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## Shrubs

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Shrubs are an important component of the vegetation of the boreal forest because they provide complex structure where trees are absent or added dimensions in the forest between the herb layer and the tree layer. Shrubs are the winter food of the key species of herbivores in the boreal zone. Snowshoe hares and moose rely on browse from shrubs to get them through the winter period. One of the objectives of the Kluane Project was to obtain a good description of the changes in biomass and utilization of shrubs during the hare cycle, and in this chapter we present a summary of what we discovered.

### 6.1 The Shrub Community at Kluane

We include here the woody component of the plant community that grows between about 10 cm and 3–4 m in height in the Kluane boreal forest. We exclude from this discussion small trees (discussed in chapter 7) and the dwarf woody plants such as *Arctostaphylos uva-ursi*, which can be a dominant form of ground cover. In this section, we describe first the species that occur at Kluane and their relative abundances, the successional sequence in the shrub community, and the chemical defenses shrubs use against herbivores.

#### 6.1.1 Species Composition

The shrub community in the Kluane region is dominated by gray willow (*Salix glauca*). For the 1700 shrub clip plots that we measured on control areas from 1987 to 1996, gray willow is 98.1% of the above-ground shrub biomass, bog birch (*Betula glandulosa*) is 1.25%, *Potentilla fruticosa* is 0.33%, and soapberry (*Shepherdia canadensis*) is 0.14%, on average. There are two other species of shrub willows in the Kluane area, but they are restricted in distribution (*S. alaxensis*, *S. scouleriana*).

Different experimental areas within the study region have highly variable shrub communities. Table 6.1 (Beals 1960) summarizes the prominence values for shrubs from the different treatment areas. Gray willow is common and is the dominant shrub on all the areas. A few differences stand out. Bog birch is prevalent on the two fertilizer treatments, food 2, and on the fence grid but nearly absent on control 1 and hare enclosure 1. Both soapberry and *Potentilla* are patchy in the study area.

The patchy nature of the shrub vegetation is difficult to portray with conventional measures and techniques, and we had to develop new methods to describe site heterogeneity. In this part of the boreal forest, it would be possible for a snowshoe hare to live in a 5-ha home range dominated by bog birch with soapberry very common. In other areas of the valley, no birch or soapberry would occur at all in the same size of home range, and the most general statement one can make is that every hare would have abundant gray willow within its home range anywhere in the valley.

#### 6.1.2 Pattern Changes and Succession

Vegetation pattern analysis describes the spatial heterogeneity of the vegetation as well as the way this heterogeneity changes with time (Dale and Zbigniewicz 1997). We examined the effects of the experimental manipulations on the spatial pattern of the two major

Table 6.1 Prominence values of the major tall shrub species in the treatment areas in 1987–1988.

Grid	<i>Salix glauca</i>	<i>Betula glandulosa</i>	<i>Potentilla fruticosa</i>	<i>Shepherdia canadensis</i>
Control 1	92	4	14	0
Control 2	183	84	68	0
Fertilizer 1	57	164	33	0
Fertilizer 2	131	123	0	1
Food 1	106	15	0	0
Food 2	98	169	5	3
Fence	104	234	1	0
Fence + food	123	10	0	0
Hare enclosure 1	102	0	4	4
Hare enclosure 2	101	58	1	2

Prominence is measured by the relative cover and the relative frequency of the species in quadrats (Beals 1960). Because these values are means of only two 100-m transects, they give only a general view of the variation among sites. (Data from M. Zbigniewicz, personal communication.)

shrub species, *Salix glauca* and *Betula glandulosa*, before and after the 1989 population peak of the snowshoe hare. In this context, *spatial pattern* refers to the predictability of the locations of plants. A simple pattern is a regular alternation of high-density patches and low-density gaps. The intensity of such a pattern is the difference in density between the two phases. The scale of the pattern is the average of the patch and gap sizes (Dale and MacIsaac 1989). The scale of pattern of the vegetation may be an important habitat characteristic for herbivores, because for the same average density of plants, larger scales of pattern mean greater distances between patches of food plants or of cover.

Vegetation may have more than one scale of pattern, as when the patches occur in clusters. The effect of herbivores may be to break up patches into smaller units, causing a new small scale of pattern to develop in the vegetation. We predicted that treatments that increased snowshoe hare density would decrease the intensity of shrub pattern and cause the appearance of smaller scales of pattern. Treatments that decrease browsing or enhance the plants' ability to grow should increase intensity and cause the loss of small-scale pattern. We also predicted that moderate herbivory would decrease shrub patch size. Therefore, we investigated both pattern scale and intensity and patch size and used the data collected before and after the hare population peak to test our predictions.

We selected level areas occupied by shrub vegetation 0.5–2 m in height. Within each area we established two or more transects of 1001 contiguous quadrats, each 10 cm × 10 cm, and these were sampled in 1988 before the hare peak and in 1993. We recorded ocular estimates of the cover of all species in each quadrat.

We compared the 2 years by looking at the number of nonempty quadrats in each year and the density in them. We used two-sample *t* tests to compare the average densities of quadrats that were not empty in both years (Dale and Zbigniewicz 1997). The *t*-tests on the quadrat densities showed an overall positive effect on shrub cover attributable to fertilizer addition, even in the presence of herbivores, and to herbivore enclosure. The high and prolonged hare peak, caused by food addition and predator enclosure, reduced shrub

cover, especially of *Betula*, due to a smaller proportion of the quadrats being occupied. The increase at fertilized sites could not be attributed to an increase in nonzero quadrats. The increase in *Betula* in the herbivore enclosure with fertilizer was due to increases both in the number of occupied quadrats and in the density. In the food-only grids and the untreated grids, the proportion of quadrats occupied decreased, while the average density in those occupied increased.

To investigate spatial scale, the data were analyzed using Hill's (1973) three-term local quadrat variance (3TLQV) because it is the best method to detect the scale of the pattern (Lepš 1990). The method calculates variance as a function of *block size*, the number of quadrats that are combined into larger units. Peaks and shoulders in the plot of variance as a function of block size reflect scales of pattern in the data (Dale and Blundon 1990). We concentrated on the smallest and most obvious scales of pattern revealed by the plots of variance. We compared years by looking at the intensity of individual peaks in the variance plot and at the total variance over the range of block sizes examined. The positions of peaks in the variance graphs were also compared between years to see whether the scales of pattern had shifted or whether scales had been gained or lost. Where there was a good match between the positions of variance peaks, we compared the intensity of pattern at that scale (for the calculation of intensity, see Dale and MacIsaac 1989).

Most of the sites showed some increases in total variance attributable to the proportional change in total cover. There were few dramatic changes in the 3TLQV graphs: most of the peak shifts are small, as are changes in intensity. For both species, the average scale of pattern was between 3 and 4 m. There was no consistent evidence of the appearance or disappearance of small scales of pattern.

Whereas Hill's 3TLQV analysis is used to detect the scale of pattern, Galiano's (1982) new local variance detects patch size by producing peaks in its variance plot at block sizes equal to the sizes of the patches or the gaps, whichever is smaller. In our data, the patches were almost always the smaller phase, and we looked at the smallest block sizes that produced clear peaks in the plot of variance.

There are some clear trends in patch size, such as an increase in *Betula* patch size at the three fertilized sites. At the control and food addition sites, patch sizes decreased or the variances associated with smaller sizes increased, showing that the smaller patches became more common (Dale and Zbigniewicz 1997).

The conclusion is that our early predictions were not supported by the data. The peak density of the herbivore between the years sampled seems to have had little effect on the pattern of the food plants. The intensity of pattern increased slightly at most sites as the cover in occupied quadrats increased. This applied particularly to sites that experienced normal or near normal peak densities. In spite of high rates of twig browsing during the peak, at most sites the basic characteristics of the spatial pattern recovered quickly. Only where food addition and predator enclosure enhanced and prolonged the hare density peak was there a sharp decline in the intensity of spatial pattern of the preferred winter food plant *Betula*. The addition of fertilizer produced favorable conditions for the plants' regrowth, whereas the combination of food addition and predator enclosure produced a clear effect at Hungry Lake, strongly reducing pattern intensity and patch size for *Betula*. The spatial pattern of these shrubs is resilient to normal changes in herbivory and therefore may persist for decades through several hare population cycles.

