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## SEASONAL MOVEMENT OF NUTRIENTS IN PLANTS OF DIFFERING GROWTH FORM IN AN ALASKAN TUNDRA ECOSYSTEM: IMPLICATIONS FOR HERBIVORY

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### SUMMARY

(1) The seasonal pattern of biomass distribution and of amounts of N, P, K, Ca and Mg was examined in plants of a variety of growth forms in an Alaskan tundra ecosystem. The growth forms examined were: deciduous shrub, evergreen shrub, deciduous forb, tussock graminoid, moss and lichen.

(2) The deciduous shrubs *Salix pulchra* and *Betula nana* had 70–80% of their biomass below ground, of which about half was roots. The evergreen shrub *Ledum palustre* had less than 50% of its biomass below ground.

(3) In deciduous shrubs, up to 14% of the total plant capital of nitrogen and phosphorus was translocated from stems and large roots into leaves during the 3 weeks following snow-melt. The amount in stems and roots was not fully replaced by uptake until late autumn. At this time, 50–60% of the nitrogen and phosphorus which had been in leaves was removed. In contrast, the evergreen shrub translocated nitrogen and phosphorus to leaves gradually throughout the growing season, and showed no evidence of large stores of nutrients in stems or roots. By late August 46% of the total nitrogen of evergreen shrubs was present in leaves.

(4) Potassium was not effectively back-translocated to stems of the deciduous species sampled.

(5) In the graminoid *Eriophorum vaginatum*, spring production of roots as well as leaves depleted nitrogen reserves in the rhizome. Similar dependence of root production upon stored nutrient reserves is suggested in deciduous shrubs.

(6) The differences in nutrient allocation between the mosses *Aulacomnium* spp. and *Polytrichum* spp. were just as pronounced as those between evergreen and deciduous vascular species, and may relate to the source of nutrients. Lichens had a uniformly low content of the major nutrients.

(7) Some implications of seasonal nutrient patterns for herbivores are discussed.

### INTRODUCTION

Most major ecosystem-types such as grassland, wet tropical forest and temperate coniferous forest are dominated by a single physiognomic type. Tundra, by contrast, is characterized by a variety of communities in which graminoids, deciduous shrubs, evergreen shrubs, deciduous forbs, lichens and mosses may each be community dominants within a small area (Bliss *et al.* 1973). Studies comparing growth-form distribution among various communities (Beadle 1954; Monk 1966; Webber 1978), and studies comparing

nutrient use by species of differing dominance within a single community (Chapin, Van Cleve & Tieszen 1975; Thomas & Grigal 1976; Schlesinger & Chabot 1977), both suggest major differences among growth forms in patterns of nutrient movement. Here we report a study of the seasonal pattern of nutrient movement in a variety of dominant growth forms growing in the same (tundra) macroclimate, and consider some implications for interactions between plants and herbivores.

### THE STUDY AREA

The Atkasook study area is on the Meade River (70°27'N, 157°55'W, 23 m altitude), 108 km S.S.W. of Barrow, Alaska, where the arctic coastal plain merges with the northernmost foothills of the Brooks Range. The area is characterized by a heterogeneous mixture of partially-drained lake basins and upland tussock-tundra (Clebsch 1957; Tieszen & Johnson 1968; Peterson & Billings 1978). The soils are underlain by permafrost, and have a 10–20 cm organic mat intermixed with and underlain by sand (Rickert & Tedrow 1967). The growing season is both longer and warmer than in the coastal tundra at Barrow, with the season of active plant growth at Atkasook lasting approximately 75 days (12 June–30 August). In 1975, the year of this study, Atkasook had a mean July air temperature of 7.2 °C and a summer precipitation of 80 mm.

### METHODS

One species was chosen to represent each of five growth forms, and two to represent the deciduous shrubs. For one of these deciduous shrub species, two morphologically-distinct populations were chosen for sampling. In this way we encompassed the range of growth forms, but included some comparison within a growth form and within a species. The growth forms and species sampled were: the deciduous shrubs *Betula nana* L. ssp. *exilis* (Sukatsch.) Hult., and two populations of *Salix pulchra* Cam.; the evergreen shrub *Ledum palustre* L. ssp. *decumbens* (Ait.) Hult.; the deciduous forb *Rubus chamaemorus* L.; the tussock-forming graminoid *Eriophorum vaginatum* L. ssp. *spissum* (Fern.) Hult.; the mosses *Aulacomnium* spp. and a mixture of polytrichaceous mosses, *Polytrichum* spp. and *Pogonatum* spp.\*; and ten lichen species.

Each species was sampled from a community where it was a dominant. Plants in the two populations of *Salix pulchra* differed greatly in size. One population consisted of erect shrubs 1.2 m tall, and was dominant along creek margins. *Pyrola grandiflora* Radius and various moss species predominated in the understory. The meadow *Salix* population was prostrate (10–20 cm tall) and co-dominant with *Carex aquatilis* Wahlenb. ssp. *aquatilis* along the margin of a partially-drained lake. *Aulacomnium* spp., *Polytrichum* spp. and *Pogonatum* spp. were common here.

Lichens were sampled from a dry lichen heath populated by a mixture of lichens and the vascular plants *Empetrum nigrum* L. ssp. *hermaphroditum* (Lange) Böcher, *Dryas integrifolia* M. Vahl ssp. *integrifolia* and *Diapensia lapponica* L. ssp. *obovata* (F. Schm.) Hult.

All other species (*Betula*, *Ledum*, *Eriophorum*, *Rubus* and the mosses) were sampled from an area of tussock-tundra with high-centred polygons, dominated by the species sampled, in mixture with *Carex bigelowii* Torr. and *Sphagnum* spp. This community-type,

\* Hereafter referred to as *Polytrichum*.

dominated by *Eriophorum vaginatum*, characterizes broad expanses of northern Alaska (Britton 1967).

Samples were taken between June and August. Lichens were sampled twice, mosses three times, *Rubus* four times, *Ledum* five times, and all other species seven times (at approximately 10-day intervals). The same populations were sampled at each date, but an individual plant was never sampled more than once. At each date, samples were collected in the morning from at least twenty randomly-chosen places. An 'individual' was defined as all above-ground biomass issuing from a stem that goes into the ground. Because of extensive vegetative reproduction in all the species studied, this individual was considerably smaller than the clone. A minimum of 20 individuals of each *Salix* population, 40 individuals of *Ledum*, *Betula* and *Rubus*, and 50 individuals (vegetative tillers) of *Eriophorum* were sampled at each sample date. The individuals were cut into appropriate parts (leaves, stems, etc.) within 12 h. After pooling material from all individuals, each plant part was separated into four replicate samples, dried at 40 °C for 48 h, and later re-dried at 60 °C for 24 h before grinding and analysis. At one sample date in mid-July, surgical gloves were worn while collecting and separating plants for subsequent sodium analysis.

Below-ground biomass of shrubs was measured in early August by excavating the below-ground stem and all roots larger than 3 mm for six clones composed of 5–12 individuals. *Salix* and *Betula* clones selected for excavation were at least 5 m distant (i.e. beyond the rooting radius) from other individuals of either species. Fine-root biomass (roots smaller than 3 mm diameter) of these species was determined from 4.7-cm-diameter cores taken at 20, 50, 100 and 150 cm from the centre of each clone and separated under a dissecting microscope. Both species had club-shaped mycorrhizal roots which were readily distinguishable from roots of other species. At 150 cm no *Betula* or *Salix* roots were found. Two cores at each distance from the clonal centre were used to estimate fine-root biomass per clone. Biomass per individual shoot was then calculated for each clone and averaged among clones of each species. Fine roots of *Ledum* remained attached to the below-ground stem and were separated as plants were excavated. Microscopic examination revealed that most fine roots were unbroken during excavation from the low-bulk-density peat. All *Eriophorum* roots were removed from 4.7-cm-diameter cores taken in the centre of tussocks (Chapin, Van Cleve & Chapin 1979). Root biomass per tiller (individual) was calculated. Live *Eriophorum* roots were white and unbranched, and readily distinguishable from dead brown roots and from live roots of other species. Roots from *Rubus* and the creek margin *Salix* population were not quantitatively excavated.

The high potassium concentration of newly-produced, unuberized *Eriophorum* roots early in the season suggested that leaching of nutrients from roots during washing was not a serious problem (Tukey 1970).

