SEASONAL CHANGES IN CRUDE PROTEIN AND LIGNIN OF TEN COMMON FORAGE SPECIES OF MOOSE IN NORTH-CENTRAL BRITISH COLUMBIA

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Abstract: Monthly levels of crude protein and lignin were determined for current annual growth of nine woody plants and whole plant samples of one lichen, from May 1972 to April 1973. Crude protein averaged 6.7% for the nine woody species over the year. All these species had a similar annual pattern for protein: levels jumped sharply to peaks of about 14-16% in May and June, declined gradually until October, and remained unchanged at 4-6% until the following spring. Generally, protein levels in leaves were 1.5 to 3 times those in current twigs. Crude protein content in the lichen, *Lobaria pulmonaria*, remained relatively constant through the year at about 12%. Lignin averaged 9.8% in five of the woody species over the year. Annual means varied between species, with *Sorbus* spp. having the lowest, and *Salix* spp. and *Betula papyrifera*, the highest lignin contents. The annual pattern of lignin showed a decline to a mid-summer minimum and then increase until October, after which levels remained steady.

The forested habitats of moose (*Alces alces*) in central British Columbia are increasingly being modified by changing forest practices. Over the past 20 years, harvesting has gone from selective cutting to clearcutting; cut blocks have increased in size; the rate of cut has accelerated; and wildfires have been largely controlled. Thus the future habitats of moose will differ considerably from natural ranges.

With these changes, the wildlife manager faces two important questions. First, how will these modifications affect moose habitat and second, how can these activities be altered either to reduce adverse impacts or to enhance habitat. Answers to these questions depend upon an adequate knowledge of habitat needs of moose. The present paper is part of a general study (Eastman 1977) designed to help provide that understanding. It focused on levels of crude protein and lignin in moose forages, and had the following objectives:

1) to provide a basic nutritional description of forage, including both species and seasonal differences, and
2) to determine if habitat, stand age, and substrate affected levels of these components.

STUDY AREAS

Field work was conducted on the following three important moose winter ranges in north-central British Columbia near Prince George, 525 km north of Vancouver: Eagle, Grove, and Salmon. All areas occur in the sub-boreal spruce biogeoclimatic zone (Krajina 1959; Revel 1972), within an elevational range of 750 ± 75m. Climatically, the areas have cold, snowy winters with an abrupt transition to short, cool summers. The mean annual temperature at Prince George is 3.3°C; the average precipitation is 621 mm, of which 63% is rain.

The Eagle winter range occupies 390 km^2, approximately 40 km northeast of Prince George. Lying between 590-950 m, it has soils derived from mostly silty and clayey lacustrine deposits. The vegetation is about one-third forested with white spruce (Picea glauca) and subalpine fir (Abies lasiocarpa), one-quarter burned over from fires in 1932 and 1937, with the remainder covered by various kinds of post-logging vegetation.

The Grove study area occupies approximately 450 km^2, situated 30 km east of Prince George. Unlike Eagle, this study area lies mostly above the upper limit of lacustrine deposits (790 m). Thus soils are derived from till except the soils of the northern one-quarter that are clays and silts. Vegetative cover is about three-quarters seral willow and birch, resulting from a 320 km^2 fire in 1961 that burned through logging slash and some mature timber. The remaining vegetation consists of pine-spruce-fir forests along the northern and eastern boundaries of the study area.

The Salmon winter range covers about 300 km^2 between 610-780 m, approximately 30 km north of Prince George. Straddling the Salmon River, this winter range is more heterogenous than the other two from a soils and landform perspective, with recent alluvium, beach ridges, lacustrine deposits and glacial till all present. Vegetation is also quite diverse, with various successional stages of spruce-cottonwood along the river; aspen and mixed forests at the southeastern end, resulting from a fire about 75 years ago; pine and pine-spruce stands in the northeast; and cutovers and cleared fields dotted in the northern and southern ends of the study area, respectively.

METHODS

Based on the winter diet of moose in the area (Eastman 1977), ten species were selected for analysis: subalpine fir (Abies lasiocarpa), paper birch (Betula papyrifera), red-osier dogwood (Cornus sericea), trembling aspen (Populus tremuloides), willow (Salix spp.), mountain ash (Sorbus spp.), saskatoon (Amelanchier alnifolia), black cottonwood (Populus balsamifera), mountain bilberry (Vaccinium membranaceum), and lungwort (Lobaria pulmonaria). Protein levels were determined for all ten species and lignin levels were determined for the first six.

Forage samples were collected monthly from April 1972 to April 1973, at 15 sites within the three study areas. Species sampled at each site are listed in Table 1. Site features were determined from historical records, on-site vegetation sampling, and soil maps (see Eastman 1977 for details). Each sample of 200-500 g wet-weight, consisted of current annual growth clipped at the previous bud scale scar from ten or more plants per species. Since current production of lungwort was not easily distinguishable, these samples consisted of material torn from branches, avoiding the tree's bark and other lichens.

Samples were oven-dried at 50°C for 24 h. Drying at higher temperatures than this may increase lignin artificially (Goering and Van Soest 1967). All dried plant samples were ground first in a hammer mill, and then in a Wiley mill equipped with a 1 mm mesh stainless steel screen. Subsequently, this coarsely ground material was mixed thoroughly. A sub-sample was withdrawn, ground in a Wiley mill with a 40 mesh screen, and stored in a plastic bag until analysis.

Table 1. Study area, habitat, substrate, and species collected for analysis of crude protein and lignin in central British Columbia, April 1972 - April 1973.

