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EIGIL REIMERS

ELDAR GAARE

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NUTRIENT DYNAMICS OF CARIBOU FORAGE ON ALASKA'S ARCTIC SLOPE

K. R. Whitten and R. D. Cameron

Alaska Department of Fish and Game, 1300 College Road, Fairbanks, Alaska 99701, USA

ABSTRACT

Selected forage species (*Salix pulchra,* Cham., *Pedicularis Langsdorffii,* Fisch., *Eriophorum vaginatum,* L., and *Carex aquatilis,* Wahlenb.) were collected from 9 equally spaced sites on caribou (*Rangifer tarandus granti,* Banfield) range between the Beaufort Sea and the Brooks Range on the arctic slope of Alaska. Phenological progression was also monitored at these sites by recording flowering dates of conspicuous forbs. Forage samples were analyzed for N, P, K, Ca, Mg, Na, and total nonstructural carbohydrates (TNC), and data from sites within each of 4 latitudinal intervals were combined. Generally, within each region N, P, and K composition decreased steadily for all species through the growing season, while Ca content usually increased; changes in the amounts of other nutrients were less consistent. Phenology progressed from south (initiation of growth ca. 8–10 June) to north (ca. 1 July), and temporal changes in nutrient composition were consistent with the northward delay in phenology. The dicots analyzed were higher in N, P, Ca, and Mg than the monocots. TNC and K also showed consistent differences among species, but Na content was similar for all species. Some sampling sites were apparently deficient in Ca. Caribou have the opportunity to maximize forage nutrient quality during spring and summer by migrating north as phenology progresses and also by selecting among species and among local feeding sites.

1. INTRODUCTION

During the summer growth season, forage quality for herbivores is usually correlated with nitrogen (N) and phosphorus (P) content. These nutrients are usually most concentrated during the early stages of plant growth. As plant tissues mature, minerals and organic matter of low digestibility (i.e. crude fiber, lignin, etc.) accumulate, thus diminishing N and P levels by dilution. Later, N and P are further reduced in availability to grazers through active translocation to storage tissues in roots and stems. Soluble carbohydrates tend to increase during the plant growing season and then decrease during senescence. After senescence, even some inorganics may be lost from standing dead plant tissues through leaching and bleaching. Thus, N and P availability during the growing period and carbohydrate or total energy content during non-growth periods (e.g. winter), are both related to plant phenology (Stoddart and Smith 1955, Oelberg 1956, Klein 1970).

Factors which affect plant phenology may vary along several environmental gradients, including latitude, altitude, and slope/aspect. On any grazer's range these factors can work in concert or in opposition to determine local plant phenology. A varied topography, or ability to move over long latitudinal distances, provides a wide variation in initiation of plant growth and duration of early growth stages over the range of a grazer (Klein 1970).

Several workers have suggested that caribou follow plant phenological events (Lent 1966, Kelsall 1968), tending to maximize their intake of N and P (Klein 1970). The objective of this study was to determine if this general pattern applies to the Central Arctic Caribou Herd (CAH).

2. DESCRIPTION OF THE STUDY AREA

The study was conducted along the Trans-Alaska Pipeline haul road from the arctic coast at Prudhoe Bay to the north side of the Brooks Range near Galbraith Lake (Fig. 1). Over this 270-km distance, the road cuts perpendicularly across the major physiographic provinces (Wahrhaftig 1965) on the arctic slope in Alaska. A poorly drained coastal plain of low relief extends 140 km inland. The shallow depth of thaw and flat terrain result in extensive areas of wet meadows and oriented lakes and ponds. Mean elevation is about 180 m where the plain joins the foothills. The foothills consist of a northern section of rolling, rounded hills extending inland to about

The mountains rise steeply to over 2000 m at the southern end of the study area.

Single-stemmed sedges of the genera *Carex* and *Eriophorum* dominate the vegetation of the coastal plain, the tussock-forming sedge *Eriophorum vaginatum* typifies the foothills, and *Dryas octapetala,* L. characterizes the mountains. Stream margins and outwash plains in the mountains, foothills, and southern portion of the coastal plain are lined by tall willows (*Salix* spp.). The dense stands of riparian willow give way to scattered low-growing or prostrate willows farther north near the arctic coast.

