Variations in plant forage quality in the range of the Porcupine caribou herd [1]

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Abstract: Understanding potential impacts of vegetation change on caribou energetics requires information on variations in forage quality among different plant types and over time. We synthesized data on forage quality (nitrogen, neutral detergent fiber and dry matter digestibility) for 10 plant growth forms from existing scientific literature and from field research in the Arctic National Wildlife Refuge, Alaska. These data describe forage quality of plant species in habitats found within the summer and winter range of the Porcupine caribou herd in northwestern Canada and northern Alaska, U.S.A. We compared mean levels of summer forage quality among growth forms and, where possible, estimated seasonal changes in forage quality. Preferred forage groups (deciduous shrubs, forbs, and cottongrass flowers) had higher nitrogen and digestibility, and lower fiber content, than other growth forms. Nitrogen concentration in green biomass peaked at the onset of the growing season in forbs and deciduous shrubs, whereas graminoids reached peak nitrogen concentrations approximately 15-30 days after growth initiation. *In vitro* dry matter digestibility (IVDMD) and concentration of neutral detergent fiber (NDF) of green biomass differed among growth forms, but did not show strong seasonal changes. IVDMD and NDF concentrations were correlated with nitrogen concentrations in studies that had paired sampling.

Key words: Arctic National Wildlife Refuge, digestibility, neutral detergent fiber, nitrogen, plant growth forms, range ecology, tundra.

Introduction

Identifying mechanisms that may regulate ungulate populations has been an important focus of many wildlife research studies. In some populations predators are implicated (Bergerud, 1978; Seip, 1992). However, large migratory populations appear largely regulated by density-dependent resource limitation (Sinclair *et al.,* 1985; Fryxell *et al.,* 1988; Messier *et al.,* 1988). The linkages among nutrition, body composition and reproductive performance in ungulates, particularly caribou (*Rangifer tarandus*), are well documented (White & Trudell, 1980a; Albon *et al.,* 1986; Adamczewski *et al.,* 1987; Cameron & ver Hoef, 1994;

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Russell *et al.,* 1998). For this reason, interpretation or prediction of caribou population dynamics under changing environmental conditions needs to be based on a solid understanding of quality, availability and use of forage resources.

A recent survey of the large migratory caribou herds (Russell *et al.,* 2000) indicated that there was a wide difference in the state of knowledge of baseline population or environmental characteristics among herds. For many herds, the survey indicated that basic food resource information was lacking. In contrast, a large amount of information has been collected for the Porcupine caribou herd (PCH; Russell *et al.,* 2000). These data have been integrated into a computer model (Kremsater *et al.,* 1989) that projects impacts of climate change and industrial development to the population level. Application of this type of model to other large caribou herds, however, will require tools to generate forage quality estimates from limited data sources. Understanding how forage quality varies within the relatively well-studied range of the PCH is an initial starting point for predicting similar patterns in other areas.

Our objectives were to quantify seasonal patterns of nutritional quality of forage utilized by the PCH in northeastern Alaska, USA and northwestern Canada (Yukon and Northwest Territories). Information on forage quality, generalized by plant growth form types, is required as input to the model of caribou energetics parameterized for the Porcupine herd (Kremsater *et al.,* 1989). Specifically, the caribou energetics model uses information on forage biomass, nitrogen content, fiber content, and digestibility. Concentration of nitrogen in plant tissues (N) is an indicator of the summer nutritional value of different forage types with respect to protein deposition. Neutral detergent fiber (NDF) concentration reflects the portion of plant material contained in cell wall, and gives information on controls over rate of processing by the animal. In vitro dry matter digestibility (IVDMD) provides information on the availability of energy by estimating the proportion of plant material that is readily digestible. Combined, these values exert a strong control over food processing, which may affect frequency of feeding and total intake of biomass and nutrients. Although other chemical constituents of plants can play critical roles in animal nutrition, we focused our effort on developing generalized relationships for those variables directly used in our modeling efforts.

This study represents an amalgamation of species, sites, and annual climate conditions found within the range of the Porcupine caribou herd.

From these reported studies we have tried to make generalizations about plant forage quality. For any given sample, variability among species, sample sites and annual environmental conditions likely affected observed forage quality. In particular, variations in plant phenology across a landscape may have significant effects on the quality of forage that is available to caribou (Whitten & Cameron, 1980; Jorgensen & Udevitz, 1992; White *et al.,* 1992; Walsh *et al.,* 1997). However, because caribou use of seasonal habitats varies from year to year (Russell *et al.,* 1993), it is important to have a regional picture of forage quality as a basis of models of caribou energetics under 'average' conditions.

Methods

We assembled two forage quality data sets. One was derived from a literature review of published forage quality records collected within the range of the PCH (*ca.* 67-70°N, 135-150°W), or in physiographically similar areas. A second data set was based on our own field measurements of forage quality within the PCH calving grounds. We focused on the three variables required by the PCH energetics model (Kremsater *et al.,* 1989): nitrogen (N), neutral detergent fiber (NDF), and *in vitro* dry matter digestibility (IVDMD; Van Soest, 1964; Robbins, 1983). We included studies that documented biomass in our literature review (Table 1), but limited our analysis to the forage quality variables listed above. Only IVDMD obtained from a 48-hour two-stage procedure of Tilley & Terry (1963) was used in our analyses. Data were taken from graphs or tables in the literature, and therefore often represented means of individual measurements. For those studies reporting experimental manipulations, we used only values from experimental controls. To increase our sample size in evaluating correlations between different measures of forage quality, we included paired forage quality data from comparable habitats in other geographical locations (*e.g.* Manseau, 1996).

We reviewed 19 published studies that estimated vegetation biomass or forage quality relevant to the PCH range. No single study contained information on all four parameters of interest (biomass, N, NDF, IVDMD; Table 1). Most research on forage quality has been conducted during the snow-free season. As a result, there was much more information applicable to the tundra summer range of the PCH than to the taiga winter range. The exceptions were taiga lichen species (Chapin *et al.,* 1980; White & Trudell, 1980a) and some forest understory shrubs (Chapin, 1983). We found no

Table 1: Sources of information on plant forage biomass and nutritional quality relevant to the geographic range utilized by the Porcupine Caribou Herd. Checks in biomass, % N (nitrogen), % NDF (neutral detergent fiber), or IVDMD (*in vitro* dry matter digestibility) columns indicate the source contains data on those variables. The season and plant community type of collected samples are listed, along with the plant growth forms that were included in the study.

ID	Citation	Sample area	Biomass	N %	NDF %	IVDMD	Season	Growth form*	Plant community
1	Chapin, 1980	Atkasook, Alaska		X			summer	6,8	tussock
2	Chapin *et al.*, 1975	Barrow, Alaska		X			summer	5, 6, 8, 9	sedge meadow
3	Chapin *et al.*, 1980	Barrow, Alaska		X			summer, winter (lichens only)	1-2, 5-8, 10	tussock, sedge meadow
4	Hobbie, 1996	Foothills region, Toolik Lake, Alaska		X			late summer (senescent)	6, 7, 9	tussock
5	Jorgensen & Udevitz, 1992	Alaska National Wildlife Refuge (ANWR)	X	X	X		summer	5-6, 8, 10	coastal plain (incl. sedge meadow & tussock)
6	Klein, 1990	Arctic Alaska and other circumpolar arctic		X	X	X	summer, winter	5-8, 10	unspecified, summarized from (species pooled) multiple sources
7	Kuropat, 1984	Western Arctic herd calving grounds, NW Alaska		X	X	X	summer	6-8, 10	riparian, sedge meadow, tussock
8	Person *et al.*, 1980	Prudhoe Bay region, Alaska		X	X	X	summer	2	coastal plain, taiga
9	Russell *et al.*, 1993	Yukon PCH calving grounds	X	X	X		summer	2, 4-8, 10	alpine, gravel, heath, riparian, sedge meadow, tussock
10	Shaver & Chapin, 1986	Interior and foothills Alaska	X				summer	5-8	tussock
11	Shaver & Chapin, 1991	Foothills region, Toolik Lake, Alaska	X	X			summer	1-2, 5-8	heath, sedge meadow, tussock
12	Walsh *et al.*, 1997	ANWR		X			summer	6, 8	tussock
13	Webber, 1978	Barrow, Alaska	X				summer	1-2, 5-8	sedge meadow
14	White & Trudell, 1980a	Prudhoe Bay region, Alaska			X		summer, winter	2	coastal plain, taiga
15	White *et al.*, 1975	Prudhoe Bay region, Alaska			X	X	summer	2	coastal plain
16	White *et al.*, 1992	ANWR			X	X	summer		coastal plain (incl. sedge meadow & tussock)
17	Whitten & Cameron, 1980	Prudhoe Bay region, Alaska		X			summer	5-6, 8, 10	coastal plain (incl. sedge meadow & tussock)
18	Williams *et al.*, 1975	Prudhoe Bay region, Alaska	X	X			summer	1-2	tussock, sedge meadow
19	Williams *et al.*, 1978	Barrow, Alaska	X	X			summer	1-2	sedge meadow
	This study	ANWR	X	X		X	summer	5-6, 8-10	coastal plain (incl. sedge meadow & tussock)

* Key to plant types: 1= moss, 2= lichen, 3= mushroom, 4= *Equisetum* sp., 5= forbs, 6= deciduous shrub, 7= evergreen shrub, 8= graminoid, 9= standing dead (graminoid), 10= cottongrass flowers.

information on availability or forage quality of mushrooms that was applicable to our geographic area (however, see Grønwall & Pehrson, 1984).

In our second data set we included previously unpublished estimates of forage quality that were obtained as part of PCH range ecology research in the Arctic National Wildlife Refuge (ANWR), Alaska. We measured N concentration and IVDMD for several key caribou forage plants: willow (*Salix pulchra*), sedge (*Carex aquatilis*), tussock cottongrass (*Eriophorum vaginatum*), narrow-leaf cottongrass (*E. angustifolium*), and forbs (species pooled). Samples were collected during calving and post-calving (late May to late June) in 1993 and 1994. The data included here are averages calculated for five-day intervals within each year. Methodology for the ANWR samples followed methods reported in Russell *et al.* (1993).

We grouped forage quality data for plant species into plant growth forms. The selection of plant growth forms was based on the documented diet of the Porcupine caribou herd (Russell *et al.*, 1993) and consisted of the following groups: mosses, lichens, fungi (mushrooms), horsetails (*Equisetum* spp.), forbs (herbaceous dicots), deciduous shrubs, evergreen shrubs, and graminoids. The graminoid group was further subdivided into live green tissues, standing dead tissue (*Eriophorum angustifolium* and *Eriophorum vaginatum* only), and flower heads of tussock cottongrass (*E. vaginatum*). Only plant parts used as forage by caribou were considered. For most growth forms, this included all green biomass, flowers, and current-year stem growth. Exceptions were lichens, mushrooms, and standing dead graminoid tissue. In these, all above ground biomass was considered to be forage material.

We used a two-factor analyses of variance (ANOVA) to test for significant differences in forage quality ($P < 0.05$) between growth forms and seasons (SAS, 1990). Seasons were divided into early summer (May–June) and late summer (July–September). Means (calculated by growth form and season) from individual studies and from single years of our ANWR research were treated as experimental units. We calculated type III partial sums of squares for the analysis because replicates were distributed unequally across growth forms and season (SAS, 1990). Separate ANOVA's were performed for N, NDF and IVDMD. Significant interaction and main effects were examined graphically. Where there were significant season effects, seasonal patterns in forage quality were examined by plotting observations against calendar date. To obtain maximum temporal resolution in these graphs, we used all available values reported in the literature, rather than means from each study. We constructed seasonal plots only for growth forms with more than ten samples.

We examined correlations among forage quality variables when more than one forage quality parameter was measured for the same samples. This analysis was only possible for pairwise comparisons of N with NDF and IVDMD.

Results

Plant tissue concentrations of N and NDF, and IVDMD differed significantly among growth forms ($P < 0.001$, df=7, 6, and 5 for N, NDF, and IVDMD respectively; Fig. 1). Nitrogen concentration also differed between early and late season ($P < 0.001$, df=1) but the amount of seasonal change varied among growth forms (season and growth form interaction, $P < 0.05$, df=4).

Nitrogen concentrations of deciduous shrubs, forbs, and cottongrass flowers in early summer were substantially higher than for other growth forms at the same time or for the same groups in late summer (Fig. 1). Growth forms with lower mean N concentration showed little change in N concentration between early and late summer. Deciduous shrubs and forbs had the lowest concentrations of NDF, while cottongrass flowers and graminoid leaves had the highest. IVDMD was highest in forbs, cottongrass flowers and graminoid leaves. Deciduous shrubs and lichens were intermediate in digestibility between this group (forbs, cottongrass flowers, and graminoid leaves) and a low digestibility group consisting of evergreen shrubs and standing dead graminoid leaves.

The combination of high nitrogen concentration, high digestibility and low fiber content made forbs rank highest in overall forage quality (Fig. 1). Deciduous shrubs and cottongrass flowers also had generally high forage quality, but ranked lower that forbs because of lower digestibility (deciduous shrubs) or higher concentrations of NDF (cottongrass flowers). Graminoid leaves showed patterns of forage quality similar to cottongrass flowers but had lower early-season N concentration. Evergreen shrubs, standing dead graminoids, and lichens had the lowest overall forage quality due to relatively low concentrations of nitrogen, combined with moderate to low digestibility and intermediate fiber concentration. The limited information available for horsetails and mosses suggested that these growth forms also fit within the low forage quality group.

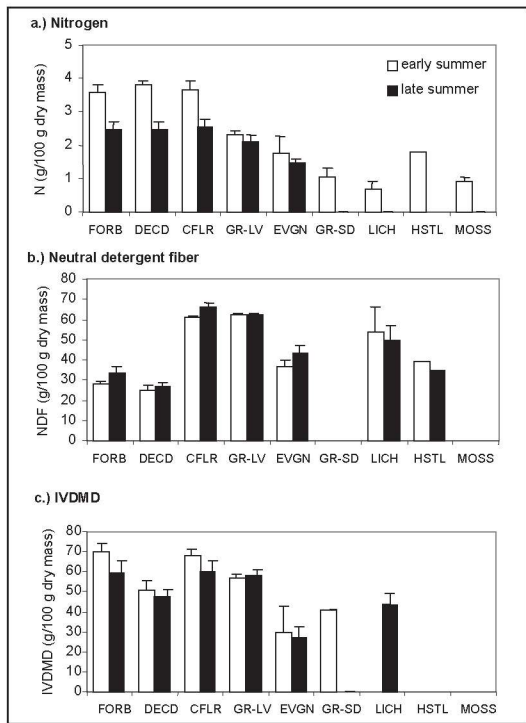We examined seasonal changes in N concentration in more detail for five growth forms for which