The shrubs differed greatly in size, and these differences masked any seasonal trend in weight of parts per individual except for current year's leaves and current year's stems. Therefore, in calculations of seasonal nutrient budgets, we assume no significant weight change in plant parts other than current year's growth. Nutrient budgets for current year's stems were calculated using the seasonal weight changes obtained in this study. Nutrient budgets for leaves were calculated using the seasonal weight changes reported by Johnson & Tieszen (1976). Using the same populations in the same year (1975), they measured non-senescent leaf length on marked leaves throughout the growing season, and estimated weight per leaf at each sample date from weight-length regressions of destructively-sampled leaves. This leaf weight was multiplied by the average number of

leaves per individual to give the total leaf weight per individual. At the last sample date, however, leaves had begun to senesce, so the regression method was invalid, and leaf weight per individual was estimated from biomass separations.

Nutrient analyses were carried out at the University of Alaska Agricultural Experiment Station, Palmer, Alaska. Samples were ground in a Wiley mill with a No. 60-mesh sieve or, for samples smaller than 1 g, with a Wig-L-Bug 600 dental grinder. Nitrogen was analysed by a micro-Kjeldahl method. Phosphorus was determined colorimetrically by the ammonium molybdate method on 100 mg wet-ashed subsamples, and calcium, potassium, magnesium and sodium were measured by atomic-absorption flame spectrophotometry on the same subsamples. Nutrient concentrations in above-ground and below-ground stems of each species at each sample date were nearly the same, so these parts are reported as 'main stem'.

A *t*-test with pooled variance was used to test difference between means, after checking for homogeneity of variance.

## RESULTS

### *Vascular plants*

#### *Biomass*

Deciduous shrub species sampled at Atkasook differed from evergreen species in their patterns of biomass distribution. The two deciduous-shrub species had about 75% of biomass below-ground, a significantly larger ( $P < 0.01$ ) proportion than in the evergreen shrub *Ledum palustre* (Table 1). Qualitative observations suggested that *Vaccinium vitis-idaea* L., another evergreen shrub, also had a relatively small below-ground biomass. At the time of maximum leaf biomass, new growth as a proportion of above-ground biomass ranged from 10% in creek margin *Salix*, through 14% in *Betula* and 19% in meadow *Salix*, to 29% in *Ledum*. The leaves of *Ledum*, which live for more than 1 year, made up nearly half the above-ground biomass of that species, twice the proportion of photosynthetic tissue in the deciduous shrubs.

TABLE 1. Biomass (mg per individual)\* of various plant parts in Alaskan tundra determined at time of maximum above-ground biomass; values are mean  $\pm$  S.E.,  $n = 6$ ; inflorescence values are calculated from a single lumped sample of 20–50 individuals

Sampling date	<i>Salix</i>	<i>Salix</i>	<i>Betula</i>	<i>Eriophorum</i>	<i>Ledum</i>
	(meadow)	(creek margin)			
	7 August	7 August	5 August	5 August	25 August
Current leaves	740 $\pm$ 20	1370 $\pm$ 110	350 $\pm$ 20	20 $\pm$ 3	210 $\pm$ 10†
Current stem	180 $\pm$ 30	310 $\pm$ 40	90 $\pm$ 8	—	—
Inflorescence	70	10	40	1	0
1-year leaves	—	—	—	—	120 $\pm$ 20
1-year stem	250 $\pm$ 25	430 $\pm$ 30	140 $\pm$ 20	—	40 $\pm$ 10
2-year-and-older leaves	—	—	—	—	120 $\pm$ 10
2-year-and-older stem	850 $\pm$ 160	2850 $\pm$ 260	890 $\pm$ 70	—	150 $\pm$ 30
Above-ground main stem	1810 $\pm$ 230	9400 $\pm$ 1400	920 $\pm$ 100	—	350 $\pm$ 30
Below-ground stem	5900 $\pm$ 1400	—	3800 $\pm$ 500	24 $\pm$ 1	440 $\pm$ 80
Roots	3100 $\pm$ 130	—	6200 $\pm$ 370	39 $\pm$ 3	280 $\pm$ 60
Total biomass	12 900 $\pm$ 1600	—	12 430 $\pm$ 960	84	1710 $\pm$ 140
Percentage below ground	70 $\pm$ 4	—	80 $\pm$ 1	74	43 $\pm$ 6

\* An individual is defined as a tiller or branch that extends below ground.

† Includes current stem.

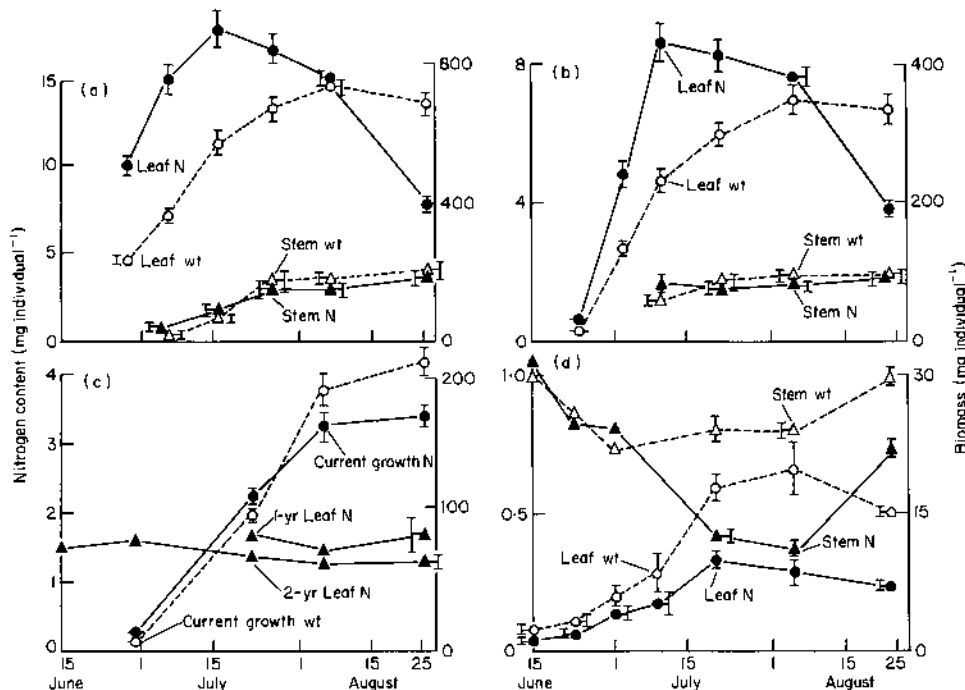


FIG. 1. Seasonal course of above-ground biomass (unfilled symbols, pecked lines) and nitrogen (filled symbols, continuous lines) per individual (mean  $\pm$  S.E.) in four species in Alaskan tundra (a) *Salix pulchra* (meadow), leaves and current year's stems,  $n = 20$ ; (b) *Betula nana*, leaves and current year's stems,  $n = 20$ ; (c) *Ledum palustre*, results for current year's leaves and stems combined,  $n = 40$ , but nitrogen in 1-year-old leaves and in older leaves shown separately; (d) *Eriophorum vaginatum*,  $n = 50$ , results for leaves and rhizomes shown separately. Values without standard error shown are calculated from a single lumped sample containing the indicated numbers of individuals.