### 6.1.3 Secondary Chemicals in Kluane Shrubs

Plant defense theory argues that shrubs that are browsed by herbivores should attempt to defend themselves chemically to reduce herbivore damage (Bryant et al. 1994, Coley et al. 1985). Earlier studies (Sinclair and Smith 1984, Sinclair et al. 1988) have shown that phenolic compounds change over the hare cycle and are the most sensitive compounds to browsing. Phenolic compounds have been identified in other birch species (Reichardt et al. 1984), but they appear to be at low levels in willow species. A crude index of phenolic compounds can be obtained from methanol extraction. A 20-g fresh weight sample was taken from the twigs of gray willow and bog birch collected in the autumn for growth measurements. One 2-g sample was ground in a blender and then soaked in methanol for 2 days. The solvent was decanted and replaced with fresh methanol twice more. The combined solvent was then evaporated and the remaining extract weighed, and the results were expressed as a percentage (gram extract per gram wet weight of twig). We were unable to do replicate samples for many of the treatments, and our evaluation of significant changes in these indices of secondary chemical levels must rely on the replicates done on two control and two fertilizer grids. For birch and willow, differences of 4% or more among years or among treatments are approximately statistically significant.

For bog birch, this crude methanol extract showed a pronounced cycle coinciding with the hare cycle (table 6.2). All treatments except fence + food showed an initial low index in 1986 and 1987, followed by an increase in 1988, a peak in 1989, and still high but declining values in 1990. The index then fell to low values in 1991 and remained there until 1994, the last year of records. Birch values on the fence + food treatment remained low throughout the hare peak, but then dropped to even lower levels after 1991. Fertilizer treatments showed the same cycle as other treatments. These changes in secondary chemicals in birch are large (table 6.2).

In contrast, for gray willow there was much less apparent change from 1987 to 1994 (table 6.3). Values increased sharply for controls and food and fence treatments from 1987

Table 6.2 Crude methanol extract of secondary chemicals from bog birch (*Betula glandulosa*) current annual growth taken as a pooled sample from winter twigs in May of each year.

Year	Controls	Fertilized	Food	Predator Exclosure	Predatore Exclosure + Food	Hare Exclosure + Fertilizer
1986	26.2					
1987	26.7	22.3	25.1	22.3		
1988	39.1	27.1	30.1	38.3	27.9	20.6
1989	40.1	36.4	43.2	39.7	25.9	40.1
1990	?	30.4	31.4	35.1	28.5	30.8
1991	?	18.8	26.5	22.5	29.2	26.3
1992	23.8	20.5	20.5	18.9	18.9	19.3
1993	19.7	19.4	21.5	25.3	23.4	21.1
1994	26.3	19.8	22.5	20.0	23.6	19.5

Data are expressed as a percentage of the wet twig weight. The average standard deviation for replicate samples was 1.75, but on most areas only a single sample was analyzed. Unfortunately, there was no birch on the hare exclosure that was not fertilized.

Table 6.3 Crude methanol extract of secondary chemicals from gray willow (*Salix glauca*) current annual growth taken as a pooled sample from winter twigs in May of each year.

Year	Controls	Fertilized	Food	Exclosure Predator	Predator Exclosure + Food	Hare Exclosure	Hare Exclosure + Fertilizer
1986							
1987	14.4	13.0	13.3	17.8		15.8	
1988	19.1	17.1	21.8	20.5	13.9	19.7	13.3
1989		18.2	22.4	19.0			15.2
1990	16.3	15.9	17.4	18.0	14.9	15.8	12.1
1991	18.2	18.7	18.7	17.4	17.6	19.7	14.1
1992	17.2	15.6	17.1	16.6	17.1	17.5	13.6
1993	17.0	16.9	17.8	16.3	17.9	17.1	14.5
1994	15.5	13.2	15.5	15.8		16.8	13.1

Data are expressed as a percentage of the wet twig weight. The average standard deviation for replicate samples of controls and fertilized plots was 1.78, but on most areas only a single sample was analyzed.

to 1988 and then declined gradually to 1994. The index values for fence + food were lower than those for the controls or the fertilized grids. There was no clear cycle in the willow methanol extracts for fertilizer treatments, in contrast to the results for birch. Where hares were excluded, application of fertilizer appeared to result in a lower value of extract compared with that for the control area, but the differences were small.

There was thus a major difference in the secondary chemical responses of the two main shrubs at Kluane to the snowshoe hare cycle. Bog birch increased the level of chemical defense as hare numbers increased but did not maintain these high levels during the years of snowshoe hare decline from 1991 to 1994. The gray willow results, in contrast, suggest little change in secondary chemical levels through the hare cycle and only minor changes associated with the treatments.

## 6.2 Biomass Dynamics

Because of the intensity of browsing on shrubs associated with the snowshoe hare cycle, we put considerable effort into measuring the biomass dynamics of bog birch and gray willow through the 1986–1996 period. Because earlier studies by Keith et al. (1984) and Smith et al. (1988) indicated that snowshoe hares rarely browsed large twigs, we divided biomass for both birch and willow into small twigs (<5 mm diameter) and large twigs (>5 mm diameter). In this section we discuss the methods we used to measure biomass and the effects of the treatments on biomass of the two major shrubs in this part of the boreal region.

### 6.2.1 Methods of Estimation

In our previous studies we used nondestructive sampling to measure browsing responses over a hare cycle (Smith et al. 1988). We decided to change in this study to destructive sampling ("clip plots") because the repeatability of nondestructive methods

would be low with so many individual observers involved. We used two general methods of destructive sampling to estimate standing biomass at the end of winter.

**Quadrat Sampling** We began in 1987 by setting out random quadrats of  $1 \times 2$  m on two control areas, two fertilizer areas, and one hare exclosure. In 1990 we began sampling the predator exclosure + food area as well. The variance of  $1 \times 2$  quadrats was so large that we looked for a better quadrat shape in 1988. The basic problem was that many quadrats contained no shrubs at all. We found in a trial analysis that long, thin quadrats,  $10 \text{ m} \times 20 \text{ cm}$ , could reduce sampling variation (CD-ROM frame 46). And so from 1989 onward we used these long, thin quadrats.

In spite of a statistical power analysis that indicated a sample size of 50 quadrats would give us precision of  $\pm 20\%$  of the mean, we continued to find high variability from year to year in the estimates of standing crop. This variability resulted from habitat heterogeneity on a fine spatial scale. We classified the habitat around each sampling point into six categories, but we were unable to improve precision by this stratification. Because we were unable to sample more than 50 quadrats in each sampling area, we had to be content with the data obtained.

**Transect Sampling** In 1993 we adopted a second approach to biomass determination. This approach was based on six transects of  $6 \times 600$  m within each sampling area. In each transect the size of each willow or birch bush was measured (basal diameter, height, number of main stems). By destructive sampling of a series of bushes of variable sizes, we developed multiple regressions for each area to predict standing crops of these shrubs from these measurements. In all cases regressions with high levels of predictability were obtained. These transects had to be sampled only once if we assumed that the standing crop of large stems did not change much from year to year. We could then compute the standing crop in any given year by correcting the biomass estimates by the spring ratios of small twigs to total biomass (these ratios were obtained from the clip plots). Because these spring ratios could be estimated precisely, this gave us biomass estimates of higher precision than we obtained from simple clip-quadrat sampling. The limiting assumption of no change in large twig biomass would be true over a few years but would not hold over the time scale of succession (15+ years).

In all our analyses of bog birch and gray willow, we separated two size classes of twigs. Small twigs are  $<5$  mm in diameter and represent the growth point of the shrubs. These form the main winter food for snowshoe hares, and thus we are particularly interested in the growth dynamics of this size class for these shrubs. Large twigs are  $>5$  mm diameter and are typically not browsed by snowshoe hares or by moose. Some large twigs are girdled each year and otherwise die from natural causes.

