Relationships of aspen (*Populus tremuloides*) to foraging patterns of beaver (*Castor canadensis*) in the Strawberry Valley of central Utah

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RELATIONSHIPS OF ASPEN (POPULUS TREMULOIDES) TO FORAGING PATTERNS OF BEAVER (CASTOR CANADENSIS) IN THE STRAWBERRY VALLEY OF CENTRAL UTAH

William J. Massieh1, Jack D. Brotherson2, and Rex G. Cates2

ABSTRACT.—Eight study sites were examined in Strawberry Valley, Utah, to assess the response of aspen (Populus tremuloides Michx.) to foraging activities of beaver (Castor canadensis Warren & Hall) and to determine patterns by which the animals utilize aspen stands. Sites utilized by beaver, along with adjacent control plots in mature, uncut aspen stands, were sampled. Age-class profiles of control plots were composed of a broad age distribution with trees ranging from 3 to 108 years old. Age-class profiles for aspen sprouts in areas previously used by beavers were composed of trees averaging seven years of age with a range of 1 to 24 years. Age distribution of sprouts in areas used by beaver show a tendency to be skewed toward younger age classes. Average density of aspen in areas used by beaver was 15,800 stems per hectare compared to 2,950 stems per hectare in controls. Stump densities in use areas ranged from 900 to 5,066 stems per hectare. Densities of stumps in the 0-5-cm size class were greater in areas used by beavers than in the corresponding size class in the mature forests. A regression equation describing age versus diameter relationships was calculated using data from 312 aspen trees.

Total phenolics and mineral nutrients in the twigs and bark of mature aspen trees and aspen sprouts were also examined to determine if variations could explain foraging patterns of beaver in the valley. Total phenolics were highly variable between sampling groups, and differences were not significant. Twigs from mature aspen and aspen sprouts were significantly higher in nitrogen, phosphorus, and iron. Zinc was significantly higher in the bark of mature aspen trees and twigs of aspen sprouts. Calcium concentrations were significantly higher in mature aspen bark, and magnesium was significantly higher in mature aspen twigs.

Aspen (Populus tremuloides Michx.) is the most widespread forest type in Utah, occupying approximately 1,425,000 acres (Choate 1965). Aspen is a prolific root sprouter and is considered to be important in erosion control, wildlife habitat, and wildlife and livestock forage (Barton et al. 1983, Crouch 1983, Reynolds 1969). Commercially it is used for pulpwood, furniture core stock, excelsior, fuelwood, and building material (Keays 1972).

Beaver (Castor canadensis Warren & Hall) rely heavily on aspen for food and building material. Aldous (1938) found that aspen is the most important food species for beaver, with birch, alder, and willow next in rank. Some authors suggest that the distribution of beaver is largely governed by the distribution of aspen (Stegeman 1954, Hall 1960). Several workers have studied the compatibility of aspen and beaver (Hall 1960, Hiner 1938, Shadle and Austin 1939) and have questioned whether aspen can survive under cutting pressure from beaver. Hall (1960) suggested that any combination of aspen and beaver eventually leads to the complete loss of aspen. In contrast, Yeager and Hill (1950) suggested that a colony of beavers can maintain itself for many years or even permanently because aspen sprouts will grow to usable size as the cutting of older stems progresses. They also contend that livestock utilization of young sprouts is the main reason for loss of aspen during the time that beavers are utilizing a stand.

Aspen is an important species in the ecology of beaver; where they coexist, beaver rely heavily upon it (Aldous 1938). Some authors suggest that the distribution of beaver in North America is largely influenced by aspen distribution (Stegeman 1956, Hall 1960). Several studies of beaver ecology have focused on patterns by which they utilize aspen. For example, Aldous (1938) studied the importance of aspen stem size as related to the cutting activities of beaver. Although relative availability of aspen was not documented in his study, the greatest numbers of trees cut were in size classes 10–15 cm in diameter. Once the trees were cut, the percentage of biomass utilization of downed trees was...
greatest in the 2- and 5-cm-diameter classes, with increasing wastage as stem diameter increased. In diameter classes greater than 8 cm, a large percentage of trees had only the tops utilized.