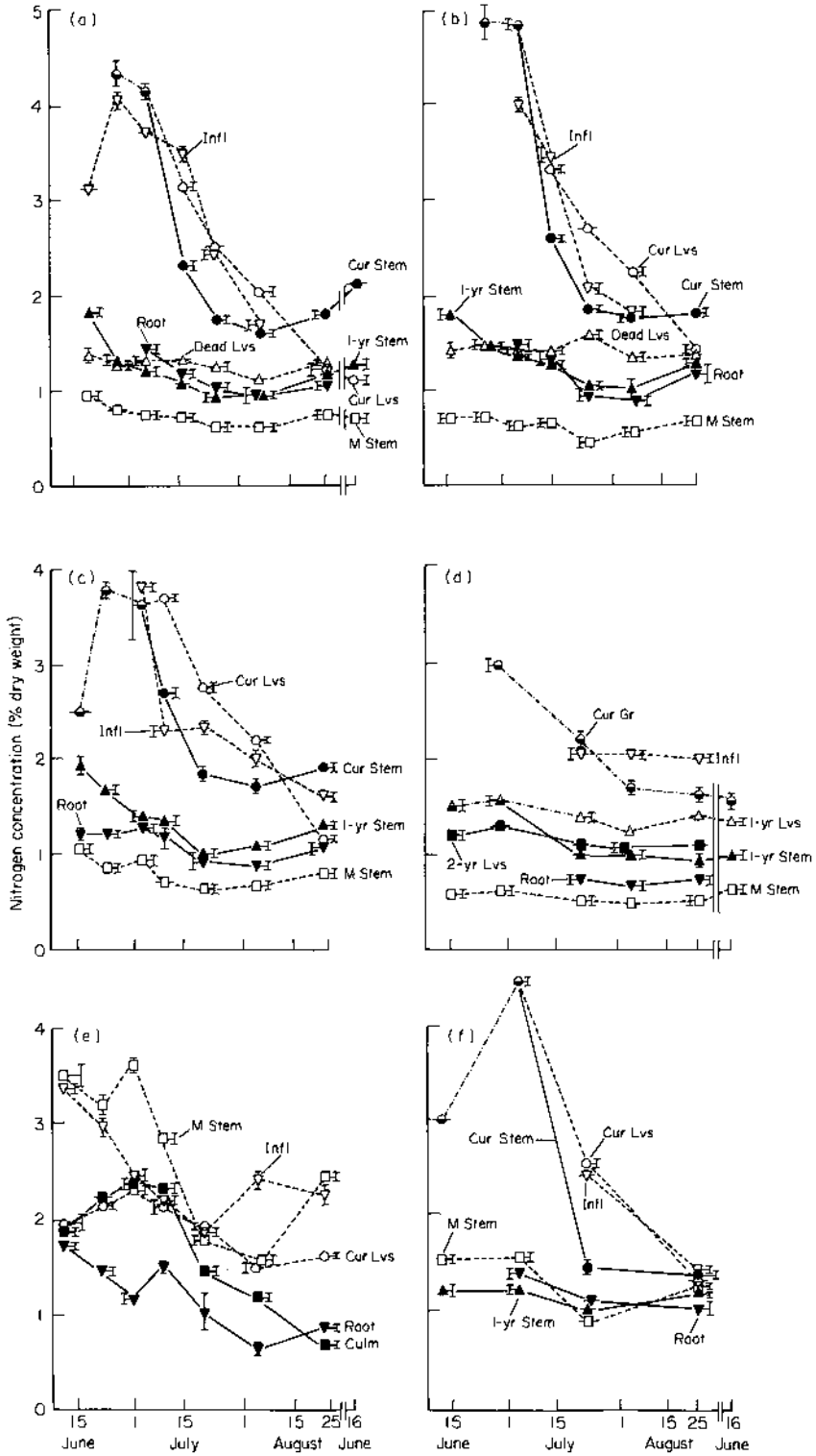
In the tussock graminoid *Eriophorum vaginatum*, low individual variability permitted detection of seasonal changes in stem (rhizome) weight. Rhizome weight decreased by 25% during the first 2 weeks of the growing season (Fig. 1), coincident with initiation of root growth, and presumably resulting from some combination of rhizome respiration and movement of reserves to roots and perhaps to leaves. After 1 July, average rhizome weight remained relatively constant until maximum leaf biomass was attained, after which time rhizome weight returned to its initial spring value.

### Nitrogen

Although the two *Salix* populations differed sufficiently in height (15 and 120 cm) to be placed in different Raunkiaer life-form groupings, and although *Rubus* stems were less woody than those of *Salix* and *Betula*, all these deciduous species showed a similar magnitude and timing of seasonal changes in nitrogen concentration (Fig. 2). The evergreen shrub *Ledum* differed from the deciduous species, however, in having lower nitrogen concentration and less pronounced seasonal changes. For example, the nitrogen concentration in *Salix* leaves decreased four-fold from 4.5% N during the first growing season, whereas that in *Ledum* leaves declined only 50% from 3.0% N.

A substantial quantity of nitrogen moved into and later out from leaves of the

*Nutrient movement in tundra plants*



deciduous shrubs. At the time of maximum nitrogen content in the standing crop (Fig. 1), *Salix* and *Betula* had about twice as large a proportion of their total nitrogen in the leaves (7–14% of total plant N, or 27–41% of above-ground N) as they did biomass (3–6% of total plant biomass; Tables 1 and 2). Flowering preceded or coincided with leaf production and must have further strained nitrogen reserves, judging from the high nitrogen concentration of inflorescences. Maximum nitrogen content of the leaves was reached within 3–4 weeks after snow-melt, whereas the biomass of leaves continued to increase over a 6-week period (Fig. 1). If it is assumed that non-current stems did not change weight during the phase of rapid leaf production (late June and early July), a maximum of half of the nitrogen appearing in the leaves during this period could be accounted for by the decline in nitrogen in the above-ground stems.

The spring decrease in the nitrogen concentration of below-ground stems and roots of the deciduous shrubs (Fig. 2) also suggests that much of the nitrogen in the leaves was moved from below ground. Because nitrogen was needed for leaf production at a time when most of the soil was still frozen and there were few newly-produced roots, nitrogen was probably supplied largely from below-ground reserves in the plant rather than by uptake from the soil. Between mid-July and late-August, 56% of the maximum leaf-nitrogen content was removed from the leaves of *Salix* (Table 2). Movement downwards within the plant was presumably more important than leaching in explaining this nitrogen removal from leaves, because (1) no precipitation occurred during the last 2 weeks of August when nitrogen declined most rapidly in the leaves, and (2) leaching might be expected to remove elements in the order  $K > N > P$  (Tukey 1970), whereas the observed disappearance from leaves tended to be in the reverse order (see below).

All stem-categories of *Salix* and *Betula* continued to decline in nitrogen concentration (Fig. 2) for 2–4 weeks after the leaves began to lose nitrogen (Fig. 1). This decline may reflect leaching, but it seems more likely that root growth, which was still rapid, could not be totally sustained by concurrent uptake from the soil and so depended upon stored nitrogen. Catkin production preceded or coincided with leaf production in the deciduous shrubs examined, and therefore was unlikely to be a major sink for nitrogen at this time. Demands for nitrogen, firstly for leaf and inflorescence production, then for root production, and also to replace losses by leaching, were not balanced by nitrogen uptake from the soil until later in the growing season. A similar movement of nutrients from shoots to support root growth has been suggested for *Rubus chamaemorus* (Sæbø 1968).

Nitrogen movement into new growth of the evergreen *Ledum* occurred later in the season and more gradually than it did in the deciduous shrubs. Consequently in mid-July, when the leaves of deciduous shrubs reached their maximum nitrogen content, current growth of *Ledum* had only 65% of its end-of-season nitrogen content (Fig. 1). Of the total nitrogen content of *Ledum*, a maximum of 24% was present in new growth and 46% in all age-classes of leaves. This is more than three times the maximum proportion in leaves of any of the deciduous species (Table 2). In contrast to the deciduous species, nitrogen concentrations in leaves and stems of *Ledum* changed in parallel through the season, although the magnitude of these changes was small in all tissues except current

FIG. 2. Seasonal course of nitrogen concentration in various plant parts of (a) *Salix pulchra* (meadow), (b) *Salix pulchra* (creek margin), (c) *Betula nana*, (d) *Ledum palustre*, (e) *Eriophorum vaginatum* and (f) *Rubus chamaemorus* in Alaskan tundra. Mean  $\pm$  S.E. is shown,  $n = 4$ . Infl = inflorescence; Cur, 1-yr, and 2-yr Lvs = current year's, 1-year-old and 2-year-and-older leaves, respectively; Cur, 1-yr, and M Stem = current year's, 1-year-old and main stem, respectively; Cur Gr = current year's stem and leaf material combined.



## Nutrient movement in tundra plants

TABLE 2. Total nitrogen (mg per individual)\* in different plant parts in mid-July and late-August in Alaskan tundra; values are mean  $\pm$  S.E.,  $n = 4$ 

