Phytochemical Deterrence of Snowshoe Hare Browsing by Adventitious Shoots of Four Alaskan Trees

Abstract. *After snowshoe hares have severely browsed deciduous trees and shrubs, these woody plants produce adventitious shoots that are extremely unpalatable to them. The adventitious shoots of four common boreal forest trees contain significantly higher concentrations of terpene and phenolic resins than the mature-growth-form twigs of the same species. These resins are experimentally shown to be repellent to snowshoe hares and appear to explain the avoidance of adventitious shoots by hares. The production of adventitious shoots after intense hare browsing and the avoidance of these shoots by hares may play an important role in the 10-year hare cycle.*

In North America's boreal forest, the number of snowshoe hares (*Lepus americanus*) increases dramatically at approximately 10-year intervals (*1*). At times of high populations intense hare browsing severely damages the snowshoe hare's preferred food supply, namely, early and mid-successional deciduous trees and shrubs (*2*). A consequence of this damage is the production of adventitious shoots (*3*), which are extremely unpalatable to snowshoe hares (*4*). I now report that the adventitious shoots of four common boreal forest trees produce exceptionally large quantities of terpene and phenolic resins and experimentally demonstrate that these resins can account for the low palatability of these adventitious shoots to snowshoe hares.

Small-diameter (< 4 mm) twigs were collected from adventitious shoots and mature-growth-form plants of the Alaska paper birch [*Betula papyrifera* Marsh. ssp. *humilis* (Regel) Hult.], quaking aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L. ssp. *balsamifera*), and green alder [*Alnus crispa* (Ait.) Pursh ssp. *crispa*] (*5*) at five sites near Fairbanks, Alaska. At each site, 25 clones of each species were randomly selected, and both adventitious shoots and mature-growth-form twigs were collected from each clone. Analyses of these twigs show that the adventitious shoots of these species contained significantly more nitrogen, phosphorus, and terpene and phenolic resins than their mature-growth-form twigs (*6*) (Fig. 1). These analyses suggest that, in these species, resins rather than proximal nutrients or energy are responsible for the low palatability of adventitious shoots.

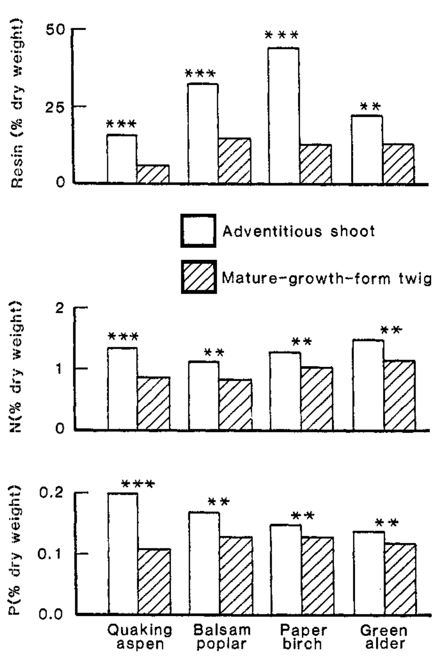

Fig. 1. Nitrogen, phosphorus, and resin contents of adventitious shoots and mature-growth-form twigs. Mean and significance level of difference shown (**, $P < .01$; ***, $P < .001$); $N = 5$ replications.

To verify this hypothesis I coated mature-growth-form twigs of feltleaf willow [*Salix alaxensis* (Andress) Cov. ssp. *longistylis* (Rydb.) Hult.] with the adventitious shoot resins of these species. Feltleaf willow was chosen as a substrate for resin application because it is a nonresinous, highly palatable, winter hare browse in Alaska; the lipid fraction (2.5 ± .14 percent, dry weight) of this species is primarily fatty acid (*7*).

Resins were extracted at room temperature from freshly collected winter dormant twigs of each experimental species in reagent grade diethyl ether and stored under nitrogen at −40°C until used in feeding experiments. Resin concentrates were diluted to the appropriate concentrations (0 to 160 mg of resin per gram of willow twig, dry weight) in reagent grade diethyl ether and applied to freshly collected willow twigs (3 mm in diameter). Treated twigs were dried for 48 hours at −40°C before being offered to hares. Exposure of oven-dried twigs with a similar resin coating to high vacuum for 15 minutes indicated that after 48 hours of drying at −40°C all detectable ether had evaporated from the experimental twigs. Control twigs dipped in the reagent grade ether also discounted the possibility that the ether altered twig palatability.

Free-ranging snowshoe hares were attracted to five feeding stations by baiting with both adventitious shoots and mature-growth-form twigs of all the species to be tested for resin repellence. The feeding stations were widely separated, each serving a different group of hares. The day prior to each experiment all browse bait was removed from the feeding stations. On the day each experiment began, 30.0-g bundles of resin-treated twigs, diethyl ether–treated control twigs, and untreated control twigs were placed in a random array at the feeding stations. A complete range of resin concentration of each tree species was placed at each of the feeding stations at least once. Because the number of hares visiting the stations varied (*8*), the feeding stations were considered blocks in a randomized block experimental design, and two-way analysis of variance was used to estimate the effect of hare density on resin repellence. The experimental bundles were collected and weighed after 24 hours. Palatability was measured by the disappearance of biomass.

