm^2) wounding on tree trunks compared to treated trees ($P \leq 0.05$).

Prior to placing hares into pens containing untreated trees, these animals lost 11.4±0.5% (n=12) of their initial body weight, while those placed into pens containing thiram-treated trees lost 11.0±1.3% (n=12). Hares in pens with thiram-treated trees lost 27.3±34.4g (n=12), whereas hares in pens with untreated trees gained 58.8±31.1g (n=12) during the course of the experiment. Hares exposed to thiram-treated trees had a mean daily intake of 31.8±2.5g (n=9) for rabbit ration and 31.6±2.5g (n=9) for willow. The mean daily intake of rabbit ration and willow for hares exposed to untreated trees was 31.3±2.4g (n=9) and 31.2±2.4g (n=9), respectively.

The concentration of thiram on tree twigs averaged 114.2±25.2ppm (n=6).

3.4 Discussion

3.4.1 Anispray and Anipel

In general, Anispray and Anipel did not affect snowshoe hare preference for or acceptability of treated white spruce trees at the rates of application tested. Both types of Anipel tablets as well as both methods of tablet application had no repellent effects. The greater browsing of treated trees in Experiments 4, 6 and 7 suggested that Anipel may have even attracted browsing by hares. Only undiluted concentrations of Anispray showed any evidence of consistently deterring snowshoe hare browsing of spruce seedlings, though differences in browsing were not statistically significant. Although, hares may find extremely high concentrations of Anispray less palatable than untreated trees, there was no indication of aversive properties for this chemical.

There may be species differences in response to Anispray and Anipel. For example, a study by MacMillan Bloedel found Anispray effective in deterring deer (Odocoileus hemionus columbianus) as well as elk (Cervus elaphus) and moose (Alces alces) depredation of western red cedar (Thuja plicata) and Douglas-fir (Pseudotsuga menziesii) seedlings in British Columbia (R.T. McLaughlin, pers. comm.). In Quebec, Anipel did not produce repellent effects on deer browsing of white and black spruce (P. mariana) (R. Jobidon, pers. comm.). However, preliminary results indicated that both Anipel and Anispray reduced damage from deer browsing of yellow birch (Betula alleghaniensis) and red oak (Quercus rubra).

In addition to the absence of a deterrent gustatory stimulus, the data indicate that the olfactory stimulus provided by these chemical products through the offensive odor of mercaptan, a chemical related to that contained in skunk or mink scent glands, did not affect snowshoe hare forage preferences in any experiments. A repugnant olfactory stimulus of adequate intensity should deter browsing of a forage species without requiring a gustatory stimulus. Furthermore, olfactory stimuli should decrease the initial taste sampling necessary for lagomorphs to experience either an unsavory taste sensation producing repellent effects or gastrointestinal dysfunction or a related illness associated with a particular taste, thereby initiating a learned food aversion.

In Experiment 7, ACl trees had significantly fewer twigs browsed and total points of browse, suggesting this chemical treatment deterred hare browsing. However, these trees initially had fewer twigs (94.3±17.1 twigs, n=108) and were shorter (3.1±1.2cm, n=108) relative to the other three chemical treatments, owing to the one-year age difference in tree stock. In contrast, ACl trees suffered more browsing in Experiment 6. A single untreated tree remained unbrowsed throughout the trial. This likely contributed to the statistically significant difference among the two treatments, though it was not significant biologically. This tree was located adjacent to a plywood shelter and was perhaps awkwardly located in the pen for browsing. Periods of feeding activity and inactivity as depicted in the step-like increments in the amount of browsed material in Experiments 3 and 4 reflected the crepuscular and nocturnal feeding habits of snowshoe hares.

The ineffectiveness of Anispray and Anipel against snowshoe hare depredation of conifer seedlings may be related to a number of factors. For instance, the gustatory and olfactory cues these chemicals generated may not have been sufficient to attain a threshold level, if one existed, required to affect feeding preferences. The effectiveness of repellents are often species-specific. Thus, the chemosensory mechanisms of snowshoe hares may be less sensitive to Anispray and Anipel than those of ruminants. This difference might be associated with detoxification systems that were better equipped for metabolizing the active ingredients in Anispray and Anipel. Jobidon (pers. comm.) found Anispray and Anipel to reduce damage by deer to deciduous but not coniferous species, and therefore, effectiveness may be related to the browse species as well. For example, the uptake of the active ingredients in Anipel tablets may have been translocated much easier by deciduous species than conifers. Furthermore, it was possible that the root systems of the trees did not absorb the chemical initially. However, this could not be substantiated due to the inability to perform chemical analyses.