Within the study area snow melt proceeds from south to north, with windswept ridges and river floodplains in the mountains and foothills generally snowfree by mid- to late May. There is a pronounced maritime influence on weather over the coastal plain. Snowfree ground does not usually occur along the coast before 1 June, and snowmelt is not complete until 10–15 June.

3. METHODS

Nine sampling sites (A–I) were located approximately every 13′ of latitude along the haul road from the extreme southern arctic foothills (68°40′N) to the coast at Prudhoe Bay (70°20′N). Most sites were on or adjacent to the Sagavanirktok River floodplain. However, the southernmost site was located on the upper Kuparuk River, and the northernmost site was located on the coast about 12 km west of the Sagavanirktok Delta (Fig. 1). To minimize effects of slope and aspect, only level sampling sites were selected. The sites were visited biweekly

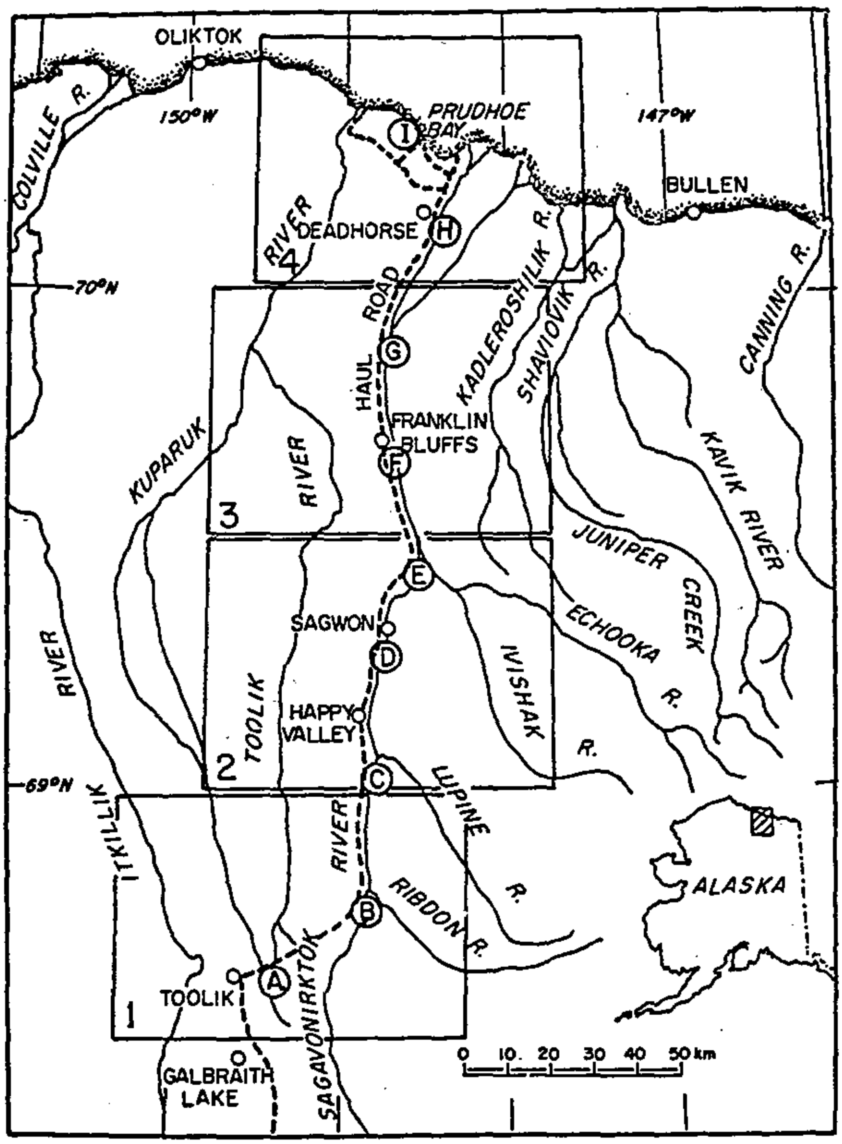

Fig. 1. The study area, with sampling sites (circled letters) and regions used for analysis of forage nutrient dynamics (rectangles).

on or near the 10th and 25th of each month, beginning in June and continuing through September. However, no visits were made on 10 September, and not all sites were sampled on 25 August.