### 6.2.2 Impacts of Treatments

The different treatment areas differed considerably in their average standing crop of gray willow and bog birch, as indicated in table 6.1, and these differences were present before any of the treatments were applied to experimental areas. From previous studies (Smith et al. 1988), we had expected the pattern of change in shrub biomass shown in fig-

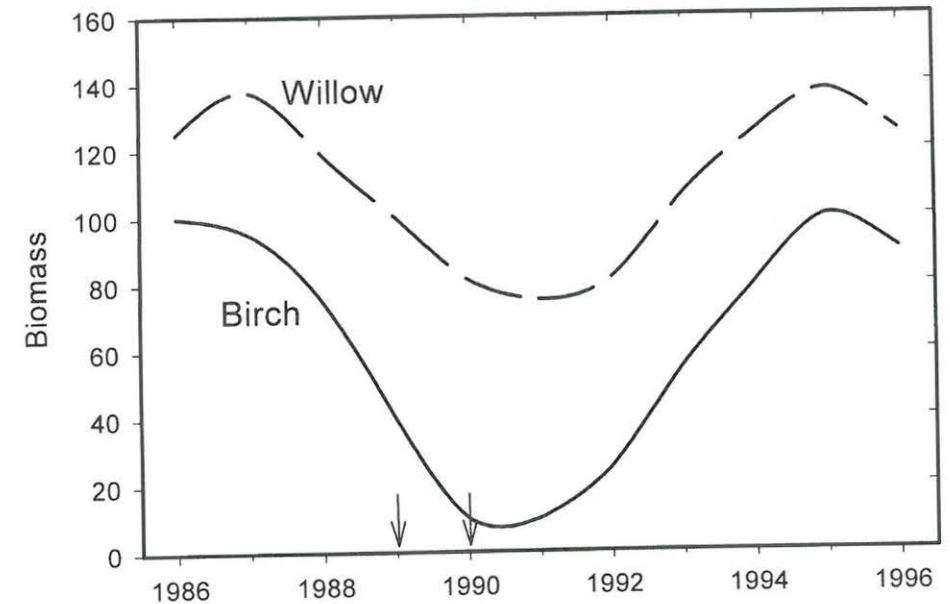


Figure 6.1 The expected pattern of biomass changes in small twigs ( $<5$  mm diameter) of gray willow and bog birch in the Kluane area. Arrows indicate the peak density of snowshoe hares. Snowshoe hares can depress standing crops each winter by browsing, and, because they prefer bog birch over gray willow, we expected the impact to be much greater in bog birch. We also expected a time lag of 1–2 years in the recovery of the vegetation after the hare peak passed.

ure 6.1. Both willow and birch biomass should be depressed by snowshoe hare browsing, and this depression should be more severe in the preferred winter food plant, bog birch (Sinclair and Smith 1984).

Because there was so much variation in average standing crop of shrubs on the different treatment areas, we standardized the shrub biomass data. We used the midpoint of our data (1990) as the standard and calculated all shrub biomass relative to 1990. Figure 6.2 shows the relative standing crop of all shrubs on the two control sites and illustrates a completely unexpected pattern of biomass change. Shrub biomass increased as hare numbers increased, and did not decrease as predicted in figure 6.1. Shrub biomass peaked 2–3 years after hares peaked in abundance, and it appears that snowshoe hares, in fact, stimulated shrub growth as a side effect of their browsing. We had not anticipated that browsing would enhance productivity, as shown in figure 6.2. Note that figure 6.2 includes total shrub above-ground biomass.

Shrub biomass as well as species composition varied greatly among different sites. Figure 6.3 illustrates this for the two major shrub species, gray willow and bog birch, on each of the study sites and emphasizes three important points. First, bog birch was much less abundant overall than gray willow. Only 6.6% of the shrub biomass on all the areas studied was bog birch, and even on sites with the greatest birch abundance, birch reached only 15% of total shrub biomass. Second, the control areas in particular had very little birch

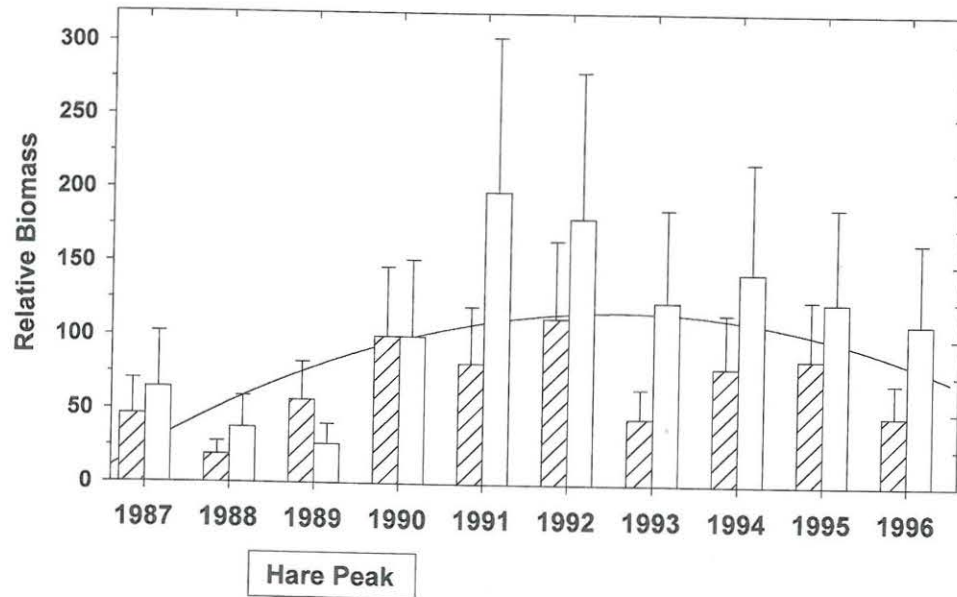


Figure 6.2 Relative biomass of all shrubs combined on two control areas at Kluane, with a second-degree polynomial regression and 95% confidence limits. Biomass peaked in the springs of 1992 and 1993, 3 years after the snowshoe hare peak. Biomass was standardized to spring 1990 = 100% on each area in order to compare them. For control 1, average biomass dry weight per square meter was 173 g, and for control 2 it was 913 g in 1990.

(1.2% of total shrub biomass). On some areas birch was virtually absent and thus cannot be a required food for hares. Third, small twigs made up a small fraction (9.7% on average) of the total standing crop of these shrubs.

Changes in standing crop of small twigs of willow and birch from year to year were highly variable because they were the result of two conflicting pressures: browsing off-take by hares and growth stimulation by hares (figure 6.2). The expected patterns are thus not easy to see in these data. One way to investigate the changes in standing crop is to determine the rate of change of standing crop from one year to the next. We define the rate of change as:

$$\lambda_t = \frac{\text{biomass in May of year } t+1}{\text{biomass in May of year } t}$$

Table 6.4 gives the average values of these rates of change for large and small twigs of willow and birch, and figure 6.4 plots the yearly changes for both species of shrubs.