	Salix (meadow)		Salix (creek margin)		Betula		Eriophorum†		Ledum	
	16 July	26 August	15 July	25 August	10 July	24 August	21 July	24 August	23 July	25 August
Current leaves	17.9 $\pm$ 0.9	7.9 $\pm$ 0.4	36.9 $\pm$ 3.2	20.4 $\pm$ 1.4	8.7 $\pm$ 0.5	3.9 $\pm$ 0.2	0.34 $\pm$ 0.02	0.24 $\pm$ 0.01	2.2 $\pm$ 0.1§	3.4 $\pm$ 0.04§
Current stem	1.6 $\pm$ 0.3	3.6 $\pm$ 0.5	7.2 $\pm$ 0.9	6.1 $\pm$ 0.6	1.6 $\pm$ 0.2	1.8 $\pm$ 0.2	-	-	-	-
Inflorescence†	2.3	1.1	0.4	0.2	0.8	0.6	-	-	0.0	-
1-year leaves	2.8 $\pm$ 0.2	3.0 $\pm$ 0.3	5.5 $\pm$ 0.3	5.6 $\pm$ 0.4	1.9 $\pm$ 0.2	1.8 $\pm$ 0.2	-	-	1.7 $\pm$ 0.2	1.7 $\pm$ 0.2
1-year stem†	-	-	-	-	-	-	-	-	0.4 $\pm$ 0.1	0.4 $\pm$ 0.1
2-year-and-older leaves	6.8 $\pm$ 1.1	7.5 $\pm$ 1.2	23.7 $\pm$ 2.0	28.5 $\pm$ 2.4	8.0 $\pm$ 0.5	8.9 $\pm$ 0.7	-	-	1.3 $\pm$ 0.1	1.3 $\pm$ 0.1
2-year-and-older stem†	-	-	-	-	-	-	-	-	1.0 $\pm$ 0.2	1.0 $\pm$ 0.2
Above-ground main stem†	12.7 $\pm$ 1.4	14.5 $\pm$ 1.6	63.9 $\pm$ 8.5	70.5 $\pm$ 9.6	6.4 $\pm$ 0.6	6.9 $\pm$ 0.8	-	-	1.8 $\pm$ 0.1	1.9 $\pm$ 0.2
Below-ground stem†	46.0 $\pm$ 9.5	41.3 $\pm$ 8.8	-	-	27.7 $\pm$ 3.3	32.3 $\pm$ 3.9	0.43 $\pm$ 0.02	0.53 $\pm$ 0.03	2.3 $\pm$ 0.4	2.2 $\pm$ 0.3
Roots†	37.2 $\pm$ 1.6	33.5 $\pm$ 1.6	-	-	74.4 $\pm$ 5.8	67.0 $\pm$ 4.1	0.39 $\pm$ 0.03	0.33 $\pm$ 0.05	2.1 $\pm$ 0.4	2.1 $\pm$ 0.4
Total nitrogen	127	112	-	-	130	123	1.16	1.10	12.8	14.0

\* An individual is defined as a tiller or branch extending below ground.

† Assumes constant weight through season; sample variability precluded measurement of seasonal weight changes.

‡ Allocation pattern is given for non-flowering tillers that constitute more than 99% of the population.

§ Includes current stem.

growth. The small but parallel changes in leaf and stem nitrogen suggest that there were no specialized winter storage organs in *Ledum*.

The tussock-forming sedge *Eriophorum vaginatum* has leaves that overwinter and resume elongation the following spring (Johnson & Tieszen 1976). The relatively constant nitrogen concentration in the leaves during August is similar to the seasonal pattern of *Ledum*, but different from the continued loss of nitrogen from the leaves of deciduous shrubs and from the senescing green culms of *Eriophorum* (Fig. 2), suggesting that *Eriophorum* leaves may store nitrogen for leaf growth in the following spring. The decline in nitrogen content of the rhizomes of *Eriophorum* during June and July is about twice the increase in nitrogen in the leaves (Fig. 1), and may reflect movement of nitrogen into newly-produced roots. *Eriophorum* roots do not overwinter, but are rapidly initiated following snow-melt (Chapin, Van Cleve & Chapin 1979), and have a relatively high concentration of nitrogen (Fig. 2).

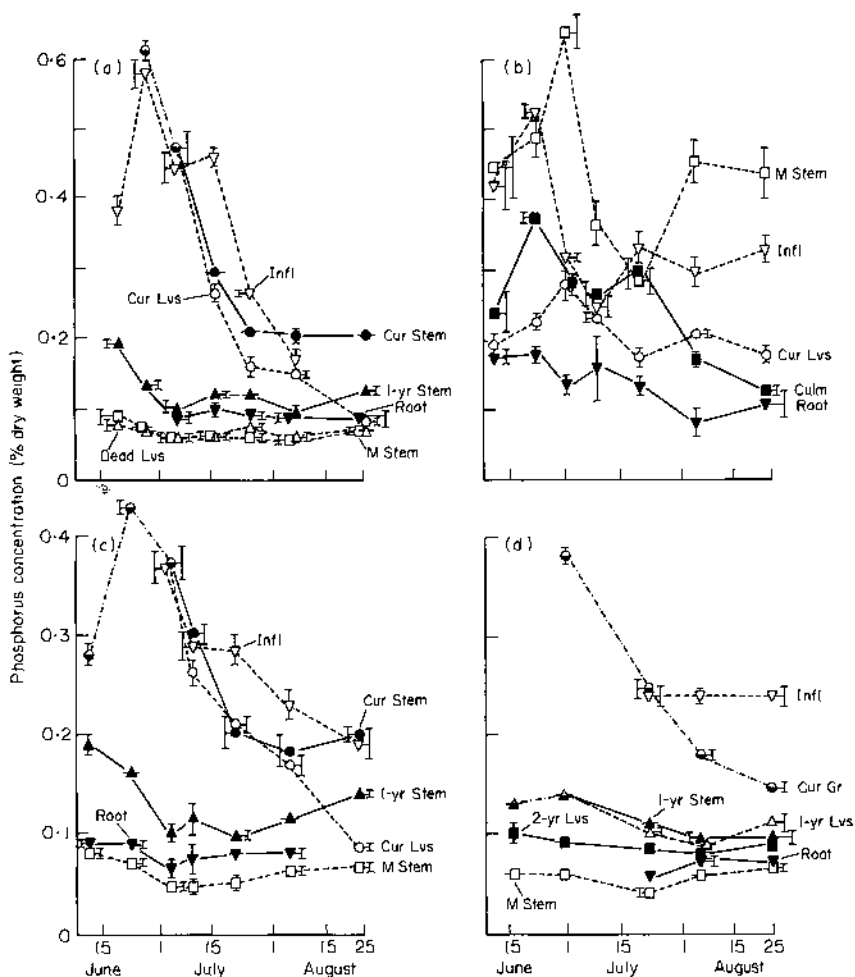


FIG. 3. Seasonal course of phosphorus concentration in various plant parts of (a) *Salix pulchra* (meadow population), (b) *Eriophorum vaginatum*, (c) *Betula nana* and (d) *Ledum palustre* in Alaskan tundra. Mean  $\pm$  S.E. is shown,  $n = 4$ . Note differences in scale on the y-axis. Abbreviations as in Fig. 2.

Other elements

Seasonal changes in the concentration and amount of phosphorus, potassium and magnesium in the two *Salix* populations were very similar, and therefore are shown for the meadow *Salix* plants alone. Likewise, seasonal nutrient patterns in *Rubus* were similar to those in the other deciduous species, and are shown in the Appendix. The distribution of phosphorus and potassium among plant parts was similar to that for nitrogen (Table 2), and is not shown; the distributions of calcium and magnesium were similar, and only calcium is shown (Table 3). Results not shown are available from the authors.