Fig. 1. Mean (+ 1 standard error of the mean) early (May-June; light bars) and late (July-September; dark bars) summer estimates (g/100 g dry mass) of a) nitrogen, b) neutral detergent fiber, and c) *in vitro* dry matter digestibility (IVDMD) for 10 tundra plant growth forms. Codes for growth forms are: FORB=forbs, DECD=deciduous shrubs, CFLR=cottongrass flower, GR-LV=graminoids live, EVGN=evergreen shrubs, LICH=lichen (forage species), GR-SD=graminoids standing dead, HSTL=horsetails, MOSS=moss. Means depicted here were calculated from the following data sources (see Table 1 for source list): a) nitrogen: 1-7, 9, 11, 17, 19, this study; b) NDF: 5, 6, 8, 9, 15; and c) digestibility: 6-8, 14, 15, 16, this study. Only values for forage tissues utilized by caribou are included. Bars without error bars indicate $n=1$.
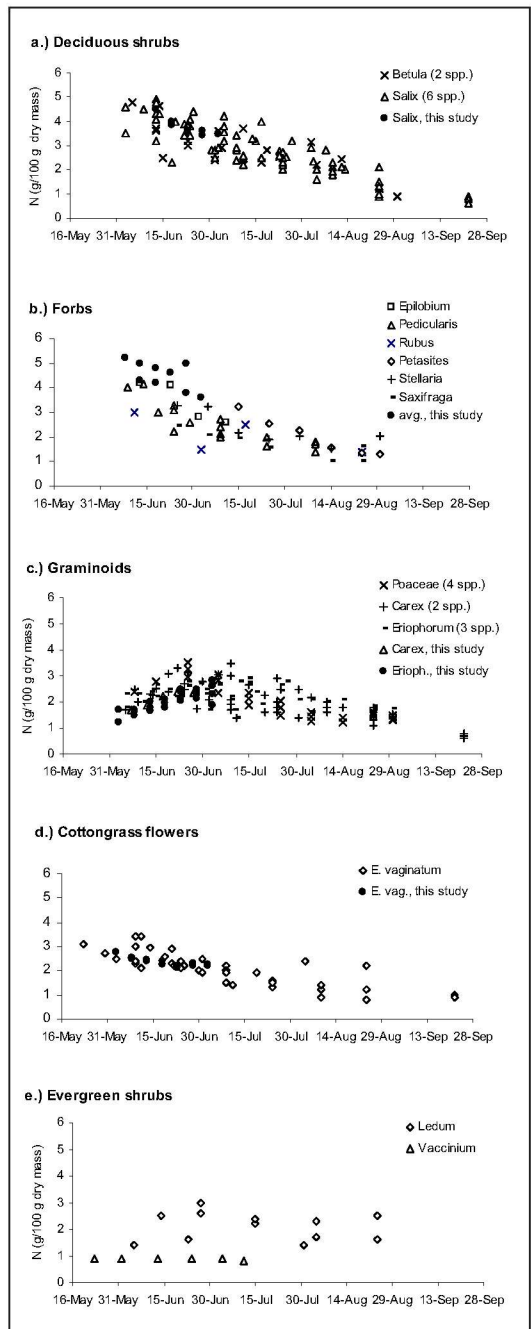

Fig. 2. Nitrogen concentrations (g/100 g dry mass) in major vascular growth form types during the growing season. Plant tissue classes represented in each graph are as follows: a.) deciduous shrubs: green leaves or current year growth (stem+leaf), b.) forbs: current year aboveground tissues, c.) graminoids: leaves or aboveground tissues, d.) cottongrass flowers: current year flowers, and e.) evergreen shrubs: green leaves (current year only or current year + previous years). Different symbols are used to represent data obtained for each genus within the functional group; the 'spp. pooled' category indicates values for different species in a growth form were averaged in the original publication. Values not designated as «this study» were taken from published field studies in northern Alaska and Yukon Territory (1-5, 7, 9, 12, 17; see Table 1 for source list). Exact values are approximate for some studies.
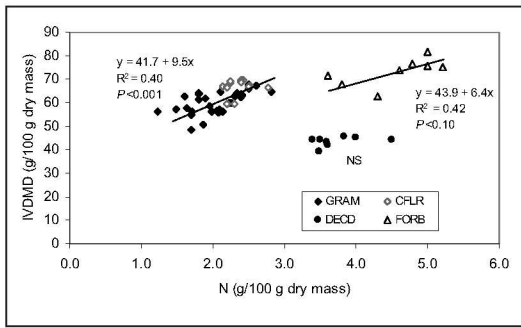
Fig. 3. The relationship between nitrogen concentration and *in vitro* dry matter digestibility (IVDMD) plotted for four plant growth forms (GRAM = graminoid, CFLR = cottongrass flower, DECD = deciduous shrub, FORB = forb). Data for graminoid leaves and cottongrass flowers are analyzed together. NS denotes a non-significant relation between N concentration and IVDMD for deciduous shrub data. Data are from the Arctic National Wildlife Refuge, Alaska (this study).
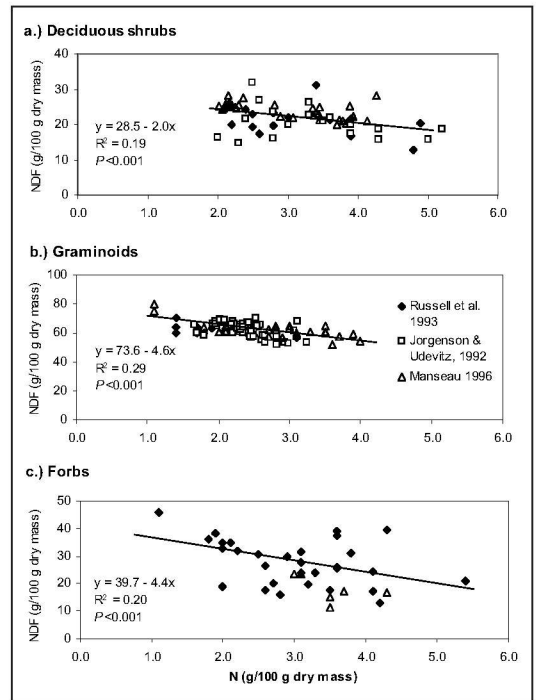