In a study comparing relative availability of aspen and observed cutting by beaver, Hall (1960) concluded that size preference by beaver was very slight. He also found increased preference for 5-cm trees while dam building was occurring within a colony. As building declined, differential preference for the smaller trees diminished. Jenkins (1978, 1979) suggested that beaver exhibit spatial and temporal preference in food items. Seasonal variation in the concentrations of stored nutrients in the bark of various tree genera was thought to explain switches in preference. Pine was favored during spring months when carbohydrate reserves were greater than in the bark of neighboring deciduous trees. Jenkins (1980) also studied food selection by beaver with respect to an optimal foraging model of size-distance relations. His data suggest that beavers are more selective in cutting behavior as the distance from shore increases. A smaller range of sizes was cut far from shore, with greater numbers of small trees cut and fewer large ones.

Studies addressing the relationship between beaver and aspen have focused mainly on patterns by which the animals utilize the trees. For instance, do size-class preferences exist? Little documentation is available quantifying the effects on aspen of utilization by beaver.

The objectives of the present study were to determine the pattern of aspen utilization by beaver near Strawberry Reservoir, Wasatch Co., Utah, and to quantify the sprouting response of aspen in areas where beaver have utilized stands over long periods of time. Also, we wish to present ideas concerning the foraging patterns of beaver on aspen in central Utah and to discuss the relative value of aspen as a forage species for beaver.

**STUDY SITE**

This study was conducted in the Strawberry Valley, Wasatch Co., Utah, on the east slopes of the Wasatch Mountains (lat. 40°11’15”N, long. 111°21’30”W) at an elevation of approximately 2,325 m. The study site was character-ized by broad valleys and low, rolling hills. Several valleys accommodate perennial streams and are wide and flat in their lower reaches. The valleys head at elevations of approximately 2,743 m along the Strawberry Ridge, range in length from 6 to 10 km, and drain into Strawberry Reservoir.

The climate of the area is characterized by cool summers and cold winters with heavy snow cover. Average annual precipitation taken at the east portal of the Strawberry Reservoir is 610 mm of which 60% falls as snow. The area lies within the Heber Ranger District of the Uinta National Forest and has been grazed by cattle since the 1860s.

Vegetation on the study area is a combination of montane sagebrush (*Artemisia* spp.) steppe in the valleys and aspen-conifer (*Abies, Picea, Pseudotsuga*) forests higher on the slopes (Walker and Brotherson 1982). The riparian areas along stream banks in their lower reaches are dominated by willow (*Salix* spp.).

**METHODS**

Eight study sites were selected based on a high degree of past utilization by beaver. Slope and aspect were recorded for each site. The size of the area affected by beavers was estimated by pacing. A plot measuring 20 × 20 m (0.04 ha) was established in the center of the cutting area. Corners were permanently staked and a line was strung to mark the plot. A second control plot with equal dimensions was also established at each study site. It was located in the aspen forest as close as possible to the study site but beyond any evident beaver activity and on areas with similar slope and aspect.

The quarter-method (Cottam and Curtis 1956) was used to determine density of trees or stumps in the study plots. Ten sampling points were randomly located within each plot, yielding data on 40 trees per plot. In each quarter, the following measurements were recorded: distance to nearest aspen stem; height of stem or stump (measured up to 6 m with a retractable tape), stem diameter at 0.3-m height; and stem age. Diameters were taken at 0.3 m above the ground so that the stem diameter of living trees could be compared to that of the stumps (which rarely reached breast height).
Table 1. Site factor data from areas used by beavers and adjacent control areas in Strawberry Valley, Wasatch Co., Utah.