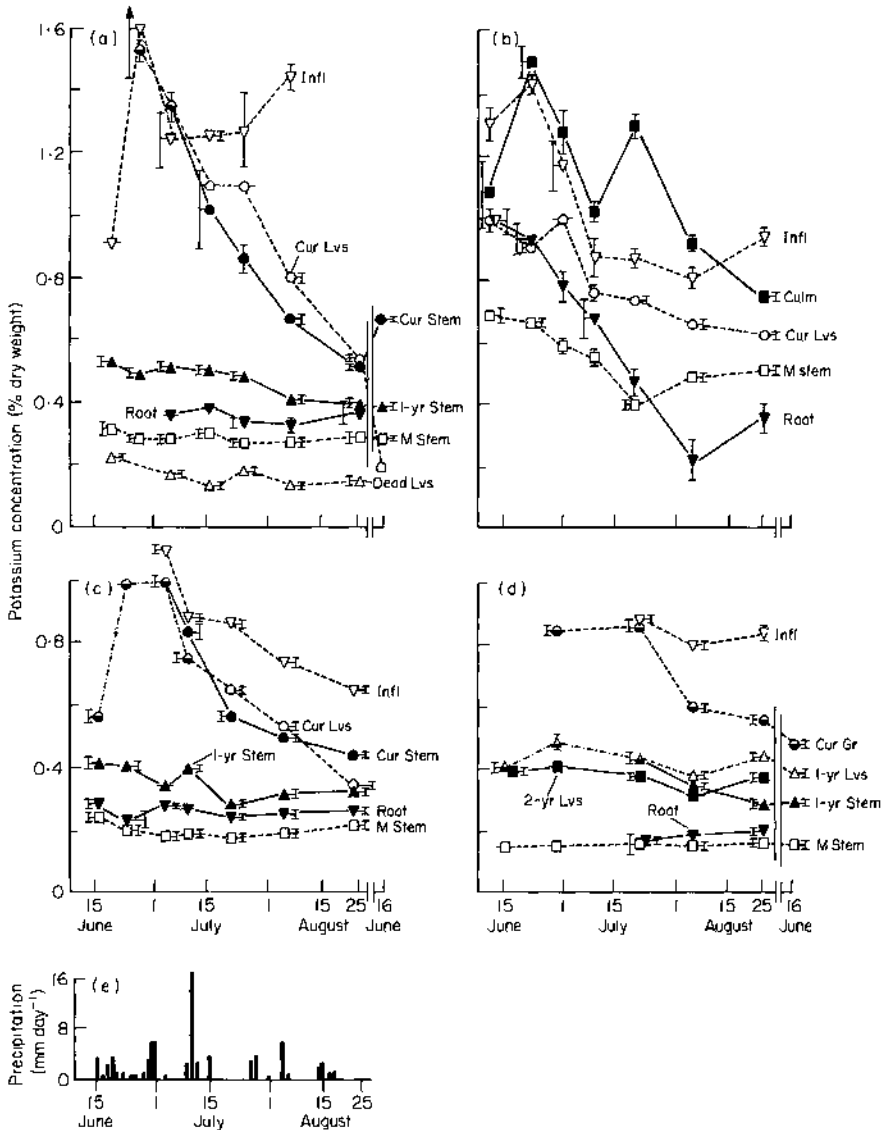


FIG. 4. Seasonal course of potassium concentration in various plant parts of (a) *Salix pulchra* (meadow population), (b) *Eriophorum vaginatum*, (c) *Betula nana* and (d) *Ledum palustre*—note differences in scale on the y-axis—and daily precipitation in Alaskan tundra. Mean  $\pm$  S.E. is shown,  $n = 4$ . Abbreviations as in Fig. 2.

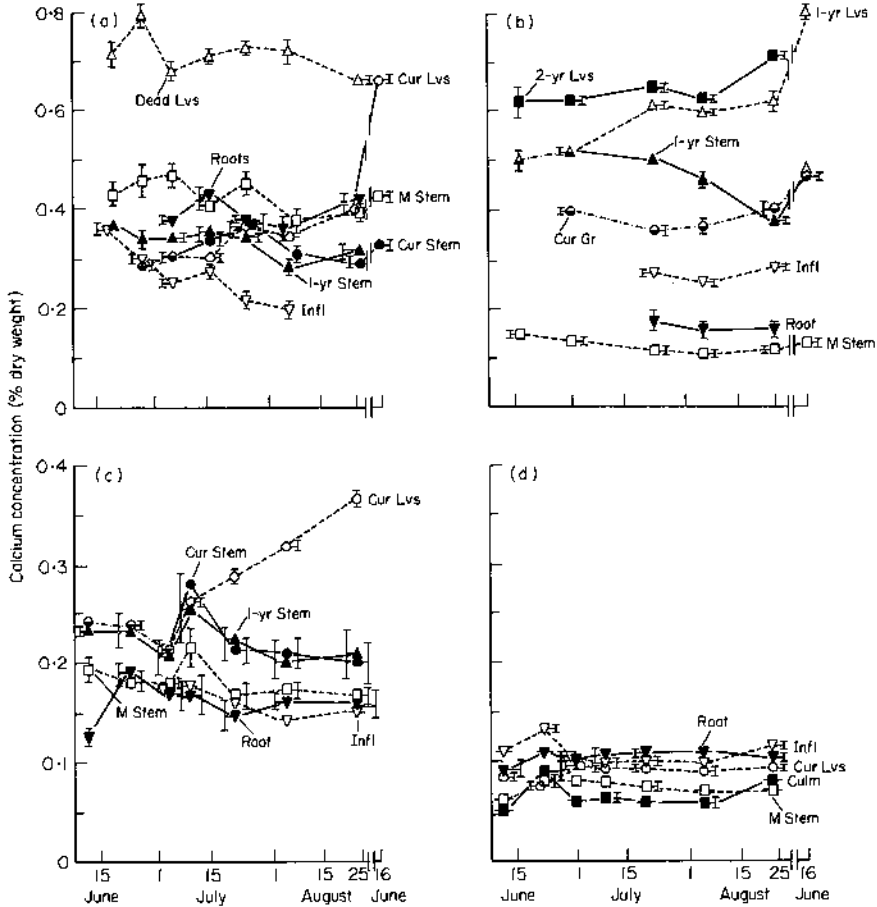


FIG. 5. Seasonal course of calcium concentration in various plant parts of (a) *Salix pulchra* (meadow population), (b) *Ledum palustre*, (c) *Betula nana* and (d) *Eriophorum vaginatum* in Alaskan tundra. Mean  $\pm$  S.E. is shown,  $n = 4$ . Note differences in scale on the y-axis. Abbreviations as in Fig. 2.

The concentrations of phosphorus and potassium followed the same general seasonal trend as nitrogen for all species, the two *Salix* populations being quite similar to one another, and *Betula* having somewhat lower concentration and less pronounced seasonal fluctuations than did *Salix* (Figs 3 and 4). In *Ledum*, phosphorus and potassium concentration was generally lower than in the deciduous shrubs and showed less seasonal fluctuation. From 53 to 64% of the phosphorus and 35 to 53% of the potassium disappeared from the leaves of the deciduous shrubs before the leaves dropped from the plants, indicating substantial autumn translocation or leaching. The tendency of current and 1-year-old stems to show increased concentration of nitrogen and phosphorus but not of potassium in autumn (Table 2, Figs 2-4) suggests that the mechanism for internal movement and storage of potassium in these deciduous species is less effective than that for nitrogen and phosphorus. This difference among elements was not evident in the evergreen *Ledum*, which shows no evidence of nutrient-storage in stems.

In contrast to the mobile elements (i.e. N, P and K), calcium increased in concentration and total content in leaves of all species except *Eriophorum*, indicating the lack of

## Nutrient movement in tundra plants

TABLE 3. Total calcium (mg per individual)\* in different plant parts in mid-July and late-August in Alaskan tundra; values are mean  $\pm$  S.E.,  $n = 4$

	<i>Salix</i> (meadow)		<i>Salix</i> (creek margin)		<i>Betula</i>		<i>Eriophorum</i> †		<i>Ledum</i>	
	16 July	26 August	15 July	25 August	10 July	24 August	21 July	24 August	23 July	25 August
Current leaves	1.7 $\pm$ 0.1	2.6 $\pm$ 0.1	4.9 $\pm$ 0.4	8.7 $\pm$ 0.6	0.6 $\pm$ 0.0	1.2 $\pm$ 0.1	0.017 $\pm$ 0.001	0.015 $\pm$ 0.001	0.37 $\pm$ 0.01§	0.86 $\pm$ 0.04§
Current stem	0.2 $\pm$ 0.0	0.6 $\pm$ 0.1	1.4 $\pm$ 0.2	1.3 $\pm$ 0.1	0.2 $\pm$ 0.0	0.2 $\pm$ 0.0	-	-	0.00	-
Inflorescence†	0.2	0.1	0.0	0.0	0.1	0.0	-	-	0.74 $\pm$ 0.11	0.00
1-year leaves	-	-	-	-	-	-	-	-	0.20 $\pm$ 0.04	0.75 $\pm$ 0.11
1-year stem†	0.9 $\pm$ 0.1	0.8 $\pm$ 0.1	2.2 $\pm$ 0.2	1.8 $\pm$ 0.1	0.4 $\pm$ 0.1	0.3 $\pm$ 0.0	-	-	0.79 $\pm$ 0.06	0.15 $\pm$ 0.03
2-year-and-older leaves	-	-	-	-	-	-	-	-	-	-
2-year-and-older stem†	3.2 $\pm$ 0.5	2.8 $\pm$ 0.5	16.0 $\pm$ 1.3	9.8 $\pm$ 1.8	2.3 $\pm$ 0.2	1.8 $\pm$ 0.2	-	-	0.38 $\pm$ 0.07	0.84 $\pm$ 0.06
Above-ground	6.8 $\pm$ 0.8	6.6 $\pm$ 0.7	56.4 $\pm$ 7.3	46.5 $\pm$ 6.4	2.0 $\pm$ 0.2	1.5 $\pm$ 0.1	-	-	0.46 $\pm$ 0.08	0.35 $\pm$ 0.06
Below-ground	26.6 $\pm$ 5.5	25.4 $\pm$ 5.2	-	-	8.4 $\pm$ 1.1	6.3 $\pm$ 0.8	0.018 $\pm$ 0.001	0.021 $\pm$ 0.001	0.48 $\pm$ 0.08	0.45 $\pm$ 0.03
Root†	13.5 $\pm$ 0.6	13.2 $\pm$ 0.5	-	-	10.5 $\pm$ 1.0	9.9 $\pm$ 0.8	0.042 $\pm$ 0.003	0.041 $\pm$ 0.003	0.50 $\pm$ 0.10	0.51 $\pm$ 0.08
Total calcium	53.1	52.1	-	-	24.5	21.2	0.077	0.077	3.92	4.37

\* An individual is defined as a tiller or branch extending below ground.