3.4.2 Thiram

3.4.2.1 Acceptability of Thiram

Thiram afforded white spruce trees with excellent protection during the first winter; twigs removed per tree were 14% for thiram-treated white spruce and 88% for untreated white spruce. A three-year study in western Washington reported snowshoe hare clipping of thiram-treated Douglas-fir (Pseudotsuga menziesii) seedlings to be 18% compared to 87% for untreated trees (Besser and Welch 1959). White and black spruce plantings treated with thiram sustained ≤2% damage as opposed to ≥50% of untreated spruce in Minnesota (Krefting 1958). Field-tests of thiram-treated Douglas-fir indicated small and large untreated seedlings sustained 88% and 94% damage, respectively, over four months, with survival estimated at 33% and

52%, respectively (Hartwell 1969). Four percent of treated stock was damaged and 76% of these damaged trees survived.

Deciduous trees treated with thiram in South Dakota, Wisconsin and Colorado sustained 18% damage by cottontails (Sylvilagus floridanus) and jackrabbits (L. townsendii) (Besser and Welch 1959). Thiram-treated Chinese elms (Ulmus pumila) with stems ≥1.28 cm in diameter were protected from damage by cottontails over a six-month period, whereas the chemical on other shrub species with stems of lower diameter (≤1.28 cm) ranged from 68-90% effective. Goldie (1955) and Hayne and Cardinell (1958) found thiram to protect apple (Malus spp.) rootstocks and shoots from European hares (L. europeaus) in Ontario and cottontails in Michigan.

Not only were fewer twigs removed on thiram-treated trees, but the length of stem removed was less compared to untreated seedlings. Hares browsed 13% (5.4±1.0cm, n=72) of thiram-treated trunks compared to 43% (18.1±1.0cm, n=72) of untreated trunks in Experiment 8. Furthermore, 99% and 56% of white spruce apicals were clipped on untreated and thiram-treated trees, respectively. In Colorado, jackrabbits clipped stems ≥10.2 cm in length from untreated apicals of apple trees and treated apicals remained intact (Besser and Welch 1959). Hartwell (1969) reported that treated Douglas-fir seedlings averaged 79.4 cm and 41.0 cm more vertical growth than the small and large untreated stock, respectively.

The applied solutions of Bartlett Ropellent consisted of 13% active thiram, which was similar to the amount typically used (10%) in other studies (Besser and Welch 1959; Dodge 1969; Hayne and Cardinell 1958; Walter and Soos 1961). Evans (1974) reported 20% hare damage to seedlings treated with 10% thiram whereas hare damage increased to 50% and 70% when 6% and 3% thiram, respectively, were used.

Some browsing of thiram-treated trees occurred. This probably represented sampling by the hares and involved browsing the lower or underparts of the tree, where a lower concentration of the chemical would be expected as a result of the spraying technique. Similarly, when barking injuries were sustained, particularly during the second winter, portions of the trunk had likely received a lower concentration of chemical upon initial application, but had also weathered sufficiently during the summer months such that these areas were substantially more palatable. In the case of untreated trees, however, the depletion of twigs likely instigated the increased amount of barking during the latter stages of both spring and fall experiments. The tendency for animals to strip foliage from thiram-treated trees in order to bark and girdle seedlings suggested that animal appetite was sufficient when feed was restricted to cause the animals to select the most palatable portions of the tree for consumption, though not likely the most nutritious or digestible, which was similar to behavior displayed by hares during peaks in the population cycle (Wolff 1980).

In general, hares prefer twigs ≤4 mm (dpb) (Bookhout 1963; Pease et al. 1979; Sinclair et al. 1982; Sinclair and Smith 1984; Wolff 1980). The consumption or browsing of white spruce tree trunks in the present study was an indication of hunger stress because the dpb exceeded 6 mm (Pease et al. 1979; Wolff 1980). Hunger stress was also demonstrated in an Alaskan study when browsing intensity attained 100% during two cycle peak winters and dpb ranged from 6-15 mm (Wolff 1980).

The use of smaller diameter twigs may be correlated with nutritional value of those twigs (Pease et al. 1979; Sinclair et al. 1982). Bailey (1967) reported that high protein levels occurred in terminal parts of twigs. Greater concentrations of protein, zinc, calcium, magnesium and potassium were correlated with twigs 3 mm in diameter as opposed to 6-10 mm in willow and alder (Alnus spp.) (Wolff 1980). Also, studies by Lindlof et al. (1974), Miller (1968) and Radwan and Campbell (1967) associated general feeding preferences of hares with a high content of nitrogen, phosphorous and carbohydrates. However, the hares used in the study in Chapter 2 did not appear to display nutritional wisdom. Smaller twigs are also more digestible as there is a reduced amount of lignin (Pehrson 1981; Sinclair and Smith 1984).

Thiram still provided some protection after one year of weathering, with 73% of twigs per tree clipped on treated trees as compared to 98% on untreated trees. This degree of protection was less than that provided before weathering as 59% more twigs were removed on thiram-treated trees the second year. Similarly, 10% more twigs were removed on untreated trees during the second experiment. This may be attributable to lower mean temperatures during the experiment the second winter. Mean temperatures during the March 1990 and November 1990 experiments were +3.25°C and -12.65°C, respectively. Furthermore, the slopes among treatments did not appear to differ the second winter for the number of twigs browsed, number of bark wounds or percent of apicals browsed. Browsing by hares beyond current annual growth demonstrated that repellent effects were decreasing. Even though there was a significant difference, the protection provided after one year of weathering was inadequate to be considered effective biologically.

