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GROWTH AND PHYSIOLOGICAL RESPONSES OF TUNDRA PLANTS TO DEFOLIATION

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ABSTRACT

In addition to extreme abiotic conditions, biotic factors such as grazing influence the growth of tundra plants. Strategies of carbon assimilation, accumulation, and utilization must not only satisfy the requirements of a rigorous physical environment but also must simultaneously adjust to the impacts associated with herbivory. Representatives of four growth forms found in northern Alaska (a deciduous shrub, an evergreen shrub, a single-shooted graminoid, and a tussock-forming graminoid) were subjected to various defoliation regimes and their physiological and morphological responses were documented. Re-

sults from this study support the hypotheses that (1) carbon allocation patterns are a function of growth form and dictate plant responses to defoliation; (2) maximum photosynthetic rates are a function of growth form and are inversely related to leaf longevity; (3) the impact of grazing is reduced in plant species with rapid leaf turnover and little supportive tissue; (4) defoliation results in an immediate adjustment in carbon allocation pattern within the defoliated plant; and (5) carbon allocation to maintenance tissue or long-lived productive tissue is accompanied by mechanisms that reduce grazing.

INTRODUCTION

Until the recent discovery of petroleum reserves, the most important use of arctic tundra for man has been as grazing grounds for native ungulates and domesticated animals (Dahl, 1975). And yet our understanding of grazing relationships, at least from the point of view of the plant, is poorer than both that of other ecological processes in tundras and of herbivory in other biomes (see Tieszen and Archer, 1979).

There are several characteristics of tundra systems which have special implications for

plant-herbivore interactions. First, the soil and biological communities of tundra are relatively young and are nutritionally impoverished both in the Arctic (Ulrich and Gersper, 1978) and in alpine regions (Costin, 1967). Although their evolution is not known well, tundra floras and faunas can be considered depauperate (see Hoffman and Taber, 1967) due perhaps to the recent and severe Pleistocene extirpations. Second, tundras which evolved in the total absence of ungulates have a similar physiognomy to those with large grazers. Thus gross community structure has not been directly determined by large mammalian herbivores, although they can be important in determining species composition (Mark, 1965, 1969; Klotzli, 1977). Third, the

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“extreme” nature of some environmental factors—low temperatures, low soil nutrients, and short growing seasons—all help to account for low values of primary production. As a result, green biomass of high nutrient quality, although predictable in occurrence, is often a scarce resource (Figure 1). Fourth, plants which inhabit tundra systems have evolved a variety of adaptations which enable them to successfully cope with the complex of short growing seasons, long winters, low temperatures and light intensities, and limited availabilities of nutrients.

Five growth forms of vascular plants (Table 1), all represented by perennial species that reproduce vegetatively, illustrate the array of vascular plants common at Atkasook, Alaska, and represent different evolutionary responses to the same environmental problems. The degree to which differences in growth form are related to functional differences is not thoroughly documented; however, work of Bliss (1962), Hedberg (1964), and Mooney and Dunn (1970) has suggested that growth forms have functional importance and that each

growth form is characterized by a particular allocation of nutrients which presumably allows successful exploitation of particular habitats. Lewis and Callaghan (1975) and Tieszen and Wieland (1975) have described distinct growth strategies of meadow grasses, tussock sedges, and fellfield forbs, and these growth forms have been related to specific environmental complexes (Webber, 1978; Komárková and Webber, 1980, this volume).