† Assumes constant weight through season; sample variability precluded measurement of seasonal weight changes.

‡ Allocation pattern is given for non-flowering tillers that constitute more than 99% of the population.

§ Includes current stem.

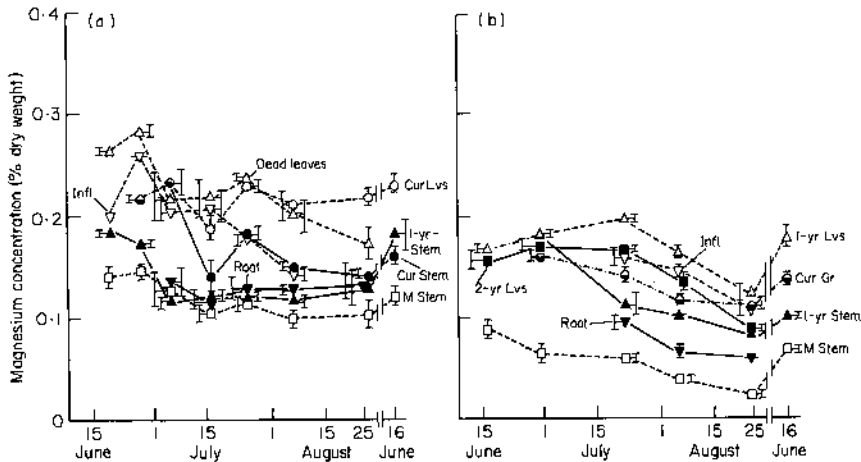


FIG. 6. Seasonal course of magnesium concentration in various plant parts of (a) *Salix pulchra* (meadow population) and (b) *Ledum palustre* in Alaskan tundra. Mean  $\pm$  S.E. is shown,  $n = 4$ . Abbreviations as in Fig. 2.

movement of calcium from senescing leaves (Fig. 5 and Table 3). The concentration of calcium in stems, however, decreased throughout the latter half of the growing season (Fig. 5), suggesting that the stems serve as a calcium store.

The large differences in calcium concentration among species and populations bore no apparent relation to growth form. For example, the creek margin population of *Salix* had a calcium concentration about 50% higher than that shown for the meadow population (Fig. 5), and the evergreen *Ledum* had concentrations intermediate between the two *Salix* populations. *Eriophorum*, the tussock-forming sedge, differed strikingly from all other species examined in the low value and seasonal stability of calcium concentration, the maximum concentration in *Eriophorum* being about equal to the minimum observed in any of the other species.

Concentration of magnesium in the leaves of all species remained relatively constant throughout the growing season (Fig. 6), suggesting that it was removed from senescing leaves to a greater extent than calcium, but less than nitrogen, phosphorus or potassium.

The concentration of sodium in most plant parts of most species was very low. In contrast to the other mobile elements (N, P or K), sodium concentration was lower ( $P < 0.01$ ) in leaves and 1-year-old stems (0.002%) of shrubs than in older stems or roots (0.010 and 0.014% respectively). Similarly, the sodium concentration of *Eriophorum* leaves (0.011%) and inflorescences (0.002%) was considerably lower than that of roots (0.109%).

#### Non-vascular plants

In the two moss communities sampled, of *Aulacomnium* spp. and the mixture of polytrichaceous mosses (*Polytrichum* spp. and *Pogonatum* spp.), the concentration of nitrogen was consistently lower than in the vascular plant leaves (Fig. 7). The concentration of phosphorus and potassium was also lower than in leaves of deciduous species, but similar to that in old leaves of *Ledum*. The calcium concentration in mosses was within the range for vascular plants. In *Aulacomnium*, green and brown tissues generally did not differ greatly in nutrient concentration. In contrast, *Polytrichum*, with greater differentiation into photosynthetic and conducting or support tissue, always had significantly higher

## Nutrient movement in tundra plants

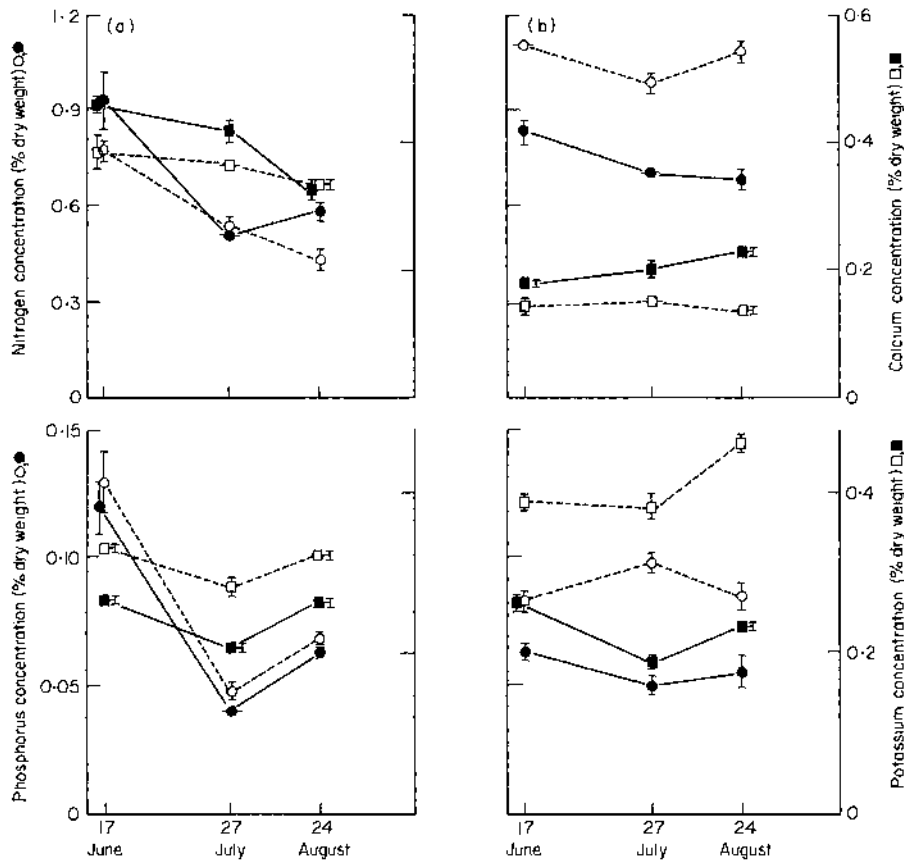


FIG. 7. Seasonal course of N, P, K and Ca concentration in green (unfilled symbols, pecked lines) and non-green portions (filled symbols, continuous lines) of (a) the moss *Aulacomnium* spp., (b) a mixture of the polytrichaceous mosses *Polytrichum* spp. and *Pogonatum* spp., in Alaskan tundra.

( $P < 0.01$ ) concentration of nitrogen, phosphorus and potassium but lower concentration of calcium in green than in non-green tissue. This pattern is the same as that generally observed in vascular plants. *Polytrichum* also showed less seasonal fluctuation in nutrient concentration than did *Aulacomnium*.

All lichen species sampled had low concentrations of nitrogen, phosphorus and potassium, but a similar calcium concentration relative to the mosses and vascular species sampled (Table 4). Among the lichen species, *Stereocaulon* spp. and *Thamnolia vermicularis* tended to have higher nitrogen, phosphorus and calcium concentration than did *Cetraria* and *Cladonia* spp. Six lichen species re-sampled in the autumn showed nearly the same concentration of nitrogen and phosphorus as those shown in Table 4.

