Nordic Society Oikos

Latitudinal patterns in consumption of woody plants by snowshoe hares in the eastern United States

Robert K. Swihart, John P. Bryant and Lucy Newton

Swihart, R. K., Bryant, J. P. and Newton, L. 1994. Latitudinal patterns in consumption of woody plants by snowshoe hares in the eastern United States. – Oikos 70: 427–434.

Previous studies have documented large-scale spatial variation in palatability of woody plants to snowshoe hares, Lepus americanus, but clear latitudinal gradients have not been demonstrated. We conducted a series of feeding trials designed to compare palatabilities of woody plants that differed either in latitude of collection, geographic distribution, or stage of development. Tests were conducted using three species of birches (Betula) and two species of aspens (Populus) found in the eastern United States within the range of snowshoe hares. When presented with conspecific juvenile- and mature-stage twigs of species with predominantly boreal distributions, hares generally avoided juvenile-stage twigs, whereas little discrimination was evident between juvenile- and mature-stage twigs with nonboreal distributions. When presented with a choice of congeneric juvenile-stage aspens, hares avoided the twigs of the boreal species. No differences in consumption were noted among birches; however, Bryant et al. have observed an avoidance of boreal birches by hares in Alaska and Connecticut. Finally, when presented with conspecific twigs collected at different latitudes, hares did not discriminate among mature-stage twigs. However, discrimination did occur when hares were offered juvenile-stage twigs; twigs from northern latitudes were eaten less than twigs from southern latitudes, and this trend was more pronounced for species with predominantly boreal distributions.

It is doubtful that the observed patterns were generated solely, or even primarily, by latitudinal gradients in temperature affecting either bioenergetics of hares or chemicals associated with cold hardiness in plants. Rather, the available evidence suggests that the elevated levels of avoidance exhibited by hares for juvenile plants with predominantly boreal distributions have resulted from more intense selection for chemical defense against herbivory in winter-dormant plants occupying boreal areas. Colder temperatures, by limiting nutrient availability, also could increase the selection pressure for antiherbivore defenses in boreal areas by magnifying the cost of herbivory.

R. K. Swihart, Dept of Forestry and Natural Resources, Purdue Univ., West Lafayette, IN 47907–1159, USA. – J. P. Bryant, Inst. of Arctic Biology, Univ. of Alaska, Fairbanks, AL 99775–0180, USA. – L. Newton, D140 Schurman Hall, New York State College of Veterinary Medicine, Cornell Univ., Ithaca, NY 14850, USA.

Herbivores can influence plant fitness and community structure. In northern temperate forests, and especially in boreal areas, twigs of woody plants often serve as an important food source for herbivorous mammals during winter (Hough 1949, Telfer 1972, 1978, Swihart and Yahner 1983, Mattfeld 1984, Keith 1990, Tahvanainen et al. 1991). When mammalian browsers are abundant, they can reduce severely the survival, growth, and distribution of woody plants in a locality (Snyder and Janke 1976, Wolff 1980, Frelich and Lorimer 1985, Alverson et al. 1988, Brandner et al. 1990, Bryant et al. 1991a). Thus, strong selective pressure presumably is exerted on plants to evolve mechanisms to deter browsing in localities where herbivorous mammals are plentiful. Indeed, resist-

ance of woody plants to mammalian browsers is heritable (Dimock et al. 1976, Silen et al. 1986, Rousi et al. 1991), and experimental evidence is consistent with the interpretation that chemical deterrents present in dormant twigs have evolved primarily in response to browsing pressure (Bryant et al. 1989, 1992).

Most investigations of plant-herbivore interactions have ignored the possibility of large-scale spatial variation in such relationships. Recently, though, Bryant et al. (1989, 1994) documented large-scale patterns of chemical defense of high-latitude woody plants against browsing by hares (*Lepus* spp.). They demonstrated that plants growing in areas characterized by high levels of browsing pressure were less palatable to hares than were plants from areas with lower levels of browsing, and they argued that these patterns were linked to geographic variation in the intensity of selective browsing by mammals, which in turn was determined largely by spatial variation in wildfire history. Although the data of Bryant et al. (1994) were suggestive of a latitudinal trend, definitive conclusions could not be drawn because collection sites varied greatly in longitude, and because comparisons among species grown solely in a common environment were not conducted. The objective of the present study was to extend the biogeographic analysis of Bryant et al. (1994) by determining whether a latitudinal gradient exists in susceptibility of winter-dormant woody plants from the eastern United States to browsing by snowshoe hares *Lepus americanus* (Erxleben). Snowshoe hares were chosen as our model herbivore because they discriminate among plants on the basis of plant defensive compounds (reviewed by Tahvanainen et al. 1991), they have been used extensively as a model in boreal systems where they are an important mammalian herbivore (Tahvanainen et al. 1991), and they occupy a broad geographic distribution which encompasses both boreal and mixed deciduous-coniferous forests (Hall 1981).

Susceptibility to browsing may vary as a function of plant ontogeny. Severe browsing by mammals disproportionately affects juvenile-stage woody plants (i.e., seedlings and saplings, sensu Kozlowski 1971) because it reduces competitive ability and increases mortality and age of first reproduction (references in Bryant et al. 1991b). An evolutionary response of woody plants should be to invest relatively heavily in defense of the juvenile growth stage (Bryant et al. 1983). Consistent with this hypothesis, juvenile-stage woody plants in boreal areas exhibit greater concentrations of deterrent chemicals and hence experience reduced consumption by browsers relative to mature-stage conspecifics (Bryant et al. 1983, Reichardt et al. 1984, 1990, Tahvanainen et al. 1985, Clausen et al. 1986, Jogia et al. 1989).

The relative susceptibility of juvenile- and mature-stage plants to browsing, then, may be a reflection of the intensity of selection for antiherbivore defense. Populations of snowshoe hares in the boreal forest exhibit cyclical fluctuations in abundance, with peak spring densities of >1300 hares/100 ha (Keith 1990). Hare populations in

the maritime provinces of Canada and in the eastern United States apparently are noncyclic, and peak densities range from 40–60/100 ha in the boreal forests of the north to 1–5/100 ha in the temperate forests farther south (Keith 1990). Based upon these data and the results of Bryant et al. (1994), we predicted that: 1) species of woody plants with boreal distributions should exhibit relatively greater protection of juvenile-stage plants than congenerics with distributions primarily within the temperate forest; and 2) juvenile-stage plants growing in northern areas should be less susceptible to browsing by hares than conspecifics from more southern areas. Note that these predictions are not independent. Thus, a consideration of both site-of-origin and geographic distribution results in a composite prediction: individuals of species with boreal distributions grown in northern latitudes should exhibit the greatest protection of juvenile-stage growth, whereas individuals of species with temperate distributions grown in southern latitudes should exhibit the least protection of juvenile-stage growth. Tests of these predictions were accomplished via feeding trials with hares.

Methods

Species and origins of woody plants

Three species of birch *Betula* and two species of aspen *Populus* were used in feeding trials. Among the birches, eastern paper birch *B. papyrifera* (Marsh.) is primarily boreal in distribution, black birch *B. lenta* (L.) is restricted to the temperate deciduous forest, and yellow birch *B. alleghaniensis* (Britton) is distributed in the temperate deciduous forest as well as in the transitional mixed deciduous-coniferous forest (Harlow and Harrar 1969). Of the aspens, quaking aspen *P. tremuloides* (Michx.) is primarily boreal in distribution, whereas bigtooth aspen *P. grandidentata* (Michx.) is distributed south of the boreal forest. In terms of geographic distributions, then, the order from north to south is paper > yellow > black for birches and quaking > bigtooth for aspens.

Twigs were collected along a latitudinal gradient in the eastern United States within the geographic range of snowshoe hares. Twigs of black birch, yellow birch, bigtooth aspen, and quaking aspen were collected from Savage River State Forest in western Maryland (39° 37' N) and from Mattatuck and Naugatuck State Forests and nearby private lands in west-central Connecticut (41° 30' N). Twigs of eastern paper birch also were collected in Connecticut. Twigs of bigtooth aspen, quaking aspen, and eastern paper birch were collected in and around Orono, Maine (44° 50' N).

Dormant twigs of juvenile-stage (2–5 yr old) and mature-stage (10–20 yr old) plants were collected from the three localities. All twigs collected were 2–5 mm in diameter, within the size range of twigs preferred by hares (Wolff 1980). Immediately following collection in

Table 1. Summary of feeding trials conducted with snowshoe hares, in relation to tests of predictions regarding (1) the effects of geographic distribution and (2) latitude of origin of birches and aspens.

Trial	Test of prediction	Experimental variable	Levels of analysis (No. of comparisons)
1	1	Ontogenetic stage (juvenile versus mature)	Latitude of origin × Species: Maryland (4) Connecticut (10)* Maine (3)
2	1	Geographic distribution	Latitude of origin × Genus: Maryland (2) Connecticut (2) Maine (1)
3	2	Latitude of origin	Ontogenetic stage × Species: mature (4) juvenile (4)

*Includes five comparisons with captive hares in Connecticut.

the latter half of December, twigs were sealed in air-tight plastic bags and stored at −10 to −20°C.

Feeding trials

Three sets of trials were conducted with free-ranging hares in Maine, and an additional set of trials was conducted with captive hares in Connecticut (Table 1). For trials with free-ranging hares, sixteen feeding stations were established at the Dwight B. DeMerrit Experimental Forest, Univ. of Maine, Orono, Maine, USA. Dominant overstory vegetation at the site included eastern white pine *Pinus strobus* (L.), balsam fir *Abies balsamea* (L.), and eastern hemlock *Tsuga canadensis* (L.), with an understory consisting primarily of red maple *Acer rubrum* (L.), birch *Betula* spp., and brambles *Rubus* (L.) spp. Snowshoe hares and white-tailed deer *Odocoileus virginianus* (Zimmermann) were the dominant herbivores at the Forest. Feeding stations were placed at locations suitable for snowshoe hares but difficult for white-tailed deer to access. Stations were configured so that adjacent stations were ≥200 m apart. Before the trials began, we baited each station with alfalfa pellets for 5–7 d, followed for 2–3 d by presentation of twigs of all species from all sites and both developmental stages. The procedures for trials with captive hares in Connecticut followed Bryant et al. (1994), except as described below.

Feeding trials with free-ranging hares were conducted during January and February 1990. For each trial, 50-g bundles of twigs were placed in the snow at selected stations. An exception was the trial with juvenile quaking aspen from the three localities, for which limited quantities of twigs were available; hence, 25-g bundles were used. After 24 h, bundles at sites that had been visited by hares were removed and weighed. Bundles at the remaining sites were checked daily until hares had visited, at

which time bundles were collected and weighed. Bundles browsed by deer were replaced with new bundles, and stations visited by deer were repositioned to avoid further disturbance. A station was omitted from statistical analysis for a particular trial if browsing by hares at the station resulted in consumption of <10 g of twigs. The 16 stations were divided into two groups of eight stations each. Group 1 was used for conducting trials with *Populus*, whereas Group 2 was used for conducting trials with *Betula*. Stations were assigned to groups in a staggered design to ensure that no two stations in use from the same group were <400 m apart. Trials were conducted concurrently at both groups of stations.

In the first set of trials with free-ranging hares, we tested prediction 1 by presenting simultaneously one bundle each of juvenile and mature twigs collected from the same site to hares at feeding stations. Thus, 12 trials of this type were conducted (three species from Maine, five from Connecticut, and four from Maryland). A similar protocol was used during January and February 1989 with captive hares. Hares were maintained individually in outdoor cages with unlimited access to commercial rabbit chow and water (Bryant et al. 1994). Each trial consisted of offering a hare two 100-g bundles of the same species overnight, one composed of juvenile twigs and one composed of mature twigs. Twigs for trials with captive hares were collected only in Connecticut. We used as our dependent variable the proportion of the total biomass consumed that consisted of juvenile twigs. Two-way analyses of variance (distribution × origin) were performed separately on results of birch and aspen trials. Because of missing cells for the birch trials (e.g., no paper birch from Maryland), the interaction term was excluded from the analysis.

The preceding trials served only as an indirect test of prediction 1, because species with different distributions were not presented simultaneously to hares. As a more direct test of prediction 1, a second set of trials was conducted in which bundles of juvenile-stage twigs of congeneric plants collected at the same latitude were offered simultaneously to free-ranging hares at feeding stations. Four trials of this type were conducted (Maryland aspens, Connecticut birches, Connecticut aspens, Maine aspens). A one-way analysis of variance, with feeding stations as a blocking factor, was performed on the proportion of bundles consumed for the trial with birches from Connecticut; paired, one-tailed t-tests were performed for all other trials.

In the third set of trials with free-ranging hares, we tested prediction 2 by comparing palatability of twigs from different localities, after grouping according to species and ontogenetic stage; i.e., bundles of conspecific twigs of the same ontogenetic stage but differing in latitude of origin were presented to hares at feeding stations. We failed to collect sufficient quantities of black birch from Maryland to permit testing of the hypothesis for this species. Hence, eight trials were conducted (trials for each ontogenetic stage of yellow birch, eastern paper

Table 2. Consumption ($\bar{X} \pm 1$ SE) by snowshoe hares of juvenile-stage and mature-stage twigs for each species × locality combination. Consumption is expressed as the percentage of each bundle eaten. Means that are significantly different are highlighted in bold type. Unless otherwise noted, trials were conducted during 1990 with free-ranging hares in Maine. Geographical distributions are denoted as N (northern), I (intermediate), S (southern).

Locality	Species	n	Consumption (%)		P
			Juvenile	Mature	
Maryland	Black birch (S)	7	43.8±14.7	49.4±10.2	0.234
(39°)	Yellow birch (I)	7	49.4± 4.9	50.7± 6.2	0.410
	Bigtooth aspen (S)	8	49.0±10.1	36.0± 9.6	0.791
	Quaking aspen (N)	7	13.2± 4.2	25.4± 7.0	0.067
Connecticut	Black birch (S)	5	64.7± 4.3	70.6± 7.7	0.191
(41°)		*7	27.2± 4.3	25.4± 5.9	0.713
	Yellow birch (I)	**10**	**25.7± 4.1**	**40.4± 3.5**	**0.006**
		*8	18.4± 2.6	18.1± 3.1	0.558
	Paper birch (N)	**5**	**58.6± 4.3**	**75.4± 7.2**	**0.049**
		*7	**3.8± 0.5**	**39.6±10.6**	**0.002**
	Bigtooth aspen (S)	5	63.9± 8.0	45.4±17.1	0.866
		*5	18.8± 3.6	48.7±16.0	0.112
	Quaking aspen (N)	***4**	**3.0± 1.0**	**53.8±11.6**	**0.006**
		9	26.3± 4.3	33.3± 9.5	0.297
Maine	**Paper birch (N)**	**9**	**28.2±10.4**	**57.0± 8.2**	**0.003**
(44°)	Bigtooth aspen (S)	7	44.1± 7.1	36.4±10.1	0.852
	Quaking aspen (N)	**5**	**6.5± 2.2**	**32.2± 6.8**	**0.017**

*Trials conducted with captive hares in Connecticut during 1989.

birch, bigtooth aspen, and quaking aspen). The proportion of each bundle consumed by hares was compared using either paired, one-tailed t-tests (birch) or analysis of variance with feeding stations as a blocking factor (aspen). For all trials, proportions were subjected to arcsine transformation before analysis (Zar 1974).

Results

Palatability and geographic distribution

Species with more northern distributions consistently elicited greater discrimination between juvenile and ma-

Table 3. Consumption ($\bar{X} \pm 1$ SE) by free-ranging hares of bundles of juvenile-stage twigs of congeneric species. Trials compared twigs collected from the same locality. Consumption is expressed as the percentage of each bundle eaten. Means that are significantly different are highlighted in bold type. Symbols for geographic distributions are given in Table 2.

Origin	n	Species (Distribution)	Consumption (%)	P
Maryland	7	Black birch (S)	56.9± 5.6	0.146
(39°)		Yellow birch (I)	50.6± 5.1	
	8	**Bigtooth aspen (S)**	**54.4± 5.5**	**<0.001**
		Quaking aspen (N)	**5.4± 2.0**	
Connecticut	7	Black birch (S)	46.1± 6.3	0.910
(41°)		Yellow birch (I)	40.1± 2.5	
		Paper birch (N)	48.2±11.1	
	6	**Bigtooth aspen (S)**	**68.1± 5.2**	**0.001**
		Quaking aspen (N)	**21.5± 4.0**	
Maine	**8**	**Bigtooth aspen (S)**	**70.0± 8.5**	**<0.001**
(44°)		**Quaking aspen (N)**	**9.5± 3.1**	

ture twigs by hares. Relative to mature-stage twigs, juvenile twigs of boreal species were consumed less than juvenile twigs of nonboreal species for aspens (F = 11.25, 1,42 df, P < 0.0025) and birches (F = 17.53, 1,62 df, P < 0.0005). Juvenile and mature twigs of black birch, a temperate-zone species, were always consumed equally, and significantly greater consumption of mature twigs of yellow birch, another predominantly temperate-zone species, occurred only once. In contrast, mature twigs of eastern paper birch, a boreal species, always were eaten preferentially (Table 2). Similar results were obtained for aspens; juvenile and mature twigs of bigtooth aspen, a temperate-zone species, were consumed equally, whereas mature twigs of quaking aspen, a boreal species, were consumed in greater amounts than juvenile conspecific twigs. Overall, differential consumption of mature and juvenile twigs was demonstrated in only 10% (1/10) of trials with aspens and birches characterized by nonboreal distributions, whereas hares preferred mature twigs in 71% (5/7) of trials with species characterized by predominantly boreal distributions. Moreover, of the two trials with boreal species in which differential consumption was not statistically significant, both were characterized by a tendency for greater feeding on mature twigs (P = 0.067 for the Maryland quaking aspen trial).

Additional evidence for the influence of geographic distribution on palatability was obtained from trials in which hares were presented with juvenile-stage congeneric twigs from a single collection site (Table 3). For all sites, juvenile twigs of the boreal aspen (quaking) were eaten significantly less than juvenile twigs of the nonboreal aspen (bigtooth). We failed to note a similar trend in birches, perhaps partly because tests of boreal and

Table 4. Consumption ($\bar{X} \pm 1$ SE) by free-ranging snowshoe hares of bundles of twigs collected from different localities. A trial consisted of comparing conspecific twigs of a particular ontogenetic stage. Consumption is expressed as the percentage of each bundle eaten. Means that are significantly different are highlighted in bold type. Symbols for geographic distributions are given in Table 2.

Ontogenetic stage	Species (Distribution)	Consumption (%)				P
		n	Maryland (39°)	Connecticut (41°)	Maine (44°)	
Mature	Yellow birch (I)	7	53.6 ±9.6	42.0 ± 6.1	–	0.095
	Paper birch (N)	7	–	55.2 ± 8.6	47.3 ±4.1	0.204
	Bigtooth aspen (S)	7	21.5 ±5.7	48.5 ±12.2	34.0 ±7.8	0.166
	Quaking aspen (N)	8	16.0 ±2.4	9.1 ± 2.9	11.4 ±2.4	0.190
Juvenile	**Yellow birch (I)**	7	**41.2 ±2.5**	**32.5 ± 5.1**	–	**0.026**
	Paper birch (N)	7	–	**48.8 ± 5.5**	**36.7 ±7.6**	**0.028**
	Bigtooth aspen (S)	7	36.9 ±8.3	34.9 ± 7.0	34.2 ±4.7	0.998
	Quaking aspen* (N)	5	**32.6[a]±2.4**	**21.3[b]± 2.8**	**10.9[c]±3.4**	**0.001**

*Means with different superscripts were significantly different (P < 0.05).

nonboreal birches from Maine and Maryland were not conducted. However, other tests have demonstrated that boreal birches are less palatable in the juvenile stage than are nonboreal birches. Bryant et al. (1994) presented juvenile-stage twigs of black, yellow, eastern paper, and Alaska birch (*Betula resinifera*) to hares in Alaska and in Connecticut. They found that hares at both sites consumed significantly greater amounts of the species with nonboreal distributions.

Palatability and latitude

Conspecific trials of twigs collected from different latitudes revealed that hares consumed mature twigs without regard to collection site (Table 4). However, hares discriminated among collection sites for juvenile twigs of yellow birch (P = 0.026), eastern paper birch (P = 0.028), and quaking aspen (P = 0.001). Moreover, juvenile twigs from southern latitudes were preferred over twigs from northern latitudes for each of these species (Table 4). Hares did not discriminate among collection sites for juvenile twigs of bigtooth aspen (Table 4). Interestingly, bigtooth aspen also was the only species of the four that showed no effect of ontogenetic stage on palatability (Table 2).

Discussion

The results tend to support our predictions. Latitudinal differences in collection locality and geographic distribution both were correlated with differential consumption by snowshoe hares of juvenile- and mature-stage twigs of birch and aspen. Hares in general appear to discriminate more strongly between juvenile- and mature-stage twigs from plants with boreal distributions (Tables 1, 2; Swihart and Bryant unpubl.). Conspecific trials also indicated that hares discriminated among juvenile-stage twigs from different latitudes, with plants growing in northern latitudes

eaten less, especially for species with boreal distributions (Table 4).

Geographical patterns in consumption of woody plants by hares may be caused by climatic effects on hares, by climatic effects on plants, or by geographic variation in plant adaptations to browsing by hares. We explore these mechanisms below, with the understanding that they need not operate independently, nor do they encompass all possible explanations for the patterns observed.

Climatic constraints on browsers

Energetic constraints on hares, imposed by colder temperatures at higher latitudes, may explain some of the variation in consumption of woody plants reported previously. For instance, when presented with twigs from the same locality, snowshoe hares in Alaska exhibited greater discrimination among twigs than hares in either of two more southerly latitudes, Maine and Connecticut (Bryant et al. 1994). Hares living in colder northern latitudes may be forced to discriminate more carefully among food plants in order to achieve a net energy intake permitting maintenance of homeothermy. In other words, when energy is at a premium, undue expenditures of energy in detoxification of secondary metabolites (McArthur et al. 1991) should be avoided by discriminating carefully among potential foods. Such constraints may be diminished for hares occupying more southerly latitudes where energy loss to the environment is less severe. Energetic constraints fail to explain the patterns observed in the present study, though, because a set of trials was conducted within a short time period at a single locality.

Climatic constraints on plants

Climate could possibly explain why woody plants growing in northern latitudes or with evolutionary affinities for boreal areas are consumed less in the juvenile stage than their southern counterparts. Colder temperatures, a

shorter growing season, and winter desiccation in northern regions place a selective premium on a plant's ability to survive extended periods of subfreezing weather and drought; thus, minimum winter temperatures and water stress are important determinants of the northern range limits of many woody species (Larcher and Bauer 1981, Yoshie and Sakai 1982, Sakai 1983, Marchand 1987, Woodward 1987). Intraspecifically, trees from northern provenances are much hardier than trees from southern areas (Sakai and Weiser 1973). Conversion of stored starch into sugars, sugar derivatives, and secondary metabolites such as resins may be related to the development of winter hardiness and winter drought tolerance (Vasil'yev 1961, Sakai 1983), thereby contributing to survival of boreal trees. Increased respiration by plants in southern latitudes, by magnifying depletion of carbohydrate reserves (T.T. Kozlowski, pers. comm.) required to produce these substances (Kramer and Kozlowski 1979), could further contribute to the limited cold and drought adaptations of more temperate forest species. Thus, increased winter hardiness among northern species and genotypes may increase the production of substances that secondarily provide resistance against browsers. For instance, Scots pine *Pinus sylvestris* (L.) from northern Fennoscandia exhibits greater dry matter content of needles and apparently greater levels of terpenoids and phenols than conspecifics from southern Fennoscandia (Niemelä et al. 1989 and references therein). These heritable differences may be related to adaptations for winter hardening (Hansson 1985, Niemelä et al. 1989; but see Bryant et al. 1992), which subsequently confer upon more northern plants an enhanced ability to deter mammalian browsers.

Although the preceding arguments indicate that climate could influence the chemical composition of plants in a manner which could secondarily deter herbivores, two lines of evidence cast doubt on the importance of climate-induced changes in plant chemistry as the principal mechanism generating the geographical patterns of herbivory that have been observed. First, Rousi (1989) found no correlation between damage caused by voles (*Microtus* spp.) and characters related to winter hardening of Scots pine. Second, it is unclear how climate might mediate the ontogenetic patterns of browse selection that we observed. For instance, winter desiccation can contribute to mortality of boreal plants, and resin secretions may reduce water loss during winter (Sakai 1983), but desiccation in species such as paper birch is a more severe problem in the canopy of mature plants than in the canopy of juveniles (Hutnik and Cunningham 1961). Our trials indicate no latitudinal patterns in selection of mature-stage twigs by hares (Table 4). In addition, resins that deter browsing in boreal species are most abundant in the juvenile stage, even though the juvenile stage is less susceptible to drought than the mature stage (Bryant et al. 1992).

Biogeographic variation and plant-mammal interactions

Although it is possible that antiherbivore defenses have arisen as a serendipitous byproduct of evolution for cold hardiness, results of studies of the resistance of boreal woody plants to browsing indicate that defense against herbivory is the primary function of these substances (reviewed by Bryant et al. 1992, 1994). Geographic variation in consumption and chemical defenses of boreal birches and willows (*Salix* spp.) correlate strongly with the historical abundance of mammalian browsers, particularly hares (Bryant et al. 1989). Specifically, Bryant et al. (1989) showed that juvenile birches from Iceland, an island lacking an assemblage of mammals before Norse colonization (Darlington 1957), were eaten more by mountain hares *Lepus timidus* (L.) and contained fewer chemical defenses than birches from Finland and Siberia, areas with browsing mammals. Likewise, hares preferentially browsed birches and willows from Finland rather than from Alaska or Siberia. Finnish hare populations are not cyclic, whereas hare populations in Alaska and Siberia undergo dramatic fluctuations in abundance with roughly a 10-yr periodicity (Keith 1983). Alaskan and Siberian plants have evolved correspondingly greater levels of chemical defense against browsing by hares, apparently in response to greater levels of browsing pressure relative to plants in Finland (Bryant et al. 1989). In North America, snowshoe hares are more abundant in boreal than in temperate forests (Grange 1965, Keith 1990). Hence, the elevated levels of avoidance exhibited by hares for juvenile plants with predominantly boreal distributions (present study, Bryant et al. 1994) could reflect responses to evolutionarily derived differences in investment in antiherbivore chemistry during the juvenile stage that are directly related to the risk of predation.

Although it appears that herbivores have directly influenced the chemical defenses of the juvenile stage, we are not suggesting that a cold climate has had no effect. In fact, the more severe climate of northern latitudes could influence interactions between plants and herbivores in at least two ways. First, the net effect of a decrease in temperature is a decline in nutrient availability, because cold decreases the rate at which nutrients are mineralized from organic matter (Chapin and Shaver 1985). Thus, with increasing latitude plant growth becomes more nutrient limited. As a result, boreal woody plants could be more strongly selected for defenses against winter browsing by mammals than temperate woody plants, because nutrient limitation of growth favors increased selection for chemical defense (Janzen 1974, Grime 1977, Bryant et al. 1983, Coley et al. 1985). Second, herbivore pressure on woody plants may be increased in northern latitudes because of the longer period of time each year during which woody browse must be relied upon before other, more nutritious, food becomes available. Thus, latitudinal differences in duration of the browsing season could result in greater selective pressure on woody plants in the

absence of differences in herbivore abundance (or biomass).

With the exception of our data (Table 4), direct evidence for latitudinal variation in browse selection by mammalian herbivores is limited to conifers. Hansson (1985) observed damage by field voles *Microtus agrestis* (L.) to seedlings of lodgepole pine *Pinus contorta* (Dougl.) in Sweden. Seedlings were derived from seeds originating in numerous provenances in North America. Seedlings from northern sources in North America incurred significantly less damage than seedlings from southern sources (Hansson 1985). Similarly, common garden experiments with Scots pine in Finland revealed lower levels of browsing by moose *Alces alces* (L.) on pines originating from more northern latitudes (Niemelä et al. 1989). Because of the economic importance of many woody plants, and their susceptibility to mammalian browsing, additional studies are needed that test for latitudinal or distributional differences in palatability, and the relation of these differences to the chemical composition of plants.

Implications for distribution of woody plants

Spatial variation in susceptibility to browsing by hares could influence the rate at which woody vegetation is expected to migrate northward in response to global warming (Woodward 1987, Overpeck et al. 1991, Bryant and Reichardt 1992). Our data (present study, Bryant et al. 1994) suggest that woody colonists from eastern North American forests are more likely to be browsed by mammals such as hares than colonists of Beringian origin, and temperate plants are more likely to be browsed than boreal plants. Thus, the northward spread of plants from the temperate forest may be slower than predicted by climate change alone, because of elevated mortality rates resulting from their selective use by browsers. Of course this scenario assumes that mammalian browsers such as hares respond primarily to shifts in plant communities, which in turn are driven primarily by changes in climate (Vrba 1992).

References

Alverson, W. S., Waller, D. M. and Solheim, S. L. 1988. Forests too deer: edge effects in northern Wisconsin. – Conserv. Biol. 2: 348–358.

Brandner, T. A., Peterson, R. O. and Risenhoover, K.L. 1990. Balsam fir on Isle Royale: effects of moose herbivory and population density. – Ecology 71: 155–164.

Bryant, J. P. and Reichardt, P. B. 1992. Controls over secondary metabolite production by Arctic woody plants. – In: Chapin III, F. S., Jefferies, R. L., Reynolds, J. F., Shaver, G.R. and Svoboda, J. (eds), Arctic ecosystems in a changing climate. Academic Press, New York, pp. 377–390.

– , Chapin III, F. S. and Klein, D. R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. – Oikos 40: 357–368.

– , Tahvanainen, J., Sulkinoja, M., Julkunen-Tiito, R., Reichardt, P. and Green, T. 1989. Biogeographic evidence for the evolution of chemical defense by boreal birch and willow against mammalian browsing. – Am. Nat. 134: 20–34.

– , Provenza, F. D., Pastor, J., Reichardt, P. B., Clausen, T. P. and du Toit, J. T. 1991a. Interactions between woody plants and browsing mammals mediated by secondary metabolites. – Annu. Rev. Ecol. Syst. 22: 431–446.

– , Kuropat, P. J., Reichardt, P. B. and Clausen, T.P. 1991b. Controls over the allocation of resources by woody plants to chemical anti-herbivore defense. – In: Palo, R.T. and Robbins, C.T. (eds), Plant defenses against mammalian herbivory. CRC Press, Boca Raton, FL, pp. 83–102.

– , Reichardt, P. B., Clausen, T. P., Provenza, F. D. and Kuropat, P.J. 1992. Woody plant-mammal interactions. – In: Rosenthal, G.A. and Berenbaum, M.R. (eds), Herbivores: Their interactions with secondary plant metabolites, 2E Volume II: Evolutionary and ecological processes. Academic Press, New York, pp. 343–370.

– , Swihart, R. K., Reichardt, P. B. and Newton, L. 1994. Biogeography of woody plant chemical defense against snowshoe hare browsing: Comparison of Alaska and eastern North America. – Oikos 70: 385–395.

Chapin III, F. S. and Shaver, G. R. 1985. Arctic. – In: Chabot, B. F. and Mooney, H. A. (eds), Physiological ecology of North American plant communities. Chapman and Hall, New York, pp. 16–40.

Clausen, T. P., Reichardt, P. B. and Bryant, J. P. 1986. Pinosylvin and pinosylvin methyl ether as feeding deterrents in green alder. – J. Chem. Ecol. 12: 2117–2131.

Coley, P. D., Bryant, J. P. and Chapin III, F. S. 1985. Resource availability and plant antiherbivore defense. – Science 230: 895–899.

Darlington, P. J. 1957. Zoogeography: the geographical distribution of animals. – Wiley, New York.

Dimock, E. J. II, Silen, R. R. and Allen, V. E. 1976. Genetic resistance in Douglas-fir to damage by snowshoe hare and black-tailed deer. – For. Sci. 22: 106–121.

Frelich, L. E. and Lorimer, C. G. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. – Biol. Conserv. 34: 99–120.

Grange, W. 1965. Fire and tree growth relationships to snowshoe rabbits. – Tall Timbers Fire Ecol. Conf. 4: 111–125.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – Am. Nat. 111: 1169–1194.

Hall, E. R. 1981. The mammals of North America, 2nd ed. – Wiley, New York.

Hansson, L. 1985. Damage by wildlife, especially small rodents, to North American *Pinus contorta* provenances introduced into Sweden. – Can. J. For. Res. 15: 1167–1171.

Harlow, W. M. and Harrar, E.S. 1969. Textbook of dendrology. 5th ed. – McGraw-Hill, New York.

Hough, A. F. 1949. Deer and rabbit browsing and available winter forage in Allegheny hardwood forests. – J. Wildl. Manage. 13: 135–141.

Hutnik, R. J. and Cunningham, F. E. 1961. Silvical characteristics of paper birch. – USDA For. Serv., NE For. Exp. Stn. Pap. No. 141.

Janzen, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. – Biotropica 6: 69–103.

Jogia, M. K., Sinclair, A. R. E. and Andersen, R. J. 1989. An antifeedant in balsam poplar inhibits browsing by snowshoe hares. – Oecologia 79: 189–192.

Keith, L. B. 1983. Role of food in hare population cycles. – Oikos 40: 385–395.

– 1990. Dynamics of snowshoe hare populations. – In: Genoways, H. H., (ed.), Current mammalogy. Vol. 2. Plenum Press, New York, pp. 119–196.

Kozlowski, T. T. 1971. Growth and development of trees. Vol. 1. – Academic Press, New York.

Kramer, P. J. and Kozlowski, T. T. 1979. Physiology of woody plants. – Academic Press, New York.

Larcher, W. and Bauer, H. 1981. Ecological significance of resistance to low temperature. – In: Lange, O.L., Nobel, P.S., Osmond, C.B. and Ziegler, H. (eds), Physiological plant ecology. Encyclopedia of Plant Physiology. Volume 12A. Springer, Berlin, pp. 403–437.

Marchand, P. J. 1987. Life in the cold: an introduction to winter ecology. – Univ. Press of New England, Hanover, NH.

Mattfeld, G. F. 1984. Eastern hardwood and spruce/fir forests. – In: Halls, L. K. and House, C. (eds), White-tailed deer ecology and management. Stackpole Books, Harrisburg, PA, pp. 305–330.

McArthur, C., Hagerman, A. and Robbins, C. T. 1991. Physiological strategies of mammalian herbivores against plant defenses. – In: Palo, R. T. and Robbins, C. T. (eds), Plant defenses against mammalian herbivory. CRC Press, Boca Raton, FL, pp. 103–114.

Niemelä, P., Hagman, M. and Lehtila, K. 1989. Relationship between *Pinus sylvestris* L. origin and browsing preference by moose in Finland. – Scand. J. For. Res. 4: 239–246.

Overpeck, J. T., Bartlein, P. J. and Webb, T, III. 1991. Potential magnitude of future vegetation change in eastern North America: comparison with the past. – Science 254: 692–694.

Reichardt, P. B., Bryant, J. P., Clausen, T.P. and Wieland, G.D. 1984. Defense of winter-dormant Alaska paper birch against snowshoe hares. – Oecologia 65: 58–69.

– , Bryant, J. P., Mattes, B. R., Clausen, T. P., Chapin III, F. S. and Meyer, M. 1990. Winter chemical defense of Alaskan balsam poplar against snowshoe hares. – J. Chem. Ecol. 16: 1941–1959.

Rousi, M. 1989. Susceptibility of winter-dormant *Pinus sylves-tris* families to vole damage. – Scand. J. For. Res. 4: 149–161.

– , Tahvanainen, J. and Uotila, I. 1991. Mechanism of resistance to hare browsing in winter-dormant European white birch *Betula pendula*. – Am. Nat. 137: 64–82.

Sakai, A. 1983. Comparative study on freezing resistance of conifers with special reference to cold adaptation and its evolutive aspects. – Can. J. Bot. 61: 2323–2332.

– and Weiser, C. J. 1973. Freezing resistance of trees in North America with reference to tree regions. – Ecology 54: 118–126.

Silen, R. R., Randall, W. K. and Mandell, N. L. 1986. Estimates of genetic parameters for deer browsing of Douglas-fir. – For. Sci. 32: 178–184.

Snyder, J. D. and Janke, R. A. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. – Am. Midl. Nat. 95: 79–92.

Swihart, R. K. and Yahner, R. H. 1983. Browse preferences of jackrabbits and cottontails for species used in shelterbelt plantings. – J. For. 81: 92–94.

Tahvanainen, J., Helle, E., Julkunen-Tiitto, R. and Lavola, A. 1985. Phenolic compounds of willow bark as deterrents against feeding by mountain hare. – Oecologia 65: 319–323.

– , Niemelä, P. and Henttonen, H. 1991. Chemical aspects of herbivory in boreal forest–feeding by small rodents, hares, and cervids. – In: Palo, R. T. and Robbins, C.T. (eds), Plant defenses against mammalian herbivory. CRC Press, Boca Raton, FL, pp. 115–132.

Telfer, E. S. 1972. Browse selection by deer and hares. – J. Wildl. Manage. 36: 1344–1349.

– 1978. Cervid distribution, browse and snow cover in Alberta. – J. Wildl. Manage. 42: 352–361.

Vasil'yev, I. M. 1961. Wintering of plants. – Am. Inst. Biol. Sci., Washington, D. C. (Translated from Russian).

Vrba, E. S. 1992. Mammals as a key to evolutionary theory. – J. Mammal. 73: 1–28.

Wolff, J. O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. – Ecol. Monogr. 50: 111–130.

Woodward, F. I. 1987. Climate and plant distribution. – Cambridge Univ. Press, Cambridge.

Yoshie, F. and Sakai, A. 1982. Freezing resistance of temperate deciduous forest plants in relation to their life form and microhabitat. – In: Li, P. H. and Sakai, A. (eds), Plant cold hardiness and freezing stress. Mechanisms and crop implications. Vol. 2. Academic Press, New York, pp. 427–436.

Zar, J. H. 1974. Biostatistical analysis. – Prentice-Hall, Englewood Cliffs, NJ.