<table>
<thead>
<tr>
<th>Site factor</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size of cutting (ha)</td>
<td>0.61</td>
<td>0.18</td>
<td>0.20</td>
<td>0.18</td>
<td>0.51</td>
<td>0.30</td>
<td>0.30</td>
<td>0.40</td>
</tr>
<tr>
<td>Distance from stream to stand (m)</td>
<td>39.7</td>
<td>33.6</td>
<td>24.4</td>
<td>36.6</td>
<td>25.9</td>
<td>30.0</td>
<td>21.4</td>
<td>18.3</td>
</tr>
<tr>
<td>Beaver use area</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspect (degrees)</td>
<td>90</td>
<td>315</td>
<td>204</td>
<td>124</td>
<td>202</td>
<td>17</td>
<td>20</td>
<td>130</td>
</tr>
<tr>
<td>Slope (%)</td>
<td>28%</td>
<td>13%</td>
<td>14%</td>
<td>18%</td>
<td>23%</td>
<td>6%</td>
<td>8%</td>
<td>50%</td>
</tr>
<tr>
<td>Control plot</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aspect (degrees)</td>
<td>40</td>
<td>314</td>
<td>204</td>
<td>160</td>
<td>204</td>
<td>21</td>
<td>20</td>
<td>128</td>
</tr>
<tr>
<td>Slope (%)</td>
<td>22%</td>
<td>15%</td>
<td>12%</td>
<td>20%</td>
<td>16%</td>
<td>10%</td>
<td>10%</td>
<td>28%</td>
</tr>
</tbody>
</table>

Age of sprouts (individuals with stem diameters less than 5 cm) was determined in the field using an ax, sharp knife, hand lens, and a solution of 15% hydrochloric acid saturated with phloroglucin as a stain to increase visibility of annual rings (Alder 1970). Aging trees greater than 5 cm in diameter was done by taking a core sample with an increment bore at 0.3 m above the ground. Cores were stored in labeled drinking straws.

Core samples were permanently mounted with wood glue into grooves cut lengthwise in 90 × 30 × 3-cm boards. Portions of the core that were exposed above the surface of the board were sanded to facilitate counting. Sanded cores were stained with 15% hydrochloric acid/phloroglucin solution. Counting was done by hand using a 10X hand lens or dissecting microscope when necessary. Each ring was marked by punching a small hole in the core where needed. Annual rings were identified by the shadow created as the gradient from large to small xylem elements abruptly changed to earlywood (Maini and Coupland 1964). The few false rings encountered did not display this shading effect and were not counted. All cores were subjected to two independent counts.

Counts of all aspen stems or stumps found within each plot were conducted. Diameter was measured and each stump was placed into one of six diameter-size classes: 0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, 20–25 cm, and greater than 25 cm. Selection of size classes was partially based on studies by DeBye (1976) and Hite-Ranch (1976) where two inches of dbh was used as the size class, delineating sprouts from mature trees. We considered all stems or stumps in the 0–5 cm size class to be sprouts. All counted stems or stumps were marked with red paint to avoid counting twice.

Mean ages and standard deviations were calculated for aspen stems or stumps sampled on each of the eight study areas or their adjacent controls. Chi-square analyses were then used to determine if the age-class structure of stands used by beaver was the same as aspen stands on control areas.

Three of the eight study sites that were in the Clyde Creek drainage of Strawberry Valley, Wasatch Co., Utah, were selected and sampled in December 1983 for vegetative materials of aspen to use in determining forage quality. Even though the sampling period was later in the season than the peak period during which beaver cut aspen for dam construction and food supplies, research by Gifford et al. (1983) indicates that transpiration in aspen ceases near the end of September and does not begin again until late May. Also, Dietz (1972) found that vitamins, mineral nutrients, and crude protein in aspen did not change significantly from fall to winter.

Each of the three sites had been utilized by beaver for several years and had been cut during the late summer and fall prior to sampling. Sites were characterized by a dense growth of aspen sprouts near the stream. The area most recently utilized by the beaver was upslope and at greater distances from the dam and beyond the sprouts.

Mature, uncut aspen stands continued up the slopes beyond the cutting zone. Five sprouts ranging in diameter from 3 to 5 cm were selected at random within the sprouting area and cut down. All twigs from the top 30 cm of the sprout were trimmed and placed
into sealed plastic packages. Sprout bark was also removed using a draw knife and sealed into packages. Smaller-size sprouts were not selected because of inadequate amounts of material for analysis.

In the mature aspen stands, five mature trees of various diameters greater than 5 cm were randomly selected and cut down. Twigs from the tree top and bark from the bole at breast height were removed as described above and placed into sealed packages. Samples were kept at −5 C (ambient air temperature during sampling) in the field and were later frozen at −30 C until processed. Frozen samples were cut into smaller pieces in the laboratory and then frozen in liquid nitrogen before being ground into powder with an electric mortar and pestle. Prepared samples were sealed in bottles and kept at −30 C until laboratory analysis.

Twig and bark samples were analyzed for calcium, magnesium, sodium, potassium, phosphorus, manganese, iron, zinc, and copper using the nitric and pyloric acid digestion process (Johnson and Ulrich 1959). Percent nitrogen was determined by the Kjeldahl method (Horwitz 1983). Total phenols were determined by analyzing a 50% methanol/50% distilled-water extract with a Coleman Model 440 spectrophotometer. The standard

Fig. 1. Stand-age profiles of eight study sites and eight control plots in Strawberry Valley, Wasatch Co., Utah.
Table 2. Age-class breakdown for aspen trees sampled in study plots and control plots in Strawberry Valley, Wasatch Co., Utah.

<table>
<thead>
<tr>
<th>Age class</th>
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<th>Ctrl</th>
<th>Site 5</th>
<th>Ctrl</th>
<th>Site 6</th>
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<th>Site 7</th>
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<td>8</td>
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<td>2</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
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<td>51–55</td>
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<td>66–70</td>
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<td>0</td>
<td>0</td>
<td>5</td>
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<td>4</td>
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<tr>
<td>&gt;70</td>
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<td>0</td>
<td>3</td>
<td>0</td>
<td>1</td>
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<td></td>
</tr>
</tbody>
</table>

| s age     | 7.3   | 22.5 | 4.3   | 29.0 | 11.2  | 37.9 | 6.3   | 48.5 | 8.7   | 67.4 | 7.7  | 35.9 | 6.9  | 20.2 | 7.4  | 37.4  |
| s age     | 2.9   | 11.6 | 1.6   | 20.5 | 2.6   | 27.0 | 1.2   | 22.6 | 3.8   | 22.7 | 4.8  | 25.5 | 5.6  | 20.6 | 4.6  | 13.5  |

The curve was constructed using a buffered quebrach solution, and data were expressed as % quebrach equivalents. Tannin capacity of the extract was determined using a modification of the hemoglobin-astringency method (Bate-Smith 1973). Quebracho tannin was used in formulating the standard curve. Terpenes were analyzed with gas chromatography using a fused silica capillary column.

Means and standard deviations were calculated for the total phenolics, calcium to phosphorus ratios, and all nutrients. Two-way analysis of variance was used to test differences between sites and sampling groups (Snedecor and Cochran 1967). Means were separated using Fisher's least significant difference method (Ott 1984).

**RESULTS AND DISCUSSION**

Aspen stands occur continuously along one or both sides of all drainages studied. Distance between stands and the edge of the stream varied from 18 to 40 m (Table 1). Within this area, the flat ground adjacent to the stream was occupied by willow while the slopes above the floodplain were dominated by sagebrush steppe. Slope of areas with aspen stands utilized by beaver ranged from 6 to 50%. Aspect of study sites varied widely, with general aspects either to the north or south.

Beavers were active in all areas studied. Most aspen cutting occurred in September and October of the years the study took place. Cutting was concentrated in localized areas of mature aspen stands within 100 m of the stream.