STUDY AREAS Site	Habitat(age)	Substrate	Species collected
EAGLE			
E1	birch forest(40)	lacustrine	saskatoon, birch, dogwood, willow, ash, bilberry
E2	shrub sere(40)	lacustrine	saskatoon, birch, dogwood, aspen, willow, ash
E3	spruce-subalpine fir forest(100)	lacustrine	subalpine fir, lungwort
E4	spruce-subalpine fir forest(250)	lacustrine	subalpine fir
GROVE			
B1	shrub sere(12)	till	birch, aspen, cottonwood, willow
B2	lodgepole pine forest(50)	till	willow
B3	lodgepole pine forest(50)	till	birch, willow
G1	shrub sere(12)	till	birch, cottonwood, willow
G2	shrub sere(12)	lacustrine	birch, aspen, willow
G3	lodgepole pine forest(120)	till	subalpine fir, cottonwood
G4	spruce-subalpine fir forest(200)	lacustrine	subalpine fir, dogwood, lungwort
SALMON			
S1	spruce-cottonwood forest	recent alluvium	dogwood
S2	mixed wood forest	beach deposits	birch, willow
S3	aspen forest	beach deposits	willow
S5	lodgepole pine forest(120)	till	subalpine fir, willow

Lignin content was estimated by the acetyl bromide technique (Johnson et al. 1964; Morrison 1972a,b). The former authors described lignin determinations for woody tissues, while the latter related lignin determination to digestibilities for grasses and legumes. I assumed a similarly reliable correlation between lignin content in woody plants and their digestibility by moose. Lignin levels are inversely related to digestibility (Maynard and Loosli 1969).

Nitrogen was determined by semi-micro Kjeldahl analysis and converted to crude protein by multiplying by 6.25. The precision of analyses was checked by duplicate determinations of crude protein of approximately every tenth sample for subalpine fir (n = 4), red-osier dogwood (n = 4), trembling aspen (n = 4), cottonwood (n = 3), willow (n = 10), and mountain ash (n = 1). The mean difference between duplicate determinations was 0.25 ± 0.23 percent crude protein (n = 26).

To examine the effects of site factors on crude protein and lignin, I compared species growing on adjacent sites that differed only in the factor being examined. For example on the Grove winter range area, burned in 1961, paper birch grew both on till and neighbouring lacustrine substrates. Comparing samples collected from both substrates allowed their effect on both constituents to be examined.

RESULTS

Crude Protein

For all the woody species the average, year-round (May 1972-April 1973) level of crude protein level was 6.7 %, (Table 2). Annual means varied between species. Mountain bilberry and saskatoon had the highest mean annual levels of 8.3% and 8.1% crude protein, respectively, followed by trembling aspen and paper birch at about 7.5%. Black cottonwood ranked lowest in value at 6.5%. Thus the main food species of moose--paper birch, red-osier dogwood, subalpine fir, and willow--had intermediate levels of crude protein.

All browse species showed similar annual variations in crude protein with peak levels in May or June, and a gradual decline over the summer (Fig. 1). After leaf fall in October, all species had low crude protein levels that remained nearly constant throughout the winter. Minor fluctuations recorded between October and April likely reflected variations in experimental error than changes in the plants.

Peak protein levels varied between species and were reached in different months presumably reflecting species-specific differences in phenology (Fig. 1). Paper birch and red-osier dogwood attained in May, the highest recorded levels of 15.2 % and 16.6% crude protein, respectively. Other browse species had generally lower peaks, ranging from 11.1% to 12.7%, that were reached in June.

Increased protein content in summer browse was due to high levels in both the leaves and the stems (Table 3). Combining all data for willows revealed that in twigs crude protein increased from approximately 5.3% in late winter to almost 8% by mid-July, then declined by early fall to winter levels (Table 3). Protein levels in leaves were usually 1.5 to 3 times their corresponding twig levels: content appeared to be high in early leaf development rising to a peak probably in July, and then tapered off until leaf fall in September or early October. Paper birch, red-osier dogwood, and trembling aspen showed similar patterns (Table 3).

Table 2. Crude protein and lignin levels in major moose forages in central British Columbia, averaged over the annual cycle of May 1972-April 1973.

Species	Mean percent content ± SD(N)	
	crude protein	lignin
Subalpine fir	7.1 ± 1.7 (49)	9.4 ± 1.5 (22)
Saskatoon	8.1 ± 3.1 (4)	
Paper birch	7.4 ± 3.2 (36)	10.0 ± 1.3 (50)
Red-osier dogwood	6.9 ± 3.2 (34)	8.5 ± 2.3 (19)
Lungwort	11.9 ± 1.4 (9)	
Trembling aspen	7.5 ± 2.3 (20)	8.8 ± 0.7 (9)
Black cottonwood	6.5 ± 2.7 (19)	
Willow	6.7 ± 2.3 (90)	10.5 ± 2.1 (44)
Mountain ash	6.9 ± 2.5 (13)	8.6 ± 2.0 (4)
Mountain bilberry	8.3 ± 4.1 (2)	
Weighted mean (except lungwort)*	6.7 (267)	9.8 (148)

* All species mean for crude protein = 7.1 (276).

Table 3. Crude protein and lignin levels(%) in the current year's stems (S) and leaves (L) of selected browse species from central British Columbia, 1972.

Species sampled (N)	June		July		August		Sept.	
	S	L	S	L	S	L	S	L
CRUDE PROTEIN								
Subalpine fir (5)							5.6	7.8
Paper birch (1-4)	10.1	16.1	9.0	14.6	4.3	14.0	4.7	7.8
Red-osier dogwood (1-4)	9.8	16.9			4.0	11.8	4.4	8.3
Trembling aspen (1-2)			8.1	13.4	5.7	11.9	5.9	9.5
Black cottonwood (2)								
Willow (1-9)	7.6	12.5	7.8	13.7	4.1	11.8	5.0	8.3
LIGNIN								
Subalpine fir (3)								
Paper birch (2-4)	11.5	7.6	9.7	7.9	10.5	7.8	10.2	7.1
Red-osier dogwood (1-2)	5.2	4.0			8.1	5.5	10.2	4.1
Trembling aspen (1)								
Willow (1-7)	8.6	6.7	13.0	5.6	10.2	6.0	10.0	7.1

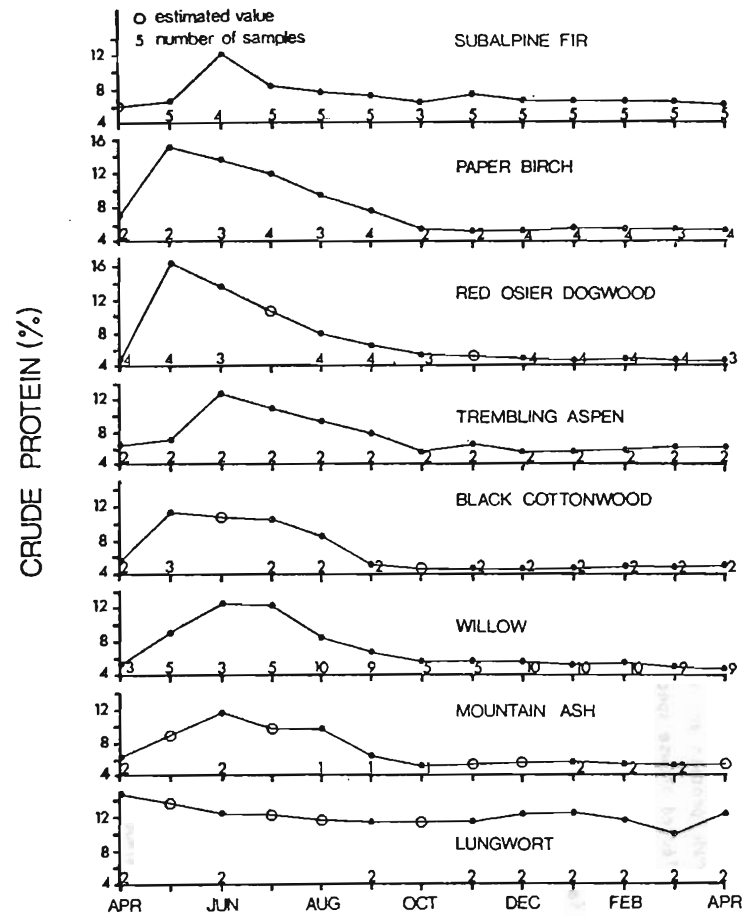

Figure 1. Annual pattern of crude protein in eight moose forages from central British Columbia, April 1972 - April 1973.

Protein levels in lungwort differed from those of the foregoing woody species. The average annual level and monthly levels were higher than all other species, except for the months of May, June and possibly July (Table 2). Also, lungwort did not show the annual pattern typical of browse species, similar to the lichen Alectoria sarmentosa (Rochelle 1980).

As well as differences between species, plant protein levels within species were modified by environmental factors. Substrate modified protein in paper birch (but not in willow) at the Grove Burn where plants on the lacustrine substrate generally had higher protein and higher lignin than plants on the till substrate (Table 4). The age of a stand also modified levels of crude protein, at least for subalpine fir (Fig. 2). Since age of stand is a surrogate for several factors that likely affect crude protein content, properly designed experiments are needed to clarify their interactions.

However, habitat type (on the same substrates) did not affect protein content for the species tested. For example, on the same substrate, at the same elevation and exposure, and originating from the same wild fire, shrubs in different habitats showed similar crude protein levels (Table 5).

Species growing at the same site differed in crude protein levels (Fig. 3). These differences were analyzed graphically by comparing annual cycles of species collected at the same site. Differences between species were not constant throughout an annual cycle, with differences in summer protein levels generally less than those in winter (Fig 3). Limited data suggested that differences between some species were consistent, whatever the habitat. At all three sites

Table 4. Comparison of protein and lignin contents of willow and paper birch collected on till and lacustrine substrates from the burn habitat at the Grove study area in central British Columbia, 1972-73.

Month	Willow protein(%) till	Willow protein(%) lacustrine	Willow lignin(%) till	Willow lignin(%) lacustrine	Paper birch protein(%) till	Paper birch protein(%) lacustrine	Paper birch lignin(%) till	Paper birch lignin(%) lacustrine
May	12.1	6.0		13.1				
June	11.1	10.1						
August	8.4	7.6						
September	6.1	7.2						
November	5.4	5.7	11.4	10.5	5.0	5.9	10.2	10.9
December	5.4	6.0			5.0		10.9	11.5
January	5.0	5.8	11.1	13.1	5.2	5.7	11.0	10.6
February	4.9	4.6			5.2	6.3	8.9	10.7
March	5.6	5.3	11.8	10.2		6.5		10.5
April	5.0	5.0	12.4	11.6	4.6	6.6	8.9	10.7
Mean*	6.9	6.3	11.7	11.3	5.0	6.1**	10.0	10.9**
SD	2.7	1.6	0.6	1.3	0.3	0.4	1.0	0.4

*Based only on those months with paired data.

**Significantly different at the 95 percent and 90 percent probability levels, respectively.

Table 5. Effect of habitat type on crude protein levels in selected browse species at the Eagle and Salmon study areas in central British Columbia, 1972-73.