## DISCUSSION

*Patterns of nutrient flux*

There is a hierarchy of similarity in the pattern of nutrient movements. The two morphologically-distinct populations of one species (*Salix*) were the most similar to one another, and all deciduous species were more similar to one another than to the evergreen

TABLE 4. Mineral-nutrient concentration (% dry wt) of lichens sampled in mid-June, single samples only

	N	P	K	Ca	Mg
<i>Stereocaulon</i> spp.	0.7	0.06	0.24	—	0.16
<i>Thamnolia vermicularis</i>	0.5	0.07	0.27	0.35	0.27
<i>Cetraria islandica</i>	0.4	0.05	0.24	0.22	0.64
<i>Dactylina arctica</i>	0.3	0.05	0.17	0.12	0.54
<i>Cladonia alpestris</i>	0.3	0.04	0.15	0.08	0.38
<i>Cetraria cucullata</i>	0.3	0.04	0.16	0.11	0.69
<i>Alectoria nigricans</i>	0.3	0.04	0.16	0.12	0.45
<i>Alectoria ochroleuca</i>	0.3	0.03	0.14	0.12	0.24
<i>Cetraria richardsonii</i>	0.3	0.03	0.17	0.48	0.48
<i>Cladonia rangiferina</i>	0.2	0.03	0.12	0.08	0.41
All species (mean $\pm$ S.E.)	0.36 $\pm$ 0.05	0.044 $\pm$ 0.004	0.182 $\pm$ 0.016	0.19 $\pm$ 0.05	0.43 $\pm$ 0.05

shrub. The deciduous species examined all had relatively high concentration of nitrogen, phosphorus and potassium in the leaves, and these changed substantially during the growing season. In contrast, the evergreen species had low nutrient concentrations which remained relatively stable throughout the growing season. These contrasts between evergreen and deciduous species are apparent in other tundra and bog species investigated (Thomas & Trinder 1947; Rodin & Bazilevich 1967; Isotalo 1971; Scotter 1972; Small 1972; Chapin, Van Cleve & Tieszen 1975; Wielgolaski, Kjølvik & Kallio 1975) and in temperate species (Gerloff, Moore & Curtis 1964; Rodin & Bazilevich 1967; Langille & MacLean 1976; Schlesinger & Chabot 1977). Thus it appears valid to generalize about patterns of nutrient movement in deciduous as contrasted with evergreen species.

Differences between species in the magnitude and seasonal variation of leaf nutrient content are consequences of differences in storage and flux from other parts of the plant. The deciduous species moved substantial quantities of nitrogen, phosphorus and potassium into the new leaves at bud-break in early spring, whereas the evergreen species moved these substances into the new leaves gradually throughout the growing season. At Atkasook, nutrient translocation into leaves by deciduous species occurs when conditions are least favourable for nutrient uptake from the soil, indicating the importance of nutrient storage, particularly below ground. Moreover, the seasonal changes in stem contents of nitrogen, phosphorus and calcium suggest a depletion and renewal of stored reserves in deciduous species but not in evergreens. Similar patterns have been observed in deciduous shrubs of Minnesota forests (Grigal, Ohmann & Brander 1976) and in *Rubus chamaemorus* in Norway (Sæbø 1968). Some deciduous tree crops are known to support leaf production primarily with nutrients stored below ground (Tromp 1970). In evergreen species, leaves may be as important as stems for nutrient-storage over winter. Both the seasonal nutrient stability and the small below-ground biomass of evergreens suggest that nutrients are not stored below ground in winter to a major extent. Evergreen-dominated heath tundras typically have a smaller proportion of biomass below ground (e.g. 30–40%) than do deciduous shrub tundras (75–85%) (Chepurko 1972; Grier 1973; Tyler *et al.* 1973; Wielgolaski, Kjølvik & Kallio 1975), and therefore presumably have less below-ground storage. Evergreen species apparently keep their nutrients *in situ* without seasonal storage in other plant parts, minimizing energy costs associated with synthesis, breakdown and translocation of storage compounds. However, this strategy places the nutrient reserves of evergreen species in a position vulnerable to herbivores, and is associated with the production of anti-herbivore defence compounds (Rhoades & Cates 1976).



TABLE 5. Potential carbon gain in relation to nutrient 'cost' of a leaf in Alaskan tundra; maximum photosynthetic rate at 15 °C, estimated duration of leaf activity in 1975 (Johnson & Tieszen 1976), and proportion of newly-initiated leaves that remain at mid-season (leaf survival) (Johnson & Tieszen, unpublished data) are used to estimate maximum seasonal carbon uptake per gram of leaf; the ratio of this carbon uptake to the quantity of nitrogen or phosphorus lost to the plant per gram of senesced leaf in autumn provides a measure of carbon gained by the plant per nutrient invested in leaves

	Maximum rate of photosynthesis (mg CO <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	Leaf longevity (days)	Leaf survival (%)	Maximum seasonal carbon gain per unit weight of leaf (g g <sup>-1</sup> )	Carbon gain for nutrient invested (g g <sup>-1</sup> )	
					C/N	C/P
<i>Ledum palustre</i>				15.7	1520	19 600
Current leaf	10 ± 1	75	100	4.9		
1-year leaf	18 ± 1	90	59	6.3		
2-year leaf	17 ± 1	90	34	3.4		
3-year leaf	11 ± 1	90	17	1.1		
<i>Salix pulchra</i>	40 ± 3	64	100	16.8	1370	20 200
<i>Betula nana</i>	37 ± 4	61	100	14.8	1290	17 400
<i>Rubus chamaemorus</i>	15 ± 1	45	100	4.4	340	4400
<i>Eriophorum vaginatum</i>	27 ± 2	90	100	15.9	1070	8900

The low nitrogen concentration found in the evergreen leaves of *Ledum* in this study is correlated with a low photosynthetic rate and slow leaf growth (Johnson & Tieszen 1976), just as in other evergreens (e.g. Mooney & Dunn 1970; Schulze, Fuchs & Fuchs 1977). The low nitrogen concentration and low photosynthetic rate results in part from dilution by a large quantity of structural carbohydrate and secondary chemical compounds in the leaves (Mooney & Dunn 1970; Rhoades & Cates 1976). It is nonetheless impressive that the major portion of the carbon acquired by *Ledum* is fixed by second- and third-year leaves (Johnson & Tieszen 1976) which have a lower concentration of nitrogen than the attached dead leaves of *Salix*.

A comparison of the potential carbon gain by a leaf with the minimum nutrient cost of producing that leaf (i.e. the nutrient loss with autumn abscission; Table 5) indicates that evergreen and deciduous shrubs at Atkasook have a similar potential for carbon uptake relative to nutrient 'investment' in leaves, despite large differences in both nutrient movement and photosynthetic rate. The actual carbon gain by plants will depend upon canopy structure and seasonal light and temperature patterns, but the ratios given in Table 5 allow a general comparison between species for a particular year. The similarity of these ratios of carbon-gain per nutrient-invested for species at Atkasook may partially answer the question posed by Schlesinger & Chabot (1977): How do different growth forms coexist in a single 'stable' community? Differences between growth forms in the ratio of carbon gain to nutrient invested in leaves might be expected in communities that are changing in growth-form composition (Horn 1974). However, this seems less likely in a stable mixed community.

The rate of photosynthesis in relation to nitrogen retention by leaves was measured by Small (1972), who concluded, as did Schlesinger & Chabot (1977), that a large photosynthetic return for nitrogen invested in leaves explained the dominance by evergreen species in low-nutrient bogs and swamps. The difference from our conclusion arises

largely in the calculation of the amount of nitrogen invested rather than in the data used. We calculated the nitrogen cost of a leaf as the nitrogen lost to the plant by autumn leaf abscission, whereas Small (1972) calculated nitrogen cost as a function of the mean seasonal concentration of nitrogen in the leaf divided by a factor correcting for movement of nitrogen out of the leaves in the autumn. This movement was assumed to occur each year in evergreen species, an assumption contradicted by the seasonal patterns of nutrient concentration in evergreen leaves obtained in our study and elsewhere (Skre, Berg & Wielgolaski 1975; Langille & MacLean 1976; Thomas & Grigal 1976). Evergreen species dominate low-nutrient environments (Beadle 1954; Loveless 1961; Monk 1966). It is possible that this may result from a lower annual requirement (absorption) or loss (by leaching and abscission) rather than from a direct relationship with rate of photosynthesis per unit of nutrient invested in the leaves.

The differences in the pattern of movement of nutrients between the two groups of mosses sampled are as pronounced as those observed among vascular plants: our original assumption of a single moss pattern was thus probably incorrect. The similarity of nutrient concentration in green and non-green tissue of *Aulacomnium* is paralleled by data for other arctic mosses elsewhere (Pakarinen & Vitt 1974; Rastorfer 1978), and presumably relates to the role of both green and brown tissues in nutrient absorption and retention on a well-developed cation-exchange complex. This maintenance of exchange capacity by the dead brown tissue may be important in exploitation of periods of high nutrient-availability, such as at snow-melt. In contrast, the relatively low nutrient concentration in brown tissue of the polytrichaceous mosses *Polytrichum* and *Pogonatum*, also evident in the data of Pakarinen & Vitt (1974), suggests a less active role by the brown tissue in nutrient-absorption in these mosses. The well-developed water-transport system of polytrichaceous mosses may allow them to acquire nutrients from the soil solution throughout the growing season, and may explain why the nutrient concentration of *Polytrichum* is more seasonally stable than that of *Aulacomnium*.