Two important points emerge from these data. Table 6.4 shows that virtually all of these rates of change were positive, so that both large and small branches of both species were increasing in biomass each year, on average, by about 20–25%. This is a reflection of the pattern shown in figure 6.2 of an increase in biomass over most of the study period. We can decompose this trend for large and small (<5 mm diameter) branches of birch and willow. Figure 6.4 shows that for bog birch the rates of change of small twigs became neg-

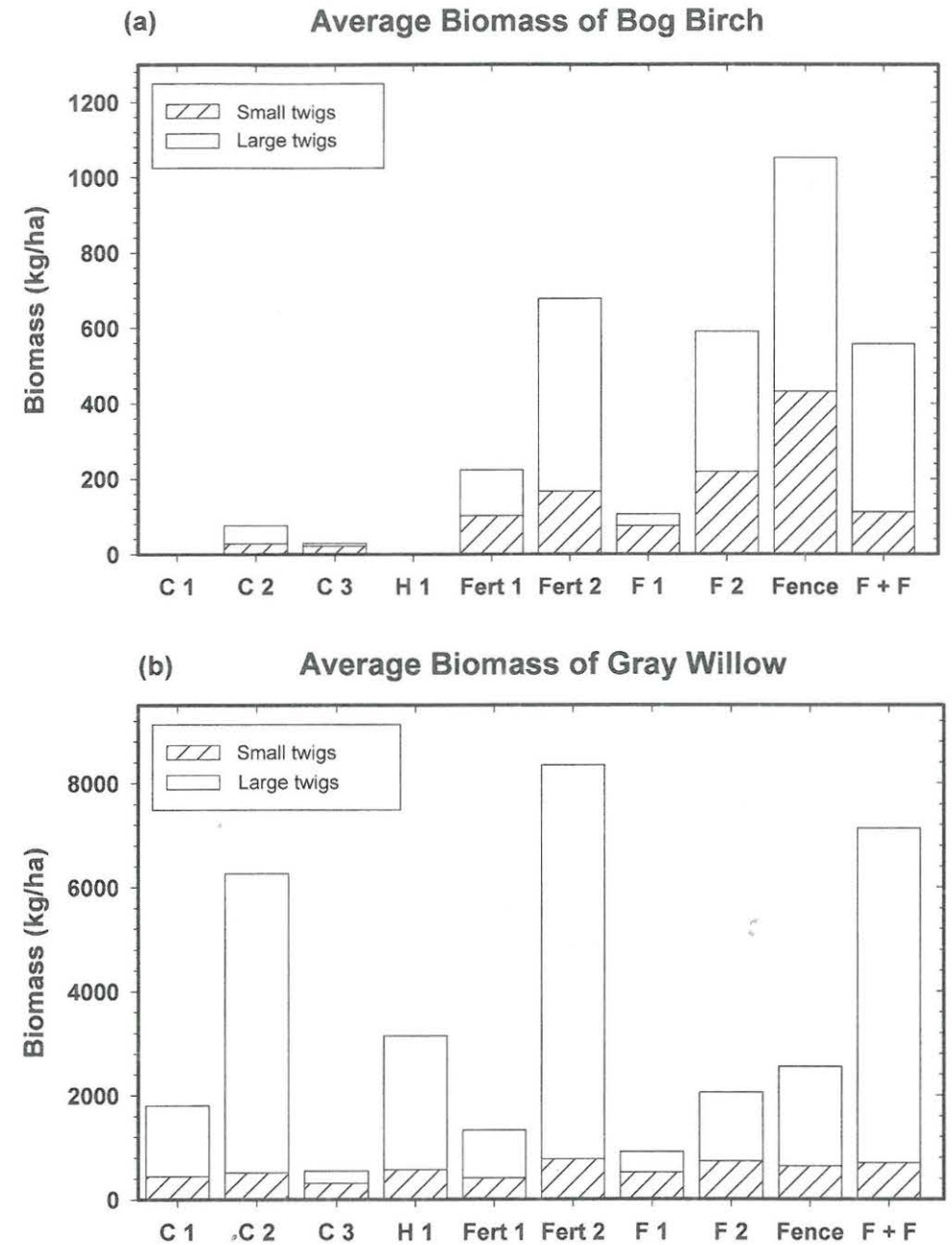


Figure 6.3 Average standing crop at the end of winter for the two major shrub species at Kluane Lake. Small twigs are <5 mm diameter; large twigs are all other above-ground stems. (a) Bog birch; (b) gray willow. C1 = control 1, H1 = hare exclusion 1, fert 1 = fertilizer 1, F1 = food 1, F2 = food 2, F+F = fence + food treatment. Data are averaged over all years.

Table 6.4 Average values of the finite rate of change of biomass per year for bog birch and gray willow for the period 1987–1996.

Treatment	<i>Bog Birch</i>		<i>Gray Willow</i>	
	Small Twigs	Large Branches	Small Twigs	Large Branches
Control 1	0.75 <sup>a</sup>	1.63	1.03	1.41
Control 2	1.48	1.39	1.19	1.32
Hare exclosure 1	—	—	1.10	1.36
Fertilizer 1	1.20	1.48	1.16	1.19
Fertilizer 2	1.07	1.13	1.18	1.32
Fence + food	1.15	1.07	1.37	1.11
Grand mean	1.23	1.27	1.17	1.28

A rate of change of 1.0 indicates no change in biomass from year to year.

<sup>a</sup>Very small samples for birch due to restricted amounts present.

ative on control areas from 1988 through 1993, following the predictions shown in figure 6.1. For willow there is no apparent pattern and no relation to the snowshoe hare peak in 1989–1990. Willow apparently compensated for the average hare browsing pressure, in contrast to the prediction shown in figure 6.1, while bog birch did not.

Two processes combine to produce these effects on shrub biomass. Growth over summer adds biomass to both large and small twigs, and browsing as well as natural deaths cause losses to standing crops in both winter and summer. From the above analysis, we can see that, on average, the growth process seemed to outweigh the loss processes. We now turn to the estimation of these two components.

### 6.3 Growth Rates of Shrubs

In a previous study we developed a new nondestructive method for measuring the growth of individual tagged twigs by photographic means (Krebs et al. 1986). In this more extensive study, the photographic method became too laborious, and we developed a new method of destructive sampling to obtain an index of small twig growth for bog birch and gray willow.

#### 6.3.1 Methods of Estimation

Each autumn, after the leaves had fallen, we collected from each of the study areas a sample of 200 live twigs of both birch and willow. These were frozen until the following May when we had time to measure them. For each twig we clipped off the terminal shoot at a diameter of 5 mm and discarded the larger pieces. We inspected each 5-mm twig for new growth from the previous summer and clipped off all this new growth. New growth was easy to distinguish on the basis of color of bark, the presence of resin glands in birch, and hairs in willow. The index of growth measured for each 5-mm twig was defined as:

$$\text{Growth index} = \frac{\text{dry weight of current annual growth on the 5-mm twig}}{\text{dry weight of the complete 5-mm twig}}$$