STUDY AREA Species	Habitat ($\bar{x}$ ±S.D.)		"t" value tab. at P = .05	calculated
	shrub-type	birch-type		
EAGLE:				
Saskatoon (2)*	8.3 ± 4.0	7.9 ± 3.4	12.71	0.78
Red-osier dogwood (10)	5.9 ± 3.0	6.0 ± 2.5	2.26	0.36
Willow (9)	6.5 ± 2.7	6.8 ± 3.1	2.31	0.90
Mountain ash (5)	7.1 ± 3.3	6.5 ± 2.1	2.78	0.85
SALMON:	aspen-type	aspen-pine type		
Willow (8)	6.1 ± 1.8	6.5 ± 2.3	2.37	2.28

*No. of pairs in sample.

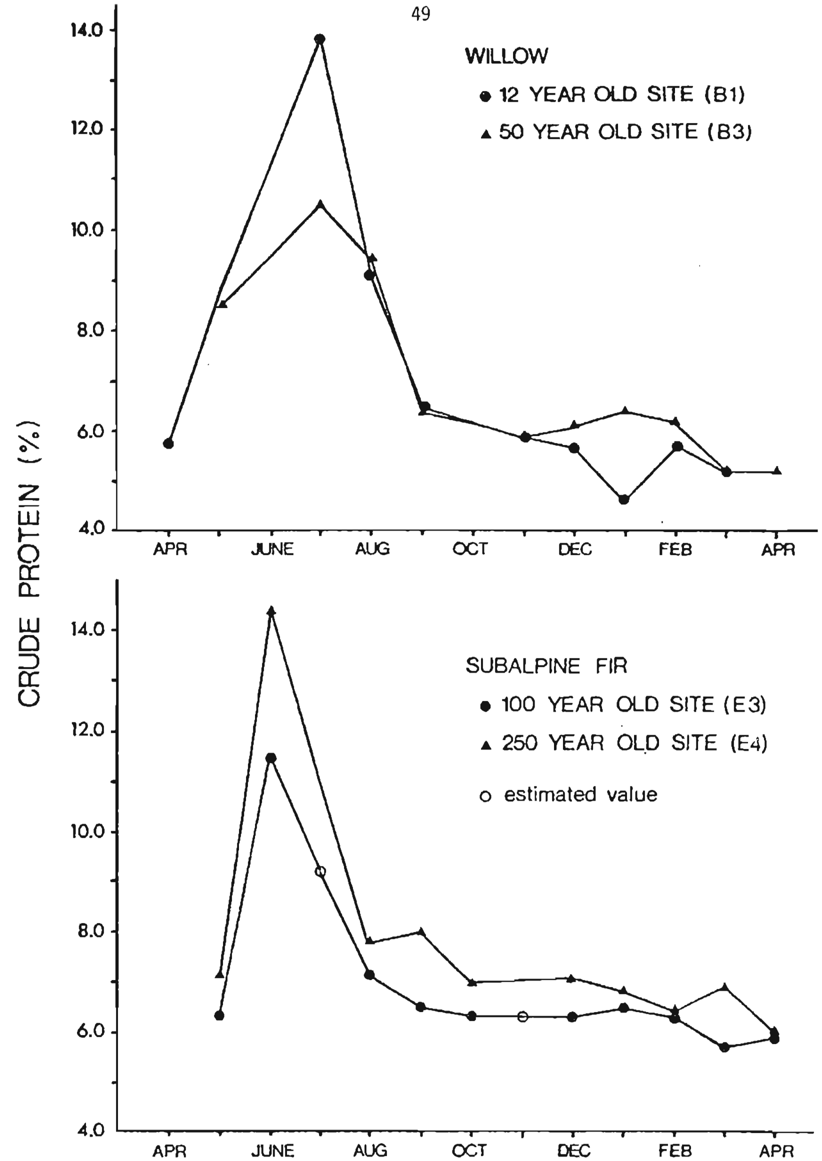

Figure 2. The effect of stand age on crude protein levels of willow and subalpine fir in central British Columbia, 1972-73.