In addition to extreme abiotic conditions, however, plant growth and perhaps community structure in arctic tundra are also influenced by biotic factors such as grazing. Tikhomirov (1959), Bliss (1975), Batzli (1975), and Batzli and Brown (1976) have reviewed the environmental impacts, both positive and negative, of herbivores on tundra plants and soils. Thus strategies of carbon assimilation, accumulation, and utilization must not only satisfy the requirements of a rigorous physical environment, but must simultaneously adjust to the impacts associated with herbivory. Our goals in this paper are to develop a quantitative understanding of the relationships be-

Seasonality of Forage Availability and Quality

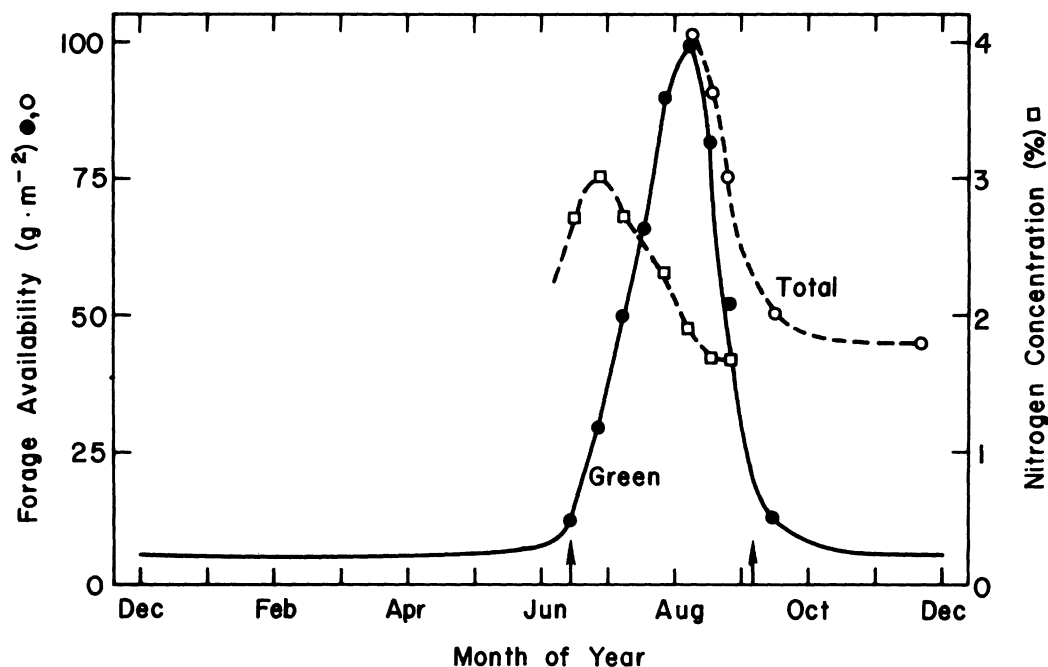


FIGURE 1. Seasonal trend in aboveground vascular plant material and nitrogen concentration in wet meadow vegetation at Barrow, Alaska, illustrating the limited availability of high quality (green) plant biomass and the displacement in time of peak biomass and peak nitrogen concentration (Tieszen, 1972; Chapin et al., 1975).

tween gross carbon and biomass allocation, leaf growth, and photosynthesis patterns in several tundra growth forms and to determine how these patterns are affected by grazing.

In a series of field experiments designed to document the physiological responses of tundra plants to simulated grazing we sought to test the general hypothesis that carbon allocation patterns, a function of life-form type, will dictate plant responses to defoliation that minimize impact on production and reproduction. For several species, photosynthetic rates, leaf longevities, and potential for re-

growth following herbivory were documented. We expected the long-term survival of an individual plant to be determined largely by its ability either to tolerate or to avoid damage, and we addressed the following specific hypotheses: (1) carbon allocation patterns are a function of growth form and dictate plant responses to defoliation; (2) maximum photosynthetic rates are a function of growth form and are inversely related to leaf longevity; (3) the impact of grazing is reduced in plant species with rapid leaf turnover and little supportive tissue; (4) defoliation results in an im-

TABLE 1
Photosynthetic capacities (mean \pm 1 SE) of species representing five arctic growth forms^a