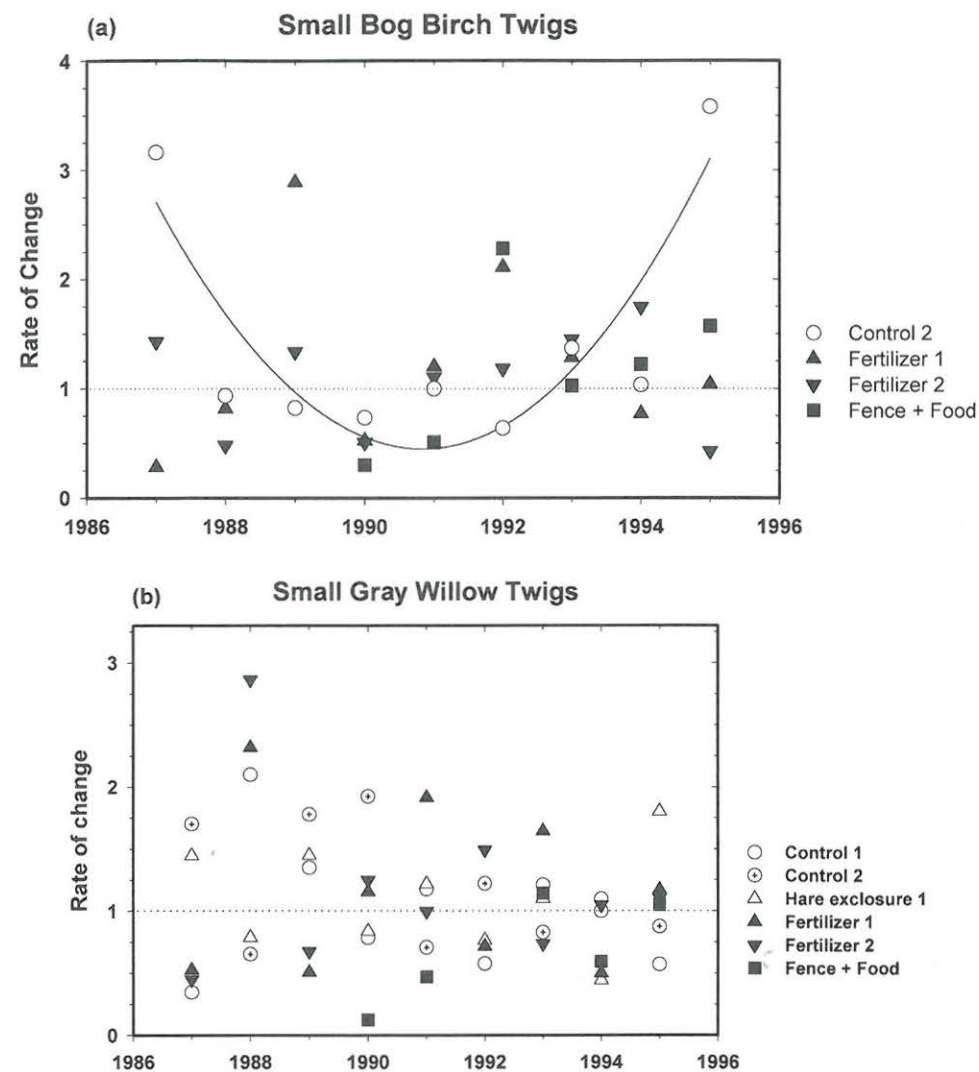


Figure 6.4 Finite rates of change in small-twig biomass of bog birch and gray willow from the various treatment areas. (a) Bog birch. Rates are <1 when hares are abundant. Curve is a second-degree polynomial fitted to control 2 data. (b) Gray willow. No trend is apparent.

and expressed as a percentage. This is not, strictly speaking, a growth rate because the twig itself also increased in diameter during the summer, and we measured only the extension growth component. Nevertheless, the true growth rate of the twig must be equal to or greater than this index of growth. The experimental unit was a single twig, and we did not take more than one twig from a single bush when we collected them in the autumn. We could have collected these twigs in spring instead of autumn, but we wanted to sample them before the snowshoe hares had removed their winter browse. All growth estimates were made on the basis of dry weights. We did not record any direct measure of large branch growth rates for shrubs.

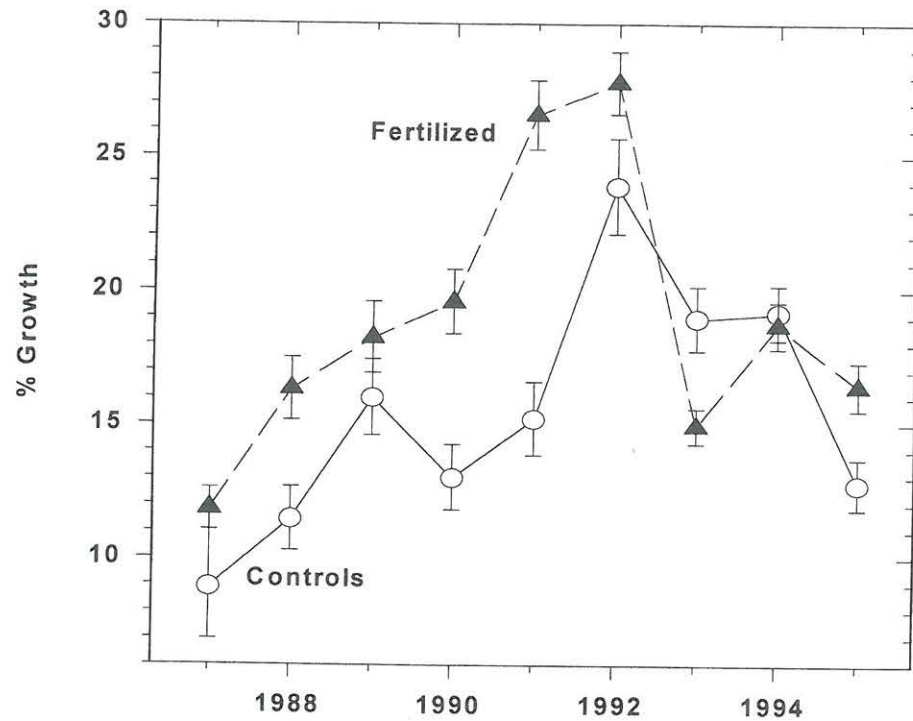


Figure 6.5 Growth rates of terminal branches of 5-mm twigs of bog birch on control and fertilized areas from 1987 growth year to 1995 growth year. Error bars indicate 95% confidence limits for each estimate. Snowshoe hares reached a peak in 1989 and 1990.

### 6.3.2 Impacts of Treatments

**Bog Birch** Areas with small amounts of bog birch became impossible to sample once hares became abundant because they ate almost all the available birch. Consequently, we do not have samples of birch from all treatments in all years. There was a strong cycle in bog birch growth rates, with peak growth occurring 1 or 2 years after the hare peak had passed (figure 6.5). This cycle in growth was evident on both the fertilized areas and on the control areas. On average, over the entire study, fertilized birch twigs showed a 26% higher growth index (20.5%) than unfertilized twigs (16.2%). This difference masks 2 years (1993, 1994) in which fertilized growth rates were at or below control growth rates during the low of the hare cycle. Growth rates of birch on the fenced grid were no different from those on the controls, but the other treatments affected growth rates in unexpected ways. The fence + food treatment had the highest growth of 5-mm birch twigs (25.2% per year), a rate 55% above the controls. In contrast, the food 1 grid showed reduced birch growth (12.1% per year), only 74% that of the controls. The hare enclosure + fertilizer treatment showed birch growth equal to the fertilized plots (20.4%), so that there was no evidence that excluding hares from this plot either increased or decreased birch growth over that expected on fertilization alone. These results are summarized in figure 6.6.

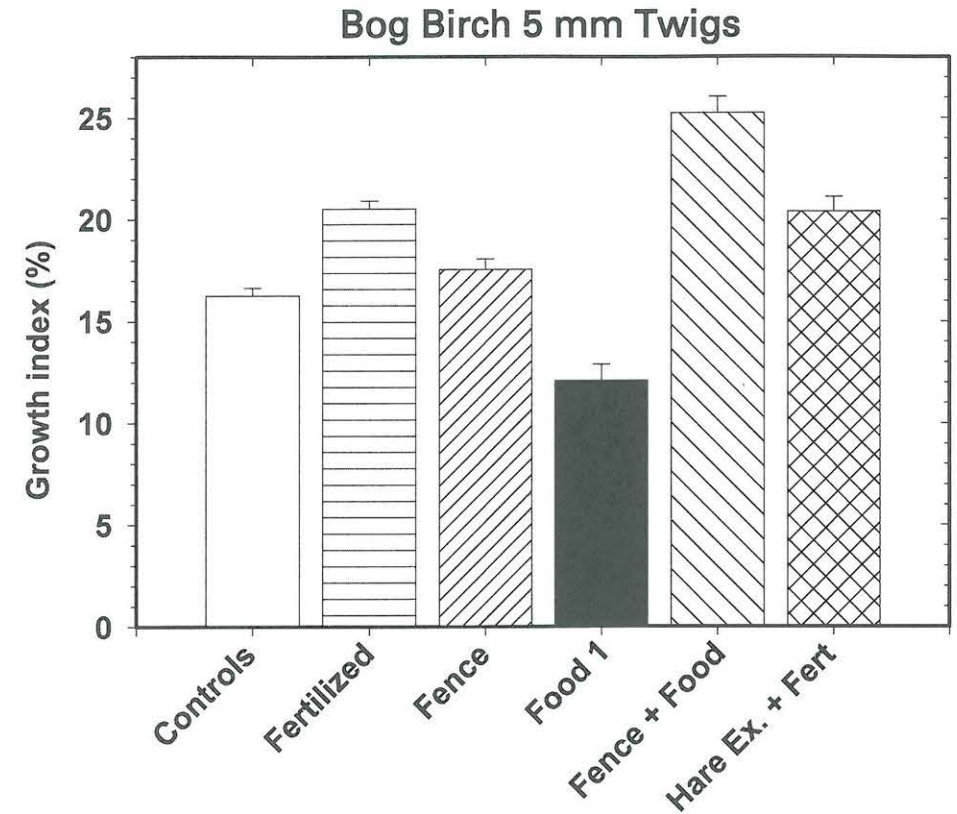


Figure 6.6 Average growth indices for 5-mm bog birch twigs for the various treatments, with 95% confidence limits. Averages were taken over 1987–1995 growth years.