During the first and second winters of the current study, untreated trees were browsed 6-fold and 1.3-fold more than thiram-treated trees. Therefore, thiram was more effective in the first winter than when unprotected current annual growth was available the following fall. Douglas-fir in British Columbia were protected from damage by hares for approximately 14 months after treatment with thiram (Walter and Soos 1961). These authors reported that following application in the fall, clipping decreased over winter but increased to approximately its original value previous to spraying over the next summer. Relative to treated sites, control plots were clipped nearly 2-fold, 19-fold and 6-fold more at the time of spraying and during the following winter and summer, respectively. Consequently, both studies observed large differences in the effectiveness of thiram as weathering occurred and current annual growth appeared.

During the summer in southwestern Oregon, snowshoe hares clipped new Douglas-fir shoots back to the point where thiram was present and feeding increased as treated portions weathered (Hooven 1966). Nevertheless, one month following planting in one plantation, no treated trees were damaged, whereas 16% of the untreated trees had the upper one-third removed and 48% were severely browsed. Another plantation exhibited 2% and 19% damage to trees treated in the spring and following fall, respectively. Damage to lateral twigs and apicals on untreated trees was estimated at 28% for both the spring and fall. Consequently, thiram-treated trees were found to be browsed 9-fold less during the first spring than the following fall after current annual growth had emerged. The apparent increased effectiveness of thiram the first year in Hooven's (1966) study may be a result of the increased availability of other natural feedstuffs.

Withholding feed to stimulate appetite added a unique element to the present research. Numerous studies have examined snowshoe hare feeding preferences for thiram-treated forage with animals under ad libitum conditions either in pen studies (A.W.L. Hawley, pers. comm.) or in a natural environment where an array of forage species were available (Besser and Welch 1959; Hartwell 1969; Hooven 1966; Walter and Soos 1961). As a result of the natural food shortages that occur at the peak of the ten-year hare cycle (Keith 1983; Wolff 1980), it is critical, particularly in the case of chemical deterrents, that hare feeding preferences be tested under conditions of feed deprivation. Feeding preferences may be masked when alternate food sources are available. For example, Zurcher et al. (1983) reported that thiram-treated corn seed repelled thirteen-lined ground squirrels (Spermophilus tridecemlineatus) during a food-choice test, though ground squirrels consumed normal amounts of treated corn when it was the only food available. For both Experiments 8 and 9, the similar losses in body weight of hares, of approximately 10%, in different groups suggested that the stimulation of appetite would have been similar between hares exposed to thiram-treated trees and untreated controls. This level of weight loss was chosen as both wild hares and rabbits were reported to sustain starvation weight losses of 18-34% (Pease et al. 1979) and 19-24%, (Mykytowycz 1961), respectively. Moreover, at daily mean temperatures above -18°C hares may sustain a 30% loss of initial body weight, while at daily mean temperatures below -18°C hares may sustain a 16% weight loss (Pease et al. 1979).

3.4.2.2 Effect of Learning on Preferences for Thiram

Numerous studies have examined the repellent effects of thiram and most researchers refer to this chemical as a repellent and not an aversive agent (Evans 1974; Holm et al. 1988; Johnson et al. 1985; Radvanyi 1987; Zurcher et al. 1983). A repellent deters an attacker, yet does not provide a mere physical barrier or act as a lethal poison (Thompson 1953). If the mode of action of thiram was one of a chemical taste repellent, it would be expected that a herbivore would immediately stop browsing a plant upon receiving unpalatable taste sensations. An aversive agent, however, has properties which create an illness or other negative reinforcement that is subsequently paired with a particular ingested substance or event (Dorrance and Gilbert 1977).

Herbivores typically develop feeding preferences and aversions as a result of exposure to a particular food and familiarity with the consequences of its ingestion. Thus, naive hares were expected to have a much higher consumption of thiram-treated twigs than experienced animals, because a negative reinforcement had not yet been associated with the gustatory stimulus afforded by thiram, within the time available. The consumption of similar amounts of thiram-treated twigs by experienced and naive hares suggested that experienced animals did not acquire a learned food aversion during exposure to thiram. The naive animals may have demonstrated feeding behavior synonymous with neophobia as evidenced by the lower feeding level of untreated white spruce twigs relative to experienced hares. It appeared as though naive hares developed a neophobia upon exposure to the novel food of thiram-treated twigs and that this neophobia was extended to untreated twigs.

As a proportion of total feed intake, experienced hares consumed 9.8% treated twigs, whereas naive hares consumed 16.5% treated twigs. If feed proportions were analyzed, the results may have coincided with the prediction that naive animals would have a higher intake of thiram-treated twigs compared to experienced animals. However, the conversion of weights of twigs consumed by hares to proportions of the total feed intake would have masked data demonstrating that experienced hares had a total feed intake exceeding that of naive animals.

Although no learned food aversion appeared to be established with experienced animals, these hares appeared to demonstrate some learned behavior as they were more adept at differentiating untreated and treated twigs as evidenced by their selection of the former. If post-ingestion effects were produced within the fourteen hour period of twig availability, consumption of treated twigs by both naive and experienced hares should have attained an asymptote, though experienced animals should, theoretically, reach that level sooner. However, cumulative consumption of treated twigs continued to increase during the course of the experiment. As a result of the varied diet of a generalist herbivore and its evolution to attain a balance between the expense of developing plant detoxification systems and the reduced consumption of unpalatable plants as well as foliar repellents, it has been suggested that the forage selection of generalist herbivores may not rely heavily on learning (Freeland and Janzen 1974; Zahorik and Houpt 1977). Although herbivores are capable of learning food aversions, they may be used very little under natural field conditions (Zahorik and Houpt 1977).

Animals may continue to show a lowered feeding response to a substance without the presence of an aversive cue once a learned food aversion is established. However, Holm et al. (1988) reported that deer mice (Peromyscus maniculatus) increased the consumption of untreated corn seed to levels comparable to controls within four days following the consumption of thiram-treated seeds for six days previous. The elevated consumption of food material during this attenuation phase following exposure to thiram suggested that thiram was merely distasteful and did not produce post-ingestion effects. Meadow voles (Microtus pennsylvanicus), exposed to thiram-treated and untreated apple twigs at consecutive intervals, consumed similar amounts of untreated twigs during the pre-treatment and post-treatment periods, which indicated that no generalized aversion was established with thiram (Swihart 1990). In the present study, clipping of untreated current annual growth down to the level of treated portions of twigs, or of extensively weathered thiram-treated twigs, also intimated that thiram only provided a taste cue and was not an aversive agent.

Several findings have indicated the potential for thiram as an aversive agent. The decomposition products of thiram are carbon disulfide and amines in acid environments and hydrogen sulfide under alkaline conditions (Horsfall 1956). Nitsche et al. (1975) suggested that the toxicity of these by-products enhances the toxicity of thiram. For example, dimethylamine, a possible carcinogen, was produced under in vitro acidic conditions but few studies have documented the production and effects of these types of metabolic by-products in the presence of gastric acid in vivo (Dalvi 1988). Nevertheless, the International Agency for Research on Cancer (IARC 1976) associated a carcinogenic by-product, N-nitrosodimethylamine, with the in vivo reaction of thiram and nitrate in the stomachs of guinea pigs. Studies have also attributed the exhalation of carbon disulfide with the breakdown of thiram in rats and humans (Dalvi and Deoras 1936; Hodgson et al. 1975). Moreover, carbon disulfide may be responsible for toxic effects to the nervous system and liver (Dalvi 1988). Diethyldithiocarbamate, another metabolite, may be responsible for cholinesterase and enzyme cofactor inhibition (Dalvi 1987).

The acute oral toxicity (LD 50) of thiram in various mammals ranges from 230-2800 mg/kg; the LD50 specifically for rabbits is 350 mg/kg (Dalvi 1988). Chronic toxicity studies in rats have associated dietary thiram with reduced growth rate, nervous dysfunctions, increased mortality rate (IARC 1976), and damage to the spleen, liver, and blood hemoglobin and enzymes (Stankevich et al. 1980). Intracutaneous administration of thiram in rabbits can produce contact dermatitis (Brusilovskiy and Fiallkovskiy 1973). The direct application of thiram solutions to the skin of rabbits, however, did not produce any skin irritation (Matthiaschk 1973). Abortion was also reported in sheep suffering chronic exposure to thiram (Dalvi 1988). However, according to some researchers, thiram does not appear to have chronic toxicological, physiological or behavioral effects on snowshoe hares, black-tailed deer or elk (Campbell and Bullard 1972; Evans 1974).

3.4.3 Research Techniques

Techniques may affect the preference and acceptability ratings observed for snowshoe hares. According to De Vos (1964), percent browsing using stem counts is significantly less accurate than using weight of material before and after consumption. The latter is feasible for cafeteria-style experiments, but not feasible for the study of standing biomass as was the case in the present study, unless the weight of material removed was estimated by the dpb (Telfer 1972). Standing biomass was selected for this study in order to represent the available forage in its natural form. The natural morphology of the tree as well as the biochemical properties would be represented which may otherwise be altered upon cutting for purposes of cafeteria-style experiments. This natural presentation was important in this study because the differential distribution of the applied chemicals on any one tree subsequently led to differential browsing of the treated seedlings, for example, the increased removal of bark relative to twig removal on thiram-treated trees.