Phenology on the sample sites was monitored by observing flowering of forbs. Forb species with conspicuous flowers were noted at each site from when they first appeared in full flower to when all or most individuals with current-year floral parts had ripened (i.e. petals and/or sepals withered or dried). All plants were identified following taxonomy in Hulten (1968). We assumed that a species flowers at the same growth stage regardless of location, and that most species at a given location tend to initiate growth and subsequent flowering synchronously. Only species which occurred on 4 or more sites were included in the analysis of flowering to avoid biasing results with species that might be restricted to microhabitats not present on all sites.

Carex aquatilis, Pedicularis Langsdorffii, Eriophorum vaginatum, and *Salix pulchra* occur throughout the study area, and were used to investigate nutrient dynamics during the summer growing season. Collections included primarily those tissues eaten by caribou; i.e. stems and leaves of *C. aquatilis* and *P. Langsdorffii,* flowering stalks of *E. vaginatum,* and leaves only of *S. pulchra.* Samples consisted of the current year's growth, including senescent and dead material late in the season. Either *C. aquatilis* or *E. vaginatum* was absent on a few sample sites, but *S. pulchra* and *P. Langsdorffii* occurred on all sites. Tissues from several individuals of a species were pooled to form a representative sample for that site. Generally, all species were collected in close proximity to each other, but at site D, about 5 km separated *E. vaginatum* from the other species, and at site I, *C. aquatilis* was collected about 1 km from the other species (see Fig. 1).

Samples were stored frozen in plastic bags until analysis. After drying at 65°C for 24–36 hours, samples were sent to the University of Alaska Agricultural Experiment Station, Palmer Research Center, for chemical analysis. Plant tissue digestion followed the method described by Isaac and Johnson (1976), and N and P were measured with a Technicon Autoanalyzer. Potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) were determined from the digest by atomic absorption. Total non-structural carbohydrate (TNC) was determined using the "Modified Weinmann Method of Removing Total Nonstructural Carbohydrates" (Smith 1969). However, the extract was analyzed for reducing power by the Technicon Autoanalyzer method for "Reducing Sugars in Tobacco Extracts" using ferricyanide reduction rather than copperidometric titration.

Other studies (Cameron et al. 1979, Cameron and Whitten 1980) have divided the study area into 4 regions for determining caribou distribution in relation to pipeline construction activities. Boundaries of these regions closely follow divisions between physiographic provinces. Sample sites within the southern and northern foothills fall into Regions 1 (sites A and B) and 2 (sites C, D, and E), respectively. The sites on the coastal plain are split evenly between Regions 3 (sites F and G) and 4 (sites H and I) (Fig. 1). Mean nutrient concentrations by species for combined sites within each region were calculated to facilitate comparisons of nutrient dynamics and forage phenology with caribou distribution.

4. RESULTS

4.1. Flowering phenology

Tab. 1 shows the progression of flowering in selected forbs from the 9 study sites. Numerical scoring was not intended to indicate a "mean flowering date," since actual flowering or senescence could have occurred any time during the 2 weeks between sample dates. Rather, it was intended to order the sites according to progression of flowering. The order correlates strongly with increasing latitude. Only sites D and E, and H and I were reversed in order. Thus, phenology followed a south to north gradient across the study area.