**Gray Willow** Gray willow is the most common shrub in the Kluane region, so there was never any difficulty obtaining samples of 5-mm twigs for estimating summer growth rates. There was a strong cycle in willow growth rates on the fertilized grids, with peak growth occurring 1 or 2 years after the hare peak had passed (figure 6.7). This cycle in growth was not evident on the control areas, which showed a nearly linear trend toward lower growth rates with time. On average, over the entire study, fertilized willow twigs showed a 30% higher growth index (20.0%) than unfertilized willow twigs (15.4%). Growth rates of willow on the fenced grid were no different from those on the controls, but the other treatments affected growth rates in unexpected ways. The fence + food treatment had the highest growth of 5-mm willow twigs (23.2% per year), a rate 51% above the controls. The food 1 grid also showed increased willow growth (22.7% per year), 48% above that of the controls. The hare enclosure + fertilizer treatment showed willow growth equal to the fertilized plots (20.2%), so that there was no evidence that excluding hares from this plot either increased or decreased willow growth over that expected from fertilization alone. These results are summarized in figure 6.8. The patterns shown by birch and willow are identical except for the food 1 grid, which had decreased birch growth but increased willow growth.

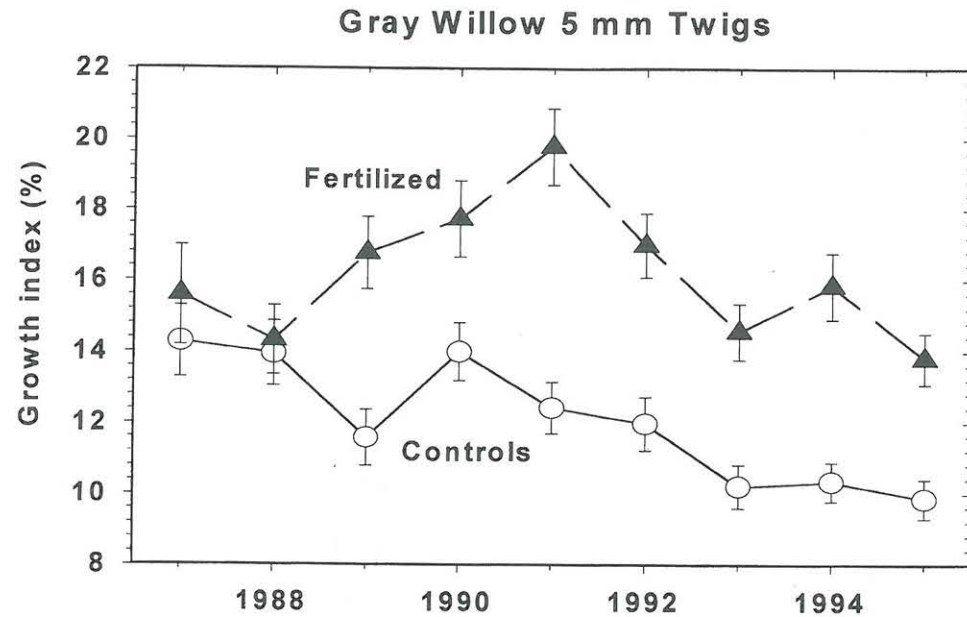


Figure 6.7 Growth rates of terminal branches of 5-mm twigs of gray willow on control and fertilized areas from 1987 to 1995 growth years. Error bars indicate 95% confidence limits for each estimate.

We interpret these effects as fertilization effects. Adding rabbit chow to the food grids also adds nutrients, either directly by the breakdown of uneaten chow or indirectly by the urine and feces of hares at high density. The amount of growth increase achieved by fertilization seems to be nearly the maximum that can be obtained for this ecosystem, and adding more fertilizer would have achieved little gain.

#### 6.4 Losses of Twigs to Browsing and Natural Mortality

The demography of 5-mm twigs from willow and birch shrubs is affected by two principal sources of loss: browsing by snowshoe hares and natural mortality. Browsing by hares leaves a characteristic angular cut from the chisel teeth, but other forms of loss are more vague, and consequently natural mortality in our terminology includes all forms of death not caused by browsing. Moose browsing could be identified, but moose were so rare on our study areas that moose browsing was never more than a trace source of loss. In this section we discuss how the sources of loss changed over the years of the study and how they were affected by the snowshoe hare cycle.

##### 6.4.1 Methods of Estimation

We determined the fate of 5-mm twigs by tagging 400 twigs from different bushes on each of 9 study areas. We studied both birch and willow on all areas except for food 2 and

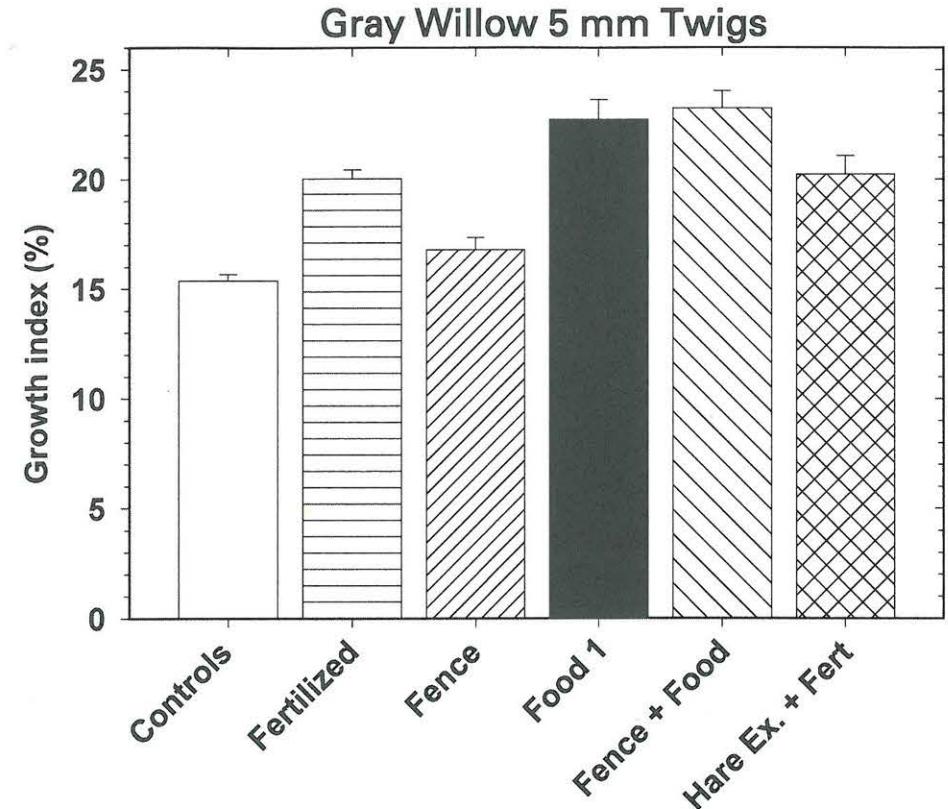


Figure 6.8 Average growth indices for 5-mm gray willow twigs from the various treatments, with 95% confidence limits. Averages were taken over the 1987–1995 growth years.

control 3. Each May we inspected each twig and classified it as intact, completely browsed by hare or moose, partially browsed, natural mortality, or accidental mortality (caused by our tagging or bending) (CD-ROM frame 47). Partial browsing removed part but not all of the live buds on the 5-mm twig, and we did not attempt to estimate the fraction removed in this study (as we did in previous work; see Smith et al. 1988). As twigs grew, we moved the aluminum numbered tags to keep each twig approximately 5 mm in diameter. Virtually all the browsing of willow and birch twigs occurs in the winter months between September and May, and we assumed all losses of twigs to be winter losses. On some areas birch was much less abundant than willow, and our sample sizes deviated from 200 of each species.