Prior to commencing the study, the most appropriate variables to estimate forage palatability were not well known for studies using standing biomass. Consequently, numerous measurements were taken in order to determine the best methods for future research. For the palatability experiments, the number of twigs removed per tree gave a better indication of snowshoe feeding preferences than the number of twigs browsed per tree. The number of twigs browsed per tree were those clipped twigs remaining on the tree at the end of the experiment. The number of twigs removed, however, was determined by subtracting the number of unbrowsed twigs remaining on the tree at the end of the experiment from those on the tree initially. A low number of twigs browsed per tree may have indicated either that few twigs were eaten with most remaining unbrowsed or that twig removal continued to depletion such that a minimal number twigs remained to estimate browsing. Compared to the raw number of twigs removed or height clipped, the percentages of these variable were the best estimators of forage acceptability or preference, particularly if the mean number of twigs or tree height available for browsing differed from treatment to treatment.

The area of bark removed appeared to be a better indicator of tree damage rather than the number of bark wounds because the number of wounds could fluctuate widely from day to day. These fluctuations resulted from two or more bark wounds becoming one or height removal causing the complete loss of bark wounds. Barking pressure on browse species has, for the most part, been estimated qualitatively (De Vos 1964).

Comparisons of the effectiveness of thiram with other studies was difficult and may not be entirely valid. Previous research was based on qualitative data, namely, whether a tree was browsed or not browsed (Besser and Welch 1959; Hooven 1966; Walter and Soos 1961). As a consequence, comparisons were made between the percentage of the mean number of twig browsed on individual trees in this study and the percentage of the total number of trees browsed in related studies.

Some studies which have examined standing biomass have differentiated apical and lateral clipping of twigs (Dodds 1960; Keith 1972; L. Roy, pers. comm.), but few have measured the height or amount of the apical stem removed (Hawley, unpubl. results). The percentage of twig length removal by hares has been used in cafeteria-style experiments by researchers as an indication of actual utilization of a browse species relative to availability (Tomm and Hudson 1978). Clipping of the apical stem is particularly important to the forestry industry, as it deforms the tree, increasing the standard rotation length as well as the likelihood of its use only for pulp rather than timber.

3.4.4 Forestry Implications

Chemical repellents which provide either a distasteful or aversive conditioned stimulus may aid in the reduction of snowshoe hare damage to seedlings in conifer plantations. Anipel and Anispray do not produce antifeeding effects on snowshoe hares. Because these products are still in the infancy stages of testing and development, new formulations may prove more effective. Since the effectiveness of most chemical compounds are species-specific, these repellents may deter ungulates or other wildlife and not hares from browsing conifer seedlings, though no research is, as yet, available to support this.

Products containing thiram, however, have been used extensively by the forestry industry for decades to deter hare browsing (Black and Hooven 1978; Dodge 1969; Thompson 1953). Duffield and Eide (1962) stated that several industrial tree-planters in the Pacific Northwest treated nursery trees with repellents prior to planting, including thiram, as early as 1958. By the late 1960's, thiram was used in many forestry nurseries and for respraying existing plantations in the Pacific Northwest (Dodge 1969).

During the first winter of this study, thiram was effective in deterring food-deprived snowshoe hares from browsing conifer seedlings. In theory, the effectiveness of thiram should increase under field conditions since other food sources would be available, even if the most preferred species were already depleted. Less preferred species may likely be consumed by hares prior to excessive clipping or barking of thiram-treated trees. However, unless the effectiveness of thiram in a natural environment exceeds that in pen trials, trees would have to be sprayed each fall during a 3-5 year span at the height of the snowshoe hare cycle, to protect established seedlings from hare browsing. Thiram has only a moderate repellent effect on deer browsing of seedlings (Besser and Welch 1959; Dodge 1969; Evans 1974; Radwan 1969). Therefore, other chemical compounds may have to be used in areas where extensive damage is perpetrated by ungulates.

Behavioral adaptations of wildlife can further influence the effectiveness of an aversive conditioning technique (Dorrance and Gilbert 1977). Snowshoe hares have crepuscular and nocturnal feeding habits (Keith 1964) and excessive amounts of time and energy are not likely expended in search of a particular food. Feeding strategies honed to a specific food type are usually more conducive to aversive conditioning (Dorrance and Gilbert 1977). The protection of specific areas through the use of an aversive agent would be simplified if hares were either gregarious or territorial because the animals would be easier to target. However, hares do not display these types of behavior, though they do establish home ranges and are fairly sedentary within these areas; but variation and extensive overlap may occur with respect to season and population density (Radvanyi 1987). Snowshoe hares can produce a large number of litters per year and large litter sizes and little maternal investment occur with precocial young (Keith 1972; Keith and Windberg 1978). Thus, the opportunity for young to learn forage selection strategies from maternal stimuli is extremely limited.