4.2. Nutrient dynamic trends

Fig. 2 shows nutrient dynamics in the 4 selected caribou forage species. N and P dynamics followed a similar trend in all species in all regions. Concentrations were usually highest on the first collection date, representing the period closest to the onset of growth. Thereafter, concentrations declined steadily. In *E. vaginatum, C. aquatilis,* and *S. pulchra,* K showed a seasonal trend similar to N and P; however, the initial concentrations were often maintained or even slightly increased in the second collection before a steady decline started. In contrast, K levels in *P. Langsdorffii* increased throughout the growing season. Ca concentrations usually increased steadily during the study period in all species, with the greatest increases in *S. pulchra* and the smallest in *E. vaginatum.* Thus, N, P, K, and Ca concentrations were all related to plant growth stage.

Dynamics of other nutrients were far less consistent among either species or regions and showed no regularity among species in relation to plant growth stage. Mg declined slightly through the season in *E. vaginatum* in all regions, but in the remaining species, Mg generally varied slightly about a mean. The most common trend in TNC concentrations was an increase through the middle of the growing season and then a decrease toward the end of the season. Na concentrations showed little variation through the season in any species or region.

Tab. 1. Flowering phenology of common (occurring at 4 or more sampling sites) dicots.

SPECIES	SITE								
	A	B	C	D	E	F	G	H	I
Anenome narcissiflora	B[1]	AB	AB	B		C			
Arctostaphylos alpinum			A	B	B	B			
Pedicularis Langsdorffii	B	AB	ABC	C	BC	C	CD		CD
Andromeda polifolia	BC	BC	B		C				
Rhododendron lapponicum		BC	B	BC		C			
Cardamine hyperborea		C		C	D	D	D	D	C
Cassiope tetragona		BC	BC	BC	B	C		D	
Hedysarum alpinum		C	C			D			
Pedicularis capitata		BC	B	C			D	D	
Pyrola grandiflora		B	C		D				
Valeriana capitata	BC	BC		C	D				
Astragalus umbellatus		C	BCD	CD		CD			
Dryas octopetela		B	BC	BCE		C		CD	CDE
Ledum palustre	BC	BC		C	C				
Papaver Macounii		C		E	D	CDE		DE	
Polemonium acutiflorum	BC	D		D					
Polygonum bistorta	BCE	BC	CD	C	C				
Saxifraga hirculus	B	CD		D	DE		DE	E	DE
Minuartia spp.						D		D	D
Pedicularis sudetica		C			C		D	D	D
Potentilla fruticosa		CDE	D	D					
Polygonum viviparum		D	CD	DE		DE	DE		
Saxifraga hieracifolia				C	C				E
Senecio spp.				D		D	D	DE	
Stelleria spp.	D		E	C					DE
Parnassia spp.		E	DE	DE					
Sausseurea angustifolia		E	D	E					E
SCORE[2]	2.67	2.72	2.85	3.41	3.27	3.59	4.10	4.17	4.14

[1] Key: A=flowering on 10 June; B, on 25 June; C, on 10 July; D, on 25 July; E, on 10 Aug.

[2] Scoring: 1 pt for each A; 2 for each B, etc. Sum for each site divided by number of entries to give final score.

4.3. Regional differences in nutrient dynamics

New plant growth was available by 10 June on the southernmost sites (Region 1), but did not appear on the northernmost sites (Region 4) until 10 July. At intermediate sites (Regions 2 and 3), new growth had appeared over a wide area by 25 June. In all regions initial concentrations of N, P, and K were similar within a species, but there were small differences in initial concentrations among regions which may be an artifact of the biweekly sampling scheme. That is, growth may have started any time during the 2 weeks before actual collection. The data show that when first collections were made simultaneously in 2 or more regions the concentrations of N, P, and K from the northern regions were usually higher and thus presumably reflect earlier stages of plant growth (see 4.2, above). The nutrient dynamic curves for N, P, and K clearly show similar seasonal patterns in each region, but there is a displacement toward later dates at the more northern regions (Fig. 2). Regional differences in concentrations of N, P, and K thus appear to correlate closely with date of collection and time since growth initiation (4.1., above).

The regional differences in nutrient concentrations described above for N, P, and K are mainly temporal, reflecting the interrelationship between phenology and latitude. Although TNC concentrations showed no consistent correlation to plant phenology, there was a tendency for TNC concentrations to be higher in Regions

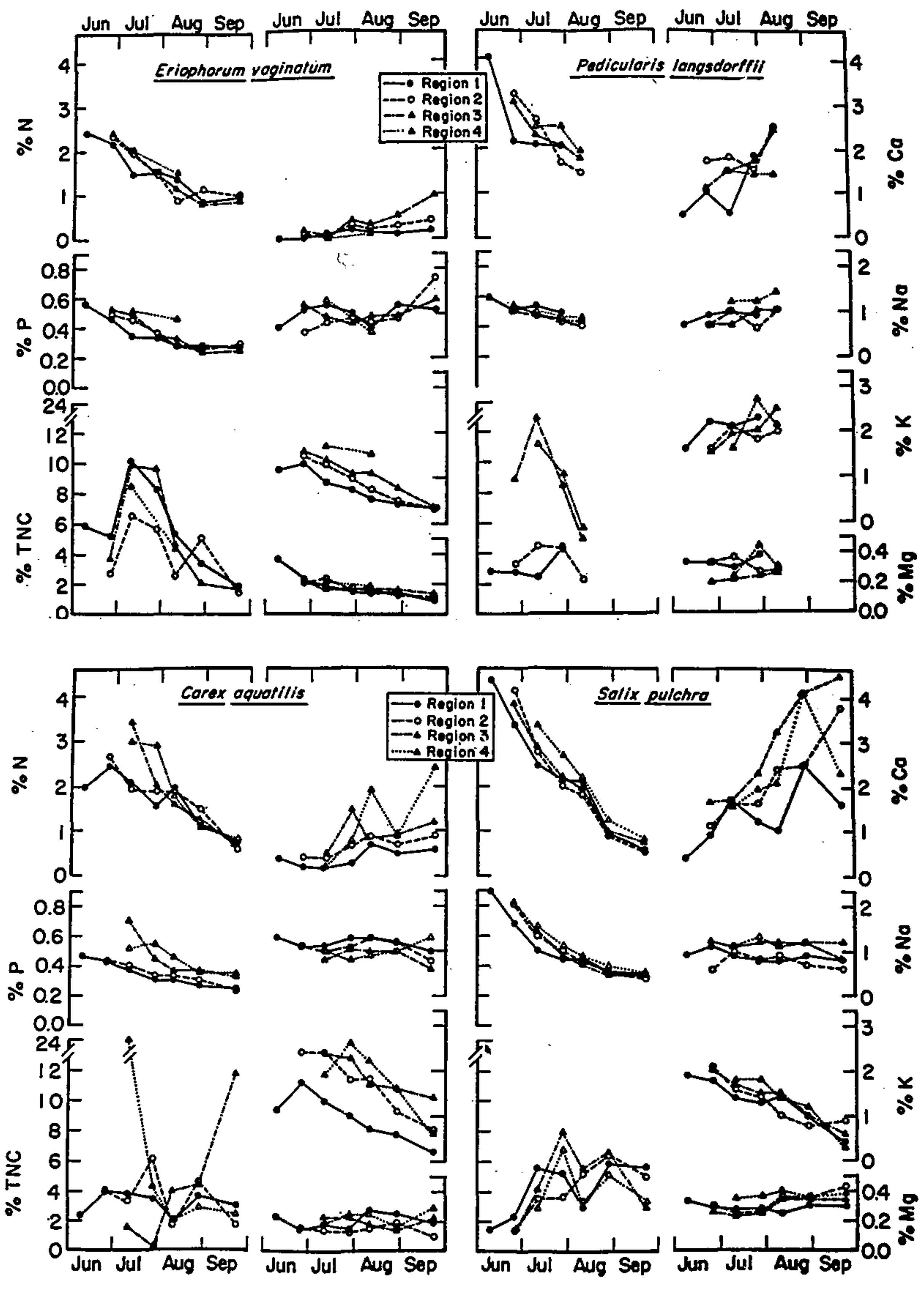

Fig. 2. Seasonal nutrient dynamics of caribou forage plants.