Species	Photosynthetic capacity ^b (mg CO ₂ · g dry wt ⁻¹ · h ⁻¹)	
	Species average ^c	Growth form average
Single-shooted Graminoids		39.3
1. <i>Arctagrostis latifolia</i>	47 \pm 7	
2. <i>Carex aquatilis</i> ^d	34 \pm 3	
3. <i>Carex bigelowii</i>	37 \pm 2	
Tussock-forming Graminoid		27.0
1. <i>Eriophorum vaginatum</i> ^d	27 \pm 2	
Forbs		21.7
1. <i>Petasites frigidus</i>	21 \pm 2	
2. <i>Polygonum viviparum</i>	29 \pm 3	
3. <i>Rubus chamaemorus</i>	15 \pm 1	
Deciduous Shrubs		38.5
1. <i>Betula nana</i>	37 \pm 4	
2. <i>Salix pulchra</i> ^d	40 \pm 3	
Evergreen Shrubs		9.0
1. <i>Cassiope tetragona</i>		
Current leaves	9 \pm 1	
Noncurrent leaves	10 \pm 1	
2. <i>Dryas integrifolia</i>		
Current leaves	10 \pm 1	
3. <i>Ledum palustre</i> ssp. <i>decumbens</i> ^d		
Current leaves	10 \pm 1	
1-yr-old leaves	18 \pm 1	
2-yr-old leaves	17 \pm 1	
3-yr-old leaves	11 \pm 1	
4. <i>Vaccinium vitis-idaea</i>		
Current leaves	7 \pm 1	
1-yr-old leaves	5 \pm 1	
2-yr-old leaves	5 \pm 1	
3-yr-old leaves	5 \pm 1	

^aAdapted from Johnson and Tieszen (1976). Nomenclature follows Hultén (1968).

^bMeasured at 15°C, high humidity, and saturating light.

^cSpecies averages are the mean of 12 to 16 replicates, except *Arctagrostis*, *Petasites*, and *Polygonum* for which there were 6 replicates.

^dUsed for defoliation experiments.

mediate adjustment in carbon allocation patterns within the defoliated plant; and (5) carbon allocation to maintenance tissue or long-

lived productive tissue is accompanied by mechanisms that reduce grazing.

METHODS

Lack of time precluded detailed observation of several representatives of each vascular plant growth form, so we selected one important species from each of four growth forms found in tundra near the Meade River at Atkasook, Alaska, for our defoliation studies (Table 1). Two populations of *Salix pulchra*, the deciduous shrub, were apparent in the Meade River area. One consisted of erect shrubs about 1.2 m tall found along creek margins. The other *Salix* population was prostrate, 20 to 30 cm tall, and was a codominant in *Carex aquatilis*-*Salix pulchra*-*Sphagnum* spp. communities. This latter population was used in our studies. *Carex* populations were examined in nearly pure stands of *Carex* tillers lightly interspersed with *Salix* and located in a moist lake margin. *Eriophorum* and *Ledum* experiments were conducted on high-center polygons at a site interlaced with a mosaic of polygon centers, rims, and wet troughs. *Rubus chamaemorus*, *Carex bigelowii*, and *Vaccinium vitis-idaea* also grew on the polygon centers. For a more complete description of community types see Komárková and Webber (1980, this volume).

In our defoliation studies plant parts were artificially clipped in an attempt to simulate an actual grazing event, because the amount of herbage removed from plants could be quantified, controlled, and held constant over time and between treatments. Plant responses could then be correlated to known frequencies, intensities, and types of defoliations. It is important, however, to acknowledge that some major differences do exist between clipping and actual grazing, and these should be considered when extrapolating results from defoliation experiments to actual grazing systems (White, 1973). For example: (1) Grazing may be more detrimental than clipping if it removes herbage from some plants and not others; unclipped plants may compete advantageously with clipped plants for resources. (2) Grazing may be less detrimental to plant vigor than clipping if some tillers of a rhizome system are left intact and ungrazed, thus allowing for a transfer of nutrients and energy from intact tillers to injured tillers. (3) Clipping

usually removes herbage at uniform heights and percentages while grazing usually results in herbage removal at various heights between plants and even within the same plant. (4) Herbivore preferences for particular plant parts, age classes of plants and phenological stages are difficult to simulate by clipping. (5) