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Biogeography of woody plant chemical defense against snowshoe hare browsing: comparison of Alaska and eastern North America

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

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Recent research has demonstrated that juvenile-stage woody plants from Alaska and eastern Siberia (Beringia) are more defended against browsing by hares (*Lepus*) in winter than the juvenile-stage of congeners from other subarctic regions. Our objectives were (1) to determine if similar biogeographical variation in woody plant defense occurs in subarctic North America, and (2) to evaluate some possible causes of this variation. To achieve these objectives we (1) conducted feeding trials that compared snowshoe hare (*L. americanus*) preferences for winter-dormant twigs of juvenile-stage tree birch and aspen from Alaska with hare preferences for the juvenile-stage of congeners and conspecifics from eastern North America (Maine and Connecticut), and (2) in the case of birch related hare preferences to twig defensive chemistry. We found that hares preferred eastern North American plants, and preferences for birch were related to defensive chemistry. Two historical explanations for such biogeographical variation in the chemical defense of juvenile-stage subarctic woody plants against browsing by hares have been suggested by Bryant et al.: (1) It is a consequence of geographic variation in the intensity of browsing by Pleistocene megaherbivores; or (2) it is a consequence of very large-scale spatial variation in intensity of browsing by hares and associated extant fire-adapted mammals.

Using the glacial history and fire history of subarctic North America, we developed scenarios that allowed us to evaluate these historical hypotheses. We also considered the possibility that biogeographical variation in defense of subarctic woody plants against browsing by mammals is a result of ecological responses of plants to the physical environment. While fully recognizing that all three processes may have contributed to the biogeographical pattern in plant defense we documented, we have concluded that browsing by hares and other extant fire-adapted mammals is likely to be the most important cause. This conclusion indicates that the climatic variation that developed across subarctic North America after the ice age has resulted in a geographical pattern in North American wildfire history, which through effects on vegetation has influenced the intensity of selective browsing by mammals in winter and thereby resulted in biogeographical variation in the chemical defense of woody plants against browsing.

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For three decades attempts have been made to determine why some plants have more effective chemical defenses against herbivory than others (reviews in Sondheimer and

Simeone 1970, Harborne 1972, Gilbert and Raven 1975, Janzen and Rosenthal 1979, Spencer 1988, Palo and Robbins 1991, Tallamy and Raupp 1991, Fritz and Simms

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1992, Rosenthal and Berenbaum 1992). Early hypotheses emphasized the importance of coevolutionary interactions between plants and insects (Ehrlich and Raven 1964, Fox 1981), and plant apparency to the evolution of defense (Feeny 1976, Rhoades and Cates 1976, Rhoades 1979). Subsequently, the importance of evolutionary and ecological responses of plant secondary metabolism to resource supply and physical disturbance was recognized (Janzen 1974, Grime 1977, Bryant and Kuropat 1980, Bryant et al. 1983, Coley 1983, Coley et al. 1985, Herms and Mattson 1992). Although these hypotheses have increased understanding of why plants growing in a locality differ in defense, none predicts very large-scale spatial variation in defense. However, such biogeographical variation occurs on land (Levin 1976, Scriber 1988, Bryant et al. 1989, Coley and Aide 1990, Swihart et al. 1994) and in the sea (Hay and Steinberg 1992, Steinberg 1989, 1992, Steinberg and Van Altena 1992). Any general theory of plant defense must take into account this variation and determine likely causes.

Biogeographical studies of antiherbivore defenses of terrestrial plants have mostly considered plant-insect interactions occurring in tropical and temperate forests (e.g., Levin 1976, Coley and Aide 1990). In comparison, high latitude forests have received little attention, and plant-mammal interactions have been largely neglected. However, recent studies indicate that chemical defenses of juvenile-stage woody plants against browsing by mammals in winter vary markedly across the vast subarctic forests of Eurasia and Alaska, and that this biogeographic variation in plant defense has both latitudinal and longitudinal dimensions (Bryant et al. 1989, Niemelä et al. 1989, Rousi et al. 1991).

The first objective of this study and its sequel (Swihart et al. 1994) was to determine if similar large-scale spatial variation in the chemical defenses of woody plants against browsing by mammals occurs in subarctic and temperate North America. To do this we experimentally studied the resistance of two widespread genera of trees, birch (*Betula*) and aspen (*Populus*), against browsing by one of their major herbivores, the snowshoe hare (*Lepus americanus*, Erxleben), and asked two questions: (1) Do the defenses of tree birch and aspen against browsing by snowshoe hares in winter vary across the subarctic forests of North America? (2) Do these defenses vary latitudinally between subarctic forests and temperate forests of eastern North America? The first question is the subject of this paper. Swihart et al. (1994) address the second question.

Our second objective was to evaluate possible causes of biogeographical variation in the defense of subarctic woody plants against browsing by mammals. Two of the hypotheses we consider invoke historical causes (Bryant et al. 1989), whereas the others appeal to ecological causes. In this paper we are primarily concerned with the historical hypotheses, and secondarily with ecological causes, which are considered in more detail by Swihart et al. (1994).

Bryant et al. (1989) found the juvenile-stages of birch and willow (*Salix*) from Beringia (Alaska and eastern Siberia, Hopkins et al. 1981, 1982) to be more defended chemically against browsing by hares in winter than the juvenile-stages of congeners from subarctic Europe (Finland) and Iceland. Rousi et al. (1991) have verified this observation for birch. Bryant et al. (1989) suggested two historical patterns of browsing that could explain their results: (1) The current biogeography of defense against browsing in subarctic forests reflects past geographical variation in the intensity of browsing by extinct Pleistocene megaherbivores. This hypothesis assumes that current antiherbivore defenses of many terrestrial plants are evolutionary responses to past herbivory by Pleistocene megaherbivores rather than responses to ongoing plant-herbivore interactions (e.g., Janzen and Martin 1982, Hay 1991). It predicts the juvenile-stage of North American woody plants originating from Pleistocene refugia that supported a large biomass of megaherbivore browsers should be more defended against browsing by extant mammals such as the snowshoe hare than the juvenile-stage of congeners or conspecifics originating from refugia that supported a lower biomass of megaherbivore browsers; (2) the second hypothesis of Bryant et al. (1989) predicts that geographical variation in an ongoing plant-mammal interaction, browsing by hares in winter, has been a more important determinant of the current biogeographical distribution of juvenile-stage defenses of subarctic woody plants against browsing. This hypothesis is based on Bryant et al.'s (1989) observation that when Alaska, Eurasia and Iceland are compared, chemical defense of the juvenile-stage against browsing by hares in winter is positively correlated with the amplitude of the ten-yr hare cycle. In this view the juvenile-stage of woody plants from subarctic regions of North America that historically have had a high-amplitude hare cycle should be more defended against browsing by snowshoe hares in winter than woody plants from regions of North America that historically have had a lower amplitude hare cycle or no hare cycle at all. Alternatively, geographical variation in the physical environment unrelated to browsing history could account for biogeographical variation in defense against browsing. The environment in which a plant grows can influence the phenotypic expression of its defenses against browsing (Bryant et al. 1983, 1987), and across the circumboreal world and between the subarctic zone and temperate zone there is variation in moisture, temperature, plant nutrient supply, and light that could affect phenotypic expression of defenses of woody plants against browsing.

Evaluation of the relative contributions of historical pressures (browsing by megaherbivores or hares) and ecological pressures (phenotypic responses of secondary metabolism to the physical environment) to a biogeographical pattern is difficult (Endler 1982). However, given this caveat, we suggest relative contributions of historical pressures can be evaluated if plausible scenarios linking the biogeographical pattern to distributions of

the presumed historical pressures can be developed. We have attempted to develop such scenarios to predict how the history of browsing by megaherbivores in North America and the history of browsing by snowshoe hares in North America might have affected the biogeography of woody plant chemical defense against browsing by snowshoe hares. In the case of megaherbivores we have used the glacial history of North America to develop our scenario. To examine the role of hare browsing, we used a relationship between wildfire and the amplitude of hare cycle that is widespread and likely to be ancient.

North American glacial refugia

The North American taiga and boreal forest where the hare cycle occurs were colonized over the last 18 000 yr by plants from two refugia. In the northwest of the continent was Beringia, which in full glacial periods included Alaska and eastern Siberia (Hopkins et al. 1981, 1982, Lozhkin et al. 1993). The other refugia was south of the Laurentide Ice Sheet in the region now occupied by temperate forest (Braun 1955, Pielou 1991). Although there is debate about the late Pleistocene environment of Beringia (Colinvaux 1980, Ritchie and Cwynar 1982, Guthrie 1985), there is a consensus that Beringia was not forested in periods of continental glaciation. It was either an arid steppe that supported a large biomass of megaherbivore grazers dominated by mammoth (*Mammuthus*), super bison (*Bison priscus*), and horse (*Equus*) (Guthrie 1968, 1982, 1984a,b, 1985, 1990), or an unproductive polar desert that supported few herbivores (Cwynar and Ritchie 1980, Ritchie and Cwynar 1982, Colinvaux and West 1984, Ritchie 1984). Irrespective of their absolute abundance, it is unlikely that Beringian megaherbivore grazers strongly selected the juvenile-stage of trees for chemical defense, because their dentition and stomach contents of their mummies indicate that they fed almost entirely on grasses and sedges (Guthrie 1985). In contrast, the refugia south of the Laurentide Ice Sheet was forested (Braun 1955, Pielou 1991), and supported a large biomass of megaherbivore browsers such as mastodons (*Mammot americanum*) and ground sloth (*Glyptodon*) that fed primarily on woody plants (Kurten and Anderson 1980). Janzen and Martin (1982) have argued that the increased thorniness and spinescence characteristic of the juvenile-stage of many new world trees (Kozlowski 1971) is an evolutionary response to browsing by megaherbivores. If megaherbivore browsers could select the juvenile-stage of trees for structural defenses, they could also have selected the juvenile-stage for chemical defense. When this paleontological evidence is taken into consideration, Bryant et al.'s (1989) glacial refugia hypothesis predicts the juvenile-stage of trees of Beringian origin should be less defended chemically against browsing by snowshoe hares in winter than the juvenile-stage of trees that colonized the subarctic from refugia south of the Laurentide Ice.

Alaskan quaking aspen (*P. tremuloides*) is likely to be of Beringian origin. Although few trees are likely to have survived the last glaciation in Alaskan Beringia (Hopkins et al. 1981, Ritchie and Cwynar 1982), macrofossil evidence and pollen evidence indicate a small population of quaking aspen may have survived (Hopkins et al. 1981). The current population of Alaskan quaking aspen may have originated from this Beringian population rather than from quaking aspen that survived the last glaciation in a refugia south of the Laurentide Ice (Hopkins et al. 1981). Thus, Bryant et al.'s (1989) glacial refugia hypothesis predicts that quaking aspen from Alaska should be less defended against browsing by snowshoe hares than the eastern north American aspens we studied. These eastern North American aspens are provenances of quaking aspen and bigtooth aspen (*P. grandidentata*) from Maine and Connecticut that almost certainly are descendants of aspens that survived the last glaciation in refugia south of the Laurentide Ice (Braun 1955, Pielou 1991).

The survival of tree birch in Beringia during the last glaciation is less certain (Hopkins et al. 1981). Birch pollen is present in at least small quantities at virtually every level in pollen sequences from Alaska, but the consensus is that most of this pollen came from resinous shrub birches (Hopkins et al. 1981) that currently occur in abundance in the tundra of Alaska and Siberia (*B. nana* ssp. *exilis*, *B. glandulosa*, Hultén 1968). Unfortunately, there is no consensus as to whether or not pollen of Beringian tree birches can be distinguished reliably from that of shrub species (Dugle 1966, Ritchie and Hare 1971, Ives 1977, Brubaker et al. 1983, Edwards et al. 1991). Consequently the pollen record tells little about the former presence or absence of tree birch, so small populations of tree birch might have co-occurred with megaherbivores in Alaskan Beringia in the last glaciation without leaving a definitive pollen record (Hopkins et al. 1981, Edwards et al. 1991).

With this cautionary note in mind, five observations indicate that Alaska paper birch (*B. resinifera*, Dugle 1966) is of Beringian origin rather than an eastern North American paper birch (*B. papyrifera*) that colonized Beringia from south of the Laurentide Ice as suggested by Hopkins et al. (1981): (1) Alaska paper birch and the morphologically similar Asian/Beringian tree birch, *B. pendula* var. *japponica* (sensu Fernald 1902) have the same chromosome number $2n = 28$, whereas the chromosome number of the eastern North American paper birch is $2n = 56-84$ (Dugle 1966); (2) the current-annual-growth (CAG) twigs of juvenile-stage Alaska paper birch (Dugle 1966, Reichardt 1981, Reichardt et al. 1984, Bryant et al. (1989) and CAG twigs of juvenile-stage *B. pendula* var. *japponica* (Fernald 1902) produce abundant resin glands. In contrast, CAG twigs of juvenile-stage eastern North American paper birch do not produce abundant resin glands (Dugle 1966, this study). This cytological and morphological evidence led Dugle (1966) to suggest that Alaska paper birch and *B. pendula* var. *japponica* (sensu Fernald 1902) are the same species; (3)

phytochemical evidence further supports the conspecific status of *B. resinifera* and *B. pendula* var. *japonica*. The secondary chemistries of resins produced by the juvenile-stage of Alaska paper birch and resins produced by the juvenile-stage *B. pendula* are similar. Both resins are rich in the triterpene papyriferic acid (Reichardt 1981, Reichardt et al. 1984, Taipale et al. 1991). Current-annual-growth twigs of juvenile-stage eastern North American paper birch do not produce this triterpene (this study). Furthermore, condensed tannin of Alaska paper birch differs significantly in structure from condensed tannin of eastern paper birch (Clausen unpubl.); (4) the secondary chemistry of resins produced by CAG twigs of juvenile-stage Alaska paper birch and resins produced by CAG twigs of shrub birch species (*B. nana* ssp. *exilis* and *B. glandulosa*) of undisputed Beringian origin (Hultén 1968, Hopkins et al. 1981, Brubaker et al. 1983) indicate that Alaska paper birch and these shrub birches are end points of a hybrid continuum (J. Dawe, P. Reichardt, M. Edwards, unpubl.); (5) the secondary chemistry of resins of the juvenile-stage of Alaska paper birch and resins of the juvenile-stage of a birch (*B. middendorfi*) common to southwestern Beringia (upper Kolyma region of northeast Russia – Lozhkin et al. 1993) are very similar (Bryant et al. 1989), and differ completely from the secondary chemistry of the juvenile-stage of eastern North American paper birch (this study). If Alaska paper birch is of Beringian origin, as suggested by this morphological, cytological, and phytochemical evidence, then Bryant et al.'s (1989) glacial refugia hypothesis predicts that its juvenile-stage should be more palatable to snowshoe hares in winter than the juvenile-stage of the 3 eastern North American birches we studied – paper birch, yellow birch (*B. alleghaniensis*), black birch (*B. lenta*). These birch species almost certainly survived the last period of continental glaciation in refugia south of the Laurentide Ice Sheet (Braun 1955, Pielou 1991).

Wildfire and snowshoe hare browsing in North America

In the taiga and boreal forest of North America, wildfire creates habitat required by early successional deciduous trees like birch and aspen (Viereck 1973, 1983, Van Cleve et al. 1991, Johnson 1992) that are preferred winter foods of snowshoe hares (Bookhout 1965, Bryant and Kuropat 1980, Keith et al. 1984, Sinclair and Smith 1984). Thus, at the peak of the hare cycle, selective browsing in winter by snowshoe hares on saplings of preferred foods such as tree birch and aspen often is most intense in fire-created early successional habitat (Grange 1949, 1965, Fox 1978, Keith et al. 1984). This browsing causes extensive mortality of juvenile trees (e.g., Seton 1911, Aldous and Aldous 1944, Grange 1949, 1965, Wolff and Zasada 1979, Wolff 1980, Sullivan and Sullivan 1982, Walker et al. 1986, Bergeron and Tardiff 1988). Thus, the relationship between hare browsing and

the biogeography of woody plant chemical defense proposed by Bryant et al. (1989) could be explained in the following way.

During succession in subarctic forests, winter browsing by snowshoe hares and associated fire-adapted mammals such as moose (*Alces alces*) favors replacement of poorly defended trees and shrubs by more defended species (Bryant and Chapin 1986, Bryant et al. 1991, MacAvinchey 1991, McInnes et al. 1992, Pastor and Naiman 1992, Pastor et al. 1993). During the 18 000-yr post-Pleistocene colonization of subarctic North America by forest plants, selective browsing by snowshoe hares and associated mammals could have had an analogous effect on vegetation. Selective browsing may have acted as a filter to survival of woody species and ecotypes, limiting survival of poorly defended species and ecotypes in regions that developed a pronounced fire regime. In regions that have developed a less intense fire regime browsing was less intense, so less defended species and ecotypes persisted. Note that this hypothesis makes no assumptions about the origins of colonizing forest plants, but it makes 3 assumptions about the history of wildfire and the history of browsing in North America, which are described below.

First, the fire history of subarctic North America developed after the ice age as forest recolonized the Beringian steppe and recently deglaciated regions. Second, there is a geographical pattern of forest fire across subarctic North America that is ancient and has affected numbers of hares for a very long time. Specifically, we propose that for a very long time the arid taiga of interior Alaska has burned more than the moist boreal forest of eastern Maine, and temperate hardwood forests have burned even less than subarctic forests (Viereck 1973, 1983, Heinselman 1981, Yarie 1981, Johnson 1992). Third, this continental-scale spatial variation in fire history is reflected in biogeographical variation in hare numbers, because the amplitude of the snowshoe hare cycle is related to fire history (Grange 1949, 1965, Fox 1978). Demographic data compiled by Keith (1990) supports this hypothesis. These data demonstrate, in peak years of the cycle, numbers of hares in the Alaskan taiga range from 400–1200 hares/100 ha. In contrast, in the boreal forest of eastern Maine snowshoe hares historically have not cycled, and in occasional years when hares are abundant their density ranges from 40–60 hares/100 ha. This density is an order of magnitude less than the density of hares at the peak of the hare cycle in Alaska. Hare populations in temperate hardwood forests of eastern North America historically have been noncyclic and of very low density, ranging from 1–5 hares/100 ha.

On the basis of these assumptions, Bryant et al.'s (1989) hare-cycle hypothesis predicts the juvenile-stage defenses of tree birch and aspen against browsing by hares in winter to be, in descending order of effectiveness, plants from the taiga of Alaska > plants from the boreal forest of eastern North America > plants from the temperate forest of eastern North America.

Methods

Birch and aspen collections

The birch and aspen we studied came from the taiga of Alaska near Fairbanks (65° 25' N), the boreal forest of eastern Maine near Orono (44° 50' N), and a temperate forest in west-central Connecticut (41° 30' N). We selected these regions of North America because they allowed us to test the 2 predictions about chemical defense against browsing by hares in winter developed in the 2 preceding sections: (1) The glacial refugia-megaherbivore browsing hypothesis predicts these chemical defenses of juvenile-stage birch and aspen from Alaska to be less effective than those of their eastern North American congeners and conspecifics. (2) By contrast, the fire history-hare browsing hypothesis predicts the chemical defenses against hare browsing of the birches and aspens we studied to be in descending order of effectiveness, plants from the taiga of Alaska > plants from the boreal forest of eastern North America > plants from the temperate forest of eastern North America.

The Alaska forest provided Alaska paper birch and quaking aspen, the Maine forest provided eastern North American paper birch, yellow birch, quaking aspen, and bigtooth aspen, and the Connecticut forest provided these 4 eastern North American trees plus black birch. Twigs were collected in mid-winter from 2–5 yr old saplings. At this chronological age the chemical defenses of winter-dormant twigs of juvenile-stage (Kozlowski 1971) birch and aspen are most pronounced (Fox and Bryant 1984). All twigs were less than 5 mm in diameter and had a similar ratio of current-annual-growth biomass/older growth biomass.

Feeding trials

For hypothesis testing we used cafeteria-style feeding trials like those successfully used in numerous studies of snowshoe hare feeding preferences (e.g., Bookhout 1965, Klein 1977, Bryant 1981, Sinclair and Smith 1984, Bryant et al. 1989). The protocol we used in our experiments is described in detail in Bryant et al. (1989). Briefly, before each feeding trial with free-ranging hares, hares were attracted to feeding stations with a subsample of twigs used in that feeding trial, and a similar subsample of twigs was used to acclimate captive hares before each trial (Fox and Bryant 1984). In all trials bundles of twigs (75 g wet mass) were simultaneously offered in a random array just before dark on day one. In the case of free-ranging hares consumption was monitored until at least 50% of one bundle of twigs was eaten, and data were recorded as percent initially offered biomass eaten. In the case of captive hares the actual wet mass of twigs consumed per hare was measured. In Alaska consumption was measured at 4 and 24 h after offering, and in Maine and Connecticut consumption was

measured 24 h after offering. The 4-h measurement in Alaska insured consumption was measured before any bundle was completely eaten: Hares in Alaska ate twigs more rapidly than hares in Connecticut, presumably because of the low temperature in Alaska (below –40°C) as compared to the near 0°C temperature in the Maine and Connecticut trials. Snowshoe hares eat more browse at low temperatures than at high temperatures (Pease et al. 1979). Birch and aspen were never offered in the same trial.

For comparisons of birch we used free-ranging hares in two feeding trials conducted in Alaska and Maine, and captive hares in two feeding trials conducted in Alaska and Connecticut. In one feeding trial using free-ranging hares the hares were offered a choice of three birch species (Alaska paper birch, eastern North American paper birch, and yellow birch), and in the other they were offered the two most ecologically similar birch species, Alaska paper birch and eastern North American paper birch from Maine. In one feeding trial using captive hares the hares were offered four birch species (Alaska paper birch, eastern North American paper birch, yellow birch, and black birch), and in the other they were offered the two most ecologically similar birch species, Alaska paper birch and Eastern North American paper birch from Connecticut. For comparison of aspen we used free-ranging hares in two sets of feeding trials conducted in Alaska and Maine. One set compared quaking aspen from Alaska, quaking aspen from Maine, quaking aspen from Connecticut, bigtooth aspen from Maine, and bigtooth aspen from Connecticut. The second set compared the two ecologically most similar aspens, quaking aspen from Alaska and quaking aspen from Maine. In these trials lower consumption of plants from Alaska than consumption of plants from eastern North America would weaken the glacial refugia-megaherbivore browser hypothesis, whereas the opposite result would weaken the fire history-hare browsing hypothesis.

Results of trials using more than two birches or aspens were analyzed by randomized block ANOVA without replication and hares as the blocking factor. The paired t-test was used to analyze results of pairwise trials. All analyses followed a general linear model procedure (SYSTAT, Wilkinson 1988). The a priori method of comparisons among means recommended by SYSTAT (Wilkinson 1988) was used for hypothesis testing, because all comparisons among means were planned. All data were log-transformed before analysis, because they contained values that ranged greatly in magnitude (Zar 1974). Additionally, data from trials with free-ranging hares were arcsine-transformed before analysis, because they were collected as proportions. We point out there is dependence among observations in our data, because two foods cannot be eaten simultaneously. If severe, this dependence can compromise results of ANOVA and the paired t-test. However, for data containing no entirely consumed twig bundles we were advised that dependence was not a serious enough problem to forego the robustness of

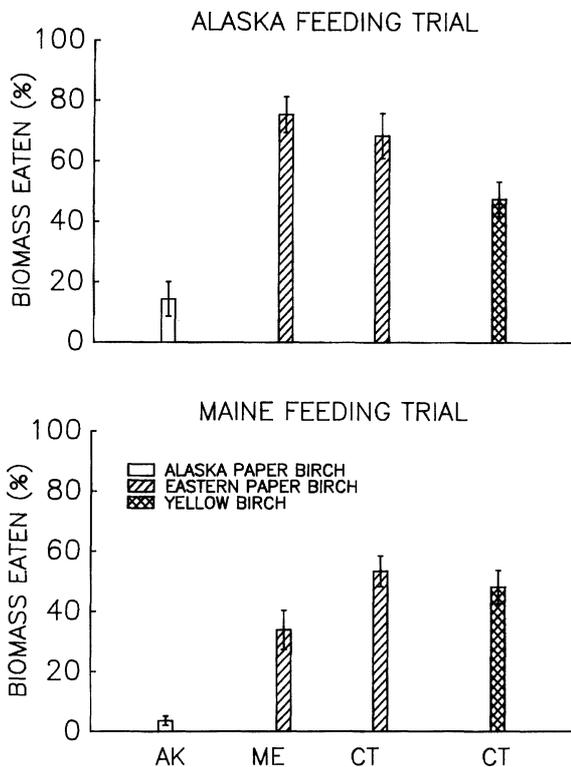


Fig. 1. Birch biomass eaten by free-ranging hares in Alaska and Maine. Acronyms in X-axis legend are origins of birch species (AK=Alaska, ME=Maine, and CT=Connecticut). Mean \pm 1 SEM presented.

ANOVA and the paired t-test (D. Sisson, Dept of Mathematical Statistics, Utah State Univ.).

Birch chemistry

In the case of birch we had preliminary information about the juvenile-stage chemical defense against browsing by hares (Bryant 1981, Reichardt 1981, Bryant et al. 1983, 1987, 1989, Reichardt et al. 1984, 1987, Sinclair et al. 1988). The palatability to snowshoe hares of winter-dormant twigs of juvenile-stage birch is largely determined by resins rich in two triterpenes, papyriferic acid (Reichardt 1981, Reichardt et al. 1984) and 3-malonyl-betulafolientriol Oxide I (Reichardt et al. 1987). Thus, for birch we measured concentrations of total resin and these two triterpenes in CAG twigs.

Results

Feeding trials

In all feeding trials hares ate less of the birch and aspen from Alaska than the birch and aspen from eastern North

America. In Alaska and Maine free-ranging hares offered Alaska paper birch, eastern North American paper birch, and yellow birch ate less Alaska paper birch than either eastern North American birch ($P < 0.0001$, Fig. 1, Table 1), and when offered Alaska paper birch and eastern North American paper birch these hares fed least on Alaska paper birch ($P < 0.001$, Table 2). Feeding trials using captive hares confirmed these results ($P < 0.0001$, Fig. 2, Tables 1, 2). Similarly, free-ranging hares in Alaska and Maine simultaneously offered three quaking aspen provenances and two bigtooth aspen provenances ate less of the quaking aspen from Alaska than either aspen species from eastern North America ($P < 0.0001$, Fig. 3, Table 1), and in pairwise trials ate less of the quaking aspen from Alaska than the quaking aspen from Maine ($P < 0.01$, Table 2). Furthermore, in two of the three feeding trials that compared boreal and temperate species, species with a generally boreal distribution (Alaska paper birch, eastern paper birch, quaking aspen) were eaten less than species with a generally temperate distribution (yellow birch, black birch, bigtooth aspen) ($P < 0.0001$, Figs 2, 3). The exception was slightly lower

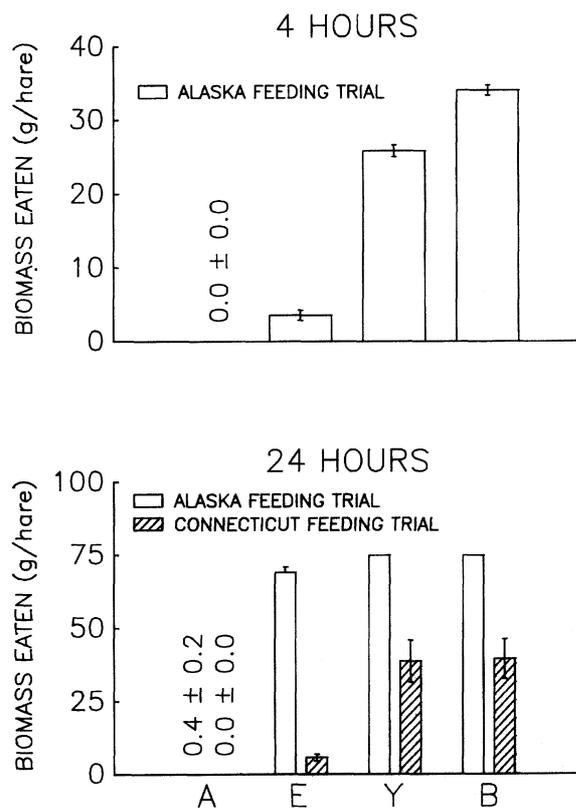


Fig. 2. Birch biomass eaten by captive hares (g/hare/24 h) in Alaska and Connecticut. Acronyms in X-axis legend are birch species offered [A=Alaska paper birch (*Betula resinifera*), E= eastern North American paper birch (*B. papyrifera*), Y= yellow birch (*B. alleghaniensis*), and B=black birch (*B. lenta*)]. Mean \pm 1 SEM presented.

Table 1. ANOVAS of cafeteria feeding trials in which hares were offered more than two birches or aspens.

Feeding trial	SS	DF	MS	F	P
Birch					
Free-ranging hares					
Alaska					
Birches	4.526	3	1.509	20	0.0000
Hares	1.311	9	0.146	2	0.0900
Maine					
Birches	2.012	3	0.671	46	0.0000
Hares	0.345	6	0.057	4	0.0100
Captive hares					
Alaska					
Birches	2.884	3	0.961	311	0.0000
Hares	0.014	7	0.002	1	0.7300
Connecticut					
Birches	2.294	3	0.765	39	0.0000
Hares	0.148	6	0.025	1	0.3200
Aspen					
Free-ranging hares					
Alaska					
Aspens	10.781	4	2.695	35	0.0000
Hares	2.370	9	0.263	3	0.0010
Maine					
Aspens	2.850	4	0.712	13	0.0000
Hares	1.307	7	0.187	3	0.0100

consumption of yellow birch than consumption of eastern North American paper birch in feeding trials with free-ranging hares (Fig. 1). It is worth noting that yellow birch characterizes the boreal forest-temperate forest ecotone in eastern North America (Harlow and Harrar 1969).

The major conclusion to be drawn from these feeding trials is that their results do not support Bryant et al.'s (1989) glacial refugia-megaherbivore browsing hypothesis.

Birch defensive chemistry

Current-annual-growth twigs of Alaska paper birch contained more total resin (range 30%-40% dry mass) than CAG twigs of the eastern North American birches (range 0.5% to 0.7% dry mass). Twigs of Alaska paper birch contained about 10% dry mass papyriferic acid, whereas twigs of eastern North American birches contained no papyriferic acid or 3-0-malonylbutulafolientriol oxide I. The pronounced difference in palatability between eastern North American paper birch and the other two birches from eastern North America indicate they contain feeding deterrents of different efficacies. However, if such substances exist, they are less effective than the chemical defenses of juvenile-stage Alaska paper birch.

The major conclusion to be drawn from this chemical

Table 2. Pairwise comparisons of Alaska paper birch and eastern North American paper birch, and quaking aspen from Alaska with quaking aspen from Maine. Data are biomass eaten. Mean \pm 1 SE are presented.

Feeding trial	Tree origins			
	Alaska	Maine	Connecticut	T P
Birch				
Free-ranging hares				
Alaska	7 \pm 2	42 \pm 4		9.0 0.0001
Maine	6 \pm 2	24 \pm 4		6.0 0.001
Captive hares				
Alaska	1 \pm 1		95 \pm 1	56.2 0.0001
Connecticut	1 \pm 1		49 \pm 1	18.2 0.0001
Aspen				
Free-ranging hares				
Alaska	26 \pm 5	60 \pm 9		5.2 0.001
Maine	2 \pm 1	15 \pm 3		4.5 0.01

analysis is that birch defensive chemistry also does not support Bryant et al.'s (1989) glacial refugia-megaherbivore browsing hypothesis.

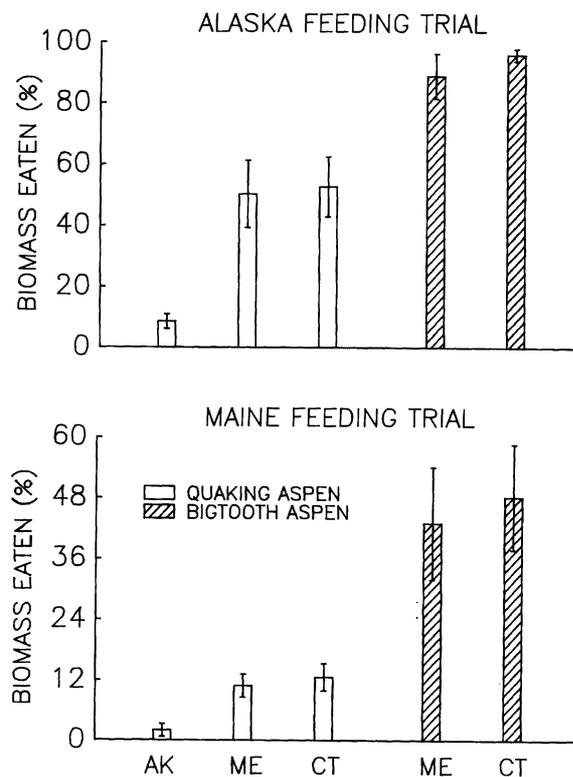


Fig. 3. Aspen biomass eaten by free ranging hares in Alaska and Maine. Acronyms in X-axis legend are origins of aspen species and provenances (AK = Alaska, ME = Maine, and CT = Connecticut. Mean \pm 1 SEM).

Discussion

Biogeography of chemical defense

Our results indicate that pronounced biogeographical variation in the chemical defenses of juvenile-stage tree birch and aspen against browsing by snowshoe hares occurs across subarctic North America. Depending on the feeding trial, hares ate 2 to 100 times more biomass of plants from eastern North America than biomass of plants from Alaska, and chemical analysis of birch twigs indicted this preference is caused by biogeographical variation in defensive chemistry. The twigs of the unpalatable Alaska paper birch contained at least three orders of magnitude more chemical defense than twigs of the more palatable eastern North American birches. Moreover, in concert with results of previous studies (Bryant et al. 1989, Rousi et al. 1991), our results strongly suggest the juvenile-stage of woody plants from Alaska is more defended chemically against browsing by mammals in winter than the juvenile-stage of woody plants from other subarctic regions with the possible exception of eastern Siberia. In the following sections we explore three possible causes for this biogeographical pattern, fully recognizing that they are not mutually exclusive and probably do not represent an exhaustive set of causes.

Phenotypic variation in defensive chemistry

The physical environments of interior Alaska, eastern Maine, and Connecticut differ greatly, and these differences could have phenotypically affected the secondary metabolism of the birch and aspen we studied, thereby causing the biogeographical pattern we documented. We cannot rule out this possibility, because we did not have the opportunity to compare the defenses of plants grown in a common environment (but see Swihart et al. 1994). However, given this caveat we suggest the biogeographical variation in plant defense we documented is primarily genetic for 2 reasons. First, other studies of tree birch indicate genotype more strongly determines the chemical defense of tree birch against browsing by mammals than phenotypic responses of birch secondary metabolism to resource supply (Rousi et al. 1991, 1993, Bryant unpubl.). For example, we found that CAG twigs of juvenile-stage Alaska paper birch contained three orders of magnitude more defensive resin than CAG twigs of the eastern North American birches we studied. By comparison, when Bryant et al. (1987) experimentally increased nutrient supply and reduced light they only halved the concentrations of defensive resins and condensed tannins in CAG twigs of juvenile-stage Alaska paper birch from the population we studied. The variation in nutrient supply and light introduced in their experiment was probably much greater than the variation in nutrient supply and light among the sites from which we collected twigs, indicating that the differences in defensive chemistry we

documented among Alaska paper birch and eastern North American birch species are genetic rather than phenotypic. Second, variation in nutrient supply and light availability have little effect on juvenile-stage chemical defenses of balsam poplar (*P. balsamifera*) against browsing by snowshoe hares in winter (Reichardt et al. 1991). The close similarity in defensive chemistry of internodes of winter-dormant balsam poplar and quaking aspen from Alaska (Mattes and Reichardt unpubl.) indicates the difference in palatability we documented among Alaskan quaking aspen and eastern North American aspens is more likely to be genetically determined than environmentally determined. Other possible causes of phenotypic variation in chemical defense of birch and aspen are considered in more detail by Swihart et al. (1994).

Browsing by megaherbivores

The probability of browsing by megaherbivores in Beringia and south of the Laurentide Ice Sheet in full glacial periods led us to predict that tree birch and quaking aspen from Alaska would be less defended in winter against browsing by extant mammals such as the snowshoe hare than tree birch and aspen from the subarctic forests of eastern North America. Our results do not support this prediction, unless the increase in intensity of browsing a woody plant can experience when it is a rare component of the vegetation (Bryant et al. 1991, Bryant and Fox unpubl.) greatly affects the intensity of selection for defense. Given this caveat, we conclude that browsing by megaherbivores is an unlikely cause of the highly effective chemical defenses that characterize the juvenile-stage of Alaskan woody plants (Bryant et al. 1989, Figs 1, 2, 3 and Table 2). It is more likely that the increasing abundance of chemically defended woody species such as resin birches that occurred in Alaskan Beringia in the Pleistocene-Holocene transition (Brubaker et al. 1983) contributed to extinction of Alaskan megaherbivore grazers by reducing their food supply (Guthrie 1984a, 1990).

Browsing by extant fire-adapted mammals

Predictions of biogeographical patterns of chemical defense based on wildfire history (Heinselman 1981, Johnson 1992) and hare population responses to early successional vegetation created by fire (Grange 1949, 1965, Fox 1978, Keith et al. 1984) were entirely consistent with our results. Generally, juvenile-stage birch and aspen were least palatable when originating in the Alaskan taiga, more palatable when from the boreal forest of eastern Maine, and most palatable when from the temperate forest of Connecticut. This result supports Bryant et al.'s (1989) suggestion that very large-scale spatial variation in the intensity of browsing by snowshoe hares is a plausible cause of the biogeography of chemical anti-

herbivore defense of winter-dormant juvenile-stage trees and shrubs in subarctic North America.

Although we have emphasized hares, we do not wish to imply that browsing by other extant mammals has not contributed to the biogeography of woody plant chemical defense in subarctic forests. Rather, there presumably is a more general relationship between browsing by extant mammals and the biogeography of woody plant defense in subarctic regions. In subarctic forests all fire-adapted browsing mammals have essentially the same food preferences as hares (Bryant and Kuropat 1980), and browsing by these mammals can in ecological time affect the distribution and abundance of woody species (Bryant and Chapin 1986, Bryant et al. 1991, McInnes et al. 1992, Pastor and Naiman 1992). Thus, the historical scenario we developed for effects of snowshoe hare browsing on the biogeography of chemical defense in subarctic forests can be extended to include all fire-adapted subarctic browsing mammals. In this view, geographic variation in the intensity of selective browsing by this herbivore guild has, since the last continental glaciation, created a circumboreal pattern in the chemical antiherbivore defense of the juvenile-stage of woody plants. This hypothesis assumes that populations of mammalian browsers have responded to shifts in plant communities driven primarily by climate (Vrba 1992), for very large-scale variation in the fire history of subarctic forests ultimately is caused by climatic variation (Johnson 1992).

Summary

Robert MacArthur (1972) stated our primary objective: "To do science is to search for repeated patterns, not simply accumulate facts, and to do the science of geographical ecology is to search for patterns of plant and animal life that can be put on a map". We and others (Bryant et al. 1989, Rousi et al. 1991, Swihart et al. 1994) have documented what appears to be a biogeographical pattern of chemical antiherbivore defense in the circumboreal world. We have explored three possible explanations for this pattern in plant defense, and have concluded that (1) climatic variation that developed across subarctic North America after the ice age has (2) resulted in a geographical pattern in North American wildfire history (3) which, through effects on vegetation, has (4) influenced the intensity of selective browsing by mammals in winter, (5) resulting in biogeographical variation in the chemical defense of juvenile-stage woody plants against browsing by mammals in winter.

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