3 and 4. Ca concentration tended to increase during the growing season in all species from all sites, but it showed no clear regional trends. This relationship was probably confused by large intersite differences in Ca concentration (see 4.5., below).

4.4. Species differences

The dicots *P. Langsdorffii* and *S. pulchra* were higher in initial N and P concentrations than were the monocots *C. aquatilis* and *E. vaginatum*, and they remained higher until senescence, when concentrations in *S. pulchra* and the 2 monocots apparently stabilized at about the same level. *P. Langsdorffii* was higher in N and P than the other species when it was last collected in early August. Cured stalks were not collected in late August or September, however, so it is not known whether those relatively high N and P levels persisted. N and P concentrations in *P. Langsdorffii* and *S. pulchra* were similar on the last dates on which both species were collected together.

Mg and Ca levels were also consistently higher in the dicots than in the monocots. *E. vaginatum* in particular had very low levels of Ca all season. One exception occurred in Region 4, where *C. aquatilis* had Ca concentrations similar to those in *S. pulchra* and higher than in *P. Langsdorffii*. However, *C. aquatilis* was collected about 1 km from the other species at the northernmost site in Region 4, and there was a possible Ca bias at that particular site (see 4.5., below).

The highest TNC levels were reached in *P. Langsdorffii* and *C. aquatilis* in Regions 3 and 4, but those peaks were of short duration. Otherwise TNC content was generally higher in *E. vaginatum* and *S. pulchra*. Peak TNC concentrations in *S. pulchra* came slightly later than the peak levels in *E. vaginatum*.

K levels were higher in *S. pulchra* and *C. aquatilis* than in *E. vaginatum*. K concentration in *P. Langsdorffii* increased through the summer, while it decreased in the other species. Therefore, K levels in *P. Langsdorffii* were the lowest of all species early in the season and the highest later. Na concentration was roughly the same for all species, and any differences did not appear to be systematic.

4.5. Site differences

Ca concentrations in *S. pulchra* and *P. Langsdorffii* were much lower in sites A, E, and I than in any of the other sites (Tab. 2). Results from *E. vaginatum* and *C. aquatilis* were less conclusive, however. Ca concentrations in *E. vaginatum* at site A were lower throughout the growing season (0.01 to 0.11%) than in the remaining sites (0.1 to 0.95%). Initial Ca concentration in *C. aquatilis* from site A was about 0.4% (possibly due to contamination with standing dead material), but declined to 0.05%, followed by a gradual increase to about 0.2%; all other sites started around 0.3–0.5% and subsequently increased to 0.7–2.7%. At site E, initial Ca levels in *E. vaginatum* were very low, similar to site A, but by senescence Ca levels there fell well within the range of the other sites; no *C. aquatilis* was collected from site E. At site I, no *E. vaginatum* was collected, and *C. aquatilis* did not show lowered Ca concentrations, but it was collected about 1 km from *S. pulchra* and *P. Langsdorffii* and may not reflect the same localized conditions.

5. DISCUSSION

Observations of flowering in dicots, onset of growth in the species collected for nutrient analysis, and comparison of regional nutrient dynamic curves all indicated a steady progression in plant phenology from south to north on similar sites across the study area. Concentrations of N, P, and, for the most part, K in caribou forage showed clear and consistent trends which were a function of phenology. In spring and early summer,

Tab. 2. Intersite differences in Ca concentration.