As indicated by the higher consumption of untreated spruce twigs by experienced hares, conditioning through negative reinforcement is more effective with naive animals. Removing experienced hares from an expansive natural environment to aversively condition naive animals would be essentially impossible because experienced animals may relocate into areas previously vacated of hares. Also, if reapplication of the aversive agent is necessary, as is the case with thiram, a time lag in exposure to the chemical may require that all animals be reconditioned. Parameters such as high population turnover, recruitment and mortality, that are characteristic at the peak of the snowshoe cycle, also make the conditioning of an entire population extremely difficult. Nevertheless, recruitment and conditioning of naive hares at the peak may be less of a factor because juveniles account for the most of the mortality (Keith and Windberg 1978).

Cost-effectiveness of the applied chemicals is extremely important to a forest manager. The costs of treatment with one pellet, 5 ml and 20 ml per six-year-old tree for Anipel, Anispray and thiram, respectively, were for Anipel $0.275, Anispray $0.215 and thiram $0.18. Volumes of Anispray used on one-year-old trees and its corresponding cost effectiveness are as follows: a)0.5 ml-$0.0215 (25%) b)1.0 ml-$0.043 (25% dual application) c)0.7 ml-$0.0258 (33%) d)1.0 ml-$0.043 (50%) e)2.0 ml-$0.086 (100%). Concentrations of the mixed solutions are given in parentheses. Anispray, therefore, may not be cost-effective, particularly with larger volumes of undiluted spray required for larger stock and the need to respray annually to ensure the protection of current annual growth. However, a cost-benefit analysis based on the necessary expenditures and quality and quantity of timber likely to be preserved within individual forest management areas may be required. For example, thiram-treated trees following the first season of application may continue to provide a potential source of merchantable timber, whereas by the second season, when current annual growth is unprotected, the trees may become too deformed for use as timber and, therefore, may only be useable for pulp.

In addition to cost-effectiveness, control strategies for snowshoe hare damage to conifer seedlings must be logistically and environmentally sound as well as acceptable to the public. To date few methods of hare control, including repellents, have fulfilled these criteria, in addition to demonstrating a high, long-term effectiveness against browsing by hares. Foresters would likely find it very difficult operationally and monetarily to individually spray each tree in the field. Treatment of trees in the nursery prior to outplanting would increase the efficiency of the chemical application the first year. Aerial spraying of cut blocks would not provide a viable alternative since all vegetation, both deciduous and coniferous, would be contaminated potentially discouraging its use by many wildlife species. Consequently, on a long-term and large-scale, chemical deterrents would not likely provide a feasible solution for the control of snowshoe damage to conifer seedlings.

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4. General Discussion

4.1 Interaction of Herbivores and Phytochemicals

Coevolution of herbivores and plants has led to numerous adaptive mechanisms by both. Plants must attain a balance between the metabolic expense of producing defensive metabolites and the risk of being consumed. The metabolic cost of producing tannins may be 2 to 6-times greater than other defensive chemicals such as alkaloids, terpenes and simple phenols yet, once formed, polymeric phenols are basically stable and do not have the rapid metabolic turnover time of 24 hours that other plant secondary metabolites do (Swain 1979). Herbivores must either evolve toward specific detoxification systems capable of metabolizing potentially toxic plant compounds or reduce the ingestion of various plant species or plant parts (Robbins et al. 1987; Zahorik and Houpt 1977). In lagomorphs, caecotrophy can provide a source of nutrients and microflora (Freeland and Janzen 1974). Reingested feces may contain substantial levels of protein, vitamins and minerals, particularly phosphates, which maintain a high stomach pH conducive to bacterial degradation of plant secondary compounds (Harborne 1979; McBee 1971; Moir 1968; Yudkin 1963).

It would also be beneficial for herbivores to assess forage quality relative to nutrient and energy availability but also the extent of assimilation of these parameters in terms of digestibility and metabolizable energy. However, forage of low quality, attributable to either insufficient nutrients or high concentrations of defensive chemicals, may be consumed if the forage does not form a large proportion of total feed intake and is consequently buffered by ingestion of other feedstuffs (Klein 1977; Sinclair and Smith 1984; Zahorik and Houpt 1977).

The effects of a single dominant factor, as was the apparent case with thiram, and synergistic factors, as evidenced by the conifer preference experiments, likely influence forage selection. For example, an essential nutrient bound to an allelochemical or a nutrient at a particular concentration may act as a deleterious allelochemical and, likewise, an extremely toxic compound may be converted to a nutrient source in a highly adapted herbivore (Reese 1979). The interaction of allelochemicals may also decrease pre-absorptive and post-absorptive toxicity of one or more of these compounds (Freeland et al. 1985).

A buffering capacity may have existed between the high and low concentrations of both condensed tannins and nutrients in Siberian larch and Norway spruce, respectively. The availability of rabbit ration and willow may also have buffered the intake of conifers, as well as may have provided otherwise limiting nutrients. Moreover, the palatability of these plant species may have been related to the difference between nutrients and secondary metabolites within a species, rather than a single chemical factor as reported by Cooper et al. (1988) for browsing ruminants. Similar to the consumption of conifer species, the decreased ingestion of thiram-treated trees under restricted feed conditions may have been a result of the lack of alternative woody browse to buffer toxic effects. Earlier preference experiments with white spruce conducted by Hawley (unpubl. results) did indicate, however, that other treatments were selected prior to thiram-treated trees under ad libitum conditions, which suggested that the availability of untreated trees was not sufficient to buffer the toxicity of thiram.