Stand-age profiles provide a visual comparison between trees sampled in areas used by beavers and trees in adjacent mature forests (Fig. 1). Each graph represents approximately 80 trees, 40 from the beaver-use area and 40 from the control plot. Eight trees out of the 640 sampled could not be accurately aged because of heart rot. All aspen stems were assigned to five-year age classes to facilitate graphing. A bar in the histogram represents percentage of sampled trees that fall within each age class.

Age-class profiles of control plots show that aspen stands in the study area are composed of a broad age distribution. These data are consistent with other studies done on aspen in the intermountain area (Alder 1970). Noteworthy similarities between stands are a short period of unfavorable growth 16 to 25 years ago and a favorable growth period between 40 and 60 years ago. Variation between stands may reflect differences in site potential, genetic differences in clones, and/or local history of disturbance. The age of aspen stems sampled from the mature forest (control areas) ranged from 3 years to 108 years, with an average of 70 (Table 2).

Age-class profiles of areas used by beavers were composed of trees averaging seven years of age, with a range of 1 to 24 years. Differences between the age profiles of mature
aspen forests and areas cut by beavers are clearly illustrated in each graph. Differences are due to a combination of the following factors: (1) patterns by which the beaver cut aspen while procuring food and building materials, (2) root sprouting by aspen in response to cutting activities of beaver, (3) differential grazing pressure between sprout areas and mature forests, and (4) differences in growth potential due to site differences and genetic variation among clones of aspen.

The leftward skew in the average age profile of the use areas suggests that beavers utilize sprouts that are approaching 20 years old.
Table 3. Density of aspen sprouts and aspen stumps in areas used by beaver and density of aspen trees in control areas. Strawberry Valley, Wasatch Co., Utah.

<table>
<thead>
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<th>Sampling group</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>( \bar{x} \pm s )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sprouts (use area)</td>
<td>30,300</td>
<td>18,180</td>
<td>5,620</td>
<td>9,350</td>
<td>5,350</td>
<td>13,300</td>
<td>34,500</td>
<td>9,803</td>
<td>15,800 ± 11,095</td>
</tr>
<tr>
<td>Control (mature forest)</td>
<td>2,700</td>
<td>4,290</td>
<td>1,450</td>
<td>2,440</td>
<td>2,190</td>
<td>4,149</td>
<td>3,330</td>
<td>3,290</td>
<td>2,980 ± 974</td>
</tr>
<tr>
<td>Stumps (use area)</td>
<td>900</td>
<td>2,170</td>
<td>2,080</td>
<td>1,900</td>
<td>2,640</td>
<td>2,350</td>
<td>2,400</td>
<td>5,060</td>
<td>2,440 ± 1,183</td>
</tr>
</tbody>
</table>

More precise histograms of the age-class profiles on the sprout areas are presented in Figure 2. Each histogram represents 40 trees sampled in areas used by beaver. Age classes are in one-year increments. Bars in the graphs represent the percentage of sampled trees in each age class. The tendency for a skewed age distribution toward younger trees is seen clearly in the average profile for the eight sites.

A comparison of densities of cut and uncut aspen trees in use plots with aspen trees in control plots is summarized in Table 3. Densities of aspen stems in areas used by beaver ranged from a low of 5,617 stems per hectare to a high of 34,482 stems per hectare, with an average of 15,801. These densities exceed those found on the control areas by five times. Figure 3 represents a graph of cover values for aspen sprouts taken along a transect passing through areas used by beaver and into adjacent stands not yet utilized. Cover of sprouts in areas cut by beavers averaged 39.5%, while in mature, unutilized stands sprout cover averaged only 5.9%.

The density and cover values found on the beaver use areas approach those found in silvicultural studies on the response of aspen to clearcutting (DeByle 1976, Hittenrauch 1976, Jones 1975). The high values for aspen sprouts
found on areas cut by beaver, along with the absence of mature trees, indicate that the pattern of year-to-year utilization of mature aspen forests by beavers as they gradually cut farther up the slope effectively simulates silvicultural clearcutting practices.