	Ca Concentration (%)			
	Initial		Final	
Species	A,E,I	All Others	A,E,I	All Others
Salix pulchra	0.3-0.6	1.1-1.7	0.6-1.2	2.0-4.9
Pedicularis Langsdorffii	0.5-1.4	0.3-3.0	0.3-1.1	1.6-3.3

when recovering from winter privation, growing new tissues, or raising young, caribou have high metabolic demands for N and P (Klein 1970). Peak forage N and P concentrations described in this report were comparable to those found in other arctic tundra areas (Tener 1965, Chapin et al. 1975) and they are high compared to most temperate and tropical forages (Klein 1970). They are, however, lower than those reported for some alpine tundra areas (Johnston et al. 1968, Whitten 1975). Assuming the plants analyzed in this study were representative of other plants in the diet of caribou, the peak N and P levels should support rapid body growth. N and P concentrations peaked with or shortly after initiation of growth, but declined rapidly thereafter at any one site. A grazer such as the caribou could theoretically maximize P and N intake and growth potential over a longer time period by following plant phenology from south to north across the study area.

In the CAH, bulls tend to follow the progression of phenology more closely than cows, remaining south longer and traveling north more slowly. On south-facing slopes in the mountains and southern foothills, new plant growth is available in mid- to late May, 2–3 weeks earlier than on the level sites used in this study. By starting in the southern foothills in May and arriving on the coast in early July, most CAH bulls make use of peak quality forage over nearly an 8-week period. In some years, many caribou overwinter on the coastal plain, but proportionately fewer bulls than cows follow this pattern. Most of those bulls which remain on the coastal plain during winter move south in late May, presumably to improved forage conditions. This observation is supported by bull/cow ratios on the coastal plain in May 1977, 1978, and 1979 which averaged 67:100 while in June they averaged 5:100 (Whitten and Cameron unpubl.). Cows arrive on the coastal plain between late April and early June, when little if any new growth is present. Perhaps the survival benefits of moving to the essentially predator-free calving grounds outweigh the loss of some prime forage. Some new growth does become available on the calving grounds shortly after parturition, when nutrient demands of females are highest.

In addition to the phenological/latitudinal trends in N, P, and K concentrations, there were other consistent differences among regions, species, and/or individual sites that presented opportunities for selective foraging. TNC reached its highest concentrations during July on the coastal plain, when most of the CAH occupies that area. Chapin et al. (1975) suggested that during midsummer dicots would be better forage than monocots (assuming similar digestibility), and in the CAH there appears to be selection by caribou for dicots, which are higher in N and P than monocots. Even though dicots make up a small part of the plant biomass in wet tundras (Chapin et al. 1975), such as are dominant on the arctic coastal plain (Regions 1 and 2) where most of the CAH summers, White et al. (1975) found selection for willows by caribou at Prudhoe Bay. While we have no quantitative data on caribou diets from this study, we have observed caribou cropping *P. Langsdorffii, P. sudetica,* Willd., and prostrate willows (*Salix* spp.) from *Carex* and *Eriophorum* stands. The intersite differences in Ca concentration indicate that even small-scale movements can lead to large differences in intake of this nutrient. However, no data are available to relate this to distribution or movement of the CAH.

Within a species, regional nutrient concentrations tend to converge at senescence, which is induced by widespread frosts in mid- to late August in the range of the CAH. At this point the opportunity for selective foraging by following gross latitudinal trends in phenology, breaks down. CAH caribou disperse over a wider area, but remain in the northern half of the study area (Cameron and Whitten 1979) where N and P concentrations are slightly higher (Fig. 2). In late summer and fall local site differences in microclimate may still provide some variation in plant growth stage, and hence some opportunity for selectivity on a local level. Lake and stream margins, for example, seem to provide a frost shelter and remain green when most vegetation has senesced. Caribou make considerable use of such microhabitats, which are abundant on the coastal plain. Often plants in protected areas may freeze permanently before senescing totally, thus providing a slightly higher source of N and P and perhaps a very good source of carbohydrate during winter. Again, caribou are observed to use such plants.

Hence, caribou movments are not random, but are related in part to forage phenology during spring and early summer. Movements to and from insect relief habitats probably involve optimizing tradeoffs between energy expenditure and nutrient intake (Roby 1978), as do fall and winter movements, whether locally or on a large scale. Hence, reductions in caribou sighting and crossing rates along the haul road from 1975 to 1978 (Cameron and Whitten 1980) are reason for real concern, since they may well represent disruptions in movement patterns that have evolved over long periods of time.

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