The type and effectiveness of detoxification mechanisms used by herbivores are critical to their survival and evolutionary fitness. It appeared that snowshoe hares were able to select forage species with much higher quantities of condensed tannins and total phenols in this study and related studies (Bryant 1981; Sinclair and Smith 1984) compared to other herbivores (Cooper and Owen-Smith 1985; McKey et al. 1978; Oates et al. 1977; Swain 1976). This suggests that these animals have adapted to the intake of large quantities of woody browse and consequently have developed detoxification systems better equipped to metabolize and eliminate associated secondary compounds. African ruminants (Cooper and Owen-Smith 1985), cattle (Cooper-Driver et al. 1977) and primates (McKey et al. 1978; Oates et al. 1977) which have a much lower threshold level for tannins do not generally have a diet that consists of extensive amounts of woody browse. Leaf-eating monkeys may lack adequate detoxification mechanisms to dispose of tannins, yet these animals appear to have sophisticated detoxification systems to metabolize the high alkaloid content in forage species (Harborne 1988). Despite the apparent capacity of snowshoe hares to ingest relatively large amounts of tannins or man-made chemicals including Anispray and Anipel, the digestive physiology of these herbivores may be ill-equipped to detoxify other natural plant defensive compounds such as terpenes or synthetic taste repellents such as thiram.

The chemosensory abilities used to assess the palatability of natural feedstuffs are also used during the selection of synthetic compounds. In both cases, if a particular defensive compound becomes associated with a specific negative reinforcement such as gastrointestinal illness, a learned food aversion may be formed. Indeed, the tendency for generalist herbivores to consume a varied diet may provide a more effective mechanism than learned food aversions to ensure dietary fitness (Freeland and Janzen 1974; Zahorik and Houpt 1977). This may be true especially when exceptionally high quantities of plant defensive compounds are required for toxic effects and a herbivore has coevolved with a particular forage species. However, the establishment of learned food aversions may be more important in the case of synthetic taste repellents or aversive agents, where adaptations to metabolize these compounds have not yet evolved.

As a generalist herbivore, snowshoe hares forage indiscriminately. This suggests that the gustatory and olfactory thresholds required for the consumption of particular forage species may be higher for hares than for herbivores with highly selective diets. Subsequently, the chemosensory mechanisms and physiological systems of snowshoe hares may be less sensitive to plant secondary metabolites and synthetic feeding deterrents. White spruce in the conifer preference experiment and thiram-treated white spruce in chemical acceptability experiments were sampled even though hares displayed a preferential consumption of other treatments. Unlike snowshoe hares, herbivores with selective foraging strategies may have browsed all Siberian larch and Norway spruce entirely before clipping white spruce and furthermore, may have endured acute physiological stress or even death rather than consume portions of thiram-treated trees. Therefore, the sucess of natural and synthetic compounds to reduce snowshoe hare depredation of conifer trees may be extremely difficult as a result of this animal's feeding behavior.

4.2 Forestry Implications

Hare damage to conifer seedlings, particularly at the peak of the snowshoe hare cycle, is a well documented problem (Radvanyi 1987; Walter and Soos 1961). Despite the preference for deciduous browse, conifers may be clipped and barked extensively during cycle highs (Aldous and Aldous 1944; Keith 1972; Radvanyi 1987; Tomm 1978). The tendency for snowshoe hares to browse newly planted stock poses a serious threat to the forestry industry. Direct losses of timber are compounded by thinning of stands beyond standard densities, extending harvest rotation length and reducing timber quality. Cumulative investments, ranging from site preparation, planting, stand tending and harvesting to the potential commercial value of merchantable timber, result in a sizeable revenue loss when planted trees are browsed by hares.

Habitat patchiness and interspersion are important factors regulating the distribution of hares. Clear-cutting creates edge and cut blocks of a checkerboard or long, narrow pattern increase vegetation mosaics which are highly preferred by hares (Radvanyi 1987). The smaller the blocks or more irregular the boundary, the greater the amount of edge and, therefore, habitat interspersion. Forest clearing from cutting and forest fires increased from 50,000 ha to 70,000 ha annually between 1975 and 1980 in the prairie provinces (Brace and Ball 1982). The early successional regeneration of cut blocks offers an abundance of food, while surrounding conifer forests in burn sites or isolated pockets of coniferous species in aspen conversion sites provide shelter. Clear-cutting practices also improve the quality and quantity of browse, as early successional species produced by regeneration provide more palatable and nutritious plants (Conroy et al. 1979).