The small size and seasonal variation found in nutrient concentration of lichens at Atkasook is characteristic of tundra lichens which do not fix nitrogen (Scotter 1965, 1972; F. E. Wielgolaski, unpublished data).

#### *Implications for herbivory*

Seasonal changes in the nutrient concentrations of plants have important consequences for food preference by herbivores. At snow-melt, leaves of deciduous shrubs and the inflorescences of *Salix* and *Eriophorum* are the sources of the highest concentration of nitrogen and phosphorus among all the species and plant parts tested at Atkasook, and are strongly preferred by caribou and ptarmigan (Batzli & Brown 1976). After the end of June, both the concentration and total amount of nitrogen and phosphorus in the leaves decline rapidly in deciduous shrubs. To the extent that requirements of nitrogen and phosphorus regulate herbivory, this seasonal nutrient pattern shown by the plants would select for the observed early spring grazing by migratory herbivores (Klein 1970), the early emergence of herbivorous insects (especially sucking insects capable of tapping the translocation stream; Hodkinson, Jensen & MacLean (1979)), and early spring reproduction in non-migratory herbivores such as lemmings. Periods of rapid leaf production and high nutrient-concentration generally coincide with times of low concentration of anti-herbivore compounds (Dement & Mooney 1974; Feeny 1976) and would strengthen selection for these seasonal trends in herbivory.

However, nitrogen, phosphorus and potassium concentrations are clearly not the only

factors involved in food preference. The *Cetraria* and *Cladonia* species sampled have low nitrogen and phosphorus concentrations even for lichens, yet Scotter (1965) found them to be among the most important forage species for caribou in northern Canada. The lichen species which have the lowest nitrogen and phosphorus concentration at Atkasook are those most highly preferred by reindeer in Sweden (O. Ericksson, unpublished data).

The proportions of mineral-elements in plants tend to be favourable for animals, because both groups of organisms have roughly the same needs. The high potassium and low sodium concentration observed in plants at Atkasook and elsewhere are the reverse of animal requirements, and may have evolved in part as a defence against herbivory. High potassium concentration in spring forage can upset the Na:K balance of vertebrate herbivores, and lead to sodium-deficiency symptoms (Suttle & Field 1967; Weeks & Kirkpatrick 1978). Plants actively exclude sodium from their roots (Nye & Tinker 1977). The low sodium concentration of leaves relative to other plant parts differs from the pattern of other mobile elements (N, P and K) and may result from active exclusion of sodium from those plant parts most frequently eaten by herbivores.

The remarkably low calcium concentration of *Eriophorum vaginatum* leaves is characteristic of this species in a variety of sites (Tamm 1954; Goodman & Perkins 1968; Wein & Bliss 1973), and is lower even than the generally low calcium concentration of other tundra graminoids (Chapin, Van Cleve & Tieszen 1975; Wielgolaski, Kjølsvik & Kallio 1975; Muc 1977), and might induce calcium deficiency in a vertebrate herbivore specializing upon this species. Addition of calcium fertilizer did not increase production of *E. vaginatum* (J. D. McKendrick, unpublished data), indicating that the low calcium concentration of this species at Atkasook does not reflect calcium deficiency.

The species studied at Atkasook probably differ with respect to their degree and timing of vulnerability to grazing. Evergreens have a larger proportion of their total nitrogen, phosphorus and potassium in the leaves than do deciduous shrubs. The deciduous shrubs move a large proportion of their nutrient capital to leaves immediately following snow-melt. These shrubs would lose more nutrients if browsed 2–3 weeks after snow-melt than if browsed at the end of the season. In contrast, the nutrient investment in evergreen leaves accumulates throughout the growing season, and the impact of herbivores selecting new growth might be greatest in the autumn. In graminoids at Barrow, Alaska, calculations of nutrient balance suggested that grazing had a minimal effect upon nutrient reserves until late July, because nutrients were rapidly moved to shoots whether grazing occurred or not (Chapin 1977). Grazing in the Barrow ecosystem and at Atkasook would primarily affect nutrient reserves in subsequent years by preventing back-translocation from leaves in late July and August. These differences in extent and timing of vulnerability may, when combined with grazing, alter the composition of plant communities (Stoner *et al.* 1978).

The present study thus provides a basis for predicting quantitatively the effects of various types, times, and intensities of grazing upon the major growth forms present in an arctic tundra ecosystem.

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APPENDIX. Seasonal changes in mineral-nutrient concentration (% dry wt; mean  $\pm$  S.E.,  $n = 4$ ) in various plant parts of *Rubus chamaemorus* in Alaskan tundra

		12 June	5 July	24 July	23 August
Phosphorus	Leaves	0.36 $\pm$ 0.013*	0.38 $\pm$ 0.010*	0.19 $\pm$ 0.011	0.10 $\pm$ 0.004
	Inflorescence	-	-	0.24 $\pm$ 0.025	0.13 $\pm$ 0.020
	Current stem	-	-	0.17 $\pm$ 0.015	0.13 $\pm$ 0.010
	1-yr stem	0.07 $\pm$ 0.004	0.04 $\pm$ 0.004	0.09 $\pm$ 0.015	0.09 $\pm$ 0.003
	2-yr stem	0.14 $\pm$ 0.006	0.09 $\pm$ 0.006	0.09 $\pm$ 0.003	-
	Main stem	0.11 $\pm$ 0.005	0.08 $\pm$ 0.005	0.09 $\pm$ 0.000	0.11 $\pm$ 0.003
	Roots	-	0.07 $\pm$ 0.005	0.08 $\pm$ 0.005	0.09 $\pm$ 0.000
	Potassium	Leaves	1.25 $\pm$ 0.029*	1.20 $\pm$ 0.030*	1.00 $\pm$ 0.035
Inflorescence		-	-	1.18 $\pm$ 0.225	0.76 $\pm$ 0.060
Current stem		-	-	1.25 $\pm$ 0.150	0.62 $\pm$ 0.010
1-yr stem		0.14 $\pm$ 0.009	0.11 $\pm$ 0.010	0.29 $\pm$ 0.080	0.20 $\pm$ 0.008
2-yr stem		0.45 $\pm$ 0.019	0.42 $\pm$ 0.020	0.45 $\pm$ 0.009	-
Main stem		0.33 $\pm$ 0.015	0.35 $\pm$ 0.020	0.42 $\pm$ 0.009	0.40 $\pm$ 0.009
Roots		-	0.39 $\pm$ 0.010	0.37 $\pm$ 0.011	0.39 $\pm$ 0.010
Calcium		Leaves	0.19 $\pm$ 0.006*	0.10 $\pm$ 0.010*	0.34 $\pm$ 0.003
	Inflorescence	-	-	0.28 $\pm$ 0.003	0.35 $\pm$ 0.050
	Current stem	-	-	0.22 $\pm$ 0.000	0.26 $\pm$ 0.003
	1-yr stem	0.28 $\pm$ 0.009	0.27 $\pm$ 0.010	0.28 $\pm$ 0.005	0.30 $\pm$ 0.014
	2-yr stem	0.13 $\pm$ 0.005	0.13 $\pm$ 0.010	0.16 $\pm$ 0.006	-
	Main stem	0.16 $\pm$ 0.004	0.14 $\pm$ 0.003	0.16 $\pm$ 0.005	0.18 $\pm$ 0.013
	Roots	-	0.12 $\pm$ 0.020	0.15 $\pm$ 0.005	0.14 $\pm$ 0.005
	Magnesium	Leaves	0.31 $\pm$ 0.006*	0.25 $\pm$ 0.010*	0.42 $\pm$ 0.013
Inflorescence		-	-	0.40 $\pm$ 0.060	0.42 $\pm$ 0.030
Current stem		-	-	0.27 $\pm$ 0.025	0.30 $\pm$ 0.038
1-yr stem		0.16 $\pm$ 0.006	0.18 $\pm$ 0.010	0.16 $\pm$ 0.010	0.18 $\pm$ 0.010
2-yr stem		0.21 $\pm$ 0.006	0.22 $\pm$ 0.010	0.16 $\pm$ 0.006	-
Main stem		0.22 $\pm$ 0.005	0.20 $\pm$ 0.015	0.18 $\pm$ 0.004	0.18 $\pm$ 0.012
Roots		-	0.24 $\pm$ 0.020	0.26 $\pm$ 0.017	0.28 $\pm$ 0.025

\* Includes current stem.