Clearcutting aspen, as opposed to selective cutting, provides the optimum conditions necessary for sprouting (DeByle 1976, Jones 1975, 1976). Sprout numbers between 24,710 and 98,840 per hectare are not uncommon after clearcutting (DeByle 1976, Hittenrauch 1976). Average density of aspen on our control areas was only 2,980 stems per hectare, with a low of 1,449 and a high of 4,298. Differences in average stem densities between the control and use areas were significant (Chi square = 12.54, p < .05).

High sprout densities in areas used by beavers might also be attributed to differential grazing pressure by livestock over long periods of time between aspen stands in the control areas and areas used by beaver. Research has demonstrated that heavy grazing pressure by livestock, deer, and elk can effectively suppress regeneration of aspen stands by sprouting (Crouch 1983, DeByle 1976, Hittenrauch 1976, Jones 1975). The unutilized boles of larger aspen trees lying on the ground in areas cut over by beaver may produce an effective barrier to grazing animals by preventing their access into the area. Silvicultural studies by Hittenrauch (1976) demonstrated that unmerchantable timber left lying on the ground in clearcuts completely eliminated grazing of sprouts by cattle. Reynolds (1969) also concluded that fallen timber was an effective barrier for deer, elk, and cattle, allowing aspen sprouts to develop.

Stump densities in use areas ranged from 900 to 5,066 stems per hectare. Size-class distribution of stumps showed a similar pattern to size classes of trees in a mature forest, although densities were different (Fig. 4). In size classes greater than 5 cm, densities of stumps on the use areas were consistently lower than those of corresponding size classes in the mature forest. In the 0–5-cm size class, densities of stumps on the use areas were greater than densities of the same size class in the mature forest. Several factors may explain the disparity between stump densities on study plots versus densities of aspen trees in control plots. A proportion of the stumps on the study plots may have been lost to decay or may have been overlooked because of dense growth of aspen sprouts and associated species (which on some plots was almost impenetrable). The fact that beavers were still active in all the study areas also complicated comparisons.

Values for diameter versus values for age were plotted to develop a regression equation (Fig. 5). With this equation to predict the age of aspen tree stumps on the study area, several relationships become clear. When the upper size limit of the 0–5-cm size class is used for the diameter variable in the equation, the predicted value for maximum age of trees in that size class was approximately 23 years. Twenty-three years of age roughly corresponds to the highest age found for sprouts in areas used by beaver. These data indicate that beaver are returning to previously cut-over areas to utilize aspen sprouts as they approach 5 cm in diameter or an age of around 20 years.

The results clearly show that vegetative reproduction of aspen is enhanced by the cutting activities of beaver. However, when considering management of aspen forests and long-term impacts of continuous utilization by beavers, other factors must be considered. For example, factors controlling resources such as willow need to be better understood. Range management practices such as aerial spraying of 2,4-D (2,4-dichlorophenoxy acetic acid) to eliminate willows and improve forage for livestock may divert increased foraging pressures to aspen. It would also be valuable...
to determine optimum beaver densities for specific sites and to manage populations at levels that allow aspen stands to perpetuate themselves. In areas where utilization of aspen sprouts by cattle is preventing establishment of smaller size classes, beaver activity may be beneficial by creating physical barriers that protect suckers from heavy utilization by livestock.

Proportions of the different size classes of stems used by beaver for construction of their dams on our study sites are shown in Figure 6. Even though all size classes of aspen were cut, only stems in the smaller size classes were incorporated into the dams. Some of the smaller size class material found in the dam probably represents stems taken from the tops of larger trees. Willow accounted for 57% of all stems counted in the dams (Fig. 6). The importance of willow as an alternate food source and building material has been discussed by several researchers. Hall (1960) concluded that willow is the second woody staple of a beaver’s diet and can sustain the animals in the absence of aspen. Rasmussen and West (1943) feel that willow, not aspen, is the key plant in beaver habitat.

Data on mineral nutrient content of aspen twigs and bark showed several differences between sampling groups. For example, phosphorus and iron were significantly higher \( p < .05 \) in the twigs of both mature aspen and aspen sprouts than in the stem bark (Table 4).

In contrast, zinc was highest \( p < .05 \) in the bark of trees and sprouts while calcium concentrations were greatest in the mature bark. Magnesium was significantly higher \( p < .05 \) in the twigs of mature aspen trees. Copper showed no significant differences in concentrations among the four sampling groups. Levels of nitrogen, potassium, and manganese varied significantly among sites \( p < .01 \). Twigs from mature aspen trees had the highest values in six out of the nine minerals (N, P, K, Fe, Mn, and Mg) and second highest in two others (Cu and Ca). If the bark and twigs of mature aspen are considered together, mature trees have the highest concentrations of all the nutrients with the exception of copper.

The relative proportions of calcium and phosphorus within and between the sampling groups are also of interest. Dietary calcium to phosphorus ratios ranging from 1:1 to 2:1 are considered best for proper absorption and metabolism in most herbivores (Robbins 1983). Abnormally high ratios (greater than 7:1) have been shown to interfere with the absorption of phosphorus and other mineral nutrients, particularly magnesium, zinc, and manganese (Underwood 1966). Calcium to
Table 4. Total phenolic and nutrient content from samples of twigs and bark of mature aspen and aspen sprouts collected at Strawberry Valley, Wasatch Co., Utah.

<table>
<thead>
<tr>
<th></th>
<th>% quebracho equivalents</th>
<th>% N</th>
<th>% P</th>
<th>% K</th>
<th>PPM/Zn</th>
<th>PPM/Fe</th>
<th>PPM/Mn</th>
<th>PPM/Ca</th>
<th>% Ca</th>
<th>% Mg</th>
<th>Ca/P ratio</th>
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<tr>
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<td>x</td>
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<td>.14a</td>
<td>.29a</td>
<td>53.5c</td>
<td>23.8a</td>
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<td>6.4a</td>
<td>1.50b</td>
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<td>s</td>
<td>± .61</td>
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<td>.04</td>
<td>.07</td>
<td>10.8</td>
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<td>.31</td>
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<tr>
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<td>14.3a</td>
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<td>1.1</td>
<td>.18</td>
<td>.02</td>
<td>13.4</td>
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*Means, within a column, with the same lowercase letter are not significantly different at p < .05.

Phosphorus ratios found in the four sampling groups range from 10:1 in the sprout twigs to 37:1 in the mature aspen bark (Table 4). High Ca/P ratios have also been reported by Strickland (1987) for oak (Quercus gambeli) utilized by porcupine. He suggests that the porcupines dealt with the high levels of calcium by concentrating it in their urine (i.e., the Ca/P ratios in the porcupine urine were approximately 22:1:1). Differences in the Ca to P ratios are significant between sapling twigs and mature aspen bark (p < .05). Foraging on twigs from either aspen sprouts or mature aspen would provide Ca to P ratios closer to those considered optimal for herbivores.

Phenolic concentrations in the aspen samples were highly variable and ranged from a low of 0.72 to a high of 4.57% quebracho equivalents. The individual samples were lumped into 10 equal-width concentration units and then plotted by sample group (Fig. 7A-E). Trends were observed in the tree twig and tree bark categories. For example, 75% of the individual samples in the tree twig category were contained in the concentration groups above 1.89% quebracho equivalents, while 69% of the individual samples in the tree bark category fell below the 1.89% concentration level (Fig. 7A, B). However, because of the high variability within the individual subsamples (Fig. 7E) as well as small sample sizes, the differences in the total phenolics between the sampling groups (twigs and bark of mature trees versus twigs and bark of sprouts) were not significant (Table 4). Further, we found no terpenes or tannins as measured by astringency (protein-complexing capacity of the extract) in the samples analyzed. Although the absence of terpenes is not unusual, the absence of tannins in the samples is noteworthy. Data summarized by Rhoades and Cates (1976) illustrated that 79% of deciduous woody perennials (211 species) tested positive for tanniferous compounds.

Bryant (1981) studied the phytochemical deterrence of snowshoe hare browsing in four species of deciduous trees (including aspen) in Alaska. His data indicated that adventitious shoots of all species contained significantly higher concentrations of phenolic resins and terpenes than twigs from mature growth of the same species. The resins were experimentally shown to repel snowshoe hares and appeared to explain the avoidance of adventitious shoots by hares.

In a more recent study on green alder (Alnus crispa [Ait.] Pursh.) and snowshoe hare (Lepus americanus Erxleben), Bryant et al. (1983, Carbon/nutrient) found that total phenols had no relationship with preferential foraging of alder parts by hares. Instead, a single phenol, pinosylvin methyl ether (PME), accounted for the low palatability in foliar buds and catkins, while internode parts (older growth) did not have high concentrations of PME and were utilized heavily by hares. More specific assays of individual chemicals and individual plant parts will be required before conclusions can be made on the influence of phenolic compounds on the foraging patterns of beaver in our study area. An important class of compounds that should be
also allows the plant to survive after being heavily browsed. Still, heavy utilization during the few years when plants are within reach of browsing mammals can cause extensive growth retardation and/or mortality. Bryant et al. (1983, Carbon nutrient) suggested that early successional trees have responded to browsing pressure by evolving toxic chemical defenses (Rhoades and Cates 1976) during the juvenile life state that are not present in the mature life stages. These ideas are consistent with foraging patterns observed on our study area.

Understanding foraging patterns of beaver on aspen is a complex problem that will require consideration of additional factors pertaining to beaver ecology. First, beavers utilize plant materials for dam building as well as food supplies. If a range of size classes of materials is available, then selection of certain size classes for dam building may be independent of food selection. Certain sizes of materials may be more efficient in dam construction.

Second, we found that beaver on our study sites passed through young stands of sprouting aspen and exhibited a preference for larger trees further from their dams. Beaver traveled distances greater than 100 m from the stream to forage on mature aspen trees even though abundant aspen sprouts (5 cm or less in diameter) were highly available near the stream. The beaver mainly utilized smaller branches on the mature trees, those in the same diameter classes as the more accessible sprouts. Since the beavers must exert a certain amount of energy on foraging excursions, it may be that the animals are trying to maximize energy return. It is possible that by traveling greater distances and cutting trees in the larger size classes they make the trips more energetically efficient. Cutting trees in larger size classes would make available greater amounts of biomass, while cutting the smallest size classes near the stream may not provide sufficient plant material to make a trip energetically profitable.

Third, beavers are generalist herbivores and utilize many species of plants for food. It may be possible that they are foraging on certain plants to avoid specific secondary metabolites and on others to meet specific needs. Such trade-offs may not be evident unless complete studies of food habits are undertaken. Also, the fact that beavers store

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**Fig. 7.** Percent of aspen phenol samples contained within each concentration category plotted against increasing concentrations of total phenols. Concentration of total phenols is expressed in percent quebracho equivalents.

Included is the phenolic glycosides, which are known to occur in aspen, willow, and other potential host plants.

Bryant et al. (1983, Pinosylvin methyl ether) discussed strategies of disturbance-adapted trees relative to defense against vertebrate herbivory. Many species that invade recently disturbed sites, including aspen, have resistance to browsing because their rapid growth rate enables them to grow out of the reach of browsing animals. Root storage
food in caches for use during the winter poses a unique situation for food habit studies. Since the animals are subject to being ice-bound for periods sometimes exceeding 100 days, the nutritional value and potential changes in secondary metabolites of forage stored in winter caches could be very important.

Data on mineral nutrients from the aspen on our study area suggest that differences exist between the nutritional value of mature aspen trees and aspen sprouts. The idea that beaver can differentiate between forages of various nutritional value may help explain patterns of preferential foraging on mature aspen trees in Strawberry Valley. The influence of specific monomer phenolic and phenolic glycoside compounds on size-class selection by beavers may also be important but requires further study.

**Literature Cited**