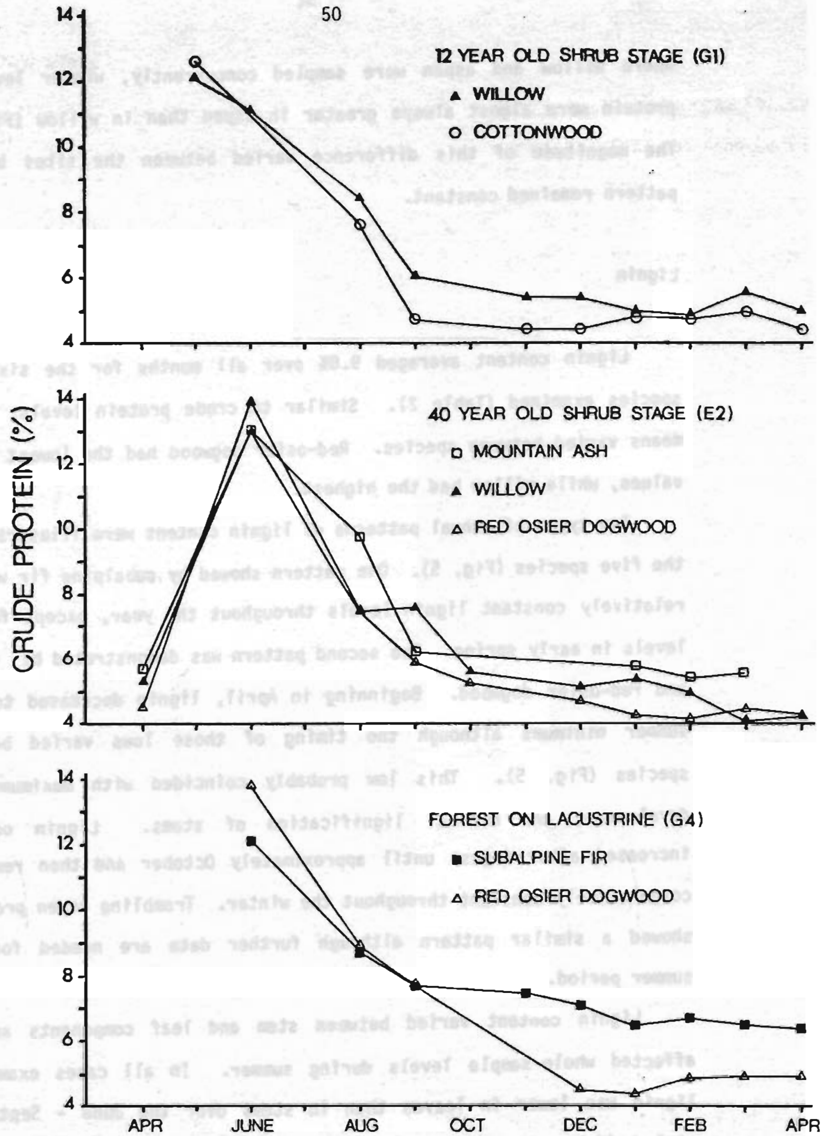

Figure 3. Differences in crude protein between selected moose browse species growing on the same sites in central British Columbia, 1972-73.

where willow and aspen were sampled concurrently, winter levels of protein were almost always greater in aspen than in willow (Fig. 4). The magnitude of this difference varied between the sites but the pattern remained constant.

Lignin

Lignin content averaged 9.8% over all months for the six woody species examined (Table 2). Similar to crude protein levels, annual means varied between species. Red-osier dogwood had the lowest lignin values, while willow had the highest.

Two types of annual patterns of lignin content were illustrated by the five species (Fig. 5). One pattern showed by subalpine fir was for relatively constant lignin levels throughout the year, except for low levels in early spring. The second pattern was demonstrated by willow and red-osier dogwood. Beginning in April, lignin decreased to mid-summer minimums although the timing of those lows varied between species (Fig. 5). This low probably coincided with maximum leaf development and minimal lignification of stems. Lignin content increased after August until approximately October and then remained comparatively constant throughout the winter. Trembling aspen probably showed a similar pattern although further data are needed for the summer period.

Lignin content varied between stem and leaf components and so affected whole-sample levels during summer. In all cases examined, lignin was lower in leaves than in stems over the June - September period (Table 3). Leaf lignin was least in red-osier dogwood and highest in paper birch. Stem samples showed a corresponding pattern.

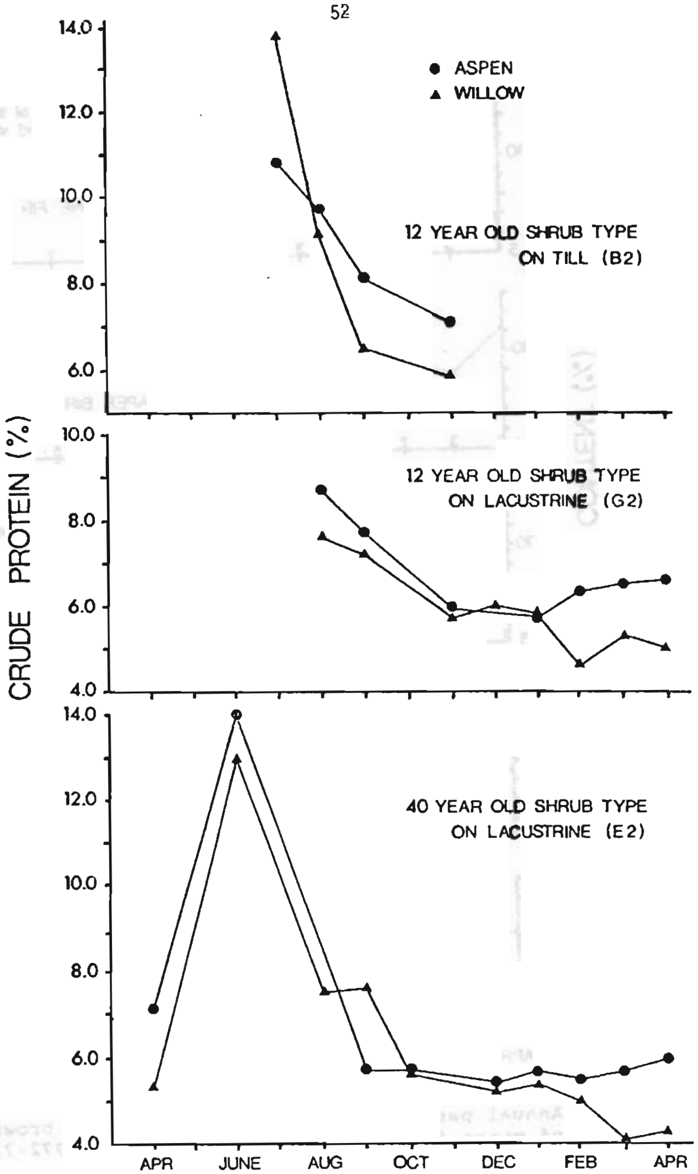

Figure 4. Consistency in the differences in crude protein between aspen and willow growing together on three sites in central British Columbia, 1972-73.

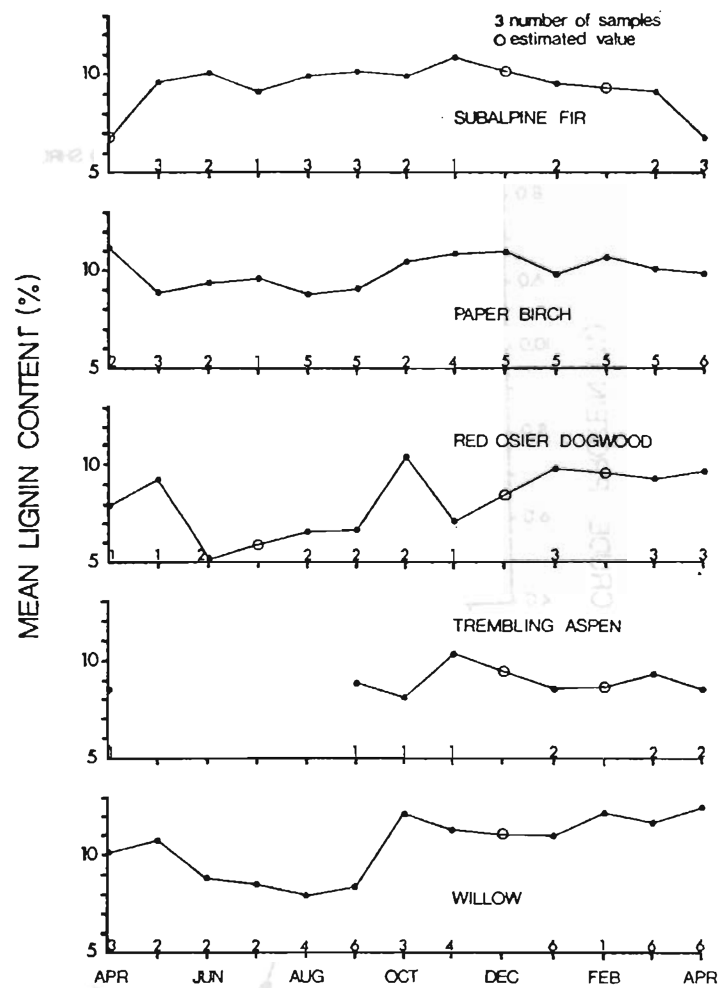

Figure 5. Annual pattern of lignin levels in five browse species of moose in central British Columbia, 1972-73.

Similar to crude protein, lignin content appeared to vary by species and by some environmental factors. Species growing at the same site had dissimilar lignin levels and the pattern of differences between species appeared to hold, whatever the site (Table 6, Fig. 6). Substrate affected lignin content, at least for paper birch (Table 6, Fig. 6). Lignin in paper birch growing on a till was generally lower than that growing on lacustrine; willow showed no significant differences. Also age of a sere appeared to modify lignin values (Table 6). The percent lignin generally declined with stand age for willow, paper birch, and trembling aspen on till and lacustrine substrates.

DISCUSSION

Crude Protein Levels in Moose Forages

Moose forages in the Prince George area had winter (November-March) levels of crude protein similar to those reported elsewhere, except for the results of Silver (1976) from northeastern British Columbia (Table 7). His levels of crude protein were approximately one-half of the average levels summarized in Table 7. Other species he sampled were also notably lower than those reported in the literature. After re-checking to rule out major sources of error, Silver (1976) concluded that these low values appeared accurate, but recommended re-sampling to substantiate his initial data.

If a dietary level of 7% crude protein is judged as minimal for the maintenance of moose (Gasaway and Coady 1974), then Prince George moose may have been at submaintenance levels for the winter. However, many herbivores can select diets higher in crude protein and other

Table 6. Annual averages of lignin content as affected by substrate, habitat, ar stand age at three sites in central British Columbia, 1972-73.

SUBSTRATE Habitat (Site)	Lignin content(%)* Subalpine fir	Paper birch	Red-osier dogwood	Trembling aspen	Willow
TILL					
12 yr old burn (B1, G1)		9.5			10.5
50 yr old pine forest (B3)					10.0
120 yr old pine forest (S5)	9.2				9.9
LACUSTRINE					
12 yr old burn (G2)		10.0		9.0	11.0
40 yr old burn (E2)		9.6	7.8	8.3	12.4
200 yr old spruce-fir forest (G4)	9.2		7.4		
250 yr old spruce-fir forest (E4)	8.9				
BEACH DEPOSIT					
Aspen forest (S2, S3)		9.4			10.2
RECENT ALLUVIUM					
Spruce-cottonwood forest (S1)			11.9		

*matched samples used in all cases. N = 4, 5, 4, 3, and 3, for species as listed above

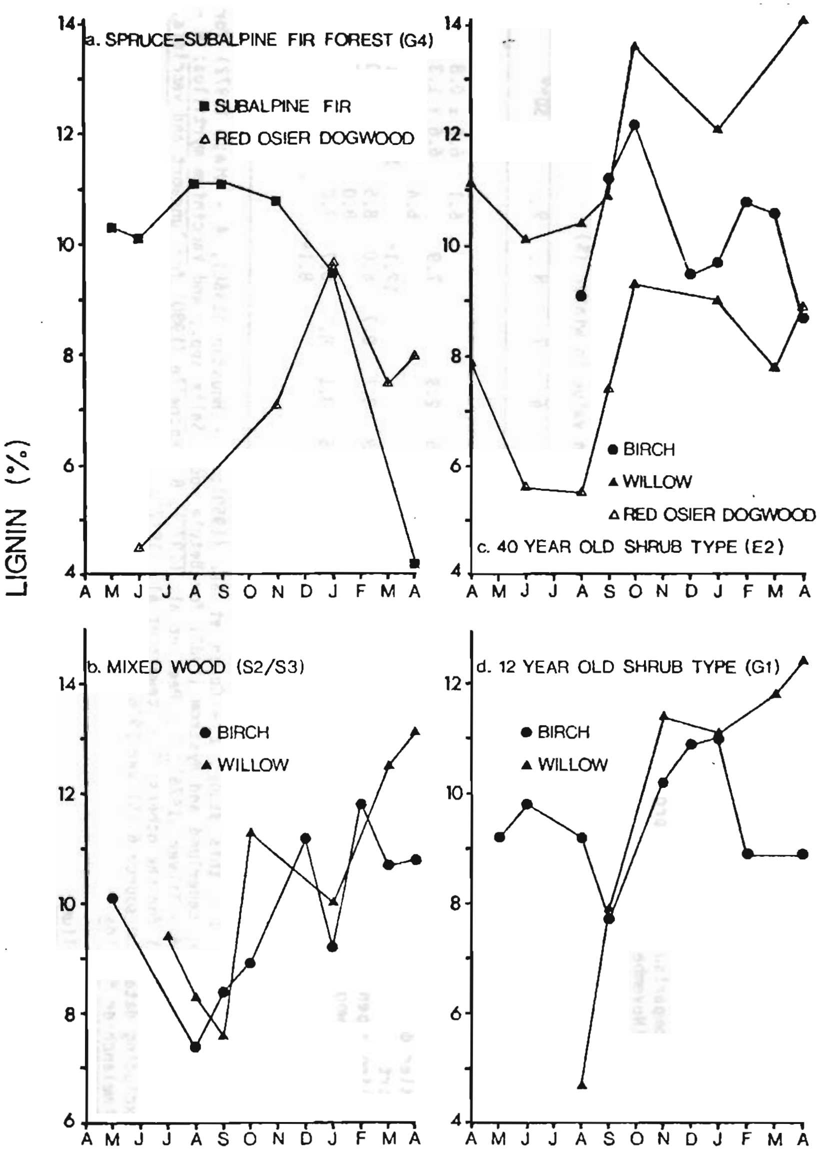

Figure 6. Effect of site on lignin levels in selected sub-boreal trees and shrubs.

Table 7. Comparisons of crude protein values for current annual growth of common winter foods of moose (November - March).

Species	Crude protein value in winter (%)									
	1*	2	3	4	5	6	7	8	9	x ± SD**
Subalpine fir	6.5	6.4	5.6							6.2 ± 0.5
Saskatoon	5.5***			7.0					6.1	6.2 ± 0.8
Paper birch	5.3	7.0		5.1	7.5	2.9		7.9		6.6 ± 1.3
Red-osier dogwood	4.8	4.8							6.4	6.5 ± 1.3
Lungwort	11.9							12.1+		12.0 ± 0.1
Trembling aspen	6.0	7.1	6.9	6.5	6.8	3.1	8.7	6.0	8.5	7.1 ± 1.0
Black cottonwood	4.7	6.1							8.0	6.3 ± 1.7
Willow	5.4		6.0	5.5	6.5	3.1	8.2	6.7	7.0	6.5 ± 1.0
Vaccinia	5.4			5.8				8.1++		6.4 ± 1.5

*Sources of data: 1 - this study; 2 - Cowan et al. (1950); 3 - Houston (1968); 4 - Dietz (1972) for saskatoon and aspen, cederlund and Nystrom (1980) for *Betula* spp., *Salix* spp., and *Vaccinium myrtillus*; 5 - Oldemeyer (1974); 6 - Silver (1976); 7 - Peek et al. (1976); 8 - Rochelle (1980) for lungwort and *vaccinia*, Kubota et al. (1970) for the others; 9 - Stewart et al. (1977).
**Excluding data from source 6 (Silver 1976)
***Amelanchier florida
+Lobaria oreganum
++Vaccinium parvifolium

nutrients than estimates based on hand-picked samples (Bissell 1959). Also, moose in the study area typically ate only the terminal portions of annual growth. These portions would have higher protein levels than those estimated from analyzing the entire annual growth as I did. Thus the dietary crude protein level for Prince George moose was probably about equal to the requirement for maintenance.

The annual average protein content of lungwort was almost twice that of the browse species (11.9% vs. 6.7%). On northern Vancouver Island, Rochelle (1980) found similar values for another Lobaria sp.. Crude protein averaged 12.1% for two samples picked from trees in December and May. This and other lichen species, made available through litterfall, formed an important part of blacktail deer winter diet in this study area. The role of litterfall as food for ungulates was summarized by Rochelle (1980). High crude protein values have been recorded for Peltigera spp., another foliose lichen, at 17.5% and 19.8% by Scotter (1965) and LeResche and Davis (1973), respectively. Lichens were not eaten by moose in greater amounts probably due to factors such as availability, palatability, difficulty of securing it, and low digestibility (Rochelle 1980). It should be noted that many other lichens have comparatively low protein levels of approximately 2-4% (Kelsall 1968).