Fig. 4. The relationship between nitrogen concentration and neutral detergent fiber concentration plotted for three plant functional types. All regressions are significant at $P < 0.01$. Data are from Russell *et al.*, (1993) and Jorgenson & Udevitz (1992) for Yukon and Alaska North Slope areas, respectively, and Manseau (1996) for the Ungava Peninsula, northeastern Canada.

sufficient data were available. In the deciduous shrub, forb, graminoid, and cottongrass flower groups, seasonal changes in N concentration were similar among the species of that group (Fig. 2). Nitrogen concentrations in evergreen shrubs showed no clear seasonal pattern. Nitrogen concentrations in deciduous shrubs and forbs followed a similar pattern of peak nitrogen levels at the start of the growing season, with a subsequent decline to low levels at the end of the season. In cottongrass flowers, N concentrations also declined through the growing season, although less dramatically than in deciduous shrubs or forbs. Among graminoids, N concentrations peaked approximately 15-30 days after the start of the growing season (usually June 1–June 15), and then declined over the rest of the summer.

There were no seasonal patterns in NDF or IVDMD evident in our analysis of reported values ($P > 0.5$, df=6 and 4 for NDF and IVDMD), although a few studies have reported seasonal changes in digestibility at a given site for some species (Kuropat, 1984; White *et al.*, 1992). We found significant negative relationships between concentrations of N and IVDMD in forbs and graminoids, but not in deciduous shrubs (Fig. 3). Changes in N concentration accounted for 40% of the variation in IVDMD for forbs and for a pooled graminoid class consisting of leaves and cottongrass flowers. NDF concentration was also positively correlated with N concentration in some plant groups (Fig. 4). For deciduous shrubs, graminoids and forbs, approximately 20% of the variation in NDF concentration was related to variance in N concentration.

Discussion

By combining multiple data sets, we attempted to characterize patterns in forage quality for most major plant growth forms within the region used annually by the PCH. Rankings of forage quality based on concentrations of N, and on NDF and IVDMD for different growth forms generally corresponded to the relative forage preference of these classes by caribou (White & Trudell, 1980b; Russell *et al.*, 1993). Cottongrass flowers, deciduous shrubs, and forbs are typically preferred by PCH caribou in spring and summer (Russell *et al.*, 1993). Graminoid leaves, although similar in forage quality to cottongrass flowers, are not strongly preferred by caribou or reindeer grazing on North Slope vegetation and routinely make up a minor portion of the diet (White *et al.*, 1975; White &

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Trudell, 1980b). Differences in forage preference by caribou may be explained by the timing of forage availability. Cottongrass flowers emerge shortly after snowmelt and are available to caribou before green-up of most other vascular species (Kuropat, 1984). New graminoid leaves do not become available until the more nutritious deciduous shrub leaves and forbs have already appeared. In addition, new leaves of single-stemmed graminoids are surrounded or subtended by dead leaves that restrict access to green leaves (White *et al.,* 1975). Generally moss and evergreen shrubs are avoided during the summer, while lichens increase in the diet as shrubs and forbs begin to senesce in late summer and fall (White & Trudell, 1980b; Russell *et al.,* 1993). Rankings of forage quality during winter are likely to differ from those based on nitrogen concentrations, as energy limitations may be more important to caribou energetics than protein acquisition during the winter season (Klein, 1990). Forage quality rankings will also be affected by concentrations of additional mineral nutrients if those nutrients are limiting.

