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THE UNIVERSITY OF ALBERTA

SOME RELATIONSHIPS BETWEEN MOOSE AND WILLOW IN THE FORT PROVIDENCE, N.W.T. AREA

by

© DAVID F. PENNER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Some Relationships between Moose and Willow in the Fort Providence, N.W.T. Area submitted by David F. Penner in partial fulfilment of the requirements for the degree of Master of Science in Range Management.

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Date October 5, 1978

ABSTRACT

A study was conducted on plant communities and moose habitat use in the lowlands near Fort Providence, Northwest Territories. The purpose of this study was to examine some relationships between moose and willows on a moose winter range.

Species composition, herbage and browse production and soil characteristics were described for five plant communities: sedge meadow, patterned fen, willow-shrub, willow savanna and aspen-willow communities. Available mean annual production ranged from 530 kg/ha in the aspen-willow to 2535 kg/ha in sedge meadow communities. Available browse production ranged from 442 kg/ha in the willow savanna to 1406 kg/ha in willow-shrub communities. Available winter browse averaged 20 percent of summer browse production in shrub communities.

Moose were found to concentrate in the willow savanna and patterned fen communities in part of the study area during winter. A density of 0.9 moose per square kilometer was recorded on willow communities used as winter range.

During winter, moose exhibited a marked browse preference for *Salix candida*, *S. bebbiana* and *S. padophylla* and an avoidance of *S. maccalliana* and *S. gracilis*. Previous browse use on individual shrubs was found to increase the probability these shrubs would be rebrowsed by moose. The degree of previous use also influenced the amount of current annual browse

removed from each shrub.

The seasonal nutrient content in the current annual growth of six willow species and two browsed conditions were examined at four dates during the growing season and once during the dormant season. Seasonal levels of moisture, crude protein, acid-detergent fiber, lignin, ash, calcium, phosphorous, magnesium, sodium and crude fats were described. Although some differences in nutrient levels were found among species and between browsed conditions within species, these were not consistent throughout the sampling period. No significant relationships were found between moose browse selection and browse nutrient content. Chemical analysis of three twig portions showed a progressive decrease in moisture, crude protein and minerals and an increase in acid-detergent fiber and lignin from the terminal to lower twig portions.

Willows subjected to simulated or natural browsing during the dormant season responded with a decrease in the number of twigs and a significant, two to four fold, increase in twig weight per secondary stem in the following growing season. It was postulated that this larger twig growth may have influenced moose preference for previously browsed shrubs. This selection may be advantageous to moose by maximizing intake of palatable and perhaps more nutritious browse (terminal twig portions) while minimizing energy expended by decreasing the time spent feeding.

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TABLE OF CONTENTS

PAGE

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

It has been well established that moose *(Alces alces)* are primarily a browsing species, especially during winter. On ranges in western North America, willows *(Salix spp.)* are one of the most important food sources used by moose (Pimlott 1961; Peek 1974). However, due to the taxonomic complexity of the genus *Salix* and the difficulty in rapidly identifying willows to species, most moose food habit studies refer to willows as a collective group. Several researchers have found that moose will discriminate among species of willows by showing preferential use of some species over others (McMillan 1953; Milke 1969; Dorn 1970). Suggested factors that may influence the preferential use of a particular species include nutrient content, succulence (moisture content), shrub height and growth form, season of use and the type and abundance of associated plants (Milke 1969; Dorn 1970; Pavlov 1973; Berg and Phillips 1974).

Food habits express a fundamental relationship between moose and their environment. An understanding of moose forage preferences is a prerequisite to moose population and habitat management. This study was conducted in the northern part of moose range in North America. At this latitude, it is expected that the long and cold winters cause a considerable energy and nutritional strain on moose. Gasoway and Coady (1974) found that moose in Alaska normally experience a loss of up to 25 percent of body weight during winter. The relatively short growing season of northern latitudes would also limit the time available for weight gain from the more nutritious summer forage. Moose are large ungulates requiring 18 to 23 kg of browse per day in winter (Verme 1970). Considerable mobility and energy expenditure would be required to obtain sufficient browse to maintain the rumen fill.

This study was initiated by observations of moose browse selection of particular species of willows and further selection of individual shrubs within a preferred species. My research on the lowland ranges near Fort Providence, Northwest Territories, seeks to quantify and relate the relationships between moose and willows on a moose winter range. The objectives of this study were:

a) to describe the habitats available to moose in the lowlands near Fort Providence, N.W.T.,

b) to quantify moose browse selection in three plant communities,

c) to investigate the seasonal nutrient levels in six common willows in the study area,

d) to investigate the response of willows to browse utilization, and

e) to investigate the relationships among moose browse selection, browse nutrient levels, previous browse utilization, and willow growth form.

DESCRIPTION OF THE STUDY AREA

1. Location and Size

The study area was located thirteen kilometers northeast of Fort Providence, Northwest Territories (61°25'N; 117°40'W of the fifth meridian) and encompassed approximately one hundred square miles Figure 1).

Within this region, two similar sites, one with relatively low and the other relatively high moose utilization, were selected for detailed investigation. The legal land location is sections 33 and 34, township 142 and sections 2 and 3, township 143, range 20, west of the fifth meridian for Site One which sustained relatively low moose use; sections 13, 14, 23, and 24, township 143, range 19, west of the fifth meridian for Site Two which sustained relatively high moose use (Figure 1).

2. History of the Area

The wildlife of the Upper Mackenzie region have historically provided a natural resource base that dominated the lifestyle of nomadic Indian bands of the Slave tribe (Osgood 1931). Moose, bison, and fish provided a major proportion of their food supply. Archaeological evidence indicates that the Fort Providence region was inhabited by prehistoric cultures for more than 5,000 years, B.P. (Wormington 1957).

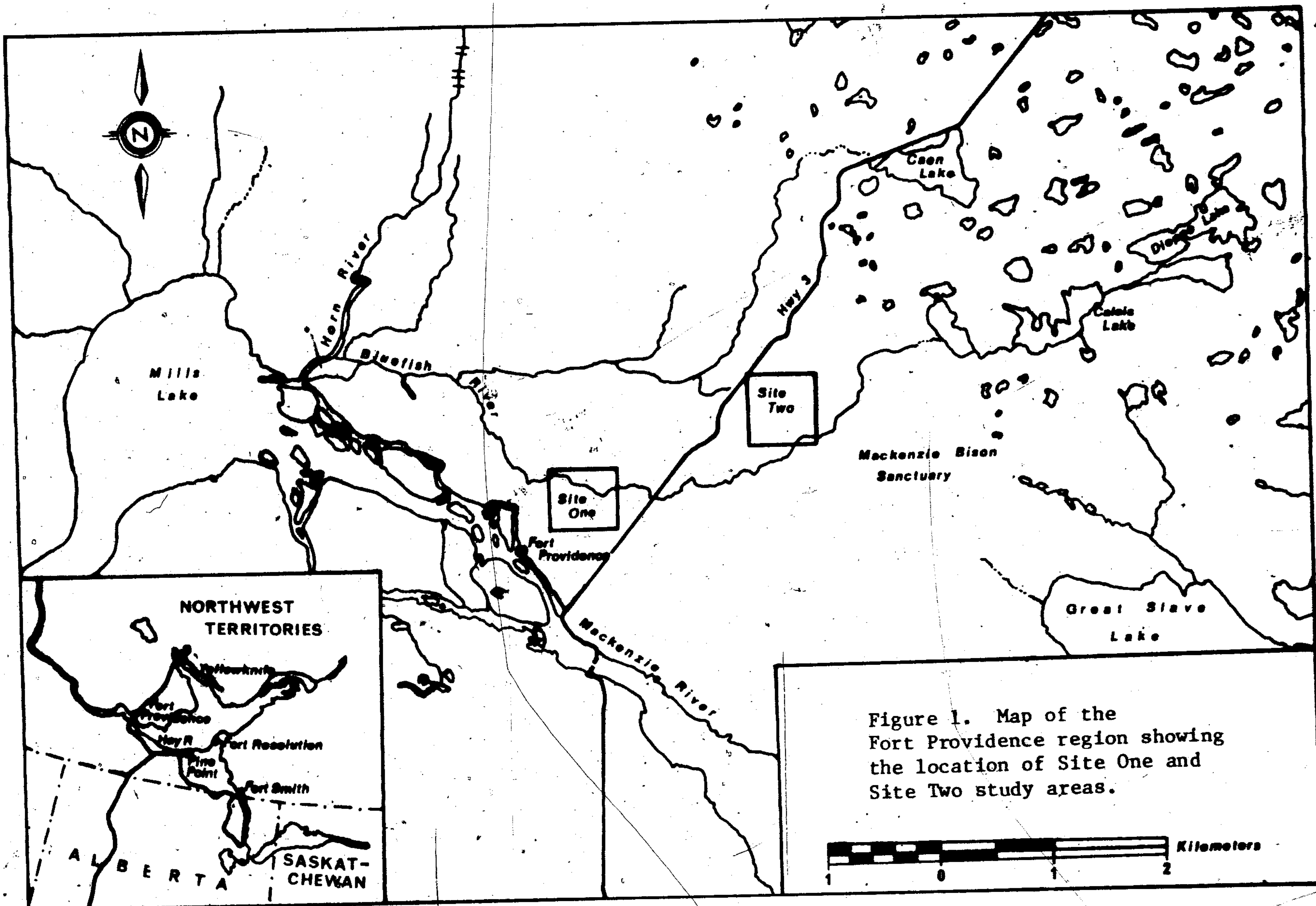


Figure 1. Map of the Fort Providence region showing the location of Site One and Site Two study areas.

The Native people are presently localized in settlements and still depend on hunting, fishing, and trapping to supplement their incomes.

Land disposition of the Fort Providence area is controlled by the Government of the Northwest Territories. Grazing leases have been established on the sedge-grasslands along the Bluefish River and at Mills Lake. Native hay and potatoes are harvested on the alluvial flats at the mouth of the Horn River. The Mackenzie Bison Sanctuary was established in 1963 with the re-introduction of wood bison. The bison sanctuary is located north of the Mackenzie River, between Highway 3 and Great Slave Lake (Figure 1).

3. Geology and Soils

The study area is underlain by Upper Devonian rocks of the Simpson formation (Douglas 1959). These rocks are described as slightly calcareous, laminated shales with inclusions of calcareous sandstone and siltstone. During the Pleistocene, the Laurentide ice sheet deposited a stony, gravelly clay drift over the entire Interior Plain (Craig 1965). During deglaciation, the till was covered by stratified lacustrine deposits derived from the sedimentation of glacial Lake McConnell. The resulting topography of the Great Slave Plain is low-lying, nearly flat ground with numerous small lakes and bogs. Numerous lineaments of varying lengths transect the study area and disturb the continuity of communities with sharp changes in vegetation (Craig 1965).

The soils of the study area were developed on moderately fine to fine textured lacustrine material that contains some stones. On well-drained sites, the vegetative cover of aspen *(Populus tremuloides)*, white spruce *(Picea glauca)*, and willows have influenced the development of Orthic Gray and Orthic Brown Luvisolic soils. Rego-Gleysol soils have developed on poorly-drained but moderately permeable sites, and are vegetated by the aspen-willow and willow-savanna community types. Where the vegetation is largely grasses and sedges, a moderate Ah horizon has developed. Poorly drained sedge meadows and patterned fens have organic soils and are often frozen at 45 or more centimeters below the surface (Day 1968).

4. Climate

The Fort Providence region lies within the Sub-Arctic climatic zone, characterized by long, cold winters, brief warm summers and light precipitation (Thomas 1953).

The mean annual temperature is -4°C and ranges from a high mean daily temperature of 16°C, in July, to a low mean daily temperature of -27°C in January. Mean daily maximum temperatures reach 23°C in July while the mean daily minimum of -32°C occurs in January. The frost-free period extends for 75 days, from about 10 June to 14 August. The mean growing season extends from 9 May to 26 September, an annual average of 140 days (Canada Department of Transport 1967).

The mean annual precipitation for the region is 26.4 cm. About one-half of the total precipitation falls during the growing season.

The mean date of drought point is reached about 22 June, forty-two days after the beginning of the growing season (Day 1968). Snowfall contributes 44 percent of the total annual precipitation. The average snowfall of 112 cm compacts to a winter maximum of 71 cm. The snow cover lasts an average of 182 days.

5. Vegetation

The Fort Providence area is in the Upper Mackenzie section of the Boreal Forest region (Rowe 1972).

The better drained soils are characterized by a climax vegetation cover of white spruce, with jack pine *(Pinus banksiana)* occurring on drier sandy ridges. Due to frequent fires, most of the uplands are covered by aspen, with an understory of willow, buffalo berry *(Shepherdia canadensis)*, rose *(Rosa acicularis)*, and grasses.

On poorly drained sites, an association of bog birch *(Betula glandulosa)*, willows, sedges *(Carex atherodes* and *Carex aquatilis)*, and grasses *(Scolochloa festucacea* and *Calamagrostis inexpansa*[1]*)* predominate. Black spruce *(Picea mariana)* muskegs with larch *(Larix laricina)*, Labrador tea *(Ledum groenlandicum)* and sphagnum moss occur

[1]Both *Calamagrostis inexpansa* and *C. neglecta* are found in the Fort Providence area but are indistinguishable by vegetative characteristics in the field. Both species are hereafter combined as *Calamagrostis inexpansa*.

in localized areas. Sites of restricted drainage are characterized by patterned sedge fens[2] and are underlain by permafrost. The intervening ridges have an overstory of black spruce, larch, bog birch and willows. Wet "grassland" communities dominated by *Carex atherodes*, *Carex aquatilis* and *Scolochloa festucacea* occur as insular meadows and along watercourses. A willow dominated grassland (willow-savanna) occurs as a relatively stable ecotone between poorly and well-drained sites.

In riverine areas and on alluvial flats, white spruce and balsam poplar (*Populus balsamifera*) form the main cover types. In these areas, willow and alder (*Alnus tenuifolia*) occur as pioneering and successional species.

6. Fauna

The Upper Mackenzie lowlands lie on the northern fringe of the Closed Boreal Forest Life Zone (Pitelka 1941; Aldrich 1963). The Upper Mackenzie lowland region is considered one of the most productive wildlife areas in the north (Canadian Wildlife Service 1972).

Seventeen species of mammals were recorded in the study area. An additional eighteen species were recorded or reported to occur in the surrounding region.

[2]Hereafter referred to as the patterned fen community.

Moose were the most common and widely distributed ungulate in the lowlands. Wood bison (*Bison bison athabascae*)[1] originally inhabited the Mackenzie lowlands (Mackenzie 1801) and were re-introduced in 1963 (Monaghan 1973)[2]. The main concentration of wood bison is located in sedge meadows to the northeast of the study area. Woodland caribou (*Rangifer tarandus*) range throughout the black spruce forests to the north and south of Fort Providence, and are occasional transients through the study area. Black bear (*Ursus americanus*) were common throughout the area.

Common mammalian predators in the area include the wolf (*Canus lupus*), red fox (*Vulpes vulpes*), lynx (*Lynx lynx*), marten (*Martes americana*), and ermine (*Mustela erminea*).

Beaver (*Castor canadensis*) and muskrat (*Ondatra zibethicus*) were common along the Bluefish River. The red squirrel (*Tamiasciurus hudsonicus*) were found throughout the region, wherever pockets of white and black spruce had escaped previous fires. The snowshoe hare (*Lepus americanus*) population was at a low point of its cycle during the study period. In preceding years, browsing by snowshoe hares had killed or seriously affected much of the bog birch in the study area.

The populations of meadow vole (*Microtus pennsylvanicus*), Arctic shrew (*Sorex arcticus*), and masked shrew (*S. cinereus*) were found to

[1]Scientific and common mammal names follow Jones *et al.*, 1973.
[2]Personal communication, H.J. Monaghan, October 17, 1973.

be locally abundant in the willow-savanna, sedge meadow and patterned fen communities.[1] The feeding and food storage activities of the meadow vole appeared to be removing up to a quarter of herbaceous forage production in sedge dominated communities. The northern bog lemming (*Synaptomys borealis*) was recorded in the patterned fen community. The deer mouse (*Peromyscus maniculatus*) and northern red-backed mouse (*Clethrionomys rutilis*) were common on drier sites under aspen, willow and white spruce cover.

Approximately 105 species of birds were observed during this study or were reported (Carbyn 1967) to breed in the western Great Slave Lake region. In addition, approximately 60 species were observed during this study or were reported (Carbyn 1967) as seasonal migrants and winter visitors.

A resident population of Sharp-tailed Grouse (*Pedioecetes phasianellus*) and a winter population of Willow Ptarmigan (*Lagopus lagopus*) were found in the study area. Both species wintered in willow-dominated communities and fed on the buds of willow and bog birch.

[1]Small mammal populations were examined by snap trapping in three plant communities in the study area. Five hundred and six trap nights were run during 3 to 5 and 11 to 12 August, 1973.

REVIEW OF THE LITERATURE

A. Plant Communities

1. Forest Communities

White spruce is generally considered to be the climax forest vegetation for mesic sites throughout northern Alberta and the adjacent Mackenzie region (Raup 1946; Moss 1953). In northern Saskatchewan Kabzems (1952) reported black spruce as the climax species, growing on a wide range of soils and forest sites, forming pure as well as mixed stands. In the more northern parts of Alberta (Moss 1953) and adjacent Mackenzie areas (Raup 1946), black spruce is commonly found on many kinds of terrain, in pure stands or intermixed with white spruce, paper birch *(Betula papyrifera)*, aspen and jack pine. For northern areas, Raup (1941) emphasized the difficulty of recognizing associations and of applying the climax concept. Raup (1941) suggested that the vegetation of the central part of the Mackenzie basin is "exceedingly young" and much of it appearing "as though it were in the process of being formed". He described the Mackenzie lowlands as a floodplain forest, developed on alluvial and lacustrine soils, and characterized by a succession from a *Populus balsamifera, Equisetum pratense, Salix bebbiana* association to a stable *Picea glauca, Salix bebbiana, Viburnum edule, Cornus stolonifera* association. On better drained sites, the upland mesophytic white spruce forest, characterized by *Picea glauca, Salix bebbiana, Hypnum Cristacastrensis, Hypnum Schrebeni* (Raup 1946) is comparable to the white spruce, shrub-herb and feather moss faciations (Moss 1953) common to northwestern Alberta.

Periodic fires that destroy the climax stands are a common occurrence in the boreal forest, and may be frequent enough to moderate or halt the natural successional processes (Moss 1932; Rowe and Scotter 1973). In northern regions, the result of fire has been the establishment of extensive stands of *Populus tremuloides*, with occasional patches of *Picea glauca*, *P. mariana*, *Populus balsamifera* and *Pinus banksiana* (Raup 1946). In the absence of fire, the slow natural succession of aspen and balsam poplar to white spruce results in a mixedwood sere that is floristically diverse but infrequently described.

Moss (1953) divided the poplar association into *Populus tremuloides* and *P. balsamifera* consociates. He also differentiated the aspen poplar association proper from the parkland. The internal structure of a typical poplar association in northern Alberta includes a closed canopy of *Populus tremuloides* or *P. balsamifera*, a discontinuous small tree -- tall shrub stratum, characterized by willow, notably *Salix bebbiana*, a rich low shrub stratum, a moderate herb strata and sporadic mats of bryophytes (Moss 1953). Important associate species include *Cornus stolonifera* in the *Populus balsamifera* consociation and *Shepherdia canadensis*, *Arctostaphylos uva-ursi* and *Elymus innovatus* in the *Populus tremuloides* consociation.

Moss (1955) stated that *Populus tremuloides* is adaptable to wide edaphic and climatic factors. Environmental variables such as soil texture, moisture and nutrients, climate, grazing, topography and past history influence the floristic composition of the understory (Raup 1946; Moss 1955; Maini 1968). Common associate species of typical stands of *Populus tremuloides* are reported by Moss (1953) for northwestern Alberta, Raup (1946) for the Wood Buffalo region, Jeffery (1961) for the Peace River area, Moss (1932) for central Alberta and the parkland, Hilton and Bailey (1974) and Sheffler (1976) for the parkland, Maini (1968) for Saskatchewan, Lynch (1955) for Montana and Kittredge (1938) for Minnesota and Wisconsin.

Moss (1932) reported *Populus balsamifera* to be restricted in distribution, due to a greater dependency upon moisture. *Populus balsamifera* reaches its best development on moist sites such as river flats, and becomes more frequent in northern Alberta. The common associate species and successional stages of *Populus balsamifera* associations are reported by Raup (1946) for the Upper Mackenzie lowlands and Moss (1932, 1953) for central and northern Alberta.

Hilton and Bailey (1974) found that herbage production under Parkland *Populus tremuloides* varied between seasons and communities. In the small poplar type, herbage yield ranged from 170 kg/ha to 104 kg/ha for grasses and sedges and 120 kg/ha to 187 kg/ha for green forbs. In the large poplar type, the herbage yield was 30 kg/ha and 32 kg/ha for grasses and sedges and 25 kg/ha and 73 kg/ha of green forbs for the 1968 and 1969 seasons respectively.

Salix bebbiana is described as a tall shrub or small tree (Raup 1959) that is widely distributed throughout the wooded parts of Alaska, and the Yukon (Viereck and Little 1972; Argus 1973), Athabasca-Great Slave Lake region (Raup 1946), and northern Alberta (Moss 1953). *Salix bebbiana* is a characteristic species of floodplain *Populus balsamifera* and *Picea glauca* associations, open *Populus tremuloides* forests, grass-land margins and burned over upland areas (Moss 1953; Raup 1959). *Populus tremuloides, Salix bebbiana* communities have been described by Sheffler (1976) and Hilton (1970) for the parkland region and by Jeffery (1961) for the Peace River area. Hilton (1970) reported that in 1968, the total green herbage production in the aspen-willow community was 374 kg/ha. Of this, grasses, including *Poa* spp., *Calamagrostis inexpansa, C. neglecta* and *Beckmannia syzigachne,* contributed 204 kg/ha and forbs 169 kg/ha.

2. Shrub Communities

Willow dominated communities are generally recognized as pioneer or early successional stages (Raup 1946; Argus 1973). Argus (1973) emphasized the relationship of willows and habitat instability characteristic of physical disturbance (river floodplains, glacial moraines, gravel outwash plains and fires) and labile successional stages. Argus (1973), Viereck (1966), Bliss and Cantlon (1957) discussed the role of willows in the vegetative succession of physically disturbed areas in Alaska and the Yukon. These authors noted a succession of willow species that dominate each seral stage. Raup (1959) recognized the dominance of willows on wet, cool soils characteristic of the margin of muskegs, wet meadows, alpine and arctic tundra as well as the role of willows in colonizing disturbed areas. Raup (1946) described willow communities of the Upper Mackenzie lowlands as generally forming a transitional zone around slough margins and along river floodplains but which may form broad expanses on delta areas. Raup (1946) recognized two types of willow succession: 1) at slough margins, where the first willow to appear is *Salix planifolia*, followed by *S. petiolaris* and *S. bebbiana*, and 2) on river sandbars, where *Salix interior* is the colonizing species, followed by *S. lutea*, *S. lasiandra* and finally by *S. bebbiana*, which persists into the forest and becomes a primary species in the shrub layer.

Raup (1935) described the floristic composition of willow dominated shrub associations of seral stages related to lakeshore, muskeg, semi-open prairies and delta ecotypes in Wood Buffalo National Park. *Salix bebbiana* occurred as a leading dominant in the shrub layer of all woodlands and in nearly pure stands over vast areas between the meadow margins and the encroaching *Populus tremuloides*. Other studies describing the seral stages and floristic composition of willow communities include: Lewis, Downing and Moss (1928) for the Cordilleran, northern forest and parkland areas of central Alberta, Moss (1953) for the marsh and bog succession in northwestern Alberta and Bird (1961), Hilton (1970) and Sheffler (1976) for slough to forest succession in the aspen parkland of Alberta. Berg (1971) described the vegetation of 14 habitat types, six of which are dominated by willows, in a moose range study in Minnesota.

Jeglum (1972; 1973) investigated the Boreal Forest wetlands in central Saskatchewan and discussed the relationship between vegetation variation and major environmental gradients. The vegetation classification included a tall shrub fen in which willows (*Salix maccalliana, S. planifolia, S. bebbiana* and *S. discolor*) and alder (*Alnus rugosa*) predominated. The understory was characterized by *Carex atherodes, C. rostrata, C. aquatilis* and *Calamagrostis inexpansa-neglecta*. Similar tall shrub associations have been described as "shrub vegetation" on predominantly mineral sub-stratum (Ritchie 1960); "thicket" (Moss and Turner 1961); "alder swamp", (Damann 1964); "shrub carr", (White 1965); "brush-land" and "brush and alder" on various provincial forest inventory maps. White (1965) considered that a minimum of 25 percent cover of tall shrubs is required to separate his "shrub carrs" from the open aspect of "meadows".

Jeglum (1972) described a low shrub fen having a shrub strata below 135 cm in height with a 20 to 25 percent shrub cover. Leading shrub dominants in separate stands included: *Salix candida, Salix pedicellaris, Andromeda polifolia* and *Betulua glandulifera*. Common understory species included sedges (*Carex aquatilis, C. chordorrhiza* and others) and *Calamagrostis inexpansa-neglecta*. Similar associations were described as "shrub fen" on predominantly peat substrata (Ritchie 1960), and a "*Drepanocladus-Carex* bog" (Moss and Turner 1961; Moss 1953). Jeglum (1972; 1973) discussed the continuum of variation resulting in an intergrading of tall shrub fens, low shrub fens and sedge fens.

Washburn (1956) reviewed the suggested origins of patterned ground and attempted a system for their classification. Bogs, characterized by sedge fens separated by shrub dominated peat ridges, have been described as ribbed fens (Zoltai 1971) patterned fens (Heinselman 1963), string fens (Drury 1956; Allington 1961) and string bogs (Thom 1972). Jeglum (1973) discussed the vegetation patterns of ribbed fens in relation to surface water movement and soil nutrient regime. Permafrost peat landforms were investigated by Zoltai and Tarnoci (1971), and Sjors (1963).

3. Grassland Communities

Moss (1953) described the successional vegetation from shallow persistent water to seasonally flooded sites as: 1) real swamp, dominated by *Scolochloa festucacea*, and *Carex atherodes*; 2) marsh, dominated by *Calamagrostis inexpansa*, *Carex aquatilis*, *C. rostrata* and *C. atherodes*; and 3) wet meadow, dominated by *Calamagrostis canadensis* and scattered willows including *Salix petiolaris (S. gracilis)*, *S. planifolia*, *S. bebbiana* and *S. maccalliana*. Other authors recognized two associations: emergent fen (Jeglum 1972) or marsh (Moss 1955; Curtis 1959) and sedge fens (Ahti and Hepburn 1967), sedge meadow (Bates and Simkim 1969) or meadow (Curtis 1959).

Thieret (1959) described three grassland communities near Fort Providence. These were *Scolochloa festucacea-Carex aquatilis-Carex atherodes* association on wet marshy sites; *Agropyron trachycaulum-Muhlenbergia richardsonis* association on mesic sites; and *Calamagrostis* *neglecta-Agropyron trachycaulum-Carex atherodes* association on intermediate sites. Shrubs and trees occurred as scattered individuals, particularly at the periphery of these grasslands. Jeffrey (1961) discussed a similar invasion of shrub and forest vegetation onto the xerophytic and mesophytic grassland communities in Wood Buffalo Park.

The floral characteristics of the Fort Providence grasslands are considered to have sub-arctic and temperate affinities (Raup 1941; Thieret 1959). These grassland communities are similar to those described for the upper Peace River country (Raup 1934) and for Wood Buffalo National Park (Raup 1933, 1935).

Raup (1941) discussed the origin and maintenance of Boreal Forest grasslands and suggested that the Mackenzie Basin prairies may have developed directly upon the new soils exposed by the drainage of the post-glacial lakes.

Forage production of sedge and sedge-grass meadows were reported by Corns and Schraa (1962), McLean *et al.* (1963), Pringle and Van Ryswyk (1968), Hilton (1970), Wroe (1971), and Corns (1974).

B. Moose Population Inventory

1. Aerial Surveys

Aerial censusing has been considered the only practical way of estimating moose numbers in most of North America (Bishop 1969; Bergerud and Manuel 1969). Banfield *et al.* (1955) summarized the strip census method generally used to obtain indices of moose densities by area. The problems of determining transect width have been discussed by Saugstad (1942), DeVos and Armstrong (1954) and Timmerman (1974). Aerial surveys of randomly selected plots, commonly referred to as the intensive search or orbiting method (Trotter 1958), were first introduced by Ontario using a 25 sq mi plot (Timmerman 1974). Recently Lynch (1971) in Alberta, Evans *et al.* (1966) in Alaska, Bergerud and Manuel (1969) in Newfoundland and Mantle (1972) in Ontario have used the intensive search on randomized blocks of 1 sq mi (2.59 sq km) in size. Lynch (1971) reported that only two-thirds the number of moose observed on block surveys were spotted during the transect counts. Evans *et al.* (1966) estimated only one-fourth as many moose were seen in a given area surveyed using linear strips as compared to intensively searched quadrats.

The inability to see all animals present generally results in an underestimation of the moose population (Timmermann 1974). In areas of dense forest cover, the average sight ability may be as low as 40 percent while in more open areas, visibility may approach 70 to 80 percent (Pimlott 1961; Edwards 1954). Benson (1966), Goddard (1966) and Bergerud (1968) have reviewed the accuracy of aerial censusing techniques and have suggested that substantial errors are inherent in most. Caughley and Goddard (1972) have suggested statistical methods for estimating these errors. Siniff and Skoog's (1964) random stratified quadrat sampling method, modified by Evans *et al.* (1966), made population estimated more plausable, but these techniques still depend upon

knowing what proportion of animals flown over were actually observed.