Approximately 20 million seedlings were planted in Alberta during 1986-87, on 22,258 ha of conifer plantations (Alberta Forest Service 1988). The Department of Forestry, Lands and Wildlife has no monetary value recently assigned to the prospective losses of Alberta's reforestation projects owing to snowshoe hare browsing. However, review of available information specific to Alberta strongly suggests that these losses are substantial, and that there is a need for effective forms of hare damage control.

The use of wildlife repellents has potential for the control of snowshoe hare depredation of conifer seedlings. Nevertheless, all commercial repellents are targeted at a wide array of domestic and wild animals and, therefore, only a limited number may possess the ingredients to consistently deter a specific species. Moreover, a chemical repellent must fulfill numerous criteria to be acceptable to the forestry industry as well as the general public. For example, an ideal chemical repellent should be: inexpensive, easy to apply, nonvolatile, insoluble in water, nonphytotoxic and remain effective throughout the season(s) of susceptibility (preferably a systemic) (Thompson 1953). Repellents should also cause neophobia through novel tastes, primary food aversion through unpalatable tastes and a learned food aversion through a negative reinforcement such as illness (Reidinger and Mason 1983). The efficacy of such products rely primarily on the gustatory and olfactory stimuli they elicit. These products often attempt to imitate one of the broad taste categories of natural plant compounds. For example, the reputed bitter qualities of Anispray and Anipel may simulate the natural bitterness of alkaloids. Despite the evidence suggesting thiram merely acts as a taste repellent, it has yet to be proven conclusively that aversive properties are not operating.

The conifer preference experiments indicated that white spruce was the most resistant conifer to snowshoe depredation. This native conifer is currently used for approximately 85% of Alberta's reforestation species. Nevertheless, white spruce is not immune to damage, particularly when food shortages occur. Just as a multiplicity of factors affect forage selection displayed by snowshoe hares, a multi-faceted approach to forestry practices must be developed to control snowshoe hare damage to seedlings in conifer plantations. For example, white spruce in both tree nurseries and established plantations should be chemically treated with thiram. Furthermore, timing planting to the low of the snowshoe hare cycle, mechanical removal of deciduous regeneration and related silvicultural techniques should support the use of a resistant conifer genotype treated with a taste repellent.

4.3 Literature Cited

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Appendix: Glossary

acceptability -a no-choice situation where an animal either finds a single food acceptable or unacceptable

alkaloid -natural heterocyclic nitrogen compounds found in plants; characterized by their specific physiological action and toxicity; used by many plants as a defense against herbivores

allelochemical -nonnutritional chemical produced by one organism that affects the growth, health, behavior or population biology of members of other species

caecotrophy -reingestion of soft mucal pellets, produced in the caecum, directly from the anus

condensed tannin -oligomer of flavan-3,4-diols (ie. catechin and epicatechin); attachs to cellulose or protein bound to fiber of cell walls; astringent taste; chemically stable

essential oils -oils of plants that contain terpenoid and phenylpropenoid compounds

hydrolyzable tannin -ester of glucose and phenolic acids (ie. gallotannins and ellagitannins); inactivate digestive enzymes; highly stringent and chemically unstable relative to condensed tannins

learned food aversion -specialized form of learning created by pairing a negative reinforcement with a particular food, space or event such that the item is avoided in the future

neophobia -suppressed consumption of novel edibles relative to familiar substances

nutrient -a compound required for the normal growth, development and maintenance of an organism's functions

nutritional wisdom -animals select foods which optimize their nutritional well-being and reject foods which are poisonous or low in nutritional value

palatability -selective intake response as determined by the interrelationship between the browsing herbivore, the plants offered the animal and the surrounding environment

phenol -plant substances that possess an aromatic ring bearing one or more hydroxyl substituents; frequently occur combined with a sugar as glycosides and usually located in cell vacuoles; classes include simple phenols, phenolic acids, phenlypropanoids, flavonoids, flavonols, flavones, xanthones; function as structural material of cell walls, regulation of growth, antiherbivore defense

phytochemical -chemical constituent of plants especially secondary metabolites

plant secondary metabolite -compounds including alkaloids, terpenoids and flavonoids which do not function directly in biochemical activities like photosynthesis, respiration and protein synthesis which support growth; function in defense against insects, fungi, in allelopathy, or as attractants to pollinators and fructivores; negative effect on herbivore fitness or a deterrent effect on herbivore feeding

preference -an animal is confronted with more than one food type and has a choice of forage species

stilbene/ß-tannin -$C_6H_5.CH{=}CH.C_6H_5$; low molecular weight tannin capable of binding protein

tannins -high molecular weight polyphenols derived either from carbohydrates and phenolic acids by condensation reactions or from flavonoids; common in leaves, fruits, seed coats, bark and heartwood of plants; capacity to bind to almost all soluble proteins; astringent taste; defend plants against feeding by herbivores and microbial and fungal attack

taste repellent -deters an animal from feeding on a certain object or plant species by the distasteful gustatory sensations it elicits

terpenoid -a group of plant secondary metabolites based on one to four or more isoprene (C_5) units, including many essential oils, gibberellins and carotenoids