We found strong seasonal patterns in N concentration in the leaves of deciduous shrubs, forbs and graminoids. Similar patterns are apparent in some of the individual studies included in this review (Chapin *et al.,* 1975; 1980; Chapin, 1980; Whitten & Cameron, 1980; Klein, 1990). Importantly, seasonal trends of N concentration were evident in several growth forms even when pooling across studies that included variations in vegetation types, annual climate patterns, and sampling techniques. The dominance of these seasonal patterns provides strong evidence for a common pattern of N concentrations within growth form types, and supports the observation that seasonal timing is a major factor controlling changes in nitrogen concentrations in tundra vegetation (Chapin *et al.,* 1975; 1980).

Tundra plants exhibit seasonal changes in N concentration as a result of nitrogen translocation to new tissue during early summer, followed by a gradual dilution of nitrogen concentrations as tissues gain dry mass over the remainder of the growing period (Chapin *et al.,* 1975, 1980; Chapin, 1980). The later peak in N concentration of graminoid leaves compared to forbs and deciduous shrubs appears to be associated with the replacement of small amounts of overwintering green biomass with nitrogen-rich current year growth during early summer (Chapin *et al.,* 1975). Evergreen shrubs retain nitrogen in overwintering leaves and consequently show relatively small seasonal changes in N concentration (Chapin, 1980; Chapin

et al., 1980).

IVDMD is a measure of the relative amounts of digestible (cell solubles, protein, hemicellulose) and non-digestible (*e.g.,* lignin, cellulose) components of forage tissue. Digestibility is expected to be greatest in new green biomass because of a lower concentration of lignin and chemical defenses. However, we did not find clear seasonal trends in IVDMD within growth forms. There were significant positive correlations between tissue digestibility and nitrogen concentration within graminoid and forb tissues, but no relationship between these variables for deciduous shrub leaves. Significant correlations between digestibility and N concentration have previously been noted for caribou forage plants, again with the exception of deciduous shrubs (Klein, 1990). A decoupling of digestibility and nitrogen concentration may be related to the capacity of deciduous shrubs to allocate substantial resources to herbivore defense compounds (Bryant *et al.,* 1983), with consequent effects on digestibility (Hanley *et al.,* 1992).

As with IVDMD, we found no evidence of substantial seasonal changes in neutral detergent fiber concentration of forage tissue within growth forms. The weak, but significant, inverse correlation we observed between NDF and N suggests a tradeoff between plant allocation to cell wall (fiber) *vs.* cell content (nitrogen). However, the shallow slope of this relationship (Fig. 3) does not indicate that this is likely to be a strong control of forage quality. Given the significant correlations of IVDMD and NDF with N, why didn't we find seasonal differences in IVDMD and NDF for those growth forms showing seasonal changes in N? Relative variation of N concentration in our data was up to 5x for a given growth form, compared to only 2-3x variation in the NDF and IVDMD. The lower variability in NDF and IVDMD may have restricted our ability to detect small seasonal changes that may have been present. Also, real seasonal patterns in IVDMD may have been obscured by different sources of rumen innoculum among the studies we analyzed and by differential chemical inhibition in the rumen system (White & Trudell, 1980b, Trudell *et al.,* 1980). Further, variations in levels of tundra plant chemical defenses that occur in response to changes in annual climate conditions (Jonasson *et al.,* 1986) may have masked seasonal patterns in IVDMD. For example, some alpine vegetation growth forms in central Alaska exhibited seasonal changes in IVDMD during a warm and dry summer, but not during a cloudy summer (Lenart, 1997). Because the studies we summarized encompassed several different years, annual weath-

er influences probably added variability to the data and could have masked real within-study seasonal trends in NDF and IVDMD.

Although substantial data exist on preferred summer and winter forage types with the PCH range, this review has highlighted a lack of adequate data on forage quality of some seasonally important forage classes, such as mushrooms, mosses, and vascular plant forages in autumn and winter (Russell *et al.,* 1993). Inaccurate estimates of nutritional quality of these classes could bias estimates of seasonal changes in caribou nutrition.

Acknowledgements

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