LeResche and Rausch (1974) investigated the accuracy and precision of aerial moose censusing under ideal weather conditions and known moose densities in Alaska. They found that experienced observers, flying fifteen minutes over each fenced square mile saw 68 percent of the moose present while inexperienced observers saw only 43 percent.

Additional factors that affect visibility bias include the number of observers, observers' fatigue, weather conditions, habitat and terrain, time of day and relative moose densities (Timmermann 1974).

Alternate moose censusing methods include track counts (Semyonov 1965; Bentley 1961; Gawley and Dawson 1965 and Priklonskiy 1965), aerial photography (Banfield *et al.* 1955; Vozeh and Cumming 1960; and Passmore 1963) and infra-red thermal imagery (Croon *et al.* 1968; McCullough *et al.* 1969; Addison 1972 and Graves *et al.* 1972).

2. Pellet Group Counts

Neff (1968) reviewed the pellet group count technique used to estimate the relative numbers of big game animals, population trends and animal distribution. Timmermann (1974) suggested the major value of pellet group counts for moose was to obtain indicies for comparison among areas and among years. These indices assisted in the estimation of the moose days use in a given area and helped determine preferred habitat types and seasonal use patterns (Neff 1968).

Neff (1968) assumed that the number of pellet groups counted in an area was closely related to the number of animal days spent in the area. Since pellet groups are usually deposited in a clumped rather than a random pattern, sampling is normally more efficient in areas of higher pellet group density (Neff 1968; Des Meules 1965). Problems associated with the pellet group technique include: observer bias and fatigue in counting groups, the small amount of coverage, rapid loss of pellets through insect attack and rain, visibility of groups as vegetation advances, size of plot and the type of surface microtopography (Timmermann 1974).

The average daily deposition rate of pellet groups has been a subject of considerable discussion. Suggested daily deposition rates include 14.9 in Wells Gray Park, British Columbia (Edwards 1956), 10.7 and 14.7 in Quebec (Des Meules 1968), 10.3 in Alaska (LeResche 1970), and 13.0 (Julander *et al.* 1963). Pellet group counts generally tend to give a higher estimate of population in winter concentration areas than aerial surveys done under ideal conditions (Hall 1964).

C. Moose Habitat Use

1. Habitat Selection

The association of moose with sub-climax plant communities is generally accepted throughout much of its range in North America (Peterson 1955). Geist (1971) described moose habitats as: a) transient communities of deciduous trees and shrubs that are unstable, short-lived and grow on burns, and b) permanent communities of climax deciduous tree and shrub associations along watercourses, alluvial deltas and avalanche slopes. In British Columbia, Hatter and Martin (1960) emphasized "...the importance of winter range upon which there is a variety of palatable seral plants, predominantly in an early stage of growth, but with an intermixture of stands of older ages, including climax associations with some palatable coniferous species." Krefting (1974) reviewed moose habitat selection in north central North America and concluded that important habitats in the boreal forest are produced in the early seral stages of plant succession. As forest succession advances, the quality of the habitats and moose populations decrease accordingly. Berg and Phillips (1974) described moose habitat selection in relatively flat areas supporting broad expanses of marsh, willow, aspen and coniferous forests that are commonly found from northwestern Minnesota to north-central Alberta. These authors found that willow and associated willow habitats supported the greater majority of observed moose use. Seasonal use of various habitats was found to be directly influenced by snow depths.

Snow conditions have been found to influence moose winter habitat selection in most moose ranges. In Ontario, Chamberlain (1972) found that under heavy snow conditions (greater than 76 cm of snow), moose preferred higher coniferous crown cover in mixedwood habitats of ridge tops and north facing slopes. During times of light snow conditions, moose preferred a more open canopy, flatter areas and south, east and west facing slopes. Telfer (1970) noted that moose in Nova Scotia often congregated on knolls and hill tops when snow depths began hindering movements. These sites supported preferred stands of young pine and juniper and an abundance of deciduous growth that was available with a limited amount of wandering. Dorn (1970) found that wintering moose often concentrated on wet lowlands in mountainous regions in Montana. In Wyoming, Harry (1957) reported that moose moved down from the mountain summer ranges to concentrate on the willow and cottonwood communities along lowland river valleys during winter. Knorre (1959) reported that moose winter habitat selection in the Pechora-Ilych Game Preserve in the Soviet Union was dependent on the availability of browse in relation to snow depth, hardness and crusting conditions. Kelsall and Prescott (1971) reported that snow depths of 70 to 90 cm are considered to restrict moose movements. Specific studies on the effects of snow on moose habitat selection have been reported by Nasimovitch (1955), Des Meules (1964), Kelsall and Prescott (1971) and Coady (1974).

Neu *et al.* (1974) and Chamberlain (1972) indicate the paucity of useable information on preferred moose winter ranges. Neu *et al.* (1974) described a statistical method of determining preference or avoidance of a given habitat in relation to its availability. He found that moose in Minnesota selected the burn periphery areas significantly more than expected according to availability, while the central burn and unburned areas were used significantly less.

2. Moose Food Habits

Peek (1974) reviewed the major findings of forty-one moose food habitat studies and concluded that willows were the primary food source for moose on western ranges. Paper birch, aspen and balsam fir *(Abies* *balsamea)* were the important browse species on eastern ranges. These findings were supported by Hosley (1949) and Pimlott (1961). Peek (1974) recognized the importance of local variations in browse preference; he also recognized that the use of herbaceous forage was related to the relative availability and palatability of forage in the area. Forbs and aquatic plants were considered to be regionally important during the growing season, while grass and grass-like plants generally assumed little importance. Recent investigations by Jordan *et al.* (1973), suggest that in Isle Royale, Minnesota, the seasonal use of herbaceous forage, especially aquatic plants, may supply moose with one or more essential nutrients, particularly sodium. Sodium was found to be comparatively low in woody browse.

In Alaska, Spencer and Chatelain (1953) reported willows and Kenai birch (*Betula kenaica*) as preferred species while aspen was important because of its abundance. The four willows *Salix bebbiana, S. scouleriana, S. arbusculoides* and *S. barclayi*, that grow to a small tree size, were particularly important to moose in the Kenai area (Spencer and Hakala 1964). In Mt. McKinley Park, Murie (1944) considered willows the major summer and winter food of moose and reported white and black spruce browse as unpalatable. Milke (1969) listed the important willows *Salix interior, S. alaxensis, S. arbusculoides, S. pulchra* and *S. niphoclada,* in a decreasing order of preference for the interior Alaska area and indicated that neither the relative abundance nor species density affected the preferential use of willows by moose.

Houston (1968) and Harry (1957) reported winter moose food habit studies for Jackson Hole, Wyoming. Harry (1957) considered red-osier dogwood (*Cornus stolonifera*), mountain ash (*Sorbus scopulina*), bog birch, snow brush (*Ceanothus velutinus*) and bitterbrush (*Purshia tridentata*) as highly palatable to moose in winter, but found their relative utilization to be less than their availability. Willows comprised about 75 percent of the winter diet and were found to contribute a greater proportion of the moose winter diets than expected from their availability. Houston (1968) found that forage preferences were related to vegetation type and reported *Salix pseudocordata*, *S. interior*, sub-alpine fir (*Abies lasiocarpa*) and bitterbrush as preferred species, those receiving greater than 50 percent of the observed use, in their respective communities. Knowlton (1960) reported willows as the major fall and winter food of moose in the Gravelly Mountains. While willows were the major summer browse species utilized, herbaceous forage contributed 71 percent of the total diet. In south-western Montana, Dorn (1970) reported that browse accounted for 90.3 percent and 99.8 percent of moose summer and winter foods, respectively. In summer, *Salix myrtillifolia*, *Betula glandulosa*, *Salix geyeriana*, and *Salix planifolia* accounted for 58.1, 11.8, 9.6 and 6.7 percent of browse use, respectively, while in winter, *S. myrtillifolia*, *S. planifolia*, *S. bebbiana* and *S. geyeriana* comprised 25.0, 24.7, 15.4, and 10.5 percent of forage use, respectively. Dorn (1970) reported that the most important factor contributing to moose browse selection was the relative availability of each species. During the winter, availability was related to shrub height and snow cover. In summer, shrub growth form and species of suitable browse heights influenced browse utilization. Smith (1962) and Stone (1971) reported that willows comprised the major proportion of moose winter diet in the Rock Creek area of western Montana. *Salix discolor* and *S. lemmoni* were preferred over *S. commutata*. Although red-osier dogwood was generally accepted to be a more palatable forage species than willows, it was less abundant and therefore less important on most winter ranges (Peek 1974). In the Cypress Hills, Alberta, Barrett (1972) reported that saskatoon (*Amelanchier alnifolia*), aspen and wild cherry (*Prunus* spp.) comprised 56.0, 21.0, and 12.0 percent of the winter moose diet. Saskatoon was considered to be a more preferred species than willows.

Additional moose food habit studies from North America have been reported by Cowan *et al.* (1950) in British Columbia, Dodds (1960), and Bergerud and Manuel (1968) for Newfoundland, Telfer (1967) for Nova Scotia, Dyer (1948) for Maine, Peterson (1953) for Quebec, Aldous and Krefting (1946), and Mech (1966) for Isle Royale, Minnesota.

Egorov (1965) reviewed the moose nutrition in Yakutia, Soviet Union. He found moose utilized a greater proportion of the available forage species during the summer (66 percent) than during the winter (39 percent). Willow leaves, *Epilobium* spp. and occasionally woody shoots were considered to be the preferred summer foods. Willow contributed 38.6 percent and *Epilobium* spp. 32.7 percent by volume of the summer diet. During the winter, willows dominated the diet of moose, followed by *Cornus alba* and *Chosenia* spp. Winter foraging on willows was reported to be influenced by their availability in relation to their proportion of the shrub vegetation and the height and density of the groves

(Egorov 1965; Borodin 1959). Willows at the periphery of thickets were found to be browsed more intensively than those within thickets.

Knorre (1959) reviewed the moose food habits of the Soviet Union and concluded that although sharply defined seasonal food preferences occurred, the importance of major browse species depended on their availability and abundance. Deciduous trees and shrubs were eaten in approximately equal quantities throughout the year while conifers, evergreen shrubs and herbaceous growth were utilized seasonally in relation to their availability due to snow cover. Moose requirement for vitamins was found to coincide with the seasonal use of conifers. The leafy coniferous growth was found to contain high levels of vitamin C and provitamin A during the winter.

D. Forage Selection by Ungulates

Different species of ungulates differ markedly in their food habits with each species showing innate preferences for certain plants, parts of plants or plants in a particular growth stage (Tribe 1952; Heady 1964). Heady (1964) described preference as selection mediated by innate behavior plus learning. Many factors interact to produce a selective response; some of these factors include: palatability, conditions surrounding available forage, history of the animal and the physiological state of the animal (Cowlishaw and Alder 1960).

Heady (1964) defined palatability as plant characteristics or characters which stimulate a selective response by animals. Similar definitions, used by Young (1948), Cowlishaw and Alder (1960), NAS/NRC (1962) and Marten (1969), insist that palatability is a relative concept that is not constant for a particular food or herbivore, but depends on the type and abundance of associated plants.

Many researchers have studied the relationships between chemical composition or nutritive value of plants and their palatability. In his review of palatability, Heady (1964) reported that high positive correlations have been found between animal preference and protein content; sugars, acetic, linolenic and butyric acids and ether extract. Lignin and crude fiber often showed a negative relationship with increased preference. Tannins were described to have a high negative relationship (Wilkins *et al.* 1953) and no correlation (Hawkins 1955) with preference by cattle. Leigh (1961) reported that grasses highest in phosphate and potash were most acceptable to livestock. Milke (1969) found that moose selected willow species higher in moisture, protein and caloric contents. Radwan and Crouch (1974) reported that fermentations of cellulose and moisture content were more closely related to preference in black-tailed deer than chemical composition.

Conflicting results from various studies have led some researchers to consider positive relationships as extremes and concluded that there appears to be no consistent correlation between chemical composition of forage and its preference (Hardison *et al.* 1954; Heady 1964). The total nutrient value of food species was considered a better indicator of palatability than any single chemical compound (Hardison *et al.* 1954; Cook *et al.* 1956).

Westoby (1974) postulated that an optimized diet by large generalist herbivores was contingent upon their selection of appropriate proportions of required nutrients from a relatively fixed bulk intake. Nutrients which are potentially beneficial (proteins, sugars and soluble carbohydrates, minerals and carotene) would either increase preference or would not change it. Chemicals which reduce food quality (crude fiber, cellulose and lignin) would either reduce preference or not change it. This pattern was illustrated by Marten's (1969) summary of the literature on the responses of preference to nutritional properties of foods. Ether extract or crude fat and organic acids showed only positive correlations. Vitamins exhibited no relationship to preference.

Westoby (1974) related an animal's ability to select an adequate diet to reinforcement learning through nutritional properties at digestion time and subsequent recognition by sensory properties of foods. This approach recognized the necessity and occurrence of sampling available foods, especially uncommon or novel ones. The observed variation in an individual animal's forage selection would thus relate to what an animal would consider palatable in specific physiological states of growth, pregnancy and/or maturity (Tribe 1952).

McClymont (1967) presented a model of food intake regulation that considered phagic behavior as a balance between facilitory and inhibitory stimuli which were integrated by the central nervous system. Facilitory stimuli included total energy demand, social facilitation and palatability. Inhibitory stimuli included rumenal distention and rate of food passage, fatigue through foraging, unpalatable foods, social inhibition, psychic stress and nutritional, disease and heat stresses.

Tribe (1952) indicated that an animal's food preferences must ultimately be explained by terms of sensory reactions, mediated by the environment and metabolic conditions. Krueger *et al.* (1974) reported that taste was the most influential sense affecting forage selection in sheep. The other senses appeared to supplement taste. Smell was found to be of minor importance while touch and sight were related to specific plant conditions as succulence and growth form. Arnold (1966) and Longhurst and Kepner (1968) reported that olfaction was the first sense used in making selection of plant parts or specific phenological stages of plants. Healy (1967) reported that in white-tailed deer, the sense of smell played a more important role in the selection of plant species and individual leaves and twigs than the sense of sight. The recognition of foods by sensory capabilities, coupled with a memory for associated cues has been described for deer (Longhurst *et al.* 1968) and other animals (Freeland *et al.* 1974). Gordon (1970) illustrated that domestic ruminants could generally sense and select for sodium but not for cobalt, magnesium or phosphorous, when deficient in these minerals. Cowlishaw and Alder (1960) found that sheep would select plants that would most readily supply their requirements for salts and energy (carbohydrates). Factors of dung contamination, fungal attack, accessibility, forage density and toughness of the forage interfered with this relationship.

The external form and physical composition of a plant are palatability factors expected to influence animal forage selection (Heady 1964). Preference may be related to presence of awns, spines, hairiness, position of leaves, stickiness and texture. Tribe (1952) described the works of Davies (1925) illustrating how palatability was influenced by the degree of harshness, hairiness and succulence in pasture grasses, and Beaumont *et al.* (1933) showing that the physical property of toughness was of importance in forage selection.

Mineral soil amendments, forage use or clipping that influence the growth and maturity of a plant also affect the relative amounts of certain chemical compounds that influence palatability (Cook *et al.* 1953; Heady 1964). Russell (1958) illustrated that nitrogen fertilization often increased the cell size without proportionate increase in cell-wall material, so the plants were more succulent and less harsh.

E. Nutritive Value of Shrubs

Studies relating the nutritional value of shrubs to wild ruminants in northern regions are limited. Chemical analysis of forage plants, including shrubs, used by barren-ground caribou (*Rangifer tarandus groenlandicus*) were reported by Scotter (1972) and for muskoxen (*Ovibos moschatus*) by Tener (1965). Kobota *et al.* (1970) examined the mineral composition of browse plants used by moose in Alaska. Milke (1969) reported the chemical analysis of four species of willow used by moose in the interior of Alaska. The chemical composition of rumen contents, rumen fermentation and energy requirements of moose in Alaska were reported by Coady and Gasaway (1972) and Gasaway and Coady (1974).

Roberts (1948) reported a survey of the carotene and ascorbic acid content of moose browse in northern British Columbia. Cowan *et al.* (1950) examined the effect of forest succession upon the nutrient values of woody plants used by moose in British Columbia. Total carbohydrates, proteins, ether extract and ascorbic acid content were found to decrease and carotene and total mineral content were found to increase as the forest approached its climax stage. Jordan *et al.* (1973) found that moose browse on Isle Royale contained extremely low levels of sodium.

Further south, studies relating the nutritional value of shrubs to white-tailed deer include reports by Alkon (1961), Hellmers (1940), Swank (1956), Urness (1969) and Swift (1948).

Ullrey *et al.* (1964; 1970; 1972) studied the digestability of cedar (*Thuja occidentalis*) and aspen (*Populus grandidentata*) browse for white-tailed deer in Minnesota. Short (1966) and Short and Reagor (1970) examined the effects of cellulose on cell-wall digestability of shrubs used by mule deer in Colorado. In Texas, Short *et al.* (1974) reported that the cell-wall constituents were negatively related to voluntary food consumption and the rate and extent of forage digestability in small ruminants. Ward (1971) reported in-vitro digestion coefficients of 34.6 and 37.3 for saskatoon and red-osier dogwood using bull elk (*Cervus elaphus*) rumen innoculum in Wyoming.

Seasonal changes in nutritive and mineral composition have been described for red-osier dogwood and mountain maple in Minnesota (Fashingbauer and Moyle 1963), sourwood leaves (*Oxydendrum arboreum*) in

Virginia (Harshbarger and McGinnes 1971), aspen (*Populus tremuloides*) in Utah (Tew 1970) and for selected shrubs used by mule deer in Colorado (Short *et al.* 1966; Dietz *et al.* 1958; 1962). Dietz (1972) illustrated the seasonal variation of nutrients and mineral content of shrubs important to deer in South Dakota. Seasonal changes of nutrients in selected shrubs used by black-tailed deer in Oregon were reported by Hines (1973).

The general trend of the above studies illustrated that protein levels were the greatest in young leaves and meristematic tissues. Protein levels in both leaves and stems decreased progressively throughout the growing season. Translocation of nitrogen from the leaves to the stems before leaf abscission was reported by Kramer and Kozlowski (1960). Protein levels remained relatively stable during the dormant season, although Dietz (1972) found that some shrubs showed an increase in protein from fall to winter. With a few exceptions, acid-detergent fiber, lignin and cellulose content of woody twigs increased from spring through winter, with the most rapid increase occurring during the transition from summer to fall. Fats tended to decrease in shrubs with seasonal progression through July, then increased in fall and winter (Dietz *et al.* 1962). Hines (1973) found considerable variation in crude fat levels of four shrubs at different seasons. Ash content of leaves tended to decrease through the growing season, then increase from summer to fall. Ash content of stems decreased during the growing season and appeared to reach a stable level during the dormant season (Dietz 1972). Calcium content in browse generally increased and phosphorous generally decreased through the growing season; no consistent trend was observed during the winter.

McHargue and Roy (1932) reported that in twenty-three species of deciduous trees, the young leaves contained the largest percentages of phosphorous, potassium and nitrogen. The mature leaves, at the end of the growing season, contained the largest percentages of ash, silica and calcium. Different species of trees showed considerable variation in their content of copper, manganese, zinc, iron and magnesium but showed no consistent trend through the growing season.

Hundley (1959) found a difference in the available nutrients in selected deer-browse species growing on different soils.

Fashingbauer and Moyle (1963) reported the protein, fat, nitrogen-free extract and mineral content of the upper one-third of twigs were greater than that of the lower two-thirds. The reverse was found with regard to moisture and crude fiber.

Kautz (1969), Bailey (1967) and Blair and Epps (1967) have shown that terminal sections of certain browse plants have a higher protein and lower fiber content than subterminal portions. Short *et al.* (1971) illustrated that in-vivo dry matter digestibility were greater in the terminal segment of American beauty berry (*Callicarpa americana*) twigs than in lower segments. Digestibility of the terminal twig portions were found to decrease abruptly when twig elongation neared completion.

F. Shrub Response to Simulated and Natural Browsing

Browse utilization studies and clipping projects in the Kaibab

National Forest have provided information on some effects of twig removal and the desirable level of use for quaking aspen (*Populus tremuloides*) and Stansbury cliffrose (*Cowania stanburiana*) (Julander 1937). Young and Payne (1948) provided similar information from a six year study on redstem ceanothus (*Ceanothus sanguineus*), saskatoon service berry (*Amelanchier alnifolia*), Utah honeysuckle (*Lonicera utahensis*) and rose (*Rosa* spp.) in northern Utah. Other simulated browsing studies to determine the optimum level of use for shrubs were reported by Steinhoff (1959), Neff (1963) and Lay (1965).

The effects of clipping [illegible]e hardwood trees and white cedar (*Thuja occidentalis*) in the [illegible]ates region were investigated by Aldous (1952). After six years of study, Aldous concluded that for white cedar, less than 15 to 20 percent of the annual growth could be removed without adverse effects. Mountain maple (*Acer spicatum*), white birch (*Betula alba*), beaked hazelnut (*Corylus cornuta*), willow (*Salix* spp.) and black ash (*Fraxinus nigra*) produced well under moderate to heavy use while mountain ash (*Sorbus americanus*), red-osier dogwood and red-berried elder (*Sambucus racemosa*) could not withstand heavy use. No attempt was made to differentiate between the species of willow used in this study.

Garrison (1953) investigated the resistance of five shrubs to various intensities of twig removal by clipping in eastern Oregon and Washington. The species studied were antelope bitter brush (*Purshia tridentata*), snow brush ceanothus (*Ceanothus velutinus*), rubber rabbit brush (*Chrysothamus nauseosus*), creambrush rock spirea

(*Holodiscus discolor*) and curl-leaf mountain mahogany (*Ceracarpus ledifolius*). The clipping intensities used were 25, 50, 75 and 100 percent, and were conducted from four to seven years. Garrison concluded that clipping generally stimulated twig production to the detriment of flower and fruit production. Changes in shrub form and an increase in average twig lengths were reported.

Cook and Stoddart (1960) reported that the clipping of herbage from one side of big sagebush (*Artemesia tridentata*) plants resulted in higher lignin and cellulose concentrations, whereas clipping of half of each twig over the entire plant gave higher yields of ether extract, protein and carbohydrates. These authors also concluded that there was little or no translocation of manufactured food from one side of the plant to the other.

Krefting, Stenlund and Seemel (1966) studied the effects of simulated and natural browsing on mountain maple during an eleven year study in Minnesota. This study concluded that natural browsing and artificial clipping of mountain maple stimulated regrowth, but that browsing intensity was not a dominant factor. On natural deer-browsed shrubs, the total number of twigs and the total and average twig lengths were greater than on unbrowsed clumps. With continued moderate clipping, the total number of twigs was found to decrease and the total and average length of twigs to increase in comparison to unclipped shrubs. The weight per 1,000 inches of annual growth was found to vary between years but illustrated a direct relationship with clipping intensity.

Harlow and Halls (1972) reported that yellow poplar (*Liriodendrom tulipifera*) seedlings whose terminal and lateral twigs were clipped in summer were significantly shorter, smaller in stem diameter and had shorter twigs than those clipped in winter. Dogwoods (*Cornus florida*) clipped in summer were significantly larger in stem diameter, lower in dry weight production and had shorter twigs than those clipped in winter.

The response of old bitterbrush shrubs to topping was studied on winter deer range in Idaho (Ferguson and Basile 1966). Topped shrubs produced nearly nine times as much twig growth as the control shrubs one year after manipulation. In subsequent years, topped shrubs out-produced control shrubs, but at a declining rate.

Shepherd (1971) examined the effects of clipping on key browse species during a twelve year period in Colorado. Plants of five species, including service berry, oak brush (*Quercus gambelli*), mountain mahogany, antelope bitter brush and big sagebrush, were subjected to 20, 40, 60, 80 and 100 percent clipping of the current annual growth[1] and a "destructive" level of treatment that removed all the CAG and a portion of the older growth. Browse production, in terms of number and weight of CAG stems, increased during the study for service berry, mountain mahogany and big sagebrush plants subjected to moderate and heavy clipping. Antelope bitter brush was found to be most sensitive to clipping at all intensities and decreased in both browse production by weight and number of current annual stems. The "destructive" clipping treatment was found to have a general debilitating effect on all species

[1]Hereafter referred to as CAG.

METHODS

A. Vegetation Measurements

The canopy cover and frequency of occurrence of all plant species in the sedge meadow, willow savanna, patterned fen and aspen willow plant communities were measured during 6 to 21 July, 1972 and 1973. In each plant community, two 200 x 500 m macroplots were established. In each macroplot, 40 to 200 microplots were located on a stratified random manner using a baseline and a random numbers table, following the method described by Daubenmire (1968). In each 20 cm x 50 cm (0.1 m^2) microplot, the canopy cover class midpoints (%) were recorded for each species present. The canopy cover classes used were:

Range	Midpoint
0 - 5%	2.5%
6 - 25%	15.5%
26 - 50%	38.0%
51 - 75%	63.0%
76 - 95%	85.5%
96 - 100%	98.0%

Frequency of occurrence was calculated as a percentage of plots in which each species occurred in a particular plant community.

The canopy cover of shrubs and trees (greater than 0.5 m in height) in the aspen-willow, willow-savanna, patterned fen and three shrub communities: *Salix maccalliana-Betula glandulosa, Salix discolor-Salix bebbiana-Salix maccalliana* and dense *Salix bebbiana* stands, were measured by the line intercept method. Ten transect lines, 30 m in length, were located in a random manner in each community. The canopy cover of each species was calculated as percent cover.

Annual herbage and browse production was measured at the end of the growing season, during 15 to 31 of August 1972 and 1973, in the sedge meadow, willow savanna, aspen-willow patterned fen and willow-shrub communities. Location of production microplots within the macroplots previously established followed the stratified random method described above. Microplot sizes were 20 cm x 50 cm (0.1 m^2) for herbaceous vegetation and woody seedlings less than 40 cm in height and 50 cm x 100 cm (0.5 m^2) for shrubs and trees greater than 40 cm in height. Herbaceous vegetation was clipped at ground level while current annual growth (CAG) of woody vegetation was clipped from ground level to 2.1 m in height. Herbage and browse were clipped by hand, sorted to species or forage type and placed in paper bags. These samples were oven-dried within 24 hours at about 60°C and weighed to the nearest 0.1 gm. The average dry weight of each species or forage type (per microplot in each community) was converted to dry weight production per unit area (kg/ha). Woody plant production was expressed as available browse, that which was readily obtainable by moose (ground level to 2.1 m in height). Summer browse was converted to available winter browse using a coefficient of twig: leaf ratios of common species in each community. Twig leaf ratios were calculated from the oven-dried weights of leaves and twigs separated for determination of moisture content as described in the methods for nutrient analysis. Forage production among the three sedge-dominated communities and among the five willow and forest communities were statistically compared by analysis of variance and Duncan's new multiple range test.

B. Moose Population and Habitat Use

1. Aerial Surveys

A general reconnaissance flight was conducted on 21 January 1974 using a Cherokee 6 aircraft. The reconnaissance flight was flown at an altitude between 90 and 150 m (agl) and an air speed of about 210 km/h. The flight covered a line between the North Channel of the Mackenzie River, the study area and Fort Providence. A brief search pattern was flown over the willow flats along the North Channel and the Site Two study area. The two observers were the pilot and the author. All moose observed and the plant community in which they were located were recorded.

A strip census of the Site Two study area was conducted on 22 January 1974 using a Cessna 180 aircraft. The strip census was flown at an altitude between 150 and 180 m (agl) and an air speed of about 140 km/h and covered 94.6 km of transect. Two observers, assisted by the pilot recorded all moose occurring within a strip 0.4 km wide on either side of the aircraft. The angle of sight to determine transect width was marked by guides: one on the observer's window and the other on the strut of the aircraft. The plant communities in which moose were observed were also recorded.

A winter moose density was calculated for the general region, using all moose observed on the two aerial surveys. Moose densities in willow-dominated communities in the Site Two study area were calculated from the observations during the strip census. Moose densities were calculated by dividing the number of moose observed by the area covered (0.8 km x transect length) in the respective surveys.

2. Pellet-group Counts

Pellet-group counts were conducted in mid-May during 1973 and 1974. A total of 947 belt transects, 2 m x 50 m (a plot size of 0.1 ha), were located in a random manner within macroplots in the aspen-willow, willow savanna and patterned fen communities in the Site Two study area. In each transect, all moose pellet-groups of the previous winter period were recorded.

Moose utilization (expressed in days use/hectare) was calculated for each plant community in 1973 and 1974, using the following formula:

$$D = \frac{\Sigma p^i \times 50}{t^i \times 13}$$

where D = days-use/ha, Σp^i = sum of pellet-groups recorded in the i^{th} plant community, and t^i = number of transects surveyed in the i^{th} plant community. The assumed moose defecation rate of 13 pellet-groups per day followed that described by Neff (1968) and Timmermann (1974).

3. Moose Winter Food Habits

Moose winter food habits were examined in the aspen-willow, willow savanna and patterned fen communities in the Site Two study area. The relative use of available browse was determined on each macroplot shortly after leaf-flush, in mid-May in 1973 and 1974. Browse species greater than 0.4 m in height were located using the point-quarter method (Smith 1966). The availability of current annual browse and the current and past use of browse by moose was recorded using the browse use and availability-hedging form classes (Tables 1 and 2).

Browse availability was determined by observation of normal minimum and maximum browsing heights occurring on the study area. A shrub was judged to be entirely available when more than 90 percent of the current annual leader production fell between 0.4 m and 2.5 m in height, partially available when greater than 10 percent and less than 90 percent of the current annual growth fell within the browse range and unavailable when greater than 90 percent of the current annual growth was above 2.5 m in height. Use of browse outside the assigned availability range, such as the breaking of branches above 2.5 m, was recorded.

Table 1. Browse use classes indicating the percent of CAG[1] removed.

RANGE	MIDPOINT
non-use	0
1-9	5
10-49	30
50-89	70
90-100	95

[1]Current annual growth.

Table 2. Browse availability and hedging form classes.

1. All available - no hedging
2. All available - lightly hedged
3. All available - moderately hedged
4. All available - heavily hedged
5. Partially available - no hedging
6. Partially available - lightly hedged
7. Partially available - moderately hedged
8. Partially available - heavily hedged
9. Decadent - due to overbrowsing
10. Unavailable

In this study the amount of previous browse utilization on a shrub is defined as a degree of hedging. The degree of hedging is used as a measure of the extent of repeated (yearly) use of a plant. A plant was judged to be slightly hedged if less than 33 percent of the annual leader growth of one preceding growing season had been utilized. Moderate hedging was defined as browse utilization of greater than 33 percent of one previous season or repeated use of less than 33 percent of the CAG. Heavy hedging was defined as repeated use of greater than 33 percent of the available leader production.

Winter use of the current annual leader growth by moose was recorded as a percentage of the available browse on each shrub and assigned the midpoint values of the leader use classes in Table 1. An age classification was assigned to each shrub to differentiate availability due to shrub height, growth form and age. The age classifications used was: seedling, young, mature, decadent and resprout.

Winter browse use was analyzed by comparing the composition and relative use of each browse species in each plant community. Browse use was converted to percent of shrubs and percent of CAG browsed of each species. The Chi-square binomial distribution (Steel and Torrie, 1960) was used to determine the goodness-of-fit by comparing the overall observed and expected frequency distributions. The expected frequency distributions were obtained by multiplying total observations of use by the proportion (percent composition) of each browse species in the plant communities following the method described by Neu *et al.* (1974). If a significant difference was found between the two distributions then it was concluded that moose were not utilizing browse species in proportion to their availability. Where a significant difference between species availability and use occurred, the Bonferroni Z statistic (Bonferroni normal statistics (Millar 1966)) was applied to the observed values, providing confidence intervals for each species (Neu *et al.* 1974). If the observed value fell within the interval, it was concluded that moose were using the species in accordance with its availability. If the observed value fell above or below the interval, moose were considered to be exhibiting an avoidance of, or preference for that browse species, respectively.

Ground observations of moose forage use during winter were recorded during 18 to 21 January, 1974. These observations were unsystematic and consisted of following recent moose tracks for approximately 100 m whenever tracks were encountered during other field work. Information recorded for each track observation included: the plant community in which they occurred, the movement pattern among shrubs during feeding, the browse species eaten, the height of browse use and other observations such as cratering activity.

4. Moose Summer Food Habits

Moose forage use during summer was recorded each time it was encountered during the May to September field seasons in 1972 and 1973 and in mid-August 1974. When recent tracks or evidence of browsing were encountered they were followed for about 100 m and the following information recorded: the plant community, the species of herbaceous or browse plants eaten and for shrubs, the plant portions (leaves and/or twigs) eaten, the amount of CAG removed and the previous browsed condition of the plant.

C. Investigation of Willow Nutrient Content

1. Collection of Browse Samples

The CAG from six species of willow was collected at four week intervals from 8 May to 1 September 1973 and in mid-January 1974. Samples of all species except *Salix candida*, were from the willow savanna community; *Salix candida* samples were from the patterned fen community. Six individual shrubs were selected as replicates for each of browsed and unbrowsed *Salix bebbiana* and *S. discolor* and browsed *S. candida*. Pooled samples of CAG were collected for unbrowsed *Salix candida, S. maccalliana, S. gracilis* and browsed *S. padophylla*. Pooled samples of browsed *Salix candida, S. bebbiana*, and *S. discolor* were collected for analysis of chemical content of twig portions (thirds).

When a sample was collected from an individual shrub, the CAG was collected to represent all aspects of lateral and terminal secondary stems within the available moose browsing range (0.4 to 2.5 m). For a pooled sample, the CAG from a minimum of ten individual shrubs was collected. Each shrub was arbitrarily divided into quadrants, and the CAG from one secondary stem at 1.5 m height was collected from each quadrant.

Individual willow shrubs were selected in a random manner within a representative portion of the plant community. Where browsed and unbrowsed individuals were compared, the closest unbrowsed shrub to a designated browsed individual was selected. On subsequent sampling dates, plants were selected that had not been disturbed by previous sampling or recent moose browsing. In this part of the study, a browsed shrub was required to have been moderately to heavily browsed by moose for three years, including the preceding dormant seasons.

The CAG of each browse sample was separated to leaves and twigs and where twig portions were to be compared, the lower, mid and upper twig thirds were separated. Leaves, twigs and twig portions were then weighed, oven-dried at 65°C for 48 hours, reweighed and the percent moisture calculated.

2. Chemical Analysis

Proximate analysis of willow browse samples was conducted at the University of Alberta. A pooled sample of each species (5 - 10 individual shrubs) from the early summer and winter collections were analyzed for crude fat (ether extract) and phosphorous at the Soil and Feed Testing Laboratory, Alberta Department of Agriculture, in Edmonton.

The nitrogen content of browse samples was determined by the Dumas method, using the Coleman Model 29A, Nitrogen Analyzer. A conversion factor of 6.25 was used to convert percent nitrogen to percent protein (Maynard and Loosli 1969). Acid-detergent fiber and acid-detergent lignin content (lignin) were obtained by the procedure described by Van Soest (1963a; 1963b). The ash content was obtained by the combustion of a 2 gm sample in a muffle furnace, following a method described by Isaac and Kerber (1971). The calcium, magnesium and sodium contents were determined with an atomic absorption spectrophotometer (Isaac and Kerber 1971).

Sample sizes of the above nutrient determinations (June to January sampling periods) were: for moisture, nitrogen, acid-detergent fiber and lignin, five or six samples each of leaves and twigs for browsed and unbrowsed *Salix bebbiana* and *S. discolor* and browsed *S. candida*, and a pooled sample of leaves and twigs from ten individual shrubs for unbrowsed *S. candida, S. maccalliana, S. gracilis* and browsed *S. padophylla* and twig portions; for ash, calcium, magnesium and sodium, three samples of twigs and a pooled sample of leaves (5 - 6 shrubs) for browsed and unbrowsed *S. bebbiana, S. discolor,* and browsed *S. candida,* and a pooled sample of each leaves and twigs (from 10 individual shrubs) of unbrowsed *S. candida, S. maccalliana, S. gracilis* and browsed *S. padophylla* and twig portions. Pooled samples of twigs (10 shrubs) of each species were used from the May collection period. Two replications of each sample were conducted for nitrogen, acid-detergent fiber and lignin. Only one measurement of ash, calcium, magnesium, sodium, phosphorous, crude fat and moisture were conducted per sample. Nutrient levels were described by a mean and standard deviation (when given) using all replications for each species and browsed condition at a particular sampling period. Nutrient levels among species and browsed conditions at each sampling period and among sampling periods for each species and browsed condition were tested for significant differences using the analysis of variance to determine whether a significant difference occurred and Duncan's new multiple range to identify which means were significantly different.

D. The Response of Willows to Natural and Simulated Browsing

1. Simulated Browsing

Browse clipping studies, which simulate moose browse use, were conducted on two species of palatable willows to examine the effect of varying degrees of browsing on CAG production. Simulated browsing treatments were conducted on *Salix bebbiana* and *S. discolor*, in the willow savanna community of Site One. This area was chosen because of its light browse use in previous years. *Salix candida* was not included in the simulated browsing study because it could not be found in adequate density in the Site One area. *Salix candida* was abundant only in the patterned fen community of Site Two, where the distances were too great to facilitate the transport and construction of protective wire cages.

Two 150 x 175 m macroplots, were delineated within representative portions of the willow savanna community in Site One. Within each macroplot, points were located in a stratified random design (Daubenmire 1968). At each point, the four closest willows were chosen if they met the following criteria: a) appropriate species, b) between 0.5 and 2.0 m in height, c) relatively distinctly separated from other shrubs, and d) had not been browsed by moose. Measurements of height, crown diameter, basal diameter (15 cm above the ground) and the number of main stems recorded. Treatments of each shrub were determined in a random manner and tagged with color coded plastic flagging. Ten replications of each treatment were established.

The simulated browsing treatments removed 50, 75 (hedged) and 100 percent of the CAG from the appropriate shrubs. The 50 and 100 percent treatment removed 50 or 100 percent of each current annual twig while the hedged treatment removed about 75 percent of the outer lateral and terminal leaders. The 75 percent clipping treatment, described in this study as "hedged", was included to approximate more closely the actual effect of heavy moose browsing; it normally concentrates on the outer, more available twigs. The control shrubs were measured and tagged, but not protected by wire cages. Ten replications of controls and each simulated browsing treatment were established for each species.

The dates of treatment were 21 June and 25 August 1972, to coincide with the expected low and high portions of the shrub carbohydrate cycle. Eight treatment replications were conducted on *Salix bebbiana* during the dormant season, 28 December 1972, to examine differences between early fall and winter effects of browsing. In both species, the <u>CAG</u> from the 100 percent clipping treatment was retained, oven-dried and weighed.

In August 1973, the CAG of treated and control shrubs were measured. Five secondary stems were removed from each shrub in a stratified manner to include one stem from each lateral quadrant and from the terminal portion of the crown. The number, lengths and oven-dried weight of the current annual twigs were measured and recorded. The diameter and age of secondary stems were measured just below the lowest branching point (Figure 2). Production and size of current annual twigs, stem ages and stem diameters were compared among treatments by analysis of variance and Duncan's new multiple range test.

In this study, a secondary stem was defined as a unit of shrub growth, comprising a major branch supporting the current annual growth and terminal branches in the foliage zone (Figure 2). Selection of this unit was based on field observations of the relatively uniform branching pattern and size of major and secondary stems that were characteristic of each willow species. This uniform branching pattern occurred in willows in both browsed and unbrowsed conditions.

2. Natural Browsing

Two willow species in Site Two were selected to examine the effect of moose browsing on the production of current annual twigs. *Salix bebbiana* was the willow selected in the willow savanna community and *Salix candida* was the other willow selected in the patterned fen community. These species were chosen because they exhibited noticeable variation in intra-specific browse preference by moose.

Subsamples of secondary stems from moose browsed and unbrowsed shrubs, were selected in a random manner from the total available within

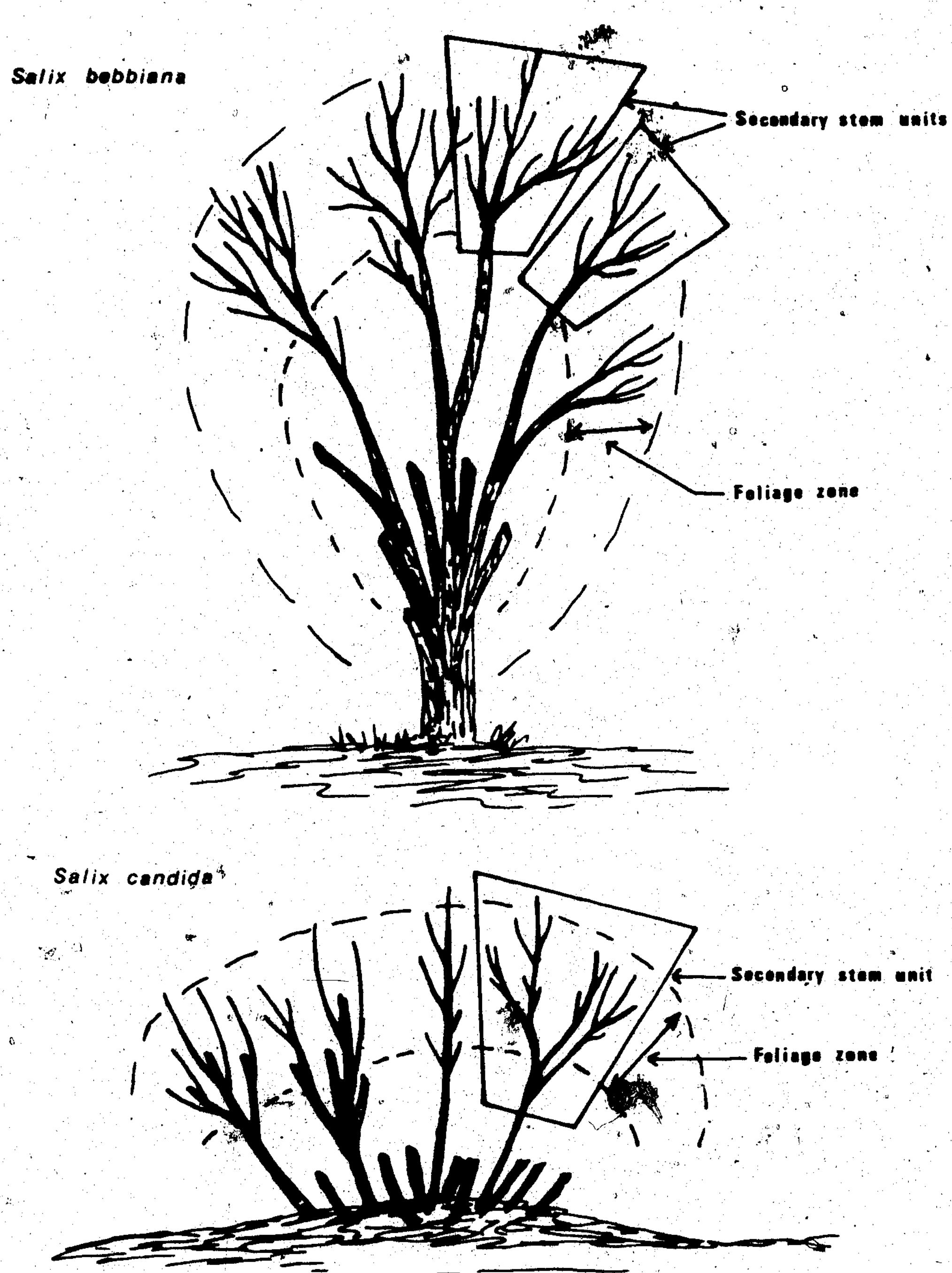


Figure 2. Characteristic branching pattern of *Salix bebbiana* and *Salix candida* shrubs, illustrating the secondary stem units. Each secondary stem unit comprises a major branch supporting the terminal branches and current annual growth in the foliage zone.

the macroplot. Moose browsed shrubs selected, were required to have three years of moderate to heavy utilization, including the preceding dormant season.[1] The number, lengths and oven-dried weights of the current annual twigs per secondary stem were measured at a point immediately below the last branch. Differences in current annual twig production and diameter of secondary stems between browsed and unbrowsed shrubs were analyzed using an unpaired Student's test.

Within mature, moderately browsed *Salix candida* clumps, the number and length of the current annual twigs were measured on secondary stems having different browse histories. These measurements were recorded in late August 1972. Differences in twig production among secondary stems were compared by analysis of variance and Duncan's new multiple range test.

F. Edaphic Variables

Soil temperature and soil moisture were monitored at four week intervals from 8 May to 1 September, 1973. The soil sampling data were coincident with sampling of willows for chemical and nutrient content.

Ten sampling plots were selected on a stratified random basis in the willow savanna, aspen-willow and patterned fen communities. At each sampling plot, one moisture sample and two soil temperature

[1]Browse use in previous years was evaluated by examining the twig branching pattern on secondary stems and counting the number of terminal bud leaf scars and dead browsing points (Figure 12).

measurements (°C) were collected at the following three depths:

Depth Class	Soil Moisture	Temperature
A	0-15 cm	8 cm
B	15-30 cm	23 cm
C	30-45 cm	38 cm

Depths to frozen soil or permafrost were recorded where applicable. In the wet sedge meadow, soil temperature and soil moisture were monitored during June July and August in conjunction with forage production experiments. No measurements were taken in May because these meadows were flooded during the spring snow melt. Thirty control sampling plots were selected on a stratified random manner. Soil moisture measurements were collected at the A, B and C depth classes previously described, and soil temperature was measured at the 10 cm and 20 cm depths.

Soil moisture samples were stored in soil moisture tins, weighed, and then oven-dried (65°C) for 48 hours. Samples were reweighed and the percentage moisture calculated using the following equation:

$$\text{Percent moisture} = \frac{(\text{wet weight} - \text{dry weight})}{\text{dry weight}} \times 100.$$

A soil pit was dug near the center of each plant community and the soil profile was classified to the appropriate order.

RESULTS

A. Vegetation and Soils

1. Sedge Meadow Communities

The wet sedge meadow or *Carex atherodes-Carex aquatilis-Scolochloa festucacea* community was characteristic of lowland sites where surface water generally persisted to the middle of the growing season. The soils were Rego Gleysols overlain by 15 to 20 cm of fibrous peat. Soil moisture levels remained high during the 1972 growing season but decreased rapidly during the 1973 growing season due to an early spring thaw and limited rainfall. Soil temperatures reached a peak of 11.2°C at 8 cm and 8.7°C at 20 cm below the ground surface in mid-July 1973. The microtopography was characterized by peaty hummocks 15 to 45 cm in height (Appendix B).

Wet sedge meadows were dominated by *Carex atherodes* which contributed about 70 percent (1,847 kg/ha) of the mean total annual production of 2,535 kg/ha (Table 3). *Carex aquatilis* and *Scolochloa festucacea* were locally abundant and had a mean production annually of 227 kg/ha and 232 kg/ha respectively. *Calamagrostis inexpansa* grew mainly on peaty hummocks and contributed 180 kg/ha. Common secondary species, including *Galium trifidum*, *Mentha arvensis*, *Scutellaria galericulata* and *Petasites sagittata*, contributed to the 46 kg/ha of forb production. Less common species recorded in this community are listed in Appendix A.

Table 3. Mean annual production (kg/ha, dry weight) of herbage and browse in sedge dominated communities.

Species or Forage Group	Wet Sedge Meadow[1]	Dry Sedge Meadow[1]	Patterned Fen-Meadows[2]
	PLANT COMMUNITY		
n[3]=	131	100	90
Carex atherodes	1,847	846	278
Carex aquatilis	228	122	455
Calamagrostis inexpansa	183	191	
Scolochloa festucacea	232	152	
Forbs	46	234	10
Salix candida			27
Salix bebbiana		100	
Salix maccalliana		16	
Total Herbaceous	2,535	1,704	742
Total Available Browse		116	27
Total Available Production[4]	2,535[a]	1,820[b]	769[c]

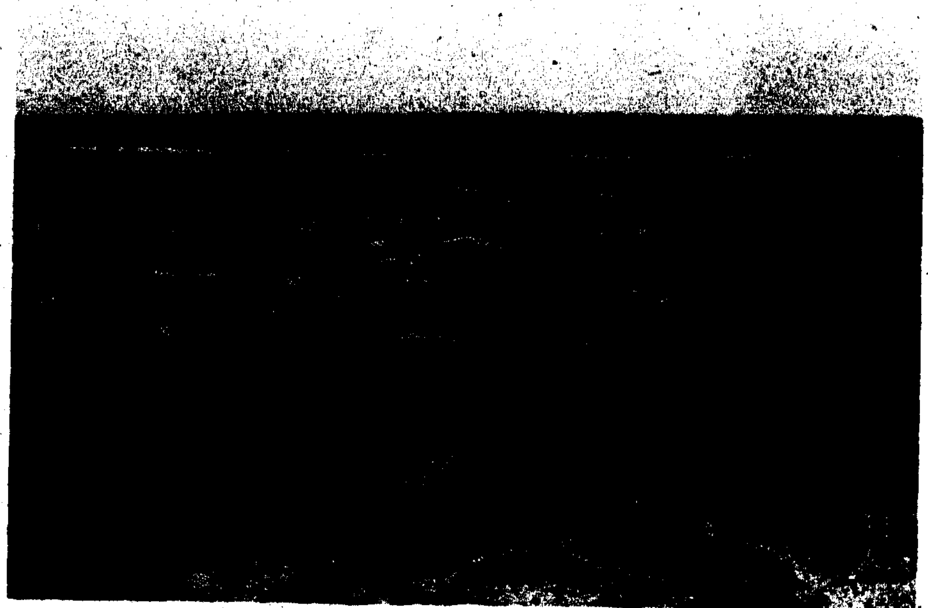
[1]Mean production from 1972 and 1973 growing seasons.
[2]Production measured only in 1973.
[3]n = numbers of 20 cm x 50 cm sample plots.
[4]Values within the same row followed by a common letter are not significantly different (P<0.05).

A "dry" sedge meadow community was recognized on better drained sites. This community was dominated by *Carex atherodes*, and had a high cover of *Calamagrostis inexpansa* (75%) and a greater variety and a higher production of forbs (234 kg/ha) than the wet sedge meadows. Mean annual production was 1,704 kg/ha of herbage and 116 kg/ha of browse (Table 3). This community appeared to be transitional between the wet sedge meadows and the willow savanna communities.

2. Patterned Fen Community

This community was characterized by small sedge fens or meadows separated by low dendritic ridges that paralleled the drainage pattern (Figure 3). The fens covered 75 percent and the ridges 25 percent of the community. The patterned fens were poorly drained; surface water was present in the troughs between the peat hummocks of the fens for most of the growing season. Although the ridges were somewhat drier, the organic soils retained a high moisture content throughout the frost-free season (Figure 4). The organic soils of the ridges and fens were described as Cryic Mesisols. They were underlain by permafrost which receded to about 75 cm in August. Temperature of surface soils at 8 cm and 23 cm reached a maximum of 10°C and 6°C, respectively, in early August 1973 (Figure 4). Anaerobic conditions and calcareous marl deposits were characteristic of the saturated fen soils.

Carex aquatilis was the dominant plant of the sedge fens with a



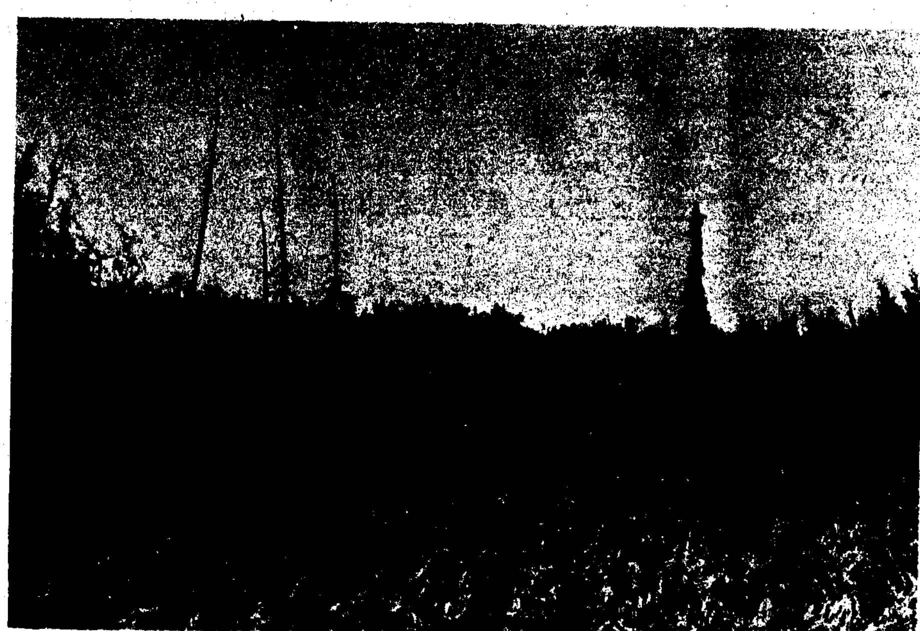


Figure 3. The patterned-fen plant community from aerial (above) and ground (below) perspectives, showing the distribution of sedge fens and the intervening willow dominated ridges.

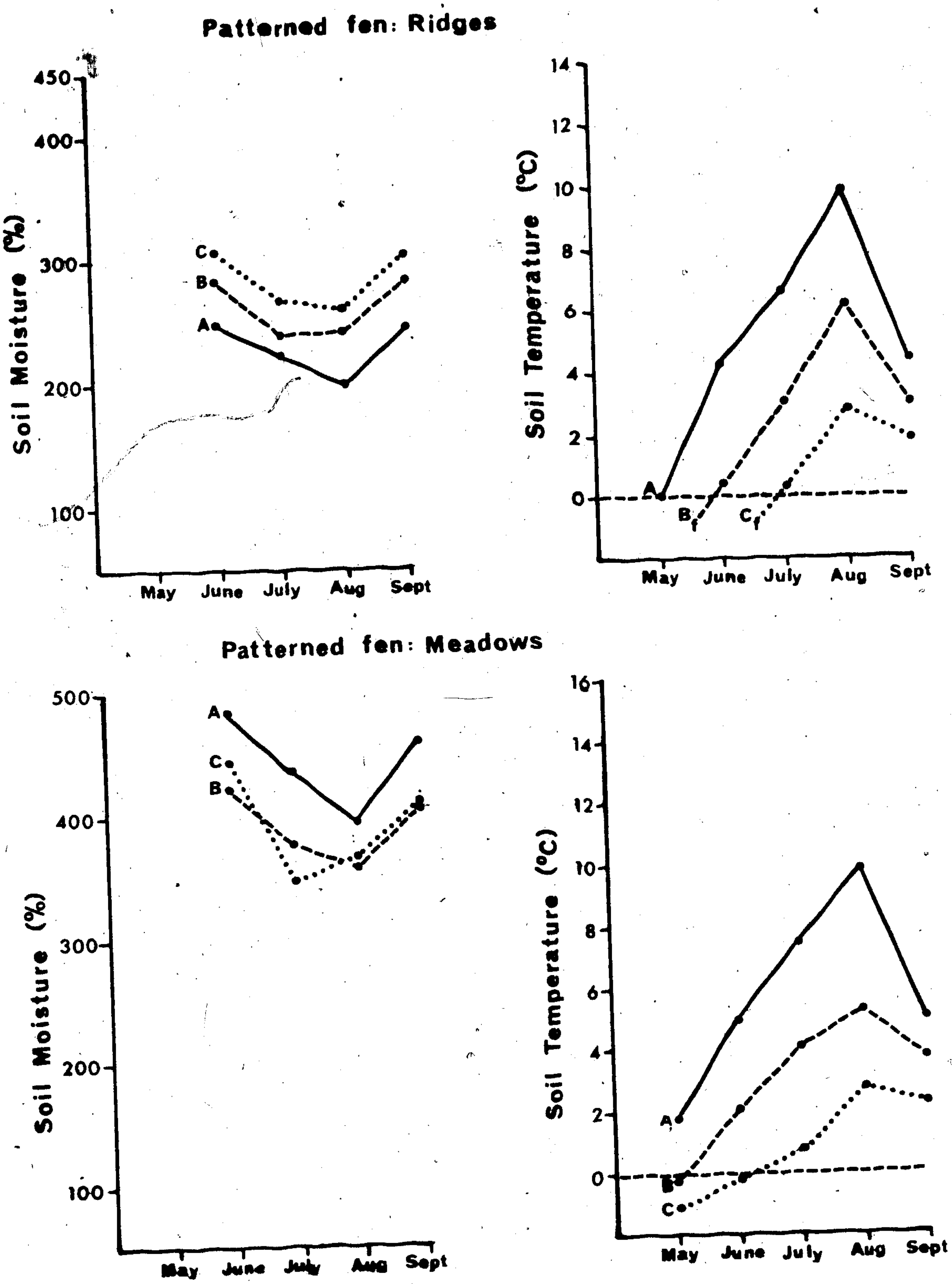


Figure 4. Moisture (%) and temperature (°C) in the 8 cm (A), 23 cm (B) and 38 cm (C) soil depth classes in ridges and meadows of the patterned fen community from May to September.
(f = frozen soil conditions).

Table 4. Canopy cover (%) and frequency of plants in the aspen-willow, willow savanna and patterned fen communities.

SPECIES		Willow Savanna	Patterned Fen: ridges	Patterned Fen: meadows	Aspen-willow
Salix bebbiana	cover	22			36
	frequency	40			55
Salix discolor	cover	3	3		2
	frequency	6	4		2
Salix candida	cover	+[1]	17	7	
	frequency	+	32	14	
Salix pedophylla	cover	2	10		
	frequency	3	18		
Salix maccalliana	cover	1	10	+	4
	frequency	4	14	1	7
Salix gracilis	cover	7			
	frequency	16			
Salix glauca	cover				8
	frequency				18
Betula glandulosa	cover	+	30	+	12
	frequency	+	43	1	24
Myrica gale	cover		18	+	
	frequency		36	1	
Shepherdia canadensis	cover		+		13
	frequency		3		31
Rosa acicularis	cover	2	5		3
	frequency	8	28		13
Ribes oxyacanthoides	cover		2		+
	frequency		4		+
Ledum groenlandicus	cover		1		
	frequency		2		
Populus tremuloides	cover	1			35
	frequency	3			38
Populus balsamifera	cover				4
	frequency				7
Picea glauca	cover	+			9
	frequency	+			19
Picea mariana	cover		4		
	frequency		8		
Larix laricina	cover		1		
	frequency		2		
Carex atherodes	cover	13	1	15	1
	frequency	36	3	1	3
Carex aquatilis	cover	6	40	60	
	frequency	15	81	94	
Carex sartwellii	cover	5			
	frequency	15			
Carex aurea	cover	1			
	frequency	3			
Carex deflexa	cover				1
	frequency				7
Juncus balticus	cover	4			
	frequency	15			
Calamagrostis inexpansa	cover	74	20	22	11
	frequency	95	49	40	39
Scolochloa festucacea	cover			1	
	frequency			4	

[1]Value less than 0.5 percent.

Table 4. continued.