In all experiments, resin treatment decreased the palatability of the willow twigs (Fig. 2). Increasing the resin concentration decreased twig palatability up to the point that all treatments above approximately 8 percent resin were al-

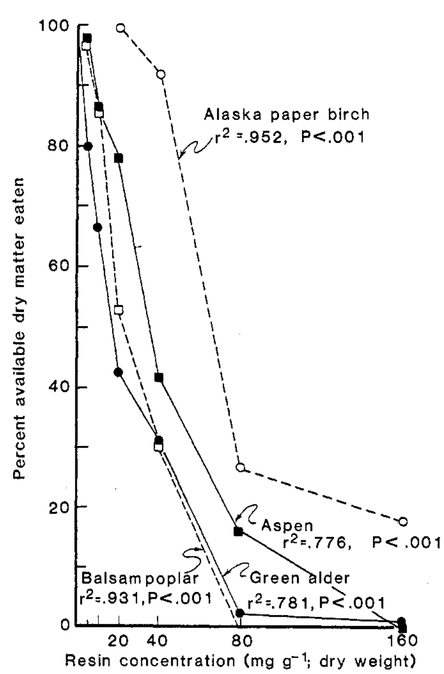

Fig. 2. Relation between resin concentration applied to mature-growth-form feltleaf willow twigs and biomass disappearance. Mean, the fraction of experimental variance explained by resin treatment, and significance of the resin treatment effect shown; $N = 5$.

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most untouched regardless of the hare density at the feeding station. Adventitious shoots of each of the above four tree species normally contain at least twice this resin concentration (Fig. 1). Furthermore, balsam poplar and green alder resins were much more repellent than those of quaking aspen and paper birch ($P < .001$), indicating that resin repellence has a species-dependent qualitative component (Fig. 2). The ether-treated and untreated control twigs did not differ in their palatability ($P > .40$), indicating that treatment with ether had no effect on twig palatability.

Although slightly more treated twigs were eaten at the feeding stations that were visited by more hares ($P < .05$), presumably because the more dense hare subpopulations were more food-limited, most of the experimental variance was explained by the resin treatments (Fig. 2). Thus, it would appear that these resins effectively repel even food-limited snowshoe hares (*8*).

While the potency of these resins as hare repellents presumably explains why the adventitious shoots of the species tested are less palatable to snowshoe hares than their mature-growth-form twigs, neither the exact chemical composition nor the mode of biological activity of these resins is known. However, alder and poplar resins contain several methylated flavonols (*9*), which may lower protein digestibility (*4*). Alder, poplar, and birch resins contain antibiotics (*10*) that may upset vitamin production and digestion in the hare's cecum (*4*). Moreover, ingestion of mountain birch (*B. pubescens*) adventitious shoots by mountain hares (*L. timidus*) results in sodium loss (*11*). Sodium loss by hares under cold conditions may lead to a shock syndrome (*12*) similar to that described (*13*) for a declining snowshoe hare population.

Regardless of the biological basis for resin repellence, the fact that preferred browse species of the snowshoe hare—such as aspen, balsam poplar, and paper birch—produce unpalatable, resinous adventitious shoots after severe browsing by peak snowshoe hare populations (*3, 4*) suggests an extreme flexibility with respect to chemical defense in the snowshoe hare's preferred browse supply. Such defensive flexibility is advantageous to woody plants of the boreal forest because energy-rich substances such as resins (*14*) appear to be produced after severe hare browsing, and carbon is allocated to growth and other processes when there is little browsing. Moreover, because (i) hare browsing during the peak phase of the 10-year hare cycle results in the production of adventitious shoots by the snowshoe hare's preferred browse species (*3*), (ii) these adventitious shoots have been experimentally shown to be of extremely low palatability to snowshoe hares (*4*), (iii) the nutritive quality of browse to snowshoe hares has been experimentally demonstrated to be directly proportional to its palatability (*15*) and (iv) the low palatability of adventitious shoots is a consequence of a high secondary metabolite content, these results suggest that browsing-induced plant defenses may play a role in the regulation of the 10-year hare cycle.

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Origin of Corn: Pollen Evidence

Abstract. *The origin of Indian corn remains controversial. Its closest wild relative is teosinte, with which it hybridizes freely to produce fertile progeny. Teosinte ears are smaller and simpler than those of corn. Searches for a more likely living ancestor have failed, but nine of its assumed pollen grains have been recovered in deep drill-core samples obtained from a stratum of soil under Mexico City, which is believed to antedate man in the Western Hemisphere. These nine largest grains are indistinguishable from pollen of modern corn. It has been assumed to be that of a postulated wild corn other than that of teosinte, but this does not account for the possibility that the pollen grains are those of a tetraploid teosinte-producing pollen with two sets of chromosomes. This likelihood has been examined by treating modern teosinte plants with colchicine, which induces tetraploidy. The result has been many teosinte pollen grains indistinguishable in size from modern corn. In interpreting this outcome it is important also to know that heat treatment of corn and other plants induces polyploidy, and that the deep drill-core pollen was recovered in a stratum of volcanic clay indicating the high temperature known to favor doubling of corn pollen volumes.*

The corn Columbus and his men found on the island of Cuba in 1492 was remarkable in more ways than they could possibly have imagined. The American Indians had made it the most important human food plant of the Western Hemisphere and had adapted it to suitable growing conditions from near the tip of South America to lower Canada. Their achievement is perhaps the most remarkable man-made plant transformation of all time, but in the process corn was so altered that it can no longer survive in the wild, for it has no means of disseminating its kernels (*1*).

When Linnaeus in 1753 assigned corn to the newly created genus *Zea* (from the Greek) and species *mays* (from the Taino language of the West Indies), he knew of no other plant that could reasonably have been placed in the genus of corn. Its closest relatives are a group of plants