Factors Affecting Nutrient Levels

Analytical demonstrations that nutrient levels vary in native North American shrubs date to at least 1911 (Knight et al. 1911, cited in Dietz 1972). Many factors have been examined for their effects on forage nutrients . Yet, wildlife-oriented reviews have found that many factors have equivocal effects on nutrient levels (Laycock and

Price 1970; Dietz 1972; Oelberg 1956;and Short et al. 1972). Probably the single most important problem in identifying and evaluating factors was defined by Laycock and Price (1970:44):

> In most of the studies reported, effects of individual environmental factors were confounded with those of other influences or with stages of plant development. Carefully controlled studies are needed to define the effects of these factors, both alone and in combinations, on the chemical composition of forage plants.

Another problem is that most studies assume that all species respond similarly to a given factor. However, since species vary in their adaptations to environmental factors, these variations could be reflected in plant nutrient levels as well. For example, Wali and Krajina (1973) demonstrated that many sub-boreal species, such as bearberry (Arctostaphylos uva-ursi), foam flower (Tiarella uniflora), and white peavine (Lathyrus ochroleucus), vary in their abundance along gradients of light and nutrients. Thus it may be that for a given level of one factor, the species best adapted to it would have the highest level of a particular nutrient.

Another major difficulty facing factor evaluation is unstandardized sample collection. Some workers collect all current annual growth while others collect only the terminal few centimetres; some separate leaves from twigs while others do not. Given the marked gradients of nutrients in plants, comparisons among these data are suspect.

Despite the foregoing problems, studies on how various factors affect nutrient levels will likely continue. Variations in nutrient levels can aid interpretation of habitat preferences by moose and other herbivores. Changes in feeding behaviour and diet will be more explainable with adequate nutrient data. Avoidance of some seemingly acceptable species of plants has been explained by studies on secondary compounds. The use of habitat management practices often depends upon knowing how forage nutrients, as well as forage abundance, changes (Peek 1974). Nutrient information also provides inputs to nutritional studies and models (Gasaway and Coady 1974; Robbins 1973).

Crude protein and lignin levels varied among the lichens, conifers, and deciduous dicots sampled. Lungwort had comparatively high crude protein values that showed little evidence of annual variation. Boreal and sub-boreal deciduous shrubs showed a definite seasonal pattern in crude protein, both in Prince George and elsewhere, (Grigal et al. 1976; Silver 1976; Tew 1970; Oldenmeyer 1974).

Changes in protein levels of both leaf and twig tissues are responsible for the dramatic changes in seasonal crude protein. Current leaves had higher crude protein levels than twigs and, even though twig crude protein levels doubled over the summer, their values were often only 50-60% those in leaves. Moreover, the majority of species had higher proportions of leaves than twigs in their current annual growth (Eastman 1977). The high crude protein levels of leaves may explain the common summer feeding behaviour of moose stripping foliage from woody shoots.

Crude protein and lignin levels in the single conifer studied, subalpine fir, were generally similar to those described for the deciduous shrubs. However, the relative ranking of this species

increased over the fall and winter so that by late winter, it had the highest protein values relative to other browse species.

Nutrient levels vary among plants within a species. This variability has both site (environmental) and genetic components although the influence of site factors is unclear. The complex and variable influence of these factors led Oldenmeyer (1974:220) to recommend that "If exact values are needed for nutrient content, they should be obtained from the area where the study is taking place and not extrapolated from other areas."

Overstory is a factor that influences forage nutrients. Overstory modifies temperatures, reduces light and through-fall precipitation, alters competitive relationships, and changes the status of soil moisture and nutrient availability. All of these factors influence forage nutrients so that overstory - nutrient inter-relationships are complex and replete with interactions. Not surprisingly, results of specific factor studies are often confounded. Laycock and Price (1970:39) explain the higher levels of protein in shade by retarded phenology, higher soil moisture (this is positively correlated with protein), succulence, and possible reduced leaching. Again, species specific adaptations must be considered.

However, these effects are not universal. In the present study, crude protein for four species was unaffected where the only difference in sites was canopy closure. Peek (1971) found that protein in twig samples from beaked hazel, trembling aspen, and willow were not correlated with canopy closure.

Genetic variability in shrubs is well recognized but its effect on nutrients is less well studied (McKell et al. 1972). However, Welch et al. (1977) demonstrated significant differences in crude protein levels of sagebrush (Artemisia tridentata). For twigs collected from plants grown under uniform conditions, crude protein levels varied from 8.7-17.1% between individual plants, and from 10.9-14.2% between three subspecies. Presumably, similar variability exists within plants and subspecies of shrubs eaten by moose. Such individual plant variations may help explain why one plant is used heavily while adjacent ones are ignored.

Nutrient variations also occur within different parts of the same plant. For moose, probably the most relevant differences are between twigs and leaves. Leaves have higher protein and lower lignin (higher digestibility) than twigs except just prior to leaf fall.

Nutrient gradients also occur within a tissue. These trends may help explain why wintering moose in Prince George and elsewhere will often remove only portions of the current annual twigs. The existence of protein gradients in native browse was known at least by 1945: Aldous (1945) found that terminal portions of current annual growth of bitterbrush (Purshia tridentata) contained more protein than proximal portions. Also, shorter annual shoots contained more protein than long ones. Cowan et al. (1970) examined this phenomenon in detail and found that the terminal 2.5 cm of black cherry and red maple contain 2.5 and 1.7 times more protein than the 23 -30 cm portion, respectively. As well, terminal buds contained approximately 1.5 and 1.3 times the protein as the terminal 2.5 cm of twig. Ahlen (1975) found similar though less marked gradients in a variety of Swedish browse species. Within tissue differences have also been documented for other nutrient components such as cellulose (Cowan et al. 1970), minerals (Ahlen

1975) and crude fiber (Aldous 1945). In general, the less easily digestible fractions decrease distally.

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