SPECIES		Willow Savanna	Patterned Fen ridges	Patterned Fen meadows	Aspen-willow
Elymus innovatus	cover				5
	frequency				23
Agropyron trachycaulum	cover	6	1		
	frequency	17	2		
Hordeum jubatum	cover	3			
	frequency	11			
Poa palustris	cover	2			
	frequency	7			
Aster junciformis	cover	4			
	frequency	40			
Fragaria virginiana	cover	7			10
	frequency	31			66
Astragalus agrestis	cover	8			1
	frequency	16			3
Stachys palustris	cover	2		2	
	frequency	25		26	
Achillea millefolium	cover	1			1
	frequency	11			21
Galium boreale	cover	1			1
	frequency	11			19
Thalictrum occidentale	cover	1			
	frequency	10			
Petasites sagittata	cover	1			1
	frequency	7			2
Mentha arvensis	cover	1		+	
	frequency	6		15	
Epilobium angustifolium	cover	1	1		5
	frequency	3	16		34
Stellaria spp.	cover	2		1	
	frequency	15		20	
Triglochin maritima	cover	1		1	
	frequency	3		1	
Rubus acaulis	cover		1	+	4
	frequency		27	4	37
Arctostaphylos uva-ursi	cover		1		4
	frequency		12		15
Linnea borealis	cover				1
	frequency				5
Potentilla palustris	cover		2	2	
	frequency		12	10	
Pyrola asarifolia	cover		1		
	frequency		14		
Equisetum scirpoides	cover		2		
	frequency		10		
Geocaulum lividum	cover		1		
	frequency		10		
Polygonum amphibium	cover			2	
	frequency			15	

canopy cover of 60 percent (Table 4) and a production of 455 kg/ha in 1973 (Table 3). *Carex atherodes* was locally abundant near the periphery of the sedge fens. Total shrub cover in the meadows was about 11 percent.

The low ridges varied from 0.3 to 1.5 m in height and 3 to 15 m in width. Many of the ridges had depressed centers and appeared to be formed by frost action in the adjacent fens. Black spruce and larch were apparently the climax species on the ridges, but only a few remnants had survived the former fires. Young black spruce and larch had a canopy cover of about 5 percent (Table 4).

The ridges were dominated by a variety of shrubs in two overlapping zones. *Salix candida* and *Myrica gale* predominated on the lower slope of the ridge while *Betula glandulosa*, *Salix padophylla* and *Salix maccalliana* shared dominance of the upper slope and top of the ridge. Secondary shrub species included: *Salix discolor*, *Rosa acicularis* and *Ribes oxyacanthoides*. The available browse production on the ridges was 1,239 kg/ha in 1973 (Table 5). Forage production in meadows is shown in Table 3.

The herbaceous cover was dominated by *Carex aquatilis* with *Calamagrostis inexpansa*, *Potentilla palustris* and *Equisetum scirpoides* as secondary species. *Carex aquatilis* produced 89 percent (223 kg/ha) of the total herbage production in 1973 (Table 5).

Table 5. Mean annual production (kg/ha) of herbage and available browse in willow and forest communities.

SPECIES OR FORAGE GROUP	PLANT COMMUNITY				
	Willow Savanna[1]	Willow-shrub Communities[1]	Patterned Fen Ridges[2]	Aspen-willow Lowlands[2]	Aspen Uplands[1]
n[4] =	60	60	54	60	54
HERBACEOUS					
Sedges	143	354	223	1	
Grass	279	151	27		158
Forbs	256	70	—[3]	38	38
BROWSE					
Salix bebbiana	249	102		280	124
Salix discolor	44	314	46	3	
Salix maccalliana	17	447	139	4	
Salix gracilis	91	63			
Salix padophylla	7		340	3	
Salix candida	22	102	361		
Betula glandulosa		370	260		
Populus tremuloides	1	4		12	55
Populus balsamifera				4	4
Shepherdia canadensis				164	230
Miscellaneous shrubs	12	3	90	21	122
Total Herbaceous[5]	678[a]	562[a]	250[b]	39[c]	196[b]
Total Available Browse[5]	442[a]	1,406[b]	1,239[b]	491[a]	535[a]
Total Winter Browse Available	87	281	272	47	52
Total Production[5]	1,120[a]	1,968[b]	1,489[c]	530[d]	731[c]

[1]Mean production from the 1972 and 1973 growing seasons.
[2]Production measured only in 1973.
[3]Forbs included with grass category.
[4]n = number of 1 sq. m sample plots.
[5]Values within the same row followed by a common letter are not significantly different ($P<0.05$).

The total available production of the patterned fen community was 948 kg/ha. Herbaceous forage contributed 65 percent (619 kg/ha) and browse 35 percent (330 kg/ha). The available winter browse was 67 kg/ha.

3. Shrub Communities

Poorly drained lowlands on minerotrophic soils were characterized by extensive stands of willow and bog birch (*Betula glandulosa*). The soils were classified as Rego Gleysols that have an organic surface layer 10 to 15 cm thick, over a thin, dark colored organic-mineral horizon over stratified silty clay. These communities were flooded during spring run-off and the soils remained wet and cool throughout the summer. Frost cracks, up to 30 cm in depth, and low spreading hummocks were common in localized areas. The dominant overstory species varied with the site characteristics and the moisture continuum from the wet sedge meadows to the willow savanna.

The *Salix maccalliana-Betula glandulosa* community formed low, dense stands, 1.2 to 2.4 m in height, with a canopy cover of about 65 percent (Table 6). Secondary shrubs included: *Salix discolor*, *S. bebbiana* and *S. candida*. Characteristic understory species were *Carex aquatilis*, *Calamagrostis inexpansa* and *Rubus acaulis*.

Dense stands of a *Betula glandulosa* community occurred infrequently in the study area; but formed extensive stands in the surrounding area.

Table 6. Canopy cover (%) of shrubs in two willow dominated communities.

Shrub Species	PLANT COMMUNITY *Salix maccalliana-Betula glandulosa*	PLANT COMMUNITY *Salix discolor-Salix bebbiana-Salix maccalliana*
n[1]=	10	10
Salix bebbiana	5.5	9.0
Salix discolor	7.7	6.2
Salix gracilis	0.1	0.4
Salix maccalliana	22.9	9.4
Salix padophylla	1.6	1.0
Salix candida	3.7	1.8
Salix spp.	0.3	0.6
Betula glandulosa	20.2	8.7
Populus tremuloides	2.4	3.5
Rosa acicularis	0.3	-
TOTAL SHRUB COVER	64.7	40.6

[1]n = number of 30 m line-intercept plots.

Salix discolor, *S. bebbiana* and *S. maccalliana* occurred as co-dominant overstory species in shrub communities characterized by numerous small sedge meadows. *Betula glandulosa* was a common understory shrub. The canopy averaged three meters in height and had a 40 percent cover (Table 6). *Carex atherodes* and *Scolochloa festucacea* dominated the meadows while *Carex aquatilis* and *Calamagrostis inexpansa* were common under the willow cover. The edge effect of these small meadows appeared to increase the availability of browse for moose.

Dense stands of mature willow, 1.8 to 4.6 m in height, were dominated by *Salix bebbiana*. Associate shrubs were *S. discolor* and *S. gracilis*. The understory was light and characterized by *Calamagrostis inexpansa* and shade-tolerant forbs. The majority of browse was unavailable to moose due to the height and maturity of the stands.

The average herbage and browse production of all willow dominated communities combined from 1973 and 1974 are given in Table 5. The mean production of available browse was 1,406 kg/ha, and ranged from a high of 2,225 kg/ha in dense low shrub communities to 702 kg/ha in dense stands of mature *Salix bebbiana*. Using the average leaf to twig ratio (3.9:1) of willows in open shrub communities, approximately 280 kg/ha of browse is available to moose in winter. The mean herbage production was 562 kg/ha. *Carex aquatilis* and *C. atherodes* contributed 62 percent and grasses, primarily *Calamagrostis inexpansa*, provided 26 percent of the total herbage production.

4. Willow Savanna Community

The willow savanna community was described as a *Calamagrostis inexpansa-Carex atherodes* grassland dominated by willows that are distributed relatively uniformly throughout the community (Figure 5). Willows were distributed singly or in small clusters with a mean distance of 6.5 m between shrubs greater than 0.5 m in height.

The soils of the willow savanna community were an Orthic Gleysol with a thin organic surface layer (L-H), 3 to 8 cm thick, over a black organic mineral horizon (AH), 8 to 13 cm thick, over stratified and gleyed silty clay. The presence of a discontinuous B horizon indicates a development toward an Orthic Humic Gleysol. The soils were imperfectly drained and retained soil moisture above drought point throughout the growing season in 1973 (Figure 6). Soil temperatures rose rapidly in June and reached a maximum of 15°C at 8 cm and 12°C at 38 cm in August 1973.

Mean frequency and canopy cover of major species in the willow savanna community are listed in Table 4. The total shrub cover was 38.6 percent and was dominated by *Salix bebbiana* (58 percent of the total cover). Secondary species: *Salix gracilis, S. discolor, S. padophylla* and *S. maccalliana* contributed 19, 7, 5, and 3 percent, respectively, of the shrub cover. *Salix candida* occurred sporadically and became more frequent toward the transition zone between the willow savanna and poorly drained communities, particularly the

Figure 5. The willow savanna plant community from aerial (above) and ground (below) perspectives, showing the scattered distribution of willows in a *Carex atherodes* - *Calamagrostis inexpansa* grassland.

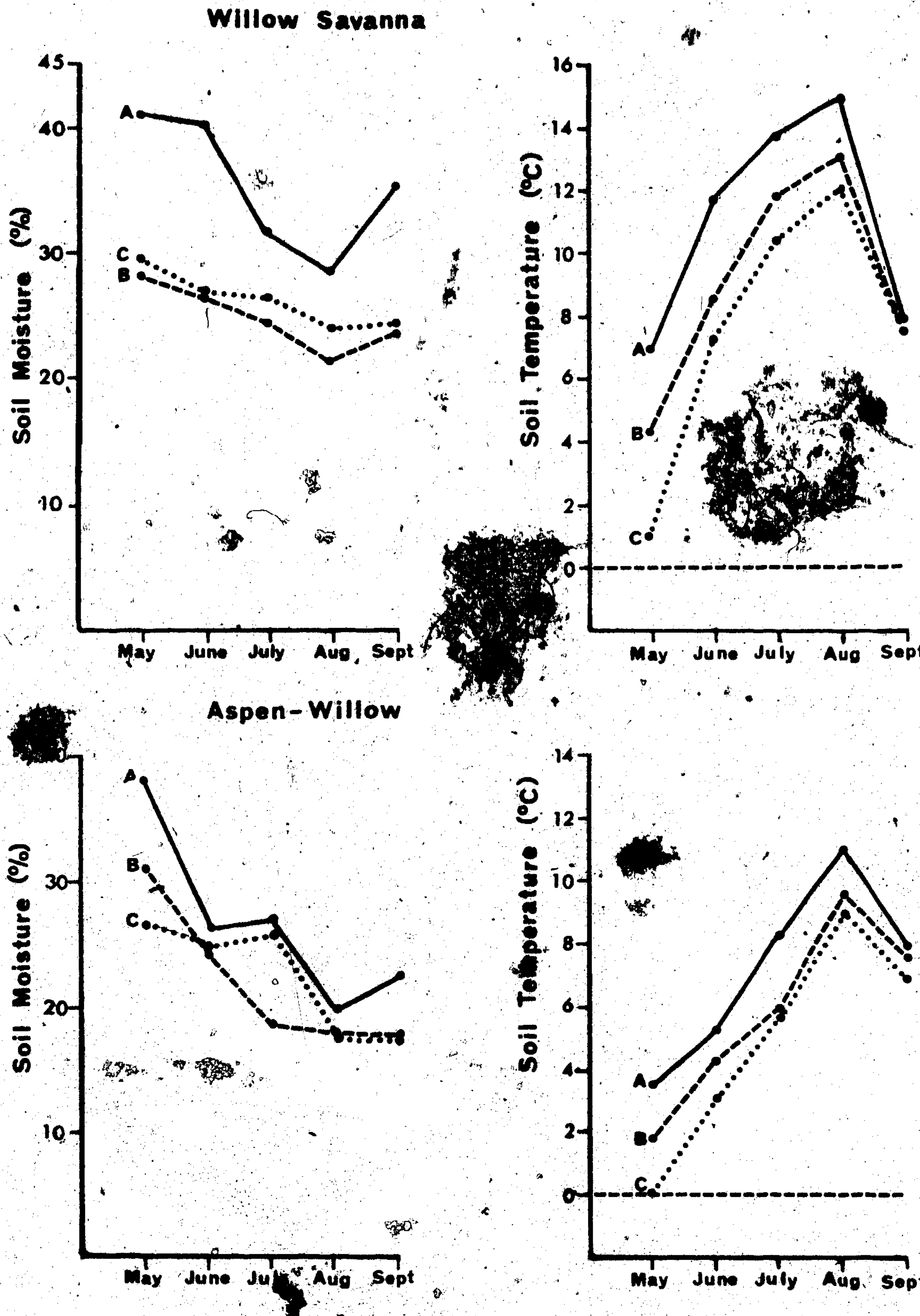


Figure 6. Moisture (%) and temperature (°C) in the 8 cm (A), 23 cm (B) and 38 cm (C) soil depth classes in the willow savanna and aspen-willow communities from May to September.

patterned fen community. Scattered aspen clones were established on better drained sites. Invasion of aspen into the willow savanna community appeared to be limited by seasonal fluctuations in soil moisture conditions. The total production of browse below 2.1 m was 442 kg/ha while the winter browse was 87 kg/ha (Table 5).

The grassland cover was dominated by *Calamagrostis inexpansa* (74.3%) with *Carex atherodes* (12.6%), *C. aquatilis* (5.5%), *C. bartwellii* (5.4%) and *Agropyron trachycaulum* (6.1%) as secondary species (Table 4). Common forbs included: *Astragalus agrestis*, *Aster junciformis*, and *Fragaria virginiana* with a cover of 7.5, 4.2 and 6.5 percent, respectively. Total herbaceous production averaged 678 kg/ha (Table 5).

5. Aspen-willow Community

The mesophytic uplands and better drained lowlands were dominated by a *Populus tremuloides-Salix bebbiana-Shepherdia canadensis-Elymus innovatus* plant community. Occasional patches of white spruce occurred as relics of the former climax forest. Evidence of previous fires were observed in the form of charred logs and fire-scarred mature aspen. Young, regenerating white spruce were common but of sporadic occurrence.

The mean frequency and canopy cover of herbaceous and browse species in the aspen-willow community are given in Table 4. Both frequency and canopy cover varied between upland and lowland sites and appeared to be related to soil moisture conditions. Generally, the aspen formed a moderately open stand of trees, 15 to 20 m in height and averaged 15 cm d.b.h.,[1] while mature trees reached 30 cm d.b.h. Aspen cover varied between 35 and 47 percent. Scattered balsam poplar, generally located in moist sites, had a mean cover of 4 percent. A distinct tall shrub layer was dominated by willows, primarily *Salix bebbiana*, and had a canopy cover of 36 percent. *Shepherdia canadensis* and *Rosa acicularis* formed a low shrub layer. Herbaceous cover was characterized by *Elymus innovatus*, *Calamagrostis inexpansa*, *Fragaria virginiana* and *Epilobium angustifolium*. *Arctostaphylos uva-ursi* formed the majority of ground cover on the drier sites.

Total available forage production varied from 731 kg/ha in upland sites to 530 kg/ha in lowland sites (Table 5). Herbaceous production was considerably higher in upland sites (196 kg/ha) than in lowland sites (39 kg/ha). The mean browse production was 520 kg/ha, of which *Shepherdia canadensis* contributed 40 percent (207 kg/ha), and willows 43 percent (224 kg/ha).

Other available browse, including *Rosa acicularis*, *Amelanchier alnifolia*, aspen and balsam poplar, had a mean production of 89 kg/ha.

[1]dbh = diameter at breast height

Willows in the aspen poplar community had a leaf to twig ratio of 9.4:1, reducing the palatable winter browse to about 22 kg/ha.

B. Moose Abundance

A total of 26 moose were observed over 309 km flown during aerial surveys in January, 1974. The average density of moose in the region was estimated at 0.21 moose per square kilometer.

Seventeen moose were recorded in the Site Two study area, yielding an observed density of 0.47 moose per square kilometer. The density of moose in willow dominated communities was 0.9 moose per square kilometer. No moose or moose tracks were observed in the aspen-willow or mixedwood communities.

C. Winter Habitat Use

1. Use of Plant Communities

The pellet-group survey showed moose used the willow savanna and patterned fen communities considerably more than the adjacent aspen-willow community (Table 7). The willow savanna community sustained 3.2 and 1.3 days-use per hectare in 1973 and 1974, respectively, while the patterned fen community sustained similar use in both years (an average of 2.4 days-use per hectare). The aspen-willow community sustained low use, averaging 0.4 days-use per hectare, in both years.

Table 7. Moose use of three plant communities in the Site Two study area; calculated from pellet-group counts in 1973 and 1974.

Plant Community	Year	Sample size[1]	Pellet-groups/ hectare	Moose days/hectare
Willow savanna	1973	230	41.6	3.2
	1974	100	16.9	1.3
	Mean		29.9	2.3
Patterned fen	1973	200	29.9	2.3
	1974	100	32.5	2.5
	Mean		31.2	2.4
Aspen-willow	1973	217	5.7	0.4
	1974	100	3.9	0.3
	Mean		4.8	0.4

[1]Number of 2 m x 50 m pellet-group plots.

Observations of pellet-group distribution within a community showed that localized areas received greater use than other portions of the same community. Field observations also indicate a change in plant community use during the winter. In mid-winter, nearly all moose and moose feeding activities were observed in the patterned fen community. In the following spring, considerably more moose winter browse activity was observed in the willow savanna than had been observed during mid-winter. Local residents reported greater movements of moose, particularly crossing the highway near the study area, during late February and in March than during early winter periods. This increase in moose activity was also reported to generally occur when snow depths increased and began crusting.

The change in intensity of use of plant communities between years shown by pellet-group counts (Table 7) is also shown by the amounts of CAG browsed by moose (Table 8). The magnitude of change in total browse use in the willow savanna between the winters of 1972-1973 and 1973-1974 is similar to the decrease in days-use per hectare between these winters. This relationship between total browse use and days-use per hectare also follows for the patterned fen and aspen-willow communities (Tables 7 and 8).

2. Moose Winter Food Habits

Moose winter browse use was examined in three plant communities by comparing the composition and relative use of deciduous browse (Table 9). Goodness-of-fit comparisons showed that the expected

Table 8. Percent of available CAG[1] browsed by moose in three plant communities during two winters.[2]

	PLANT COMMUNITY		
Winter	Willow Savanna	Patterned Fen	Aspen-willow
1972-73	12.4	5.9	2.2
1973-74	4.5	8.2	1.0
MEAN	7.8	7.1	1.5

[1]Current annual growth.
[2]Data derived from Table 9.

Table 9. A comparison of the species composition and winter use[1] of deciduous browse by moose in three plant communities.

Species	Willow Savanna: Composition (%)	Willow Savanna: % Shrubs Browsed	Willow Savanna: % CAG[2] Browsed	Patterned Fen: Composition (%)	Patterned Fen: % Shrubs Browsed	Patterned Fen: % CAG Browsed	Aspen-willow: Composition (%)	Aspen-willow: % Shrubs Browsed	Aspen-willow: % CAG Browsed
S. bebbiana	56.1	24.4	8.5	3.5	20.0	3.6	52.1	7.7	1.9
S. discolor	15.4	23.7	8.9	24.0	19.9	6.4	3.9	6.7	1.3
S. gracilis	14.5	0	0				3.5	0	0
S. maccalliana	5.3	0	0	10.7	6.6	1.4			
S. candida	4.3	36.5	18.3	37.0	39.8	13.7	0.5	25.0	2.5
S. padophylla	1.3	68.8	46.3	2.9	14.6	5.4	3.1	8.3	1.7
S. glauca							15.7	0	0
B. glandulosa				21.9	1.6	0.3	6.3	14.3	5.5
P. tremuloides	2.4	20.7	6.2				9.1	1.4	0.4
P. balsamifera	0.7	25.0	12.5						
Sample Size	1,210	248	95	1,423	309	101	776	44	11
Mean		20.5	7.8		21.7	7.1		5.6	1.5

[1]Combined data from the 1972-1973 and 1973-1974 winter seasons.
[2]Current annual growth.

distribution of browse use differed significantly from the occurrence of browse species in each plant community (Table 10).

In the willow savanna community, the number of *Salix bebbiana*, *S. candida* and *S. padophylla* shrubs browsed were significantly greater than expected according to availability. No *Salix maccalliana* and *S. gracilis* shrubs were browsed. They were considered unpalatable species avoided by moose. The number of *Salix discolor*, *Populus tremuloides* and *P. balsamifera* shrubs browsed fell within the range expected according to availability.

A similar trend of browse preference and avoidance is shown by the amount of CAG browsed from each species (Tables 9 and 10). *Salix padophylla* had the highest proportion of individual shrubs browsed (68.8%) and the most CAG browsed (46.3%), followed by *Salix candida* with 36.5% of the shrubs browsed and 18.3% of the CAG browsed. The amount of browse removed from both species was significantly greater than expected according to availability. Browse use of *Salix bebbiana* and *S. discolor*, 8.5% and 8.9% respectively, fell within the range expected. While the number of *Salix bebbiana* shrubs browsed was significantly greater than expected, the total amount of CAG removed was not, indicating that moose removed less CAG from each browsed *Salix bebbiana* shrub than browsed *Salix padophylla* and *S. candida* shrubs.

In the patterned fen community only *Salix candida* sustained significantly greater use than expected. Browsing on about 40 percent

Table 10. A comparison of the observed and expected use of shrubs and CAG of different browse species by moose in three plant communities.

Species	WILLOW SAVANNA				PATTERNED FEN				ASPEN-WILLOW			
	Number of shrubs browsed		Units of CAG[1] browsed		Number of shrubs browsed		Units of CAG browsed		Number of shrubs browsed		Units of CAG browsed	
	obs[2]	exp[3]	obs	exp	obs	exp	obs	exp	obs	exp	obs	exp
S. bebbiana	166 +[4]	139	58 o	53	10 o	11	2 o	4	31 +	23	8	6
S. discolor	44 o	38	17 o	15	68 o	74	22 o	24	2 o	2	a	a[5]
S. gracilis	0 –	36	0 –	14								
S. macalliana	0 –	13	0 –	5	10 –	33	2 –	11	0 –	2	0	a
S. candida	19 +	11	10 +	4	210 +	114	72 +	38				
S. padophylla	11 +	3	7 +	1	6 o	9	2 o	3	1 o	1	a	a
S. glauca									2 o	1	a	1
B. glandulosa					5 –	68	1 –	22	0 –	7	0	2
P. tremuloides	6 o	6	2 o	2					7 +	3	3	1
P. balsamifera	2 o	2	1 o	1					1 –	4	a	a
TOTAL	248		95		309		101		44		11	
Chi-square calculated:	80.6*		64.7*		155.9*		58.3*		25.7*		6.8 n.s.	
Tabular value P<0.05	14.1		14.1		12.6		12.6		15.5		15.5	

[1]Current annual growth.
[2]Observed.
[3]Expected.
[4]Symbols denote where browse was (+) significantly more, (–) significantly less and (o) within the range expected according to availability.
[5]'a' denotes a value less than 0.05.

of *Salix candida* shrubs removed about 14 percent of the CAG. *Salix bebbiana*, *S. discolor* and *S. padophylla* were browsed in approximate proportions of their abundance in this community. *Salix maccalliana* and *Betula glandulosa* sustained significantly less browse use than expected according to their availability.

In the aspen-willow community, the number of *Salix bebbiana* and *Populus tremuloides* shrubs browsed were significantly greater than expected. *Salix bebbiana* comprised 52 percent of the available browse shrubs and contributed 66 percent of the total browse use from about 8 percent of its population. Browse use of uncommon palatable willows including *Salix discolor*, *S. padophylla* and *S. glauca* fell within the range of use expected according to availability. *Salix maccalliana* and *Betula glandulosa* did not sustain any browse use. Because of the small sample size of CAG browsed, 1.5% of that available in the aspen-willow community, no significant differences between observed and expected use of CAG were found.

A comparison of browse use in relation to shrub height of common willows in each community showed the use of CAG on shrubs that were all available were not greatly different from shrubs that were partially available (Table 11). However, individual shrubs of *Salix bebbiana* and *S. discolor* that were all available generally had a greater amount of the CAG browsed in the 70 percent class than shrubs that were partially available.

Table 11. Use of willow browse in relation to shrub height (availability).

Plant Community	Species	Shrub Availability	% of Population	Percent of Shrubs Browsed in Each Class: Browse Use Classes[2] 0	5	30	70	95	Total CAG[1] Used (%)
Willow Savanna	*S. bebbiana*	All[3]	44	74	6	10	10	2	11.4
		Partial[4]	55	80	7	8	5	1	7.2
	S. discolor	All	46	68	6	4	23	1	17.7
		Partial	52	62	8	19	10	3	15.6
	S. maccalliana	All	49	100					0
		Partial	47	100					0
	S. gracilis	All	66	100					0
		Partial	33	100					0
Patterned Fen	*S. discolor*	All	52	80	4	11	6		
		Partial	48	88	4	8	2		
	S. candida	All	3	88		13			3.8
		Partial	93	55	15	16	14	1	15.7
Aspen-willow	*S. bebbiana*	All	41	93	4	2	2		2.2
		Partial	51	93	4	4	1		3.3

[1]Current annual growth.
[2]Range of browse use classes are shown in Table 1.
[3]All available - greater than 90% of CAG between 0.4 m and 2.5 m in height.
[4]Partially available - greater than 10% and less than 90% of CAG between 0.4 m and 2.5 m in height.

In the willow savanna and aspen-willow communities, moose were obtaining browse above the arbitrarily assigned availability height (2.5 m) by breaking down upper branches and feeding on the terminal leaders. Although a small percentage of the total shrubs were subject to this type of browse use, four or more broken upper branches was common on selected shrubs.

The degree of previous browse use of various willow shrubs was found to have a marked influence on the current winter browse use pattern (Table 12). Previously unbrowsed willows sustained very little current use while moderate to heavily hedged willows sustained much greater current use (Figure 7). In all preferred willows, the probability that a shrub would be browsed during the current winter increased with the increase in the degree of previous use. For example, in the willow savanna, only five percent of previously unbrowsed *Salix bebbiana* shrubs were browsed during the current winter while 93 percent of the shrubs that had sustained heavy use in previous years were again browsed by moose.

The degree of previous use also influenced the amount of CAG removed from a shrub (Table 12). On previously unbrowsed shrubs the intensity of current browse use was low, generally within the 5 and 30 percent use classes. On moderate to heavily hedged shrubs the current browse use removed a considerably higher proportion of the CAG, generally within the 30 and 70 percent use classes. This direct relationship of greater use of CAG on shrubs with greater levels of previous use is best illustrated by moose selection and use

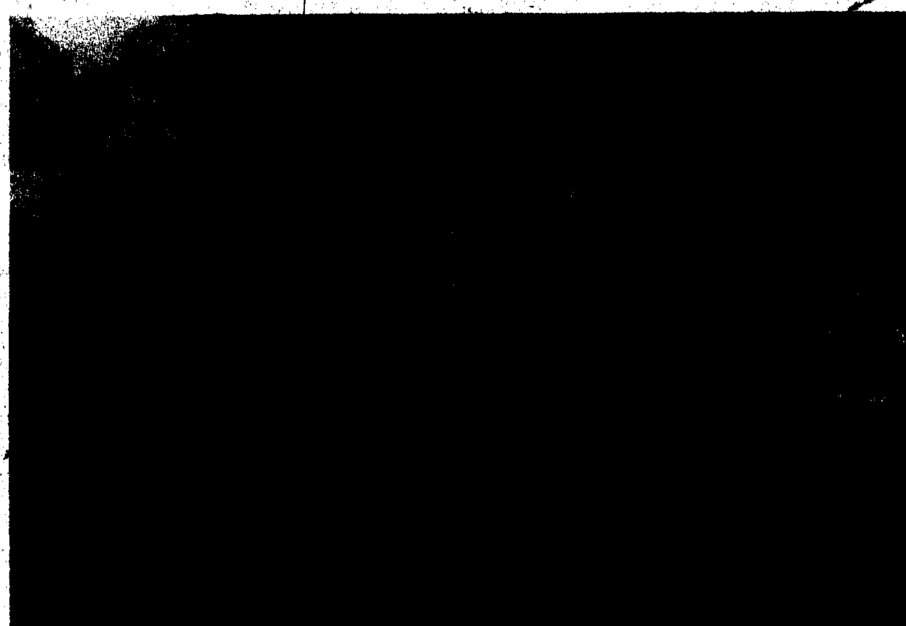


Figure 7. The difference in browse use sustained by these adjacent *Salix bebbiana* shrubs exemplifies moose browse selection in the study area; the shrub on the right sustained repeated heavy use while the shrub on the left received no apparent browse use.

Table 12. The relationship of previous browse use (degree of hedging) of individual shrubs to their current winter browse use patterns.

Plant Community	Species	Previous Use (degree of hedging)	Percent of Shrubs Currently Browsed in Each Browse Use Class					Total % of Shrubs Currently Browsed
			0	5	30	70	95	
Willow Savanna	*Salix bebbiana* n=686	none	95	2	2	1	0	5
		light	71	17	8	4	0	29
		moderate	35	22	31	13	0	66
		heavy	7	9	31	44	9	93
	Salix discolor n=184	none	92	7	0	2	0	9
		light	68	16	14	3	0	32
		moderate	29	9	50	21	0	71
		heavy	0	0	18	73	9	100
Patterned Fen	*Salix discolor* n=341	none	95	2	3	*[1]	0	6
		light	60	12	22	6	0	40
		moderate	27	0	33	40	0	73
		heavy	25	0	50	25	0	75
	Salix candida n=509	none	95	2	2	1	0	5
		light	85	10	5	0	0	15
		moderate	69	16	12	4	0	32
		heavy	26	17	27	29	1	74
Aspen-willow	*Salix bebbiana* n=405	none	98	2	*	*	0	2
		light	90	6	4	0	0	10
		moderate	41	24	35	0	0	59
		heavy	24	0	38	38	0	76

[1] '*' indicates value less than 0.05.

of *Salix discolor* shrubs in the willow savanna. The amount of CAG browsed by moose from previously unbrowsed or lightly hedged shrubs was generally within [illegible] percent use classes, while moderately and heavily [illegible], generally sustained use within the 30, 70 and 95 percent use classes.

Observations of moose track patterns in mid-winter indicated that movements between selected shrubs were not a random searching but a relatively direct movement between heavily hedged *Salix candida* clumps in the patterned fen community and between previously browsed shrubs of several species in the willow savanna community. Moderate to heavily hedged willows of taller species such as *Salix bebbiana* and *S. discolor* were visible to the author at distances greater than 100 m. Although many of the preferred *Salix candida* clumps were nearly obscured by snow cover and poorly visible, moose appeared to detect their presence and move in a direct path between clumps. In some instances a limited number of terminal shoots protruding through the snow cover may have been a visual guide used by moose to detect this low growing species.

Field observations showed that moose were cratering to obtain *Salix candida* browse from beneath the snow cover. Although the forelegs were used in some instances, the loose snow was normally moved aside by muzzle action to expose the current annual twigs.

3. Summer Habitat Use

Moose tracks and browse use were infrequently encountered in the study area during the growing season (May to September). Only a few moose were estimated to remain in the study area during the snow-free period.

Moose activity was most frequently encountered in the ecotone between the willow savanna and patterned fen communities. Use of other willow dominated communities was generally light. No moose activity was observed in the aspen-willow community in this season.

Willow browse comprised the greater portion of the observed forage use during the spring and summer. Moose commonly stripped the leaves from longer terminal leaders and rank growth but also used the upper portions of the current twig growth. *Salix bebbiana* and *S. discolor* were the major species browsed. Use of *Salix candida* was only observed on two occasions. No apparent difference in browse use was observed between previously browsed and unbrowsed willows. Use of aspen browse was recorded only once.

Small patches of seaside arrowgrass (*Triglochin maritima*) were heavily grazed by moose and appeared to be preferred to other available forage in June and July.

D. Nutrient Content of Willow Browse

1. Moisture

The seasonal trend in moisture content of the total CAG in all willows declined steadily from a mean high of 63 percent in June to a mean of 53.1 percent in September (Table 13). Winter twigs averaged 46.1 percent moisture. The moisture content of over-wintering twigs, collected at the onset of leaf-flush in May, averaged 8.4 percent higher than those during the dormant season.

In January, only *Salix bebbiana* showed a significant difference ($P<0.05$) in moisture content between browsed and unbrowsed plants. Moisture content in the total CAG of browsed *Salix bebbiana, S. discolor* and *S. candida* was generally higher than unbrowsed willows of the same species. This trend was most marked during June and the dormant season. The moisture content of the non-preferred willows, *Salix maccalliana* and *S. gracilis*, generally fell within the range of values obtained from preferred willows. A considerable variation in moisture content was found among individual willows within a species and browsed condition at each sampling period as revealed by the standard deviation of the mean.

The moisture content of leaves and twigs during the growing season showed the same seasonal trends described for the total CAG. However, the absolute moisture values were slightly lower than expected. This was apparently caused by desiccation during the separation of plant parts. The mean moisture content of leaves and twigs at each sampling period are given in Table 13.

Table 13. Moisture content[1] (mean ± SD) in the current annual growth of six willows and two browsed conditions (n=5 or 6 except as noted under footnote 4).

Species	Browsed Condition	SEASON MAY	JUNE	JULY	AUGUST	SEPTEMBER	JANUARY
Salix bebbiana[5]	BR[2]	55.1[4]	63.5 ± 0.9	56.4 ± 2.3	51.8 ± 1.6	52.5 ± 1.4	44.4 ± 0.3
Salix bebbiana[5]	UB[3]	52.1	59.3 ± 0.8	55.5 ± 1.9	51.9 ± 2.1	51.5 ± 1.9	42.5 ± 1.0
Salix discolor[5]	BR	56.9	64.5 ± 2.5	60.5 ± 0.8	56.8 ± 2.5	52.3 ± 1.7	48.5 ± 2.2
Salix discolor[5]	UB	40.8	61.4 ± 2.8	57.6 ± 1.8	54.9 ± 1.5	53.7 ± 1.2	46.5 ± 0.3
Salix candida[5]	BR	52.7	64.2 ± 1.4	56.3 ± 1.7	52.5 ± 0.5	49.5 ± 1.3	46.4 ± 0.6
Salix candida[5]	UB	-	59.7	53.0	48.3	49.1	
Salix padophylla[5]	BR	-	66.1	63.5	59.8	58.4	47.0
Salix maccalliana[5]	UB	55.9	66.7	60.3	56.9	57.2	47.3
Salix gracilis[5]	UB	-	61.6	55.1	54.6	53.7	45.0
MEAN[5]		54.5	63.0	57.6	54.1	53.1	46.1
MEAN LEAVES		-	60.1	56.9	54.0	53.5	-
MEAN TWIGS		54.5	68.1	52.1	49.6	44.2	46.1

[1]Percent of fresh weight.
[2]Browsed in previous years.
[3]Unbrowsed in previous years.
[4]Values without a standard deviation are from a single composite sample (n= 10 shrubs).
[5]Moisture content of leaves and twigs combined.

The moisture content in upper, middle and lower thirds of willow twigs showed the same seasonal trends described above. Moisture content was highest in the upper and lowest in the lower twig portions for all species and collection periods (Table 14).

2. Crude Protein

a. Current Annual Twigs

The seasonal content of crude protein was highest in June, averaging 10.4 percent, when willow twigs were actively developing, declined rapidly by July and reached their lowest levels, averaging 5.3 percent, in August (Table 15). A moderate increase in protein concentrations occurred before leaf abscission in September, followed by relatively stable protein levels, averaging 6.3 percent, during the dormant season. The protein content of overwintering twigs increased during the onset of leaf-flush in May. Unbrowsed *Salix bebbiana* willows contained considerably more protein than browsed *S. bebbiana* willows during this season.

Twig protein content varied considerably among individuals of a species and browsed condition at most sampling periods. Statistical differences between species within a browsed condition were found at each sampling period but these were not consistent throughout the year. No species of willow was markedly different in protein content in any collection period.

Table 14. Seasonal nutrient content (%) in upper (U), middle (M) and lower (L) twig portions of three willow species.[1]

Season	Nutrient	WILLOW SPECIES								
		Salix bebbiana			*Salix discolor*			*Salix candida*		
		U	M	L	U	M	L	U	M	L
May	Moisture							56.1	50.5	45.7
	Crude Protein							12.6	7.3	4.7
	A. D. Fiber							42.5	49.2	53.1
	A. D. Lignin							22.6	23.4	24.0
	Ash							3.8	2.8	2.3
	Calcium							0.61	0.52	0.53
	Magnesium							0.32	0.23	0.21
	Sodium[2]							3.7	3.0	2.7
June	Moisture							79.1	72.1	53.0
	Crude Protein							14.6	12.7	10.2
	A. D. Fiber							36.5	39.4	45.2
	A. D. Lignin							13.5	16.9	19.5
	Ash							5.3	6.2	5.0
	Calcium							0.56	0.48	0.47
	Magnesium							0.72	0.65	0.52
	Sodium[2]							8.4	3.7	5.9
July	Moisture	51.1	51.4	50.9	61.4	56.6	54.7	57.3	54.4	53.7
	Crude Protein	7.6	5.8	5.1	8.5	5.6	4.9	8.4	5.8	5.0
	A. D. Fiber	46.4	53.0	51.5	45.2	53.1	54.6	45.4	55.3	54.2
	A. D. Lignin	23.9	25.2	21.5	20.3	19.6	21.4	22.2	27.1	25.4
	Ash	3.7	3.1	2.9	3.4	2.3	2.3	3.9	3.2	3.7
	Calcium	0.53	0.48	0.53	0.44	0.38	0.40	0.55	0.45	0.49
	Magnesium	0.30	0.23	0.22	0.28	0.21	0.20	0.38	0.27	0.26
	Sodium[2]	5.5	2.7	4.0	3.2	2.5	2.9	2.9	5.0	3.8
August	Moisture	47.5	46.1	45.3	46.3	53.1	51.4	49.1	48.5	42.1
	Crude Protein	6.4	5.0	4.1	6.2	5.1	3.9	6.2	5.0	4.3
	A. D. Fiber	42.3	51.8	54.8	51.5	52.8	57.4	47.5	54.6	56.4
	A. D. Lignin	21.3	23.3	22.9	21.0	20.4	18.5	23.6	24.8	24.3
	Ash	3.1	2.4	2.3	2.5	1.8	1.8	3.0	2.6	2.6
	Calcium	0.60	0.59	0.60	0.40	0.36	0.39	0.57	0.51	0.43
	Magnesium	0.29	0.23	0.22	0.19	0.15	0.13	0.33	0.28	0.19
	Sodium[2]	2.5	3.0	2.7	3.5	3.5	2.0	4.3	3.6	2.6
September	Moisture	46.9	46.2	45.2	47.3	45.9	45.2	46.9	46.3	45.3
	Crude Protein	6.6	5.7	5.6	7.1	5.6	5.5	6.6	5.8	5.6
	A. D. Fiber	45.9	51.9	53.4	44.5	51.1	53.6	49.9	54.4	56.8
	A. D. Lignin	23.7	23.7	25.0	19.5	19.9	20.2	25.9	26.4	26.6
	Ash	3.0	2.6	2.8	1.9	1.7	1.9	3.0	2.5	2.0
	Calcium	0.76	0.65	0.72	0.45	0.38	0.40	0.66	0.56	0.60
	Magnesium	0.31	0.21	0.21	0.20	0.18	0.17	0.31	0.25	0.23
	Sodium[2]	2.3	2.3	1.7	2.6	-	2.6	3.2	3.4	1.7
January	Moisture							47.0	47.2	46.4
	Crude Protein							7.2	6.1	5.6
	A. D. Fiber							47.7	50.4	51.2
	A. D. Lignin							24.0	22.4	20.9
	Ash							3.0	2.8	2.5
	Calcium							0.67	0.64	0.61
	Magnesium							0.24	0.21	0.20
	Sodium[2]							3.0	2.5	2.5
	Phosphorous							0.12	0.10	0.09
	Crude Fat							2.4	1.1	2.2

[1]Willows browsed in previous years.
[2](% x 10^{-2}).

Table 15. Crude protein content[1] (mean ± SD) in leaves and twigs of the current season's growth in six willows and two browsed conditions (n= 5 or 6 except as noted under footnote 4).

Species	Browsed Condition	SEASON					
		MAY	JUNE	JULY	AUGUST	SEPTEMBER	JANUARY
TWIGS							
S. bebbiana	BR[2]	8.4 ± 0.2	11.4 ± 0.9	5.9 ± 0.4	5.6 ± 0.3	6.1 ± 0.6	5.9 ± 0.5
S. bebbiana	UB[3]	13.6 ± 0.2	10.9 ± 0.3	6.3 ± 0.4	6.1 ± 0.2	6.2 ± 0.4	5.7 ± 0.3
S. discolor	BR	8.5 ± 0.2	9.5 ± 0.8	6.2 ± 0.2	4.9 ± 0.3	6.7 ± 0.4	6.3 ± 0.5
S. discolor	UB	-	9.8 ± 1.2	5.9 ± 0.5	5.5 ± 0.2	6.6 ± 0.6	6.7 ± 0.6
S. candida	BR	8.1 ± 0.1	12.1 ± 1.0	6.5 ± 0.3	5.4 ± 0.3	6.2 ± 0.2	6.4 ± 0.1
S. candida	UB	-	9.7	5.6	4.9	7.0	-
S. padophylla	BR	-	9.2	5.4	4.5	5.7	6.8
S. maccalliana	UB	11.5[4]	10.2	7.8	4.9	5.7	6.2
S. gracilis	UB	-	-	7.4	5.8	6.4	6.6
MEAN		10.0	10.4	6.3	5.3	6.3	6.3
LEAVES							
S. bebbiana	BR		18.4 ± 1.2	13.8 ± 1.3	13.0 ± 1.4	9.9 ± 1.1	
S. bebbiana	UB		16.2 ± 1.0	13.1 ± 1.1	13.4 ± 1.3	9.4 ± 0.7	
S. discolor	BR		15.2 ± 0.9	14.4 ± 0.7	14.2 ± 0.9	10.2 ± 1.1	
S. discolor	UB		14.1 ± 1.7	12.8 ± 1.0	13.9 ± 1.2	9.6 ± 1.7	
S. candida	BR		14.7 ± 1.6	13.6 ± 1.2	12.1 ± 0.5	7.8 ± 0.6	
S. candida	UB		13.5	11.9	10.3	8.0	
S. padophylla	BR		-	13.8	12.0	8.1	
S. maccalliana	UB		16.1	13.7	12.0	5.7	
S. gracilis	UB		-	13.7	12.5	8.2	
MEAN			15.4	13.4	12.6	8.6	

[1]Percent oven-dry weight.
[2]Browsed in previous years.
[3]Unbrowsed in previous years.
[4]Values without a standard deviation are from a single composite sample (n= 10 shrubs).

The crude protein content of browsed and unbrowsed willows of the same species differed at each collection period; however due to the variation among individual shrubs within a browsed condition, few of these were statistically different (P<0.05). Differences between browsed and unbrowsed willows were not consistent through all collection periods (Figure 8).

Crude protein levels were highest in the terminal third and lowest in lower twig portions (Table 14).

b. Leaves

Levels of crude protein in willow leaves were highest in June when leaves were actively developing and decreased steadily with maturity (Figure 8). Protein concentrations in June averaged 15.4 percent and were significantly higher (P<0.05) than the average of 8.6 percent in September (Table 15).

Differences in protein content among species occurred at each sampling period but were not consistent throughout the growing season.

3. Acid-detergent Fiber

a. Current Annual Twigs

The acid-detergent fiber (ADF) content in willow twigs was generally lowest in June, averaging 38.3 percent, increased rapidly by July and reached an average maximum of 47.9 percent, during mid

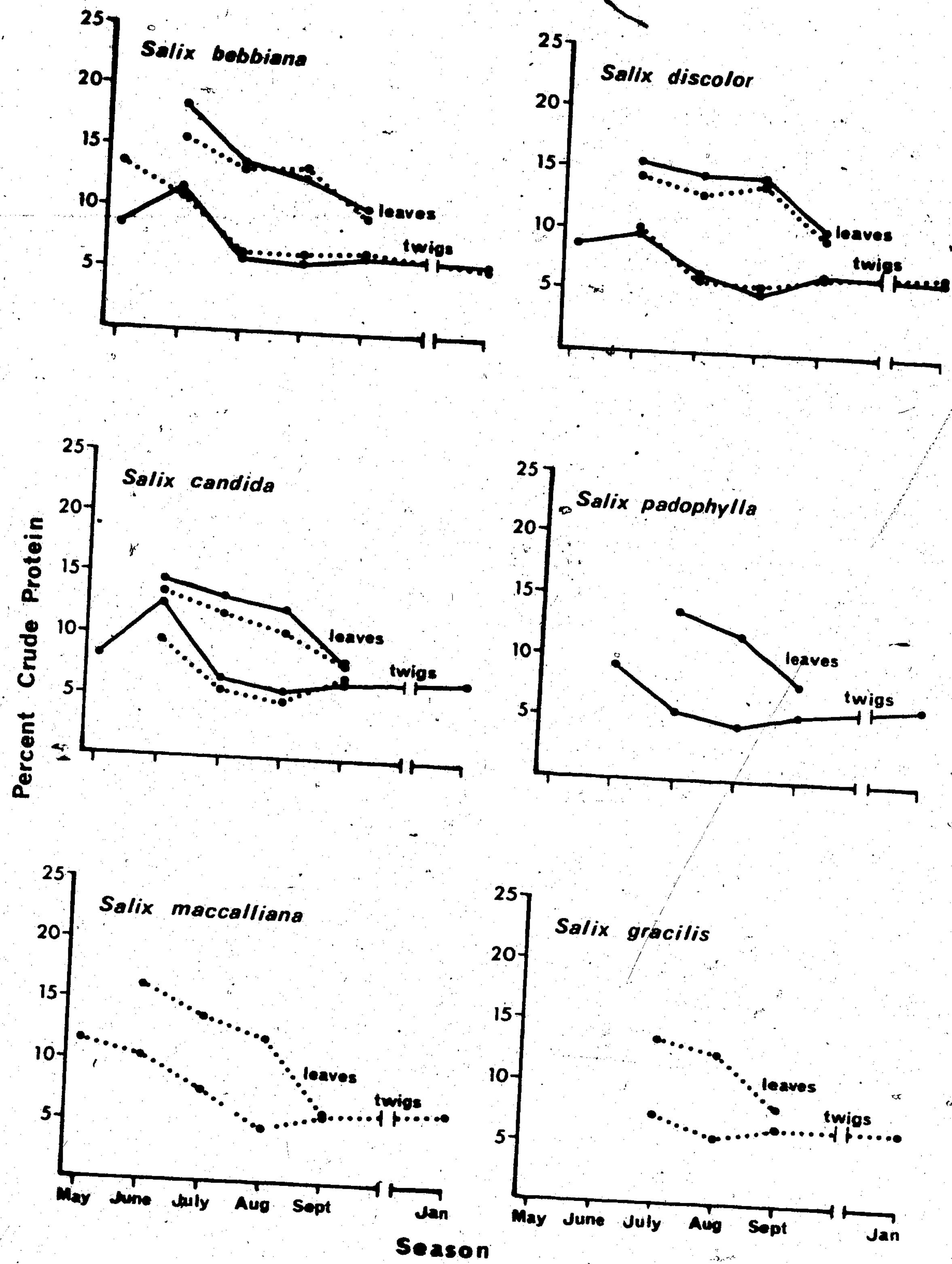


Figure 8. Seasonal variation of crude protein (%) in the current annual leaves and twigs of browsed and unbrowsed willows.
—— browsed plants
····· unbrowsed plants

or late summer (Table 16). The sampling periods when maximum ADF levels were recorded varied among species and between browsed conditions. After the seasonal high, the ADF content exhibited a slight to moderate decrease and then remained relatively stable or decreased during the dormant season (Figure 9).

Within species, all ADF levels, with the exception of *Salix gracilis*, were significantly lower in June than in July $(P<0.05)$. *Salix gracilis* maintained a relatively constant ADF content, averaging 42.7 percent, from June to September and then showed a significant decline to 38.4 percent during the dormant season. Browsed *Salix candida* and *S. padophylla* and unbrowsed *S. maccalliana* also showed a significant decline in ADF content from the September to the January collection periods.

Differences among species within a browsed condition did not exhibit a consistent pattern through the seasons. The ADF content of *Salix padophylla* maintained a relatively high level during the growing season but was significantly lower $(P<0.05)$ than other browsed species during the dormant season. The ADF content of browsed *Salix candida* was lowest in June and highest in January in relation to other browsed willows (Figure 9). Of the unbrowsed willows *Salix candida* maintained the highest and *Salix maccalliana* the lowest ADF levels in nearly all seasons.

Table 16. Acid-detergent fiber content[1] (mean ± SD) in leaves and twigs of the current season's growth in six willows and two browsed conditions (n=5 or 6 except as noted under footnote 4).

Species	Browsed Condition	MAY	JUNE	JULY	AUGUST	SEPTEMBER	JANUARY
		SEASON					
TWIGS							
S. bebbiana	BR[2]	46.6 ± 0.1	42.9 ± 4.1	49.8 ± 1.8	47.6 ± 2.7	46.2 ± 1.0	46.6 ± 3.0
S. bebbiana	UB[3]	37.1 ± 4.9	34.3 ± 4.1	47.1 ± 2.1	39.9 ± 2.2	40.6 ± 1.4	43.2 ± 3.9
S. discolor	BR	41.3 ± 0.8	39.0 ± 4.3	48.5 ± 3.4	52.2 ± 3.5	50.5 ± 2.3	47.4 ± 5.0
S. discolor	UB	32.8 ± 0.2	35.3 ± 2.9	42.4 ± 3.3	44.4 ± 1.8	41.1 ± 1.0	42.7 ± 1.8
S. candida	BR	49.0 ± 1.1	35.8 ± 0.5	48.2 ± 2.4	48.8 ± 0.7	54.2 ± 1.6	49.7 ± 1.7
S. candida	UB	-	37.4	49.6	49.3	45.7	
S. padophylla	BR	-	46.7	50.1	47.7	49.5	-
S. maccalliana	UB	35.7[4]	30.6	40.6	38.8	39.5	43.3
S. gracilis	UB	-	42.6	42.0	43.3	42.8	34.9
							38.4
MEAN		40.4	38.3	46.5	45.8	45.6	43.3
LEAVES							
S. bebbiana	BR		25.4 ± 1.0	28.2 ± 2.4	26.2 ± 3.7	26.9 ± 2.0	
S. bebbiana	UB		24.0 ± 2.3	28.1 ± 2.8	24.5 ± 1.5	26.4 ± 3.6	
S. discolor	BR		19.3 ± 1.5	22.3 ± 1.2	26.0 ± 1.2	33.3 ± 6.4	
S. discolor	UB		20.0 ± 1.4	22.4 ± 1.9	25.8 ± 3.4	29.7 ± 4.9	
S. candida	BR		33.7 ± 1.0	34.5 ± 1.9	35.5 ± 2.0	38.1 ± 1.0	
S. candida	UB		35.5	38.1	37.7	38.7	
S. padophylla	BR		18.8	18.6	19.6	19.9	
S. maccalliana	UB		26.5	22.1	19.6	23.1	
S. gracilis	UB		28.7	24.6	21.7	22.5	
MEAN			25.8	26.5	26.3	28.7	

[1]Percent oven-dry weight.
[2]Browsed in previous years.
[3]Unbrowsed in previous years.
[4]Values without a standard deviation are from a single composite sample (n= 10 shrubs).

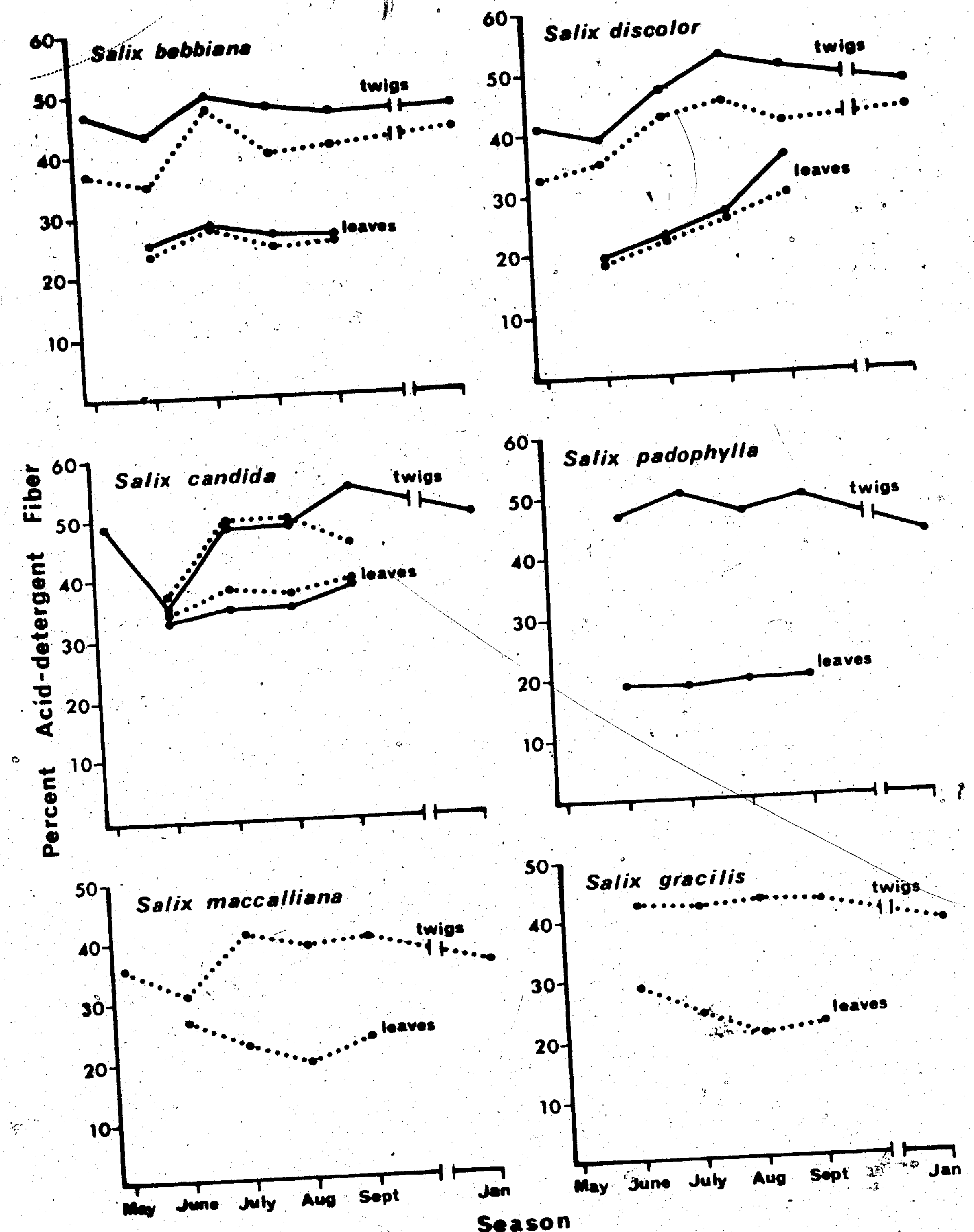


Figure 9. Seasonal variation of acid-detergent fiber (%) in the current annual leaves and twigs of browsed and unbrowsed willows.
—— browsed plants
..... unbrowsed plants

Browsed plants of *Salix bebbiana* and *S. discolor* were significantly higher in ADF content than unbrowsed plants of these species at most collection periods; an average difference in all seasons of 6.3 and 6.7 percent for *Salix bebbiana* and *S. discolor*, respectively. This relationship did not hold for browsed and unbrowsed *Salix candida* plants.

The ADF content in upper, middle and lower thirds of willow twigs showed the same seasonal trends described above. ADF content was always lowest in terminal twig portions and highest in the lower twig portions (Table 14).

b. Leaves

Seasonal trends of ADF in willow leaves varied considerably among species (Table 16). ADF content in *Salix bebbiana* and *S. padophylla* plants varied little from their seasonal means of 26.2 and 19.2 percent, respectively. *Salix discolor* showed a marked increase in ADF from a mean of 19.7 percent in June to 31.5 percent in September. *Salix candida* contained the highest seasonal ADF levels, averaging 36.5 percent, and showed a moderate increase from June to September. The ADF content in *Salix maccalliana* and *S. gracilis* decreased from June to August and then increased slightly in September.

Browsed and unbrowsed willows of the same species showed similar seasonal trends in ADF content (Figure 9). Browsed *Salix bebbiana* and *S. discolor* plants were slightly higher in ADF content than unbrowsed willows of these species. The converse relationship was found in *Salix candida* leaves.

4. Acid-detergent Lignin (Lignin)

a. Current Annual Twigs

The seasonal trends in lignin content varied among the willows examined (Figure 10). The lignin content of *Salix discolor* and *S. candida* was lowest in the developing twigs in June, increased as the twigs matured, reached a maximum level in August or September and was followed by a moderate decline by January (Table 17). *Salix maccalliana* and *S. bebbiana* showed a similar trend except for a decline in lignin content in August followed by an increase in September before decreasing or remaining relatively stable during the dormant season. The lignin content of *Salix gracilis* and *S. padophylla* was highest in June and generally decreased during the growing and dormant seasons.

Differences among species varied at each collection period. Browsed plants of *Salix candida* and *S. bebbiana* were significantly higher ($P<0.05$) in lignin content than other willows in the dormant season.

Few differences in lignin content were found between browsed and unbrowsed willows of the same species. Unbrowsed plants of *Salix discolor* contained slightly lower lignin levels than browsed plants at all sampling periods.

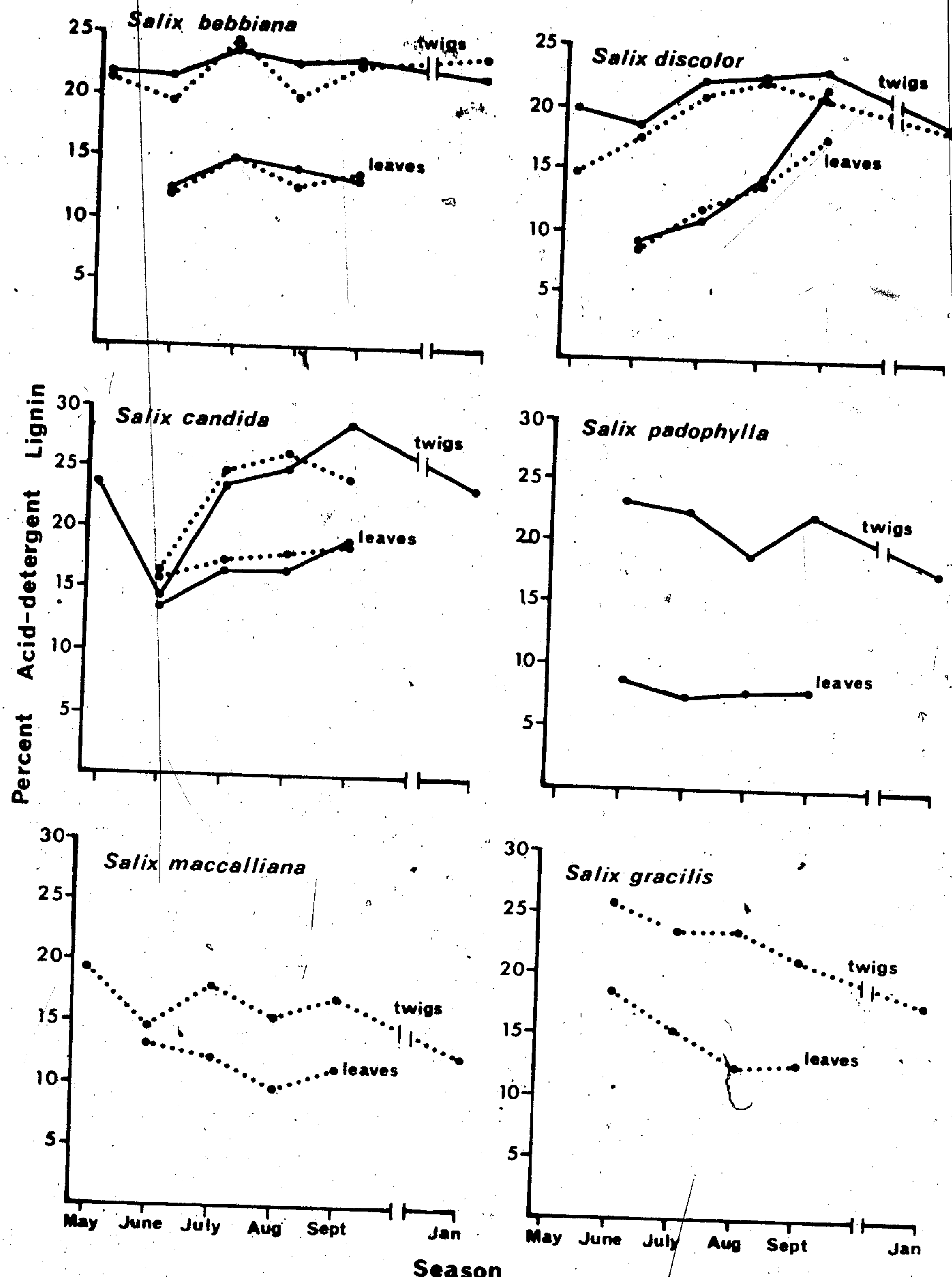


Figure 10. Seasonal variation of acid-detergent lignin (%) in the current annual leaves and twigs of browsed and unbrowsed willows.
—— browsed plants
•••• unbrowsed plants

The terminal third of willow twigs generally contained less lignin than sub-terminal portions during the growing season (Table 14). The middle portions contained the highest lignin content in July or August. The terminal third of *Salix candida* twigs contained the most lignin during the dormant season.

b. Leaves

The lignin content of *Salix discolor* and *S. candida* leaves increased steadily during the growing season (Figure 10). *Salix discolor* showed the greatest seasonal change in lignin, averaging 8.8 percent in June and 19.8 percent in September (Table 17). Lignin content of *Salix bebbiana* leaves initially increased by July, then generally declined as the leaves matured. The lignin content of *Salix maccalliana* and *S. gracilis* decreased between June and August, then increased slightly by September. The lignin content of *Salix padophylla* averaged 7.8 percent, varied little during the growing season and was significantly lower than other willows ($P<0.05$).

No significant differences were observed between leaves of browsed and unbrowsed willows of the same species.

5. ADL:ADF Ratio

a. Current Annual Twigs

The acid detergent lignin:acid-detergent fiber (ADL:ADF) ratios in willow twigs generally remained fairly constant or increased

Table 17. Acid-detergent lignin content[1] (mean ± SD) in leaves and twigs of the current season's growth in six willows and two browsed conditions (n=5 or 6 except as noted under footnote 4).

Species	Browsed Condition	SEASON					
		MAY	JUNE	JULY	AUGUST	SEPTEMBER	JANUARY
TWIGS							
Salix bebbiana	BR[2]	21.8 ± 0.7	21.2 ± 3.0	23.7 ± 1.6	22.3 ± 2.3	22.0 ± 2.3	21.4 ± 2.1
Salix bebbiana	UB[3]	21.3 ± 0.7	19.3 ± 2.8	24.3 ± 6.2	19.9 ± 1.4	22.9 ± 2.2	23.0 ± 1.9
Salix discolor	BR	19.7 ± 0.7	18.5 ± 2.1	22.2 ± 1.4	22.3 ± 2.3	23.0 ± 1.7	18.9 ± 2.6
Salix discolor	UB	14.8 ± 0.4	17.4 ± 1.4	20.8 ± 1.4	22.4 ± 1.5	21.8 ± 2.9	18.1 ± 1.0
Salix candida	BR	25.8 ± 1.0	14.6 ± 1.2	23.2 ± 0.6	24.8 ± 1.4	28.2 ± 2.4	23.2 ± 0.9
Salix candida	UB	-	16.7	24.5	25.9	24.6	-
Salix padophylla	BR	-	23.0	22.1	18.8	22.0	17.5
Salix maccalliana	UB	19.4[4]	14.8	22.9	20.4	22.0	17.3
Salix gracilis	UB	-	25.5	23.4	23.3	21.2	17.5
MEAN		20.1	19.0	23.0	22.2	22.9	19.6
LEAVES							
Salix bebbiana	BR		12.3 ± 1.0	14.8 ± 2.4	13.6 ± 1.8	13.4 ± 1.9	
Salix bebbiana	UB		12.5 ± 2.5	14.9 ± 2.0	12.4 ± 1.4	13.8 ± 2.6	
Salix discolor	BR		9.0 ± 0.9	10.7 ± 1.2	14.6 ± 2.0	22.6 ± 4.1	
Salix discolor	UB		9.4 ± 1.1	11.5 ± 1.5	14.0 ± 2.3	17.7 ± 4.1	
Salix candida	BR		13.5 ± 1.3	16.5 ± 1.3	16.9 ± 2.1	19.1 ± 1.2	
Salix candida	UB		15.8	17.1	17.9	18.6	
Salix padophylla	BR		8.2	7.1	7.8	7.9	
Salix maccalliana	UB		13.1	12.0	9.7	11.1	
Salix gracilis	UB		18.2	15.0	12.3	12.5	
MEAN			12.4	13.3	13.2	15.2	

[1]Percentage of dry weight.
[2]Browsed in previous years.
[3]Unbrowsed in previous years.
[4]Values without standard deviation are from a single composite sample (n= 10 shrubs).

slightly from early to late summer before declining during the dormant season (Table 18). *Salix gracilis* and *S. padophylla* showed a general decline in ADL:ADF with seasonal progression. Differences in ADL:ADF between species were not consistent at all collection periods. There was a consistent trend for the ADL:ADF ratios of browsed willows to be lower than that of unbrowsed willows of the same species.

b. Leaves

The ADL:ADF ratios in willow leaves showed no general trends between early and late summer collection periods (Table 18).

6. Cellulose

a. Current Annual Twigs

The cellulose content of willow twigs showed a general increase with seasonal progression; averaging 19.5 percent in early summer and 23.6 percent during the dormant season (Table 18). Previously browsed willows averaged 4 to 7 percent more cellulose than unbrowsed willows at all collection periods.

b. Leaves

Cellulose content of willow leaves remained relatively constant between early and late summer (Table 18). *Salix candida* leaves contained the highest cellulose levels, averaging 19.8 percent, in

Table 18. Composition of acid-detergent fiber (ADF), acid-detergent lignin (ADL), cellulose[1], and ADL:ADF ratio in leaves and twigs of willows during early summer, late summer and the dormant season.

		SEASON											
		EARLY SUMMER (June)				LATE SUMMER (September)				DORMANT SEASON (January)			
SPECIES	BROWSED CONDITION	ADF	ADL	Cellulose	ADL: ADF	ADF	ADL	Cellulose	ADL: ADF	ADF	ADL	Cellulose	ADL: ADF
TWIGS													
Salix bebbiana	BR[2]	42.9	21.2	21.7	0.49	46.2	22.0	24.2	0.48	46.6	21.4	25.2	0.46
Salix bebbiana	UB[3]	34.3	19.3	15.0	0.56	40.6	22.9	17.7	0.56	43.2	23.0	20.2	0.53
Salix discolor	BR	39.0	18.5	20.5	0.47	50.5	23.0	27.5	0.46	47.4	18.9	28.5	0.40
Salix discolor	UB	35.3	17.4	17.9	0.49	41.1	21.8	19.3	0.53	42.7	18.1	24.6	0.42
Salix candida	BR	35.8	14.6	21.2	0.41	54.2	28.2	26.0	0.52	49.7	23.2	26.5	0.47
Salix candida	UB	37.4	16.7	20.7	0.45	45.7	24.6	21.1	0.54	-	-	-	-
Salix padophylla	BR	46.7	23.0	23.7	0.49	49.5	22.0	27.5	0.44	43.3	17.5	25.8	0.40
Salix maccalliana	UB	30.6	14.8	15.8	0.48	39.5	22.0	17.5	0.56	34.9	17.3	17.6	0.50
Salix gracilis	UB	42.6	25.5	17.1	0.60	42.8	21.2	21.6	0.50	38.4	17.5	20.6	0.46
MEAN		38.3	19.0	19.3	0.49	45.6	22.9	22.5	0.51	43.3	19.6	23.6	0.46
LEAVES													
Salix bebbiana	BR	25.4	12.3	13.1	0.48	26.9	13.4	12.9	0.50				
Salix bebbiana	UB	24.0	12.5	11.5	0.53	26.4	13.8	11.3	0.52				
Salix discolor	BR	19.3	9.0	10.3	0.46	33.3	22.6	13.3	0.68				
Salix discolor	UB	20.0	9.4	10.6	0.47	29.7	17.7	11.9	0.60				
Salix candida	BR	33.7	13.5	20.2	0.40	38.1	19.1	19.1	0.50				
Salix candida	UB	35.5	15.8	19.7	0.45	38.7	18.6	20.1	0.48				
Salix padophylla	BR	18.8	8.2	10.6	0.44	19.9	7.9	12.0	0.40				
Salix maccalliana	UB	26.5	13.1	13.4	0.49	23.1	11.1	12.0	0.48				
Salix gracilis	UB	28.7	18.2	10.7	0.63	22.5	12.5	10.0	0.56				
MEAN		25.8	12.4	13.2	0.48	28.7	15.2	13.6	0.53				

[1]Acid-detergent fiber minus lignin.
[2]Browsed in previous years.
[3]Unbrowsed in previous years.

comparison to all other willows which averaged 11.7 percent cellulose.

7. Ash

a. Current Annual Twigs

The seasonal levels of ash content in twigs were similar in all willows (Table 19). Ash content was highest in June, averaging 5.4 percent, decreased through the growing and dormant seasons and averaged 2.7 percent in January (Figure 11). Overwintering twigs increased in ash content at the onset of leaf-flush and averaged 3.6 percent.

Differences among species and between browsed and unbrowsed willows of the same species were not consistent through the study. Unbrowsed willows often contained slightly higher ash levels than browsed willows of the same species during the latter part of the growing season and the dormant season.

Ash content in willow twigs was always highest in the terminal third and lowest in the lower third (Table 14).

b. Leaves

The ash content of willow leaves generally increased through the growing season from an average of 4.8 percent in June to 6.4 percent in September (Table 18). In *Salix discolor* and *S. gracilis*, the ash levels showed a marked decline in July before increasing in late

Table 19. Ash content[1] (mean ± SD)[2] in leaves and twigs of the current season's growth in six willows and two browsed conditions.

Species	Browsed Condition	MAY	JUNE	JULY	AUGUST	SEPTEMBER	JANUARY
		SEASON					
TWIGS							
Salix bebbiana	BR[3]	-	6.0 ± 0.7	3.3 ± 0.1	2.9 ± 0.4	3.1 ± 0.5	2.2 ± 0.1
Salix bebbiana	UB[4]	3.5 ± 0.7	5.0 ± 0.2	3.5 ± 0.4	3.7 ± 0.6	2.9 ± 0.3	2.7 ± 0.5
Salix discolor	BR	3.6	5.5 ± 0.1	3.0 ± 0.5	2.2 ± 0.3	2.2 ± 0.8	1.9 ± 0.1
Salix discolor	UB	5.2	5.0 ± 0.4	3.2 ± 0.6	2.6 ± 0.3	2.5 ± 0.4	2.0 ± 0.0
Salix candida	BR	3.1	5.6 ± 0.5	3.8 ± 0.2	3.2 ± 0.2	2.9 ± 0.3	2.5
Salix candida	UB	-	5.8	4.0	4.2	[illegible].2	-
Salix padophylla	BR	-	5.1	3.6	3.5	2.3	2.8
Salix maccalliana	UB	2.7	4.7	3.3	2.7	2.4	2.3
Salix gracilis	UB	-	5.5	3.2	2.9	2.7	2.3
MEAN		3.6	5.4	3.4	3.1	2.7	2.3
LEAVES							
Salix bebbiana	BR		5.2	4.9	6.6	8.1	
Salix bebbiana	UB		4.7	6.6	6.3	7.8	
Salix discolor	BR		6.0	4.5	5.3	6.2	
Salix discolor	UB		5.2	4.2	6.2	6.5	
Salix candida	BR		2.7	4.7	5.3	4.7	
Salix candida	UB		3.5	3.4	4.5	5.5	
Salix padophylla	BR		8.0	7.8	8.9	9.2	
Salix maccalliana	UB		3.3	4.6	5.2	5.2	
Salix gracilis	UB		4.9	3.6	4.9	4.6	
MEAN			4.8	4.9	5.9	6.4	

[1]Percentage dry weight.
[2]Values without a standard deviation were from a single composite sample (n= 5 to 10 shrubs), otherwise n= 3.
[3]Browsed in previous years.
[4]Unbrowsed in previous years.

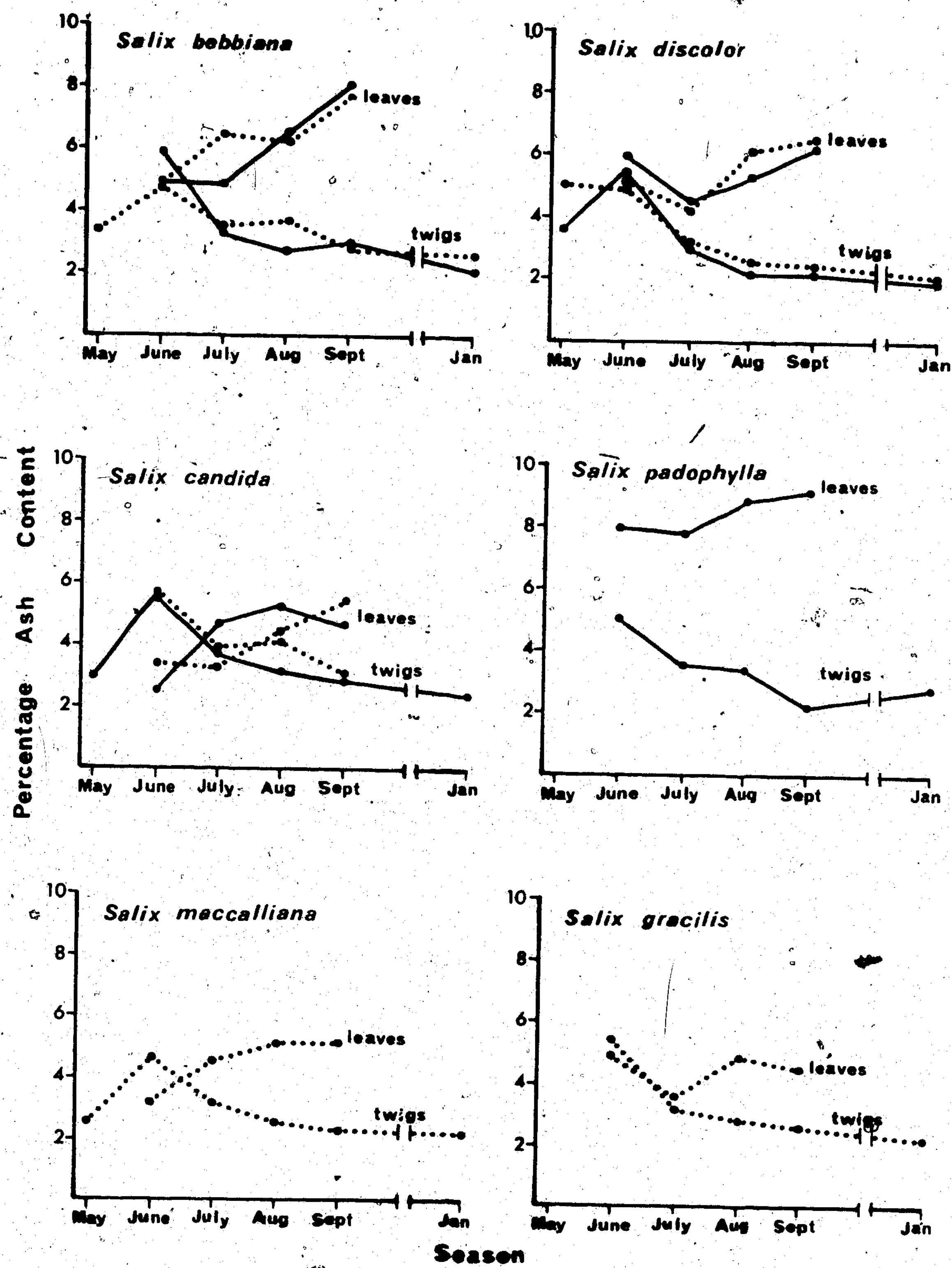


Figure 11. Seasonal variation of ash content (%) in the current annual leaves and twigs of browsed and unbrowsed willows.

—— browsed plants

····· unbrowsed plants

summer. The ash content of *Salix padophylla* averaged 8.5 percent through the summer and was significantly higher ($P<0.05$) than other willows at all sampling periods.

8. Calcium

a. Current Annual Twigs

Seasonal levels of calcium content in willow twigs were generally lowest in June and July when twigs were actively developing, reached peak levels in August or September and declined or remained relatively constant during the dormant season. Overwintering twigs of unbrowsed *Salix bebbiana* and browsed *Salix discolor* contained considerably higher calcium levels than twigs of these species during the dormant season. Calcium levels in overwintering twigs of browsed *Salix candida* and unbrowsed *Salix maccalliana* were slightly less than twigs of these species during the dormant season.

Differences among species and browsed conditions were not consistent through the study (Table 20). Calcium levels of unbrowsed preferred species ($\bar{x}$ = 3.1%) were generally higher than the non-preferred species *Salix maccalliana* and *S. gracilis* ($\bar{x}$ = 2.3%). Unbrowsed *Salix bebbiana, S. discolor,* and *S. candida* generally contained higher calcium levels than browsed willows of these species.

Calcium levels were highest in the upper third and lowest in the lower third of *Salix candida, S. bebbiana* and *S. discolor* twigs in all collection periods (Table 14).

Table 20. Calcium content[1] (mean ± SD)[2] (%) in leaves and twigs of the current season's growth of six willows and two browsed conditions.

Species	Browsed Condition	SEASON MAY	JUNE	JULY	AUGUST	SEPTEMBER	JANUARY
TWIGS							
Salix bebbiana	BR[3]	-	0.70 ± 0.09	0.61 ± 0.10	0.62 ± 0.09	0.79 ± 0.21	0.50 ± 0.08
Salix bebbiana	UB[4]	0.90 ± 0.29	0.68 ± 0.10	0.69 ± 0.25	0.84 ± 0.20	0.75 ± 0.13	0.64 ± 0.10
Salix discolor	BR	0.88	0.46 ± 0.06	0.48 ± 0.06	0.54	0.50 ± 0.17	0.38 ± 0.04
Salix discolor	UB	-	0.52 ± 0.06	0.52 ± 0.15	0.56 ± 0.13	0.48 ± 0.05	0.46 ± 0.05
Salix candida	BR	0.57	0.68 ± 0.08	0.56 ± 0.03	0.46 ± 0.12	0.69 ± 0.15	0.78
Salix candida	UB	-	0.56	0.57	0.84	0.74	-
Salix padophylla	BR	-	0.61	0.56	0.84	0.57	0.64
Salix maccalliana	UB	0.49	0.42	0.39	0.90	0.61	0.52
Salix gracilis	UB	-	0.51	0.53	0.70	0.61	0.51
MEAN		0.71	0.57	0.55	0.70	0.64	0.55
LEAVES							
Salix bebbiana	BR		0.83	1.02	1.80	1.92	
Salix bebbiana	UB		0.61	1.63	1.51	1.71	
Salix discolor	BR		0.70	0.72	1.53	1.46	
Salix discolor	UB		0.67	0.69	1.06	1.16	
Salix candida	BR		0.86	0.86	1.28	1.15	
Salix candida	UB		0.71	0.93	1.43	1.24	
Salix padophylla	BR		0.47	0.89	0.98	1.55	
Salix maccalliana	UB		0.59	0.81	1.09	1.41	
Salix gracilis	UB		1.16	1.48	1.80	1.98	
MEAN			0.73	1.00	1.21	1.51	

[1]Percentage of dry weight.
[2]Values without a standard deviation were from a single composite sample (n= 5 to 10 shrubs), otherwise n= 3.
[3]Browsed in previous years.
[4]Unbrowsed in previous years.

b. Leaves

The average calcium content in leaves of all willows combined showed a marked increase through the growing season from 0.73 percent in June to 1.51 percent in September (Table 20). The calcium content of *Salix gracilis* and *S. bebbiana* was significantly higher ($P<0.1$) than other willows at most sampling periods. Browsed willows of *Salix bebbiana* and *S. discolor* were generally higher in calcium content than unbrowsed willows of these species. *Salix candida* showed the converse of this relationship.

9. Phosphorus

a. Current Annual Twigs

The phosphorous content of willow twigs averaged 0.27 percent in early summer and 0.12 percent in the dormant season (Table 21). Differences between browsed and unbrowsed willows of the same species were not consistent among *Salix bebbiana, S. discolor* and *S. candida* or between sampling periods. *Salix padophylla* contained the highest phosphorous content (0.15 percent) of palatable, browsed species in the dormant season.

The phosphorous content in twig portions of browsed *Salix candida* during the dormant season were highest in the terminal third (0.12 percent) and lowest in the lower third (0.09 percent) (Table 14).

Table 21. Phosphorous content (%) of willow browse during early summer[1] and the dormant season[2].

Species	Browsed Condition	Early Summer leaves	Early Summer twigs	Dormant Season twigs
Salix bebbiana	BR[3]	0.38[5]	0.30	0.10
Salix bebbiana	UB[4]	0.24	0.24	0.14
Salix discolor	BR	0.23	0.28	0.11
Salix discolor	UB	0.28	0.31	0.12
Salix candida	BR	0.22	0.24	0.10
Salix candida	UB	0.19	0.20	–
Salix padophylla	BR	0.38	0.25	0.15
Salix maccalliana	UB	0.32	0.28	0.13
Salix gracilis	UB	0.33	0.32	0.10
Mean		0.29	0.27	0.12

[1]Samples collected June 6, 1973.
[2]Samples collected January 20, 1974.
[3]Browsed in previous years.
[4]Unbrowsed in previous years.
[5]Values are from one determination of a pooled sample (n= 5 to 10 shrubs) (Alberta Soil and Feed Testing Laboratory).

b. Leaves

The phosphorous content of willow leaves in early summer averaged 0.29 percent (Table 21). *Salix padophylla* and browsed *S. bebbiana* contained the highest phosphorous levels (0.38 percent) while browsed and unbrowsed *Salix candida* plants contained the lowest levels (0.22 and 0.19 percent) respectively. Differences in phosphorous content between browsed and unbrowsed plants of the same species showed the same trend as willow twigs in early summer.

10. Calcium-phosphorous Ratios

a. Current Annual Twigs

The calcium-phosphorous ratio in willow twigs averaged 2.1:1 in early summer and 4.9:1 in the dormant season (Table 22). *Salix candida* had the highest calcium-phosphorous ratios in both seasons. No consistent relationship was found between browsed and unbrowsed willows within a species.

b. Leaves

The calcium-phosphorous ratio of willow leaves averaged 2.7:1 in early summer (Table 22). Leaves of browsed and unbrowsed *Salix candida* plants contained the highest ratios (3.9:1 and 3.7:1, respectively), and *Salix padophylla* contained the lowest ratio (1.2:1).

Table 22. Average calcium-phosphorous ratios of willow browse during early summer[1] and the dormant season[2].

Species	Browsed Condition	Early Summer Leaves	Early Summer Twigs	Dormant Season Twigs
Salix bebbiana	BR[3]	2.2:1	2.3:1	5.0:1
Salix bebbiana	UB[4]	2.5:1	2.8:1	4.6:1
Salix discolor	BR	3.0:1	1.6:1	3.5:1
Salix discolor	UB	2.5:1	1.9:1	4.8:1
Salix candida	BR	3.9:1	3.1:1	7.8:1
Salix candida	UB	3.7:1	2.9:1	-
Salix padophylla	BR	1.2:1	1.6:1	4.2:1
Salix maccalliana	UB	1.8:1	1.3:1	4.0:1
Salix gracilis	UB	3.5:1	1.5:1	5.1:1
MEAN		2.7:1	2.1:1	4.9:1

[1]Samples collected June 6, 1973.
[2]Samples collected January 20, 1974.
[3]Browsed in previous years.
[4]Unbrowsed in previous years.

11. Magnesium

a. Current Annual Twigs

The magnesium content of willow twigs was highest in June, averaging 0.38 percent, declined rapidly in mid-summer and reached the lowest levels, averaging 0.24 percent, in the late summer or dormant season (Table 23). A slight to moderate increase in magnesium content occurred in most unbrowsed willows in August.

The magnesium content in *Salix maccalliana* and *S. gracilis* twigs were generally lower than unbrowsed willows of palatable species. Unbrowsed *Salix discolor* plants contained higher magnesium levels than browsed plants of this species from mid-summer through the dormant season. Differences between browsed and unbrowsed plants of *Salix bebbiana* and *S. candida* were not consistent through the season.

The magnesium content of the terminal third of willow twigs was markedly higher than the lower two-thirds (Table 14).

b. Leaves

The magnesium content in leaves of all willows except *Salix candida* and browsed *S. discolor* showed a marked increase through the growing season. The magnesium content of all species combined averaged 0.52 percent in June and 1.04 percent in September (Table 23).

Table 23. Magnesium content[1] (mean ± SD)[2] in leaves and twigs of the current season's growth from six species of willow and two browsed conditions.

Species	Browsed Condition	MAY	JUNE	JULY	AUGUST	SEPTEMBER	JANUARY
		SEASON					
TWIGS							
Salix bebbiana	BR[3]	–	0.39 ± 0.12	0.29 ± 0.04	0.32 ± 0.01	0.27 ± 0.03	0.18 ± 0.03
Salix bebbiana	UB[4]	0.21 ± 0.02	0.39 ± 0.03	0.34 ± 0.02	0.55 ± 0.01	0.26 ± 0.05	0.21 ± 0.01
Salix discolor	BR	0.20	0.36 ± 0.13	0.24 ± 0.07	0.17	0.22 ± 0.08	0.18 ± 0.02
Salix discolor	UB	–	0.31 ± 0.03	0.27 ± 0.12	0.31 ± 0.04	0.31 ± 0.02	0.25 ± 0.03
Salix candida	BR	0.25	0.59 ± 0.26	0.44 ± 0.08	0.28 ± 0.08	0.27 ± 0.06	0.25
Salix candida	UB	–	0.39	0.31	0.34	0.24	–
Salix padophylla	BR	–	0.23	0.22	0.18	0.20	0.25
Salix maccalliana	UB	0.27	0.31	0.23	0.26	0.19	0.16
Salix gracilis	UB		0.41	0.24	0.21	0.23	0.18
MEAN		0.23	0.38	0.29	0.29	0.24	0.21
LEAVES							
Salix bebbiana	BR		0.54	0.66	0.79	1.18	
Salix bebbiana	UB		0.49	0.78	0.67	1.23	
Salix discolor	BR		0.41	0.35	0.25	–	
Salix discolor	UB		–	0.47	0.49	1.23	
Salix candida	BR		0.70	0.63	0.41	–	
Salix candida	UB		0.43	0.47	0.85	0.46	
Salix padophylla	BR		0.67	0.89	0.96	1.36	
Salix maccalliana	UB		0.39	0.67	0.62	0.93	
Salix gracilis	UB		0.50	0.56	0.61	0.86	
MEAN			0.52	0.61	0.63	1.04	

[1]Percent of dry weight.
[2]Values without a standard deviation were from a single composite sample (n= 5 to 10 shrubs), otherwise n=3.
[3]Browsed in previous years.
[4]Unbrowsed in previous years.

Salix padophylla and *S. bebbiana* maintained the highest magnesium levels, averaging 0.97 and 0.79 percent respectively, through the growing season.

12. Sodium

a. Current Annual Twigs

Sodium content of willow twigs ranged from an average high of 0.029 percent in June to 0.014 percent in January (Table 24). Sodium levels generally showed a marked decrease by July when twigs were actively elongating, increased by August and then decreased again during the late summer and dormant seasons. The considerable variation in sodium content found within replicated treatments is shown by the standard deviation (Table 24). No differences between species or browsed conditions were evident.

Sodium content of *Salix candida* twig portions was generally highest in the terminal third and lowest in the lower two-thirds, averaging 0.042 and 0.034, respectively, through the growing season (Table 14).

b. Leaves

The average sodium content in willow leaves from all species during the summer was 0.026 percent (Table 24). The seasonal trends in sodium content varied among species. *Salix bebbiana* and *S. discolor* showed a general decline in sodium content through the growing season.

Table 24. Sodium content[1] (mean ± SD)[2] in leaves and twigs of the current season's growth of six willows and two browsed conditions.

Species	Browsed Condition	SEASON MAY	JUNE	JULY	AUGUST	SEPTEMBER	JANUARY
TWIGS							
Salix bebbiana	BR[3]	-	3.4 ± 3.2	1.9 ± 0.6	2.1 ± 0.5	1.7 ± 0.7	1.4 ± 0.4
Salix bebbiana	UB[4]	1.7 ± 0.2	4.1 ± 2.1	2.4 ± 0.3	2.4 ± 0.9	1.5 ± 0.3	1.8 ± 1.0
Salix discolor	BR	1.8	2.5 ± 0.9	1.1 ± 0.1	2.1 ± 1.0	1.5 ± 0.4	1.3 ± 0.8
Salix discolor	UB	-	2.2 ± 0.7	1.7 ± 0.8	2.2 ± 0.5	2.1 ± 0.6	1.8 ± 1.7
Salix candida	BR	1.6	3.6 ± 1.8	3.2 ± 1.3	2.4 ± 0.8	2.9 ± 0.5	2.0
Salix candida	UB	-	2.1	1.4	3.5	4.3	-
Salix padophylla	BR	-	3.8	1.4	2.8	1.9	1.2
Salix maccalliana	UB	1.7	3.6	1.3	2.5	1.2	0.7
Salix gracilis	UB	-	0.6	3.0	2.7	1.3	1.0
MEAN		1.7	2.9	1.9	2.5	2.0	1.4
LEAVES							
Salix bebbiana	BR		3.7	2.1	2.5	0.6	
Salix bebbiana	UB		3.3	1.5	3.4	0.4	
Salix discolor	BR		2.1	1.2	1.5	1.2	
Salix discolor	UB		2.3	2.2	2.4	0.5	
Salix candida	BR		0.9	1.6	2.4	2.4	
Salix candida	UB		4.5	2.8	1.2	2.0	
Salix padophylla	BR		0.9	8.2	1.8	4.7	
Salix maccalliana	UB		5.1	4.7	2.3	3.5	
Salix gracilis	UB		1.2	4.5	3.6	3.2	
MEAN			2.7	3.2	2.3	2.1	

[1]Percent x10^{-2} of dry weight.
[2]Values without a standard deviation were from a single composite sample (n= 5 to 10 shrubs), otherwise n= 3.
[3]Browsed in previous years.
[4]Unbrowsed in previous years.

These species also contained the lowest sodium levels, averaging 0.005 percent in September.

13. Ether Extract

a. Current Annual Twigs

Levels of ether extract (crude fat) were significantly lower ($P<0.05$) in young twigs ($\bar{x}$ = 2.1%) in early summer than in mature twigs ($\bar{x}$ = 4.0%) during the dormant season (Table 25). No consistent differences in ether extract were found between palatable and unpalatable species or between browsed conditions within species.

Ether extract in *Salix candida* twig portions during the dormant season was higher in the terminal third (2.4%) than in the lower two-thirds (1.7%) (Table 14).

b. Leaves

The ether extract content in willow leaves averaged 2.4 percent in the early summer (Table 25). Little variation was found between species and browsed conditions.

E. Effects of Browsing on Willow Twig Production

The general procedure of using secondary stem units to measure current annual twig production under various degrees of natural and simulated browsing was found to be workable and soundly conceived.

Table 25. **Ether extract (%) in leaves and twigs of six willow species and two browsed conditions during early summer[1] and the dormant season[2].**

Species	Browsed Condition	Early Summer		Dormant Season
		Leaves	Twigs	Twigs
Salix bebbiana	BR[3]	2.4[5]	1.9	4.6
Salix bebbiana	UB[4]	2.2	3.1	3.4
Salix discolor	BR	2.4	1.6	3.6
Salix discolor	UB	1.8	1.9	3.7
Salix candida	BR	2.2	2.2	3.4
Salix candida	UB	2.5	1.9	-
Salix padophylla	BR	2.9	2.0	4.0
Salix maccalliana	UB	2.2	1.8	4.6
Salix gracilis	UB	2.6	2.9	4.6
MEAN		2.4	2.1	4.0

[1]Samples collected June 6, 1973.
[2]Samples collected January 20, 1974.
[3]Browsed in previous years.
[4]Unbrowsed in previous years.
[5]Values are from one determination of a pooled sample; n=5 to 10 shrubs (Alberta Soil and Feed Testing Laboratory).

No statistical difference (P<0.05) in twig production was found between shrubs within a treatment. Some variation, found among the five secondary stem samples within a shrub, was expected due to the stratified random sampling method that included both lateral and terminal stems.

1. Simulated Browsing

a. *Salix bebbiana*

The results from the simulated browsing treatments showed that both intensity and season of clipping had a marked effect on the growth of twigs during the following season (Table 26). Season of clipping had a greater effect on twig growth than clipping intensity.

The average number of twigs per secondary stem were generally higher on shrubs clipped in spring and lower on shrubs clipped in fall and winter than the controls. The 100 percent winter clipping treatment showed the most pronounced and significant (P<0.05) decrease in twig numbers while the 50 percent spring clipping treatment showed the greatest and significant increase in twig numbers.

The average length of twigs produced on shrubs subject to the 100 percent clipping intensity in spring was significantly shorter than control shrubs. The average twig length was significantly larger on the 50 and 100 percent fall clipping treatments and all winter clipping treatments than the control shrubs.

Table 26. Comparison of browse production on *Salix bebbiana* shrubs the year following simulated browsing of varying intensities and in different seasons. Production was measured by the number, total length and total weight of current annual twigs per secondary stem, by the mean length and weight of twigs and by twig weight per unit length.

Season	Clipping Intensity	BROWSE PRODUCTION Number of Twigs[1]	Total Twig Length (cm)[1]	Mean Twig Length (cm)	Total Twig Weight (gm)[1]	Mean Twig Weight ($x10^{-2}$) (gm)	Twig Weight Per Unit Length ($x10^{-3}$) (gm/cm)
CONTROL[3]	0	22.4 b c[2]	139.5 a b c	7.5 d e	1.9 c d	10.9 c d	13.5 d e
SPRING	50%	33.4 a	172.8 a	6.0 e	2.2 b c	8.9 d	13.0 d e
	100%	25.8 a b	104.6 c	5.0 c	1.1 d	6.4 d	11.7 e
	Hedged	21.8 b c	168.7 a b	10.0 b c	2.7 b c	17.7 b c	16.0 c d
FALL	50%	18.3 b c d	181.2 a	10.9 a	3.6 a	23.1 a b	20.0 a b
	100%	11.6 c d	125.4 b c	12.0 a b c	2.7 b c	26.3 a	20.5 a b
	Hedged	16.4 b c d	149.3 a b c	9.7 c d	2.6 b c	17.6 b c	17.6 b c
WINTER	50%	13.9 c d	165.1 a b	12.5 a b	3.3 a	27.2 a	20.9 a b
	100%	10.1 d	113.3 c	12.0 a b c	2.5 b c	27.8 a	21.7 a
	Hedged	14.0 c d	137.2 a b c	11.1 a b c	2.5 c	22.0 a b	18.7 a b c

[1]Production per secondary stem.
[2]Means within the same column followed by a common letter are not significantly different ($P<0.05$).
[3]n = 8 to 10 shrubs which provided 40 to 50 secondary stems per treatment.

The total weight of twigs per secondary stem were significantly higher in the 50 percent clipping intensities in fall and winter than in control shrubs. Willows subjected to the 100 percent clipping intensity in spring responded with a decrease in total weight of twig production but were not significantly different from the controls. The remaining treatments showed a 16 to 42 percent increase in total weight of twigs produced but were not significantly higher than the control shrubs.

The mean twig weights of the 50 and 100 percent fall and winter treatments and the hedged winter treatment were significantly higher than the controls. Hedged treatments in spring and fall responded with a moderate increase in mean twig weight. The 50 and 100 percent spring treatment showed a decrease in mean twig weight but were not significantly different from the control shrubs.

The weight-length relationship showed that 50 and 100 percent clipping treatments during spring resulted in shorter-smaller twigs than the controls. These differences however were not significant ($P<0.05$). Fifty and 100 percent clipping intensities in fall and winter had significantly higher weight-length ratios than the controls.

The weight-length ratios of hedged clipping intensities in all seasons were greater than but not significantly different than the controls.

The effect of simulated browsing on twig production under all clipping intensities were similar in the fall and winter treatments. Although simulated browsing in the fall and winter seasons decreased twig production, the combined effects of increased twig lengths and weights resulted in a significant increase in the available production of twigs. Simulated browsing under 50 and 100 percent clipping in spring resulted in an increase in twig numbers but a general decrease in twig production. Hedged clipping treatments responded with a moderate increase in twig production and showed the least variation among seasons.

b. *Salix discolor*

The results from simulated browsing treatments on *Salix discolor* showed several effects on the growth of twigs in the following season (Table 27). However, only the 100 percent clipping intensity in fall showed a significant ($P<0.05$) difference from the control shrubs with an increase in mean twig weight and weight per unit length of twigs.

The average number of twigs produced per secondary stem on 100 percent and hedged spring treatments and 50 and 100 percent fall treatments were lower than the control shrubs. The 50 percent spring clipping treatment showed a 22 percent increase in twig numbers (Table 27).

All clipping treatments except the 100 percent spring and 50 percent fall treatments responded with an increase in total and mean

Table 27. Comparison of browse production on *Salix discolor* shrubs the year following simulated browsing of varying intensities and in different seasons. Production was measured by the number, total length and total weight of current annual twigs per secondary stem, by the mean length and weight of twigs and by twig weight per unit length.

		BROWSE PRODUCTION					
Season	Clipping Intensity	Number of Twigs[1]	Total Twig Length (cm)[1]	Mean Twig Length (cm)	Total Twig Weight (gm)[1]	Mean Twig Weight ($x10^{-2}$) (gm)	Twig Weight Per Unit Length ($x10^{-3}$) (gm/cm)
CONTROL[3]	0	14.4 a[2]	101.8 a	8.1 a b	1.56 a b	13.3 b c	14.8 b c
SPRING	50%	17.6 a	136.0 a	8.7 a b	2.02 a	13.9 a b c	14.7 b c
	100%	12.7 a	85.9 a	7.0 b	1.17 b	9.4 c	12.8 c
	Hedged	13.2 a	124.2 a	10.6 a	2.07 a	18.8 a b	16.3 a b
FALL	50%	12.5 a	97.2 a	8.7 a b	1.67 a b	15.2 a b c	17.8 a b
	100%	10.1 a	110.9 a	10.9 a	2.13 a	21.4 a	18.4 a
	Hedged	14.4 a	122.7 a	9.3 b	2.11 a	17.6 a b	17.2 a b

[1]Production per secondary stem.
[2]Means within the same column followed by a c[illegible] letter are not significantly different ($P<0.05$).
[3]n= 10 shrubs which provided 50 secondary stem[illegible]r treatment.

twig length and total and mean twig weight. The 100 percent spring treatment showed a decrease in these parameters. Twig production in the 50 percent fall treatment was slightly lower in total twig length and slightly higher in mean twig length, total and mean twig weight than the controls. (These differences were not significant $P<0.05$).

Fall treatments of all clipping intensities responded with an increase in twig size as expressed by the weight-length relationship. Spring treatments of 100 and 50 percent clipping intensities showed a decrease in twig size.

Hedged clipping intensities showed less variation between spring and fall treatments than other clipping intensities. One hundred percent clipping intensities showed the most variation with the greatest decrease in twig numbers in the fall treatment and greatest increase in average twig weight and length.

2. Natural Browsing

a. *Salix candida*

Woody twig production in *Salix candida* plants that were heavily browsed by moose were significantly ($P<0.05$) greater in mean length, total length, weight and weight per unit length than unbrowsed plants (Table 28).

Table 28. Current annual twig production of unbrowsed and moose-browsed *Salix candida* shrubs.

BROWSE PRODUCTION	UNBROWSED SHRUBS	MOOSE-BROWSED SHRUBS
Number of twigs[1]	11.7a[2]	7.6a
Total length of twigs (cm)[1]	42.7a	76.7b
Mean twig length (cm)	4.0a	11.0b
Total weight of twigs (gm)[1]	5.6a	22.1b
Mean weight per twig (gm)	5.4×10^{-2}a	33.6×10^{-2}b
Mean weight per unit length (gm/cm)	13.1×10^{-3}a	29.0×10^{-3}b

[1]Production per secondary stem.
[2]Means within the same row followed by a common letter are not significantly different ($P<0.05$).

Within browsed *Salix candida* clumps, the intensity of previous browse use[1] also affected twig production on those secondary stems during the following season (Table 29). In heavily browsed *Salix candida* clumps, the total length and mean length of twigs on browsed secondary stems was significantly ($P<0.05$) greater than unbrowsed stems.

In moderately browsed *Salix candida* shrubs, the twig production of unbrowsed secondary stems were compared to three intensities of browsing[1] (Table 30). Secondary stems browsed the preceding dormant season were significantly ($P<0.05$) higher in total twig lengths than unbrowsed stems or browsed stems that did not sustain any use in the preceding season. Average twig lengths were significantly ($P<0.05$) greater on secondary stems browsed only in the previous dormant season than other intensities of use. The number of twigs per secondary stem were not significantly different among treatments.

[1]Determination of intensity of previous browse use is shown in Figure 12.

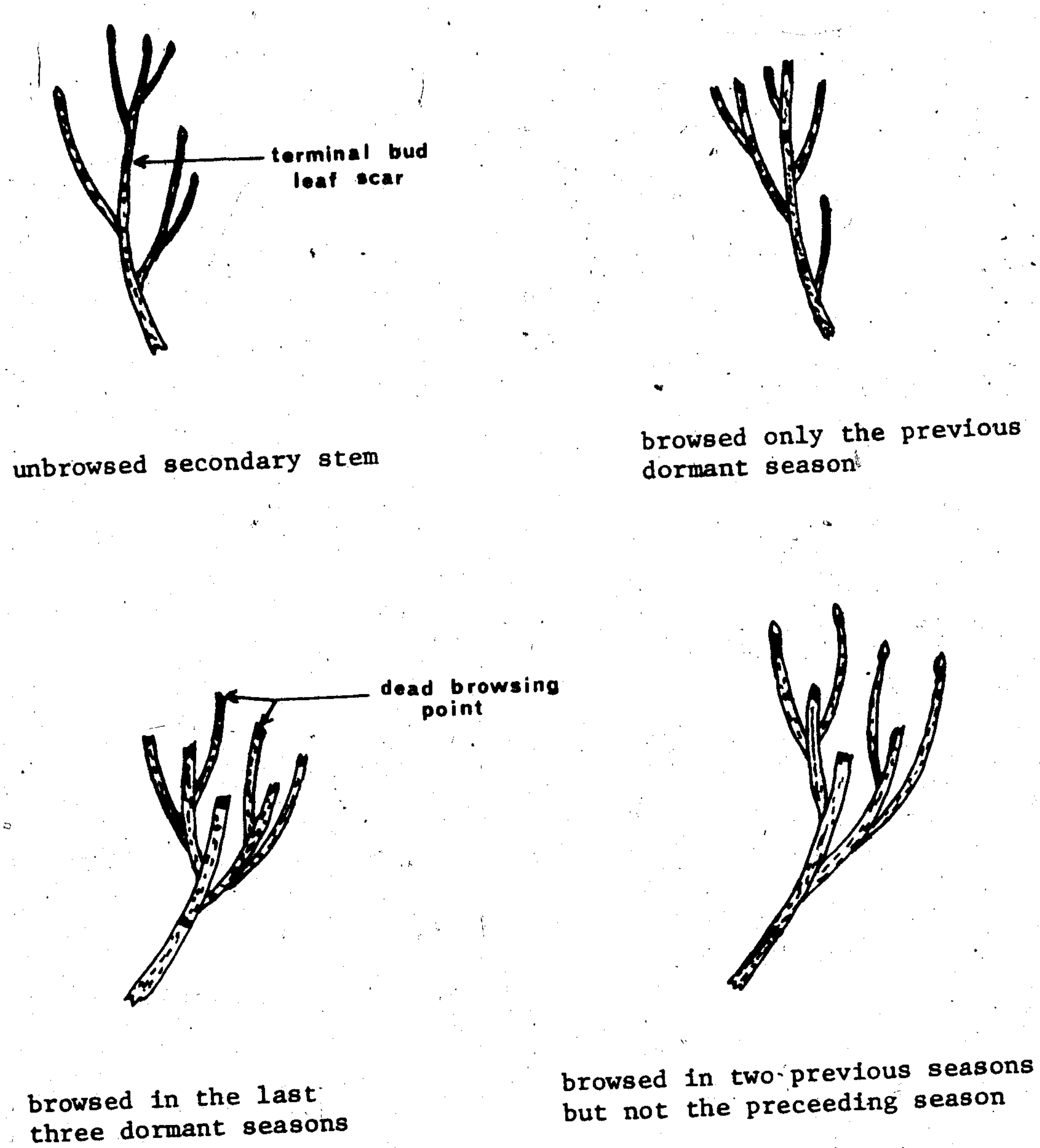


Figure 12. Comparison of *Salix candida* secondary stems with different "browse histories", showing how the degree of browse use in previous years is evaluated by examining the twig branching pattern and counting the number of terminal bud leaf scars and dead browsing points.

Table 29. Current annual twig production on browsed and unbrowsed secondary stems within heavily browsed *Salix candida* shrubs.

BROWSE PRODUCTION	UNBROWSED STEMS	BROWSED STEMS
Total number of twigs per secondary stem	4.4a[1]	3.4a
Total length of twigs per secondary stem (cm)	47.1a	65.3b
Mean length of twigs per secondary stem (cm)	10.7a	19.2b

[1]Means within a row followed by a common letter are not significantly different ($P<0.05$).

Table 30. The effect of browsing intensity on secondary stem twig production within moderately browsed *Salix candida* shrubs.

	DEGREE OF BROWSE UTILIZATION[1]			
BROWSE PRODUCTION	A	B	C	D
Number of twigs per secondary stem	16.7a[2]	13.8a	18.9a	18.6a
Total length (cm) of CAG per secondary stem	70.9a	134.2b	145.6b	103.1a
Mean twig length (cm)	5.6a	10.4b	8.5a,b	7.1a

[1]A. No previous browsing (control).
B. Browsed only the previous dormant season.
C. Browsed in two or more dormant seasons, including the preceding season.
D. Browsed in previous dormant seasons, but not the preceding season.

[2]Means within same row follow by a common letter are not significantly different ($P<0.05$).

b. *Salix bebbiana*

Twig production in browsed *Salix bebbiana* shrubs was significantly different from unbrowsed shrubs (Table 31). The mean length and weight of twigs, total twig length and mean weight per unit length of current twigs per secondary stem were significantly ($P<0.05$) greater in browsed shrubs than unbrowsed shrubs. The total weight of twig growth per secondary stem on browsed shrubs (6.7 gm) was nearly double that of unbrowsed shrubs (3.5 gm). The difference was significant at $P<0.1$. Although the total length of twig production on unbrowsed shrubs averaged about 50 percent higher than browsed shrubs, this difference was not significant ($P<0.1$). The mean age and diameter of secondary stems at the base of the first lateral branches in unbrowsed willows were not significantly different than browsed willows.

Table 31. Current annual twig production of unbrowsed and moose-browsed *Salix bebbiana* shrubs.

BROWSE PRODUCTION	UNBROWSED SHRUBS	MOOSE-BROWSED SHRUBS
Age of secondary stems (years)	7.9a[2]	7.2a
Diameter of secondary stems (mm)	11.0a	11.0a
Number of twigs[1]	171.3a	42.5b
Total length of twigs[1] (cm)	550.3a	367.8a
Mean length of twigs (cm)	3.2a	9.1b
Total weight of twigs[1] (gm)	3.5a	6.7a[3]
Mean weight of twigs (gm)	2.3×10^{-2}a	16.3×10^{-2}b
Mean weight of twigs per unit length (gm/cm)	6.8×10^{-3}a	18.1×10^{-3}b

[1]Production per secondary stem.
[2]Means within the same row followed by a common letter are not significantly different ($P<0.05$).
[3]Significantly different at $P<0.1$.

DISCUSSION

A. Nutritive Value of Willows for Moose

A good quality forage is considered to be highly palatable, having optimum levels of various nutrient components, a high apparent digestibility, optimum proportions of volatile fatty acids, adequate levels of minerals, vitamins and trace elements and is efficiently converted into the components necessary for the animal body (Dietz 1970). Kobota *et al.* (1970) found the seasonal availability of browse and herbaceous forage largely determined the levels of nutrient elements in the diet of moose. The level of nutrient intake is generally high in summer when many different kinds of plants are available, and low in winter when twigs are the primary source of feed.

1. Crude Protein

The crude protein content of willow leaves and twigs generally decreased as the current annual growth matured (Figure 8). The protein content of willow leaves declined from an average high of 15.4 percent in June to 8.6 percent in September. A more rapid decrease in leaf protein content between the August and September sampling periods coincided with a general increase in twig protein levels. Kramer and Kozlowski (1960) attributed this type of seasonal change to trans-location of nitrogenous compounds from leaves to the stems before leaf-abscission. The crude protein content of willow twigs was highest in June, averaging 10.4 percent, decreased rapidly during the period of active twig elongation in July, increased before leaf-abscission and then remained fairly constant or showed a slight increase during the dormant season. Protein levels of winter twigs averaged 6.3 percent. The seasonal changes in protein levels in willows were similar to the seasonal changes reported for three Alaskan browse plants; aspen, paper birch and willow (*Salix* spp.) (Kobota *et al.* 1970). However, the Alaskan plants showed no appreciable difference in protein concentrations between summer twigs and winter twigs. Tew (1970) found that the protein content of aspen leaves decreased with maturity, averaging about 17 percent in June, compared to 11.8 percent in September. Scotter (1972) found the crude protein levels in *Salix glauca* twigs near Inuvik, Northwest Territories, were lower during the growing season than during the dormant season.

The protein content in leaves and twigs generally showed little variation among the six species of willow at most sampling periods. Differences among species were not consistent throughout the year. This may be due to the phenological characteristics of plant nutrients that are specific to each species (Short *et al.* 1966). The protein content of willow twigs during the dormant season ranged between 5.7 and 6.7 percent. Due to the variation among willows of the same species, few significant differences were found among species of the same browsed condition. Considerable variation in nutrient content within species has also been shown for aspen in Utah (Tew 1970). The protein content in willow twigs during the dormant season was similar to protein levels reported for willows in Alaska (Milke 1969; Kobota *et al.* 1970) and Wyoming (Houston 1968).

Browsing was found to have a small influence on the protein content of the CAG. Leaves of browsed willows averaged 8 percent more protein than unbrowsed willows. Twigs of browsed *Salix bebbiana* and *S. candida* shrubs contained more protein than unbrowsed willows of these species during leaf-flush (early June), however, this difference was not consistent during other seasons. These data indicate that browsing may have delayed the phenological maturity of twigs resulting in comparatively higher protein levels early in the growing season. Nutrient quality has been shown to vary directly with growth stage (Short *et al.* 1972). The absence of consistent differences in protein content between browsed and unbrowsed shrubs of the same species agrees with the findings of other studies. Shepherd (1971) reported no significant differences in protein content in shrubs subjected to seven years of clipping treatments. Dietz (1965) concluded that prolonged heavy browsing would probably not affect shrub nutrient content.

Examination of consecutive twig segments from browsed willow shrubs showed a progressive decrease in protein content from terminal to lower twig portions (Table 14). This trend was found at all collection periods and was most marked in the overwintering twigs in May and in the new succulent growth in early June. Short *et al.* (1972) showed the relative digestibility of current twigs is directly affected by the changing nutrient content associated with phenological change. Digestibility and nutrient quality of woody cells was shown to diminish as cells matured because cell walls thickened and became lignified and cellular protoplasm decreased. Differences in nutritional quality between terminal and lower twig portions may also be related to the relative amounts of highly digestible inner bark tissues and relatively indigestible woody tissues found in each segment. Inner bark and cambial tissues contain more minerals, sugars and proteins than woody tissues during winter (Short *et al.* 1972). The progressive decrease in crude protein from the apex to the distal portions of twigs has also been found in red maple (*Acer rubrum*), black cherry (*Prunus serotina*) (Cowan *et al.* 1970), red-osier dogwood (Fashingbauer and Moyle 1963) and Rocky Mountain juniper (*Juniperus scopularum*) (Kautz 1969). Cowan *et al.* (1970) also found that the level of crude protein increased in the terminal portions of dormant twigs as the growing season approached.

The nutritional requirements for moose have not been established, but information on the nutritional requirements for domestic ruminants (NAS-NRC 1970) and white-tailed deer (Dietz 1965) provide a comparative basis. Dietary protein levels for white-tailed deer have been suggested as 13 to 16 percent for optimum growth and as 6 to 7 percent for maintenance (French *et al.* 1955). If crude protein levels fall below 6 to 7 percent, rumen functions are seriously impaired (Dietz 1965). NAS-NRC (1970) recommend a minimum of 5.9 to 7.8 percent crude protein for maintenance of beef cattle. If moose requirements are similar, the willow browse in the study area contained adequate amounts of crude protein for growth and lactation during spring and early summer, but the winter diet of woody twigs would be marginally adequate for maintenance. The average protein in winter twigs of preferred willows (6.2%) does not reach the 7 percent level recommended as a minimum for browse on good deer range (Dietz *et al.* 1962; Dietz 1965).

However, the protein content of browse selected by moose may be expected to be higher than that reported for the total CAG. Terminal portions of winter *Salix candida* twigs contained 7.2 percent protein, about 13 percent more than the total CAG. Comparison of protein levels in the entire twigs of browsed and unbrowsed shrubs of the same species reveal that terminal portions of less-rank growth would contain an even higher crude protein content. Various food habit studies have shown that domestic and native ungulates can select forage containing more crude protein than the average available on the site (Hardison *et al.* 1954; Heady 1964; McClymont 1967). Dietz and Yeager (1959) found that mule deer preference for big sagebrush in late winter and early spring was due to its having higher protein levels than other species during that period. Moose have also been found to select individual plants or species containing higher protein levels than the average available in the area (Bergerud and Manuel 1968; Milke 1969; Peek 1974).

2. Carbohydrates

The seasonal trends of acid-detergent fiber (ADF) and acid-detergent lignin (ADL) varied among species and browsed conditions within species. The generality that ADF and ADL in current annual leaves and twigs increase with seasonal progression (Dietz *et al.* 1962; Van Soest, 1966; Laycock and Price 1970) did not hold for all willows examined. ADF and ADL content in twigs of most species showed a marked increase during the summer and a moderate decline during late summer or dormant season. The leaves and twigs of *Salix gracilis* showed a progressive decline in ADL with seasonal progression. The cellulose content and ADL:ADF ratio in twigs also increased in most species from early to late summer then remained relatively stable or showed a slight decline in the dormant season. Cellulose content in leaves remained about the same or increased from early to late summer. Levels of ADF, ADL and cellulose were considerably higher in stems than in leaves, however, the ADL:ADF ratio was the same in both plant parts during the growing season. Seasonal levels of the fibrous carbohydrate components in willow browse were similar to those reported for other deciduous browse (Urness, 1973; Tew, 1970; Short *et al.*, 1972). Silver (1976) reported the seasonal levels of lignin in *Salix scouleriana* and *S. bebbiana* browse generally declined from autumn to winter. Dietz (1972) found that, with the exception of aspen and fringed sagebrush (*Artemisia frigida*) both ADF and ADL increased markedly from spring through winter in shrubs fed upon by deer in South Dakota. Aspen showed a moderate decline in both components from summer through winter.

The data show the nutrient value of willow browse generally declines with seasonal progression through September, then increases slightly during the dormant season. Urness (1973) found the consumption and nutritional value of central Arizona deer forages were primarily influenced by phenological development. He found the in-vitro digestibility of browse declined as the levels of ADF increased with seasonal progression. The digestibility of cell walls is variable and depends upon several factors of which lignin is the most important (Goering and Van Soest, 1970). Lignin acts as a barrier to micro-organisms and is negatively correlated with both dry matter and protein digestibility (Dietz, 1972). Since the digestibility of cellulose depends upon its state of lignification, the lignin fraction is best expressed as a ratio of ADF (Goering and Van Soest, 1970). Using the lignin ratio method, the estimated cell-wall digestibility of willow browse in this study varied from 13 to 21 percent. These values are lower than those reported from washed moose rumen contents in Alaska (Gasaway and Coady, 1974) and other deciduous browse (Short, 1971; Dietz, 1972).

Several factors indicate that the data may underestimate the nutritive value of willows for moose. Drying of samples at 65°C has been shown to artificially increase the acid-detergent fiber and lignin fractions through heat damage (Van Soest, 1964). Moose were also found to select plant parts and to discriminate among species of willow and among individual willow plants. The browse samples collected represent the total annual growth of leaves and twigs and do not account for selective feeding behavior or the use of only the upper portions of twigs, which contain less ADF and lignin than lower portions and are more digestible.

3. Crude Fat

The crude fat (ether extract) content of willow twigs was lower in developing twigs in early summer than in mature twigs during the dormant season. Crude fat content in shrubs generally shows a decrease with seasonal progression through July, then an increase in fall and winter (Dietz 1972). Tew (1970) found that crude fat content in aspen leaves increased greatly from spring to fall.

In this study, willow twigs in the dormant season averaged 4 percent crude fat and ranged from 3.4 to 4.6 percent. These values are comparable to the crude fat content reported for willows in Wyoming (Houston 1968) and Alaska (Milke 1969).

The nutritive value of crude fats is not considered to be as important in ruminant nutrition as they were formerly thought to be (Dietz 1972). This is because the crude fat determination includes other fractions such as terpenes, resins and essential oils which are not digestible to any extent, and may even inhibit rumen function (Nagy *et al.* 1964). It is not known whether the crude fat fraction of willow browse contains appreciable amounts of non-digestible essential oils. Smith (1950, 1952) reported the digestibility of ether extract ranged from 23.3 percent to

68.3 percent among eight shrub species of importance to wintering mule deer. Although the digestibility of crude fat in willow browse is not known, the digestible fraction may be an efficient source of metabolizable energy. This would be particularly important to moose during the long, cold winters experienced in northern regions. Essential fatty acids provide approximately 2.25 times more energy than carbohydrates or protein (Morrison 1954).

4. Minerals

Ash, calcium, magnesium, phosphorous and sodium concentrations were variable among species and between browsed conditions. The highest during the spring and generally decreased with seasonal progression. The phosphorous content of young twigs (0.27%) was more than twice that of twigs during the dormant season (0.12%). Calcium content of willow twigs was highest in late summer. In willow leaves, all minerals, except sodium, showed an increase in concentration with maturity. Sodium levels in leaves were highly variable. Similar seasonal trends for these minerals were reported for willow (*Salix* spp.) and other shrubs in Colorado (Short *et al.* 1966) and for a variety of browse species used by deer in South Dakota (Dietz 1972).

Willow browse in spring and early summer contained ample calcium levels, adequate phosphorous levels and an acceptable calcium-phosphorous ratio. In winter, willow twigs contained adequate calcium content, but appear deficient in phosphorous and had a high calcium phosphorous ratio (4.9:1). The minimum calcium and phosphorous requirements generally recommended for maintenance of domestic livestock under range conditions are 0.32 and 0.17 percent, respectively (NAS/NRC 1970). Beef cattle require 0.16 to 0.60 percent calcium and 0.16 to 0.43 percent phosphorous, depending on sex, age and condition. The desirable calcium-phosphorous ratio is 2:1 or 1:2, although ratios greater than 2:1 are permissible if sufficient vitamin D is present in the forage (Dietz 1970). McEwan *et al.* (1957) found that white-tailed deer could tolerate lower calcium levels than those recommended for domestic livestock. He concluded that the diet of deer became deficient in calcium and phosphorous at about 0.27 and 0.08 percent, respectively.

The magnesium concentration in willow twigs decreased from 0.38 to 0.21 percent and in leaves increased from 0.52 to 1.04 percent with seasonal progression. These values are considerably higher than magnesium concentrations reported for aspen leaves (0.03 to 0.25%) in Utah (Tew 1970) and for native forage plants near Inuvik (Scotter and Miltmore 1973). Short *et al.* (1966) also reported that magnesium values in willows were generally higher than those of other forage plants in Colorado. Maynard and Loosli (1969) indicated the magnesium requirements of domestic livestock for growth was in the order of 0.06 percent of the dry ration, assuming that calcium and phosphorous intakes were adequate but not excessive. If moose requirements for magnesium are similar to that reported for domestic livestock, willow browse contains ample magnesium levels.

Sodium content in willow leaves and twigs was low during all seasons. It is recommended that forage of domestic livestock contain from 0.05 to 0.15 percent sodium (NAS/NRC 1970). Sodium levels in willow leaves and twigs averaged 0.021 and 0.026 percent, respectively.

The data show considerable variation in sodium content. This may be due to contamination during handling of samples and which often is the greatest source of error in sodium determinations (Lowendorf 1974).[1] The lowest concentrations of sodium recorded are about 0.005 percent. Jordan *et al.* (1973) found that sodium concentrations in woody plants eaten by moose on Isle Royale were so low, averaging 0.001 percent, that he doubted moose could meet their minimum requirements from browse alone. He suggested that in order for moose to survive in this habitat, they needed specialized feeding strategies and unusual physiological adaptations for finding, storing, and conserving sodium. Jordan *et al.* (1973) found aquatic plants contained 50 to 500 times more sodium than terrestrial plants and felt that moose on Isle Royale and possibly in other regions where aquatics were eaten, depend in large part upon this source to meet their annual requirement for sodium.

[1]Personal communication, H. Lowendorf, 1974.

A sodium deficiency in the browse diet of moose may explain the apparent preference shown for seaside arrowgrass in the study area. Seaside arrowgrass is noted for its relatively high salt (sodium chloride) content in comparison to other herbaceous forages (McLean and Nicholson 1958). Although seaside arrowgrass is poisonous to domestic livestock (Kingsbury 1964) there are indications that native ungulates are not as susceptible to plant poisoning (Johnston *et al.* 1965).

B. Response of Willows to Natural and Simulated Browsing

Results of the simulated browsing study indicate that *Salix bebbiana* and *S. discolor* shrubs are stimulated to greater productivity when clipped during the inactive growth period or the dormant season. Although the number of twigs was reduced by all clipping intensities, the length and weight of the new CAG was greater than unclipped (control) shrubs, resulting in an overall increase in browse production the year following simulated browsing. Removal of the terminal bud and thus the apical dominance has been shown by several researchers to stimulate twig production from the dormant lateral buds (Garrison 1953, 1972; Ferguson and Basile 1966). Ferguson and Basile (1966) found that topping of bitterbrush shrubs resulted in a nine-fold increase in twig production and speculated that topping caused an imbalance of root:shoot ratio resulting in a relative abundance of water and mineral nutrients which favors shoot growth.

The response of CAG to simulated browsing in spring was more dependent upon the intensity of clipping than were the fall and winter treatments. Fifty and 100 percent clipping intensities in spring generally resulted in an increase in the number of twigs but a decrease in the length and weight of twigs produced the next growing season. In spring the 100 percent clipping treatment had a lower twig production than other treatments. These findings are similar to those reported by Garrison (1972). Garrison concluded that browse utilization was least detrimental to shrubs during fall and winter, when non-structured carbohydrates reserves are highest, and most damaging during late spring and early summer when non-structural carbohydrate reserves are the lowest.

The response of willows to natural browsing was similar to simulated browsing during the dormant season. *Salix candida* and *S. bebbiana* shrubs which were heavily browsed by moose for two or more winter seasons had fewer twigs but a greater production (weight) of woody shoots than unbrowsed shrubs. Different growth responses to browsing were also apparent between species. Browsed *Salix bebbiana* shrubs had a three-fold reduction in the number of twigs produced with a two-fold increase in total twig weight while browsed *Salix candida* shrubs responded with a small decrease in twig numbers and about a four-fold increase in total weight of twigs produced.

Within moderately and heavily browsed *Salix candida* clumps, individual secondary stems responded variously to different intensities of browse use (Table 30). Browsing during the preceding dormant season stimulated the greatest twig production. Stems browsed in previous years but not the preceding season outproduced the control stems but produced less than stems browsed the preceding season. Ferguson and Basile (1966) found the increased growth response of bitterbrush shrubs to topping continued in subsequent years, but at a declining rate. Comparison of unbrowsed stems within unbrowsed (Table 28) and browsed (Table 30) *Salix candida* clumps in my study, indicated that browsing may have stimulated twig growth (number and length of twigs per secondary stem) throughout the shrub. Cook and Stoddart (1960) however, concluded that there was little or no translocation of manufactured food from one side of a plant to the other when clipping of CAG from one side of big sagebrush plants caused death of that half of the plant while the unbrowsed half grew vigorously.

Stimulation of new twig growth as a result of removal of the terminal bud is commonly explained by suppression of apical dominance (Garrison 1972). Suppression of apical dominance generally allows two or more lateral buds to develop as new leaders. In this study, the willows subjected to simulated or natural browsing during the dormant season generally responded with a decrease in the number of new twigs or leaders. The marked increase in total twig production following browsing may be due to the change in the shrubs root:shoot ratio causing a hormonal imbalance (Berg and Plumb, 1972) or an overabundance of water and mineral nutrients (Ferguson and

Basile, 1966), both of which may favor vigorous twig growth.

C. Relationships Between Moose and Willow

Moose were found to concentrate on willow dominated communities during winter in the lowlands near Fort Providence. Aspen and aspen-willow communities were the commonest forest cover but received relatively light use. In the willow dominated communities, the willow savanna and patterned fen, willows comprised 97 and 72 percent of the available browse and 97 and 99 percent, respectively, of the browse used by moose. Similar habitat use was described by Berg and Phillips (1974) in ecologically similar areas characterized by broad expanses of willow and marsh, commonly found from north-eastern Minnesota to north-central Alberta within the transition zone between prairies and northern coniferous forests. These authors found that willow and associated willow habitats were used much more than non-willow habitats.

In this study, a marked preference was noted for certain willow species (Table 10). Comparison of the relative abundance and use of willows in each community showed moose were selecting certain species of willow and avoiding other species of willow. Browse preference varied among communities but was not related to the abundance of preferred species. *Salix candida* was preferred in the patterned fen where it was abundant and in the willow savanna where it was scarce. *Salix padophylla* was uncommon in both communities but highly preferred in only the willow savanna. This indicates that willows may be ranked in order of low to high preference, the use of a particular willow dependent upon the availability of more preferred species and the site or plant community in which it was growing. Milke (1969) also listed willows in an order of preference and indicated that neither the relative abundance nor species density affected the preferential use of browse by moose in his Alaska study area.

Although preference in this study was determined on browse use throughout the winter, field observations indicated a change in the importance of plant communities and browse species used by moose as the winter progressed. The shift in moose activities from the patterned fen, where the low-growing and highly preferred *Salix candida* was abundant, occurred about the time of increasing snow depths and snow crusting conditions (late winter). Spring observations showed the use of tall shrubs, *Salix bebbiana* and *Salix discolor*, in the willow savanna had increased in late winter. Several authors (Kelsall and Prescott, 1971; Coady, 1974; Krefting, 1974) have shown the importance of snow cover as a factor influencing the availability of browse, the distribution of moose and moose use of plant communities. Dorn (1970) found that as the snow depths increased during winter, the importance of tall species increased while that of short species decreased. While snow conditions may have influenced the use of *Salix candida* in the study area during late winter, mid-winter observations of moose cratering activities illustrate the high preference or importance attributed to this species, considering the apparent effort expended in obtaining this browse from beneath the snow.

The high degree of browse selectivity shown by moose in the study area is exemplified by their discrimination among individual shrubs within palatable species, notably a selection for those willows which had been browsed in previous seasons (Figure 7). The direct relationships between the degree of current and previous use of individual willow shrubs indicates that browsing influenced some "palatability" factor of the next season's growth which, in turn, stimulated a selective response by moose. Several other studies have also noted preferential browsing of selected shrubs within a species (Bergerud and Manuel 1968; Houston 1968). Bergerud and Manuel (1968) found moose preferred individual balsam fir with dark green needles over chlorotic, light green colored balsam fir. These authors found that protein levels in dark green fir were higher than in chlorotic fir and suggested that moose were selecting the most nutritious plants. Houston (1968) reported individual subalpine fir trees were often heavily browsed by moose and suggested that differences in palatability may occur among individual trees.

Other workers (Hardison *et al.*, 1954; Marten, 1969; Milke, 1969; Westoby, 1974) have examined the relationships between preference and palatability factors. Specifically, Heady's (1964) review of palatability showed that high positive correlations have been found between forage preference and protein content, sugars and ether extract while lignin and crude fiber often showed a negative relationship with increased preference. In my study, no significant relationships between chemical composition and browse preference of willows were found. Although differences in average nutrient content between preferred and non-preferred species of willow and between browsed and unbrowsed willows of the same species was not great, the general trend indicated that moose were selecting browse of lower nutrient content. Twigs of browsed willows were generally lower in crude protein, ash and ether extract and higher in acid-detergent fiber and lignin than willows of non-preferred species or unbrowsed individuals of the same species. Only moisture content showed a positive, although non-significant, relationship with selection for previously browsed individuals of preferred species. Moisture content of non-preferred species were similar to unbrowsed shrubs of preferred species. The influence of succulence on palatability of pasture grasses for domestic livestock was illustrated by Davies (1925). Swank (1956) found that forage with a consistent high moisture content was preferred by deer and cattle. Milke (1969) found that willows most preferred by moose also contained the highest moisture content. Pavlov (1973) suggested moose preferred balsam fir and willows during the winter because moisture does not freeze in the twigs of these species.

In this study, moose showed a marked preference for individual shrubs of palatable species that had been browsed in previous seasons. Willows browsed during the dormant season were shown to respond with a decrease in twig numbers and a dramatic, 2 to 4 fold increase in the size, length and weight, of twigs produced the next season. Descriptions of moose browsing behavior indicate that moose will often select individual twigs and manipulate them so they can be consumed butt first (Geist 1963). During mid-winter collections of browse samples and simulated browsing treatments in this study, a greater difficulty was encountered in manipulating short twigs without breakage of older wood than in manipulating longer twigs from terminal leaders or from previously browsed shrubs. These observations indicate it would be difficult for moose to select the relatively short current year's twig growth from unbrowsed shrubs without obtaining quantities of older wood. Such selection would be particularly difficult in cold weather when twigs are brittle.

Since moose consume 18 to 23 kg of browse (wet weight) per day in winter (Verme 1970), considerable mobility and energy expenditure would be required to obtain sufficient browse to maintain the rumen fill. Selection of larger twigs from previously browsed shrubs would reduce browsing time and feeding movements required to maintain rumen fill and thus be more efficient than browsing of smaller twigs from unbrowsed shrubs (Figure 13). A similar concept was described by Des Meules (1965), who postulated that heavy utilization of balsam fir by moose in late winter may save energy, since fir twigs weigh eight to thirteen times more than deciduous twigs of similar length and therefore require less time and effort to consume equivalent amounts.

In this study, moose were consuming only the upper half to two thirds of selected twigs. Chemical analysis of lower, middle and terminal twig portions showed that the terminal third contained higher concentrations of crude protein, crude fat, and minerals and

Figure 13. Comparison of current annual twig growth on secondary stems of unbrowsed and moose browsed *Salix candida* shrubs.

lower levels of acid-detergent fiber and lignin than lower twig portions or the total twigs from unbrowsed shrubs. In browsed *Salix candida* shrubs the crude protein content of terminal twig portions in January exceeded the 7 percent level considered necessary for ruminant maintenance. Selection of higher quality browse by moose may also increase food intake, digestibility and passage rate through the gut (Gasoway and Coady, 1974).

These observations lend evidence that moose in the study area were selecting for the more available as well as the more nutritious browse that was readily obtainable from previously browsed shrubs. This preference for longer twig growth may also explain why moose expended additional effort in cratering through snow to obtain browse from low growing *Salix candida* clumps or in breaking the upper branches of *Salix bebbiana* shrubs to obtain the terminal leaders.

Examination of moose food habits in this study indicates that browse abundance was probably not a limiting factor to the moose population in the Mackenzie lowlands area. In willow dominated communities where moose congregated during winter, only 7 to 8 percent of the available browse was utilized by moose; other areas and plant communities examined sustained even less use during winter. It is expected that, at this latitude, the duration and severity of winter conditions may cause a considerable energy and nutritional strain on moose. Moose normally experience a loss of up to 20-25 percent of body weight between fall and spring (Gasoway and Coady

1974). The relatively short growing season at this latitude would also limit the time available for weight gain from the more nutritious summer forage. The marked selection of winter browse, particularly from previously browsed shrubs, observed in this study may be a behavioral adaptation to maximize intake of the more palatable and perhaps the more nutritious browse available while minimizing energy expended during feeding. Energy conservation through forage efficiency may be extremely important for moose survival through the long and severe northern winters. Because of the growth response of willows to browsing and moose selection of previously browsed shrubs, this relationship also acts to perpetuate a source of preferred and perhaps important winter browse.

SUMMARY

A study was conducted to examine the plant communities and moose habitat use in the lowlands near Fort Providence, Northwest Territories. The primary objective was to examine the relationship between moose and willows on a moose winter range.

Species composition, herbage and browse production and soil characteristics were described for five plant communities: sedge meadow, patterned fen, willow-shrub, willow savanna and aspen-willow communities. Willows were the dominant browse species in all but the sedge meadow community. Mean annual production ranged from 530 kg/ha in the aspen-willow to 2535 kg/ha in the sedge meadow community. Browse production in shrub dominated communities ranged from 442 kg/ha in the willow savanna to 1406 kg/ha in the willow-shrub communities. Available winter browse averaged about 20 percent of summer browse in all shrub communities and about 10 percent in the aspen-willow community.

Moose abundance was estimated at 0.21 moose per square kilometer in the general lowland area and 0.90 per square kilometer in the willow communities used as winter range in the study area. Total browse use and pellet-group counts showed moose used the willow savanna and patterned fen communities about six times more than the aspen-willow communities.

During winter, moose exhibited a marked selection of browse from particular species of willows and from individual shrubs within preferred species. In the willow savanna community, *Salix bebbiana*, *S. candida* and *S. padophylla* shrubs received significantly more use while *Salix gracilis* and *S. maccalliana* shrubs received significantly less use than expected. Similar trends of preference or avoidance of particular browse species were also found in the patterned fen and aspen-willow communities. The degree of previous browse use (hedging) of individual palatable willow shrubs was found to have a positive influence on the probability that the shrub would be again browsed by moose. The degree of previous use also had a direct relationship with the amount of current annual growth (CAG) browsed by moose in subsequent years.

The seasonal nutrient content of six species of willows and two browsed conditions (browsed and unbrowsed shrubs of palatable species) were examined at four dates during the growing season and once during the dormant season (January). Crude protein and moisture levels were greatest in young leaves and twigs and generally decreased progressively through the growing season. A general increase in twig protein levels ($\bar{x}$ = 1% of dry weight) occurred before leaf abscission at the end of the growing season. Acid-detergent fiber and lignin levels in willow twigs increased sharply early in the growing season before showing a slight general decline in the latter part of the growing season and in the dormant season. Acid-detergent fiber and lignin levels in willow leaves showed a moderate increase throughout the growing season. Ash, calcium and magnesium levels in willow twigs showed a progressive decline and in leaves a progressive increase with seasonal progression. Phosphorous content of twigs showed a two fold decline between early summer and the dormant season. Calcium-phosphorous ratios increased from 2.7:1 in early summer to 4.9:1 in the dormant season. Sodium levels were low in willow twigs and leaves ($\bar{x}$ = 0.026 and 0.021, respectively) in all seasons. Average crude fat levels in willow twigs showed a two fold increase from 2.1 percent in early summer to 4.0 percent during the dormant season. Differences in nutrient levels were found among species of the same browsed condition but these differences were generally not consistent throughout the sampling period. Browsed willows generally contained lower levels of crude protein, ash and minerals and higher levels of acid-detergent fiber, lignin and moisture than unbrowsed willows of the same species. Variation among replicated samples resulted in few significant differences between species or between browsed conditions within species. I found no relationship between browse selection by moose and browse nutrient content.

Chemical analyses of consecutive twig segments showed a progressive decrease in moisture, crude protein, ash, calcium and magnesium and an increase in acid-detergent fiber and lignin from the terminal to distal twig portions.

Willows subjected to simulated or natural browsing during the dormant season responded with a decrease in the number of twigs and a significant (two to four fold) increase in production (total weight) of twigs per secondary stem in the following growing season. The response of shrubs to simulated browsing early in the growing season had variable results and depended upon the intensity of clipping. The 100 percent clipping treatment had the greatest debilitating effect: an increase in twig numbers and a decrease in total weight of twigs produced per secondary stem. Simulated browsing of shrubs in late summer (August) and in the dormant season had similar effects on twig production in the following growing season.

It was postulated that moose selection of browse from previously browsed shrubs of palatable species may be related to the relative ease of obtaining sufficient quantities of the current year's twig growth to maintain the rumen fill. Selection of the longer twig growth may be a behavioral adaptation to maximize intake of palatable and perhaps more nutritious browse (terminal twig portions) available while minimizing energy expended during feeding. Energy conservation through forage efficiency may be extremely important for moose survival through the long and severe northern winters.

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Appendix A. Scientific and common names[1] of plant species recorded in six communities in the study area. The prevalence of each species is indicated by the following symbols[2]: d, dominant; a, abundant; f, frequent; s, scattered and r, rare.

Scientific Name	Common Name	White Spruce	Aspen-Willow	Willow Savanna	Willow-Bog Birch	Patterned Fen ridges	Patterned Fen meadows	Sedge Meadows
TREES AND SHRUBS								
Alnus tenuifolia	river alder				r			
Amelanchier alnifolia	saskatoon		s					
Betula glandulosa	bog birch		f	s	d	d	r	
Betula papyrifera	paper birch		s					
Cornus stolonifera	red-osier dogwood		r			r		
Eleagnus commutata	silverberry		s					
Larix laricina	larch	r	r			s		
Ledum groenlandicum	Labrador tea	s	s			s		
Lonicera dioica	twining honeysuckle		r	r				
Myrica gale	sweet gale					a	s	
Picea glauca	white spruce	d	s	s	s	r		
Picea mariana	black spruce	s		r	r	d		
Pinus banksiana	jack pine		s	r				
Populus balsamifera	balsam poplar		f	s	r			
Populus tremuloides	aspen	s	d	s	s	r		
Potentilla fruiticosa	shrubby cinquefoil		s	s				

[1]Scientific plant names follow Moss (1959); common names follow Moss (1959) when given or Budd and Best (1964).
[2]Adapted from Moss (1953).

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Appendix A. continued.

Scientific Name	Common Name	White Spruce	Aspen-Willow	Willow Savanna	Willow-Bog Birch	Patterned Fen ridges	Patterned Fen meadows	Sedge Meadows
Ribes americana	wild black currant		r			r		
Ribes oxyacanthoides	northern gooseberry	s	s	s	r	s		
Rosa acicularis	prickly rose	a	a	s	s	f		
Rubus strigosus	wild red raspberry		s	s	s	r		
Salix arbusculoides	willow		s					
Salix athabascensis[1]	willow			r				
Salix bebbiana	beaked willow	a	d	d	d	s	r	s
Salix calicola	willow					r		
Salix candida	hoary willow			s	s	d	d	
Salix discolor	pussy willow		s	a	a	f	s	
Salix glauca	willow	s	a		r			
Salix gracilis	willow		s	a	r			
Salix padophylla	willow		s	a	s	a		
Salix maccalliana	willow		s	a	d	a	s	s
Salix myrtillifolia	willow			r	s	f		
Shepherdia canadensis	Canadian buffalo-berry	a	a	s	r	s	r	
Symphoricarpos occidentalis	buckbrush			s				
Vaccinium spp.	bilberry		s				r	
Viburnum edule	low-bush cranberry	s	r					

[1]Willow taxonomy follows Raup (1959).

...continued

Appendix A. continued.

Scientific Name	Common Name	White Spruce	Aspen-Willow	Willow Savanna	Willow-Bog Birch	Patterned Fen ridges	Patterned Fen meadows	Sedge Meadows
HERBS								
Achillea millefolium	common yarrow	r	f	f		r		
Achillea sibirica	many-flowered yarrow		r	r				
Agropyron trachycaulum	slender wheat grass		s	f				
Agrostis scabra	hair grass		s	f				
Allium schoenoprasum	wild chives				r			
Anemone canadensis	Canada anemone		s					
Antennaria nitida	small flowered everlasting			s				
Antennaria rosea	rosy everlasting		s	s				
Arceuthobium americanum	dwarf mistletoe	s						
Arctostaphylos rubra	alpine bearberry		s		s			
Arctostaphylos uva-ursi	common bearberry	a	f	s		f		
Arenaria lateriflora	sandwort		r	s	r			
Arnica amplexicaulis	arnica			s				
Aster alpinus	aster			r				
Aster conspicuus	showy aster		s	f		r	r	
Aster junciformis	rush aster			a	a			s
Aster pansus	prairie aster			r				
Astragalus agrestis	milkvetch		s	a				
Astragalus striatus	milkvetch			s				

...continued

Appendix A. continued.

Scientific Name	Common Name	White Spruce	Aspen-Willow	Willow Savanna	Willow-Bog Birch	Patterned Fen ridges	Patterned Fen meadows	Sedge Meadows
Bechmannia syzigachne	slough grass				s			s
Botrychium lunaria	moonwart				s			
Calamagrostis canadensis	marsh reedgrass		s					
Calamagrostis inexpansa[1]	northern reedgrass		a	d	a	f	a	a
Capsella bursa-pastoris	Shepherd's purse		s					
Cardamine pratensis	meadow bittercress					s		
Carex aquatilis	water sedge		r	f	a	a	d	a
Carex atherodes	awned sedge		s	a	a	f	a	d
Carex aurea	golden sedge		r	s				
Carex deflexa	little green sedge		r	r		s		
Carex interior	sedge		r					
Carex platylepis	sedge	s	s			r		
Carex sartwellii	sedge		r	f				
Carex simulata	sedge			s				
Castelleja raupii	Indian paint brush		s	s		r		
Chenopodium capitatum	strawberry blight		s	r				
Chenopodium leptophyllum	narrow-leaved goosefoot		s	s				

[1]Also includes *Calamagrostis neglecta*.

...continued

Appendix A. continued.

Scientific Name	Common Name	White Spruce	Aspen-Willow	Willow Savanna	Willow-Bog Birch	Patterned Fen ridges	Patterned Fen meadows	Sedge Meadows
Cicuta mackenzieana	water hemlock			r	s		s	s
Cornus canadensis	bunch berry	f	s					
Corydalis aurea	golden corydalis		s					
Crepis runcinata	hawksbeard			r				
Elymus innovatus	hairy wild rye	f	a					
Empetrum nigrum	crowberry		f					
Epilobium angustifolium	fireweed	s	a	s	f	s		
Epilobium leptophyllum	bog willow-herb						s	
Epilobium palustre	marsh willow-herb				s		s	r
Equisetum arvense	common horsetail		s					
Equisetum scirpoides	dwarf scouring rush		r			f		
Erigeron spp.	fleabane			r				
Eriophorum angustifolium	cottongrass						r	
Erysimum cheiranthoides	wormseed mustard			s				
Fragaria virginiana	strawberry	c	a	a	s	r	s	r
Galium boreale	northern bedstraw	f	a	a			f	f
Galium trifidum	small bedstraw			r	r			
Geocaulon lividum	northern comandra	f	s			s		
Gentiana affinis	prairie gentian			s				
Gentianella amarella	felwort		r	s				
Geum allepicum	yellow avens		r	r	s			

...continued

Appendix A. continued.

Scientific Name	Common Name	White Spruce	Aspen-Willow	Willow Savanna	Willow-Bog Birch	Patterned Fen ridges	Patterned Fen meadows	Sedge Meadows
Hippurus vulgarus	mare's-tail						f	
Hordeum jubatum	wild barley		s	f				
Juncus balticus	wire rush		s	f				
Koelaria cristata	June grass			r				
Lathyrus ochroleucus	peavine		r					
Lathyrus venosus	peavine		s					
Linnaea borealis	twin flower	f	f					
Lysimachia thrysiflora	tuffed loosestrife		s					
Mentha arvensis	wild mint			s	s		f	f
Muhlenbergia richardsonis	mat muhly			s				
Oxytropis spp.	locoweed			r				
Parnassia palustris	northern grass-of-Parnassus			s		r		s
Penstemon procerus	slender blue beard tongue			s				
Petasites sagittatus	arrow-leaved colt's-foot		s	f	f	s		s
Poa interior	blue grass	s						
Poa leptocoma	blue grass		r					
Poa palustris	fowl blue grass		s	s				
Poa pratensis	Kentucky blue grass		s	s	f		f	
Polygonum amphibium	water smartweed			f	s	f		
Potamogeton spp.	pondweed						f	

...continued

Appendix A. continued.

Scientific Name	Common Name	White Spruce	Aspen-Willow	Willow Savanna	Willow-Bog Birch	Patterned Fen ridges	Patterned Fen meadows	Sedge Meadows
Potentilla arguta	white cinquefoil		s	s				
Potentilla norvegica	rough cinquefoil			r				
Potentilla palustris	marsh cinquefoil			r	s	f		
Potentilla pensylvanica	Pennsylvanian cinquefoil		s	s		s		
Potentilla rivalis	brook cinquefoil			r	r			
Primula incana	mealy primrose			s				
Pyrola asarifolia	pink wintergreen	f	s	r	s	s		
Pyrola grandiflora	wintergreen		s					
Pyrola secunda	one-sided wintergreen	f	r			s		
Ranunculus cymbalaria	buttercup			r				
Ranunculus macounii	Macoun's buttercup			s				r
Ranunculus sceleratus	celery-leaved buttercup				s		s	
Rhinanthus crista-galli	yellow rattle		r	r				
Rorripa islandica	yellow cress		r				s	
Rubus acaulis	dwarf raspberry	s	a	s	f	f	f	
Rumex occidentalis	western dock		s				s	
Scirpus validus	common great bullrush						s	
Scolochloa festucacea	scolochloa			s	f		s	a
Scutellaria galericulata	common skullcap			r	r		r	s

...continued

Appendix A. concluded.

Scientific Name	Common Name	White Spruce	Aspen-Willow	Willow Savanna	Willow-Bog Birch	Patterned Fen ridges	Patterned Fen meadows	Sedge Meadows
Senecio pauperculus	balsam groundsel		r	r				
Sisyrinchium montanum	blue-eyed grass			s				
Sium suave	water parsnip				r		s	s
Solidago decumbens	mountain goldenrod		s					
Solidago gigantea	late goldenrod			s				
Stachys palustris	marsh hedge-nettle			f	s		f	s
Stellaria longipes	long-stalked chickweed		s	s		s	s	r
Stellaria spp.	chickweed			s			r	
Tanacetum vulgare	common tansey		s					
Taraxacum officinale	common dandelion		s	r				
Thalictrum occidentale	western meadow rue			f				
Triglochin maritima	seaside arrow-grass			f	r	f	f	
Triglochin palustris	marsh arrow-grass					f	s	
Typha latifolia	common cattail						r	
Utricularia vulgaris	common bladderwort						f	
Veronica scutellata	marsh speedwell						r	
Viola adunca	early blue violet			s				
Vicia americana	american vetch		s	s				

Appendix B. Mean soil moisture (% dry weight) and soil temperature (°C) at different depths in the wet sedge meadow community in 1973.

	Soil Depth Class	SAMPLING DATE 25 June	19 July	20 August
Soil Moisture n= 30	0-15 cm	67.2	56.4	56.4
	15-30 cm	28.0	23.3	22.3
	30-45 cm	22.0	19.8	19.7
Soil Temperature n= 60	10 cm	9.4	11.2	6.3
	20 cm	6.6	8.7	6.1