##### 6.4.2 Impacts of Treatments

**Bog Birch** Hares prefer to eat bog birch in winter, and consequently the browsing pressure on this shrub is intense in the Kluane region. Table 6.5 gives the percentages of birch twigs that were completely browsed by hares on the different areas during this cycle. Loss



Table 6.5 Percentage of 5-mm terminal twigs of bog birch (*Betula glandulosa*) browsed by snowshoe hares each winter.

Grid	Percentage Completely Browsed									
	1986-87	1987-88	1988-89	1989-90	1990-91	1991-92	1992-93	1993-94	1994-95	1995-96
Control 1	0	6	77	67	71	3	0	0	0	21
Control 2	0	6	41	79	91	43	1	0	3	4
Fertilizer 1	0	5	41	74	67	0	0	0	0	2
Fertilizer 2	0	2	31	46	58	9	1	1	4	1
Food 1	0	9	24	59	57	4	0	1	1	2
Fence	0	2	20	28	52	10	0	2	0	2
Fence + food	0	?	?	83	88	25	5	0	1	3
Hare enclosure 2 <sup>a</sup>	0	0	34	5	0	0	0	0	0	1
Total controls	0.0	6.0	55.6	76.9	85.7	33.0	0.9	0.1	2.1	8.5
Total fertilized	0.0	3.5	37.0	62.9	61.7	5.4	0.7	0.6	2.6	1.1

<sup>a</sup>This grid should have no browsing by hares if the enclosure is perfectly operational.

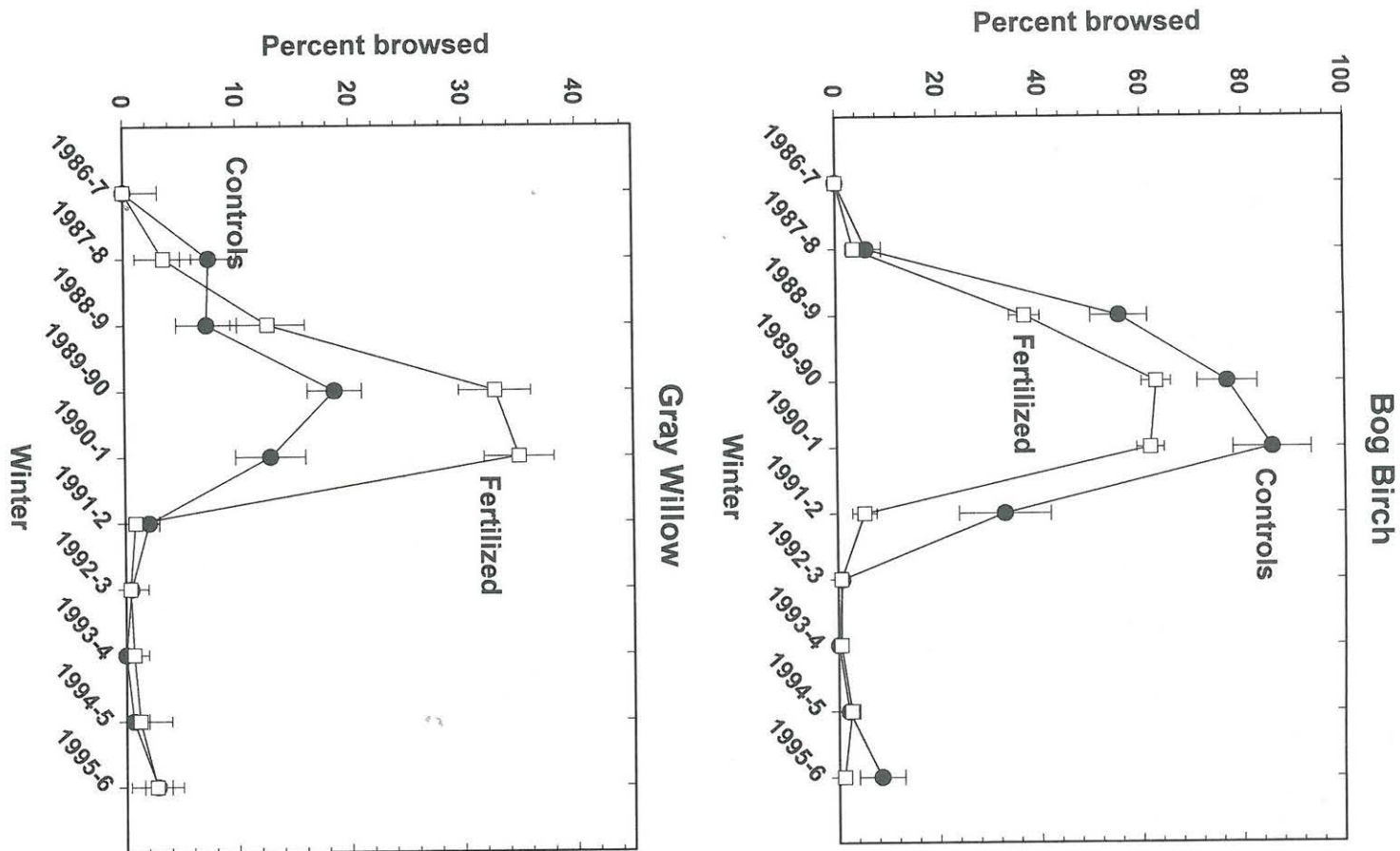


Figure 6.9 Percentage of 5-mm terminal twigs of bog birch and gray willow that were completely browsed by snowshoe hares over winter on control and fertilized areas. Two control areas and two fertilized areas are combined. Sample sizes were approximately 400 for each point. Error bars indicate 95% confidence limits.

rates due to browsing increase to 80–90% in the peak winters. Birch is not completely eliminated in this community, at least partly because of protection from snow. Once birch is buried by snow, hares do not have access to it until spring. Birch also grows well in large, open areas where hares do not often venture. Figure 6.9 shows that fertilized birch twigs were browsed at a slightly lower rate than control birch twigs, but these differences were not statistically significant. The browse rate for birch was high on the fence + food grid, which had many more hares than the controls.

In addition to complete browsing of tagged twigs, we recorded partial browsing in which the twig retained some growth buds. Partial browsing varied in tandem with complete browsing, and in the years of maximum browsing an additional 17–19% of birch twigs were partially browsed. In the 2 peak years of the hare cycle, this means that virtually every live bog birch twig had some browsing damage.

Natural mortality of small twigs also occurred, but it was always low in comparison to browsing offtake. On average, 3.3% of 5-mm birch twigs died from natural causes each winter. There was considerable variation from year to year (range 0–20%), but this variation was not associated with any particular treatment or year. In comparison with losses due to snowshoe hare browsing, natural twig deaths were relatively rare events, only about one-tenth as frequent as browsing losses.

*Gray Willow* Gray willow was browsed at much lower rates than bog birch (table 6.6). Only on the fence + food grid with very high hare densities in 1990–1991 did the rate of complete browsing exceed 50% of the marked twigs removed in one winter. On average, about 20–30% browsing of willow twigs occurred in the peak phase. Willow utilization seemed particularly low on the control areas, with less than 20% removal at the maximum.

In addition to complete browsing of tagged twigs, we recorded partial browsing in which the twig retained some growth buds. Partial browsing varied in proportion to complete browsing, and in the years of maximum browsing, an additional 8–9% of willow twigs were partially browsed.

Natural mortality of small willow twigs also occurred. On average, 6.3% of 5-mm willow twigs died from natural causes each winter. There was considerable variation from year to year (range 0–20%), but this variation was not associated with any particular treatment or year. For gray willow the losses due to snowshoe hare browsing are, on average, almost the same as natural twig deaths. Averaged over 10 years, the probability of loss per year for a 5-mm willow twig is about 5–6% for browsing and 5–6% for natural mortality.

## 6.5 What Limits Primary Production of Shrubs?

In the broad sense, primary production in the boreal forest is limited by temperature, soil nutrients, and browsing. In this section we discuss how nutrients and browsing interact, within the confines set by temperature, to alter primary production of shrubs, particularly gray willow and bog birch in the Kluane region.

### 6.5.1 Succession in Boreal Forest Shrubs

Bog birch and gray willow are present from the earliest successional stages after fire in the Kluane region of the boreal forest. They presumably reach their peak biomass in

Table 6.6 Percentage of 5-mm terminal twigs of gray willow (*Salix glauca*) browsed by snowshoe hares each winter.

Grid	Percentage Completely Browsed									
	1986–87	1987–88	1988–89	1989–90	1990–91	1991–92	1992–93	1993–94	1994–95	1995–96
Control 1	0	14	9	18	17	1	1	0	1	4
Control 2	0	1	4	15	8	3	0	0	1	1
Fertilizer 1	0	3	14	41	47	1	1	0	2	2
Fertilizer 2	0	5	10	19	20	1	0	1	1	4
Food 1	0	5	22	41	47	6	0	0	6	10
Fence	0	7	4	22	11	7	1	0	0	2
Fence + food	0	?	?	47	63	16	3	0	2	3
Hare enclosure 1 <sup>a</sup>	0	1	1	0	0	0	0	0	0	0
Total controls	0.0	7.5	7.3	18.6	12.9	2.1	0.5	0.0	0.6	2.8
Total fertilized	0.0	3.5	12.7	32.8	34.9	0.9	0.4	0.7	1.2	2.7

<sup>a</sup>This grid should have no browsing by hares if the enclosure is perfectly operational.

the early tree stage of succession, and once the forest begins to close canopy they begin to lose out, possibly to root competition by white spruce. In late successional stages mosses may dominate the forest floor and, in these stands, willow and birch are much reduced in abundance. Because the time frame of succession is so long, no one has made any direct observations on these trends. Competition for water would appear to be of minor importance in the Kluane boreal forest area, since there is typically sufficient summer rain as well as snow melt to replenish soil water. Competition for light would also seem to be minimal in most stages of succession except for the latest ones, and presumably the relative abundance of shrubs reflects more the balance between competitive ability for soil nutrients and browsing pressure by herbivores.

The addition of fertilizer increased the growth rate of birch and willow 25–30% each year. There was no indication of any differential effect on these two species, at least in biomass growth. We do not know the long-term consequences of fertilization, but it was clear that in 10 years only small changes occurred in the shrub community, in contrast to the herb community (see chapter 5). Browsing seemed to produce many more dramatic impacts than nutrient addition in this slow system.

### 6.5.2 Impact of Hare and Moose Browsing

By far the strongest pressure on the shrubs at Kluane is browsing, and almost all the browsing is done by snowshoe hares; moose are relatively rare. Snowshoe hares prefer bog birch to gray willow and gray willow to all the other shrubs. This preference for birch is, we think, the reason for the low relative abundance of birch in the forests of Kluane. Birch in the entire valley is only about one-tenth as abundant as willow. If hares could be excluded from an area, we think birch would be much more common. We did, however, see no sign of a birch resurgence on the hare exclosure plots, and we think this reflects the slow rate of change in the boreal forest ecosystem. (We had only one hare exclosure + fertilization treatment [4 ha] that had a very dense stand of birch. Unfortunately, we did not have a measurement of birch before setting up the treatment, nor were we doing clip plots to estimate the biomass of shrubs inside this plot during our study.)

Moose browsing on Isle Royale, Michigan, has been shown to have a strong impact on both tree and shrub communities. These impacts could be measured by comparing fenced and unfenced plots 40 years after they were set up (Pastor et al. 1988, McInnes et al. 1992). Snowshoe hares were able to enter the fenced plots in Michigan, but they were never the dominant browser in this system. Shrub biomass was lower in these fenced plots, presumably because of tree competition, and trees increased about 50% in biomass inside the moose exclosures after 40 years. Shrub biomass in our Kluane plots averaged 6250 kg/ha dry weight, about twice the average biomass of the Michigan plots, which had a completely different suite of species. We would guess from these results in the southern boreal zone that exclosures for Kluane hares would have to operate for at least 50 years to measure similar kinds of effects, if they would occur.

Although hare browsing exerts a dominant effect on bog birch, we were unable to see strong impacts on gray willow. There is considerable browsing on willow at the hare peak, but the large biomass of willow (95% of the shrub biomass is gray willow) reduces the impact of the hare browsing. Willow shrubs also seem to suffer more natural losses of

branches, and in this sense may be preadapted to an approximately equivalent amount of loss from browsing.

One of the most striking results of our studies on the shrub community at Kluane has been the finding that hare browsing seems to stimulate shrub production. We presume that this occurs either through nutrient recycling with a time lag of 2–3 years after the hares peak in abundance or as a physiological response of the shrubs to browsing itself. This stimulation effect is shown clearly in the fence + food treatment, which had the highest observed growth rates for both willow and birch twigs in spite of having no direct nutrient addition as fertilizer. The high densities of hares on this grid (see chapter 8) explain the growth stimulation. These results resemble the findings of McNaughton (1985), who showed that grazing in the Serengeti increased primary production.

### 6.5.3 Role of Secondary Chemicals

Secondary compounds appear to be responding directly to the influence of browsing by hares—the heavier the browsing, the higher the values of crude methanol extract. However, where browsing was extremely high in the fence + food treatment, secondary compounds were inhibited, much as the shrub growth was depressed. Thus, regrowth appears to be a compensatory response to browsing, and the secondary compounds appear to be a possible deterrent to further browsing. There is experimental evidence that such extracts do inhibit both feeding behavior and digestive abilities (Sinclair et al. 1982, 1988; Rodgers and Sinclair 1997). This effect is most apparent in bog birch and less so in gray willow. Because bog birch is the preferred species of winter food for hares, chemical defense is perhaps of higher value to this plant.

Fertilizer had the effect of reducing the secondary compounds in both species, although the effect was not large. The result is consistent with hypotheses proposing that secondary compounds may function to protect nutrients that are hard for plants to obtain (Coley et al. 1985), where nutrients are provided, there is less stimulus for the plants to produce secondary compounds to defend the nutrients.

## 6.6 Summary

Because snowshoe hare browsing can be severe at the peak of the hare cycle, we had expected shrub biomass to decline as hares increased. In contrast, we found that total shrub biomass increased with increased browsing, so that over the 10 years of study there was a net increase in shrub biomass. Browsing by hares seemed to stimulate primary production of shrubs in this system. The spatial pattern of shrub-dominated areas also recovered quickly after the snowshoe hare peak.

Hares prefer to eat bog birch in winter, and browsing rates reached 80–90% in the peak winters of 1989–1990 and 1990–1991. Biomass of small birch twigs decreased as hares increased, but the same pattern was not seen in small willow twigs. Browsing on gray willow twigs was always much less than browsing on birch and reached peaks of 20–40% on most areas. Bog birch would not exist in forested sites at Kluane if it was not protected by snow cover for much of the winter, and we suggest that hare browsing is responsible for the relatively low abundance of birch in the Kluane region.

Fertilization increased the growth rates of all the shrubs by about 25–30% over control values. Fertilized willow twigs were eaten at a higher rate than control twigs, but the opposite tendency was shown by bog birch.

Excluding hares from areas had little impact on any of our measures of biomass or growth in willow or birch, and we think that processes in the Kluane ecosystem are too slow to show impacts in less than 50 years of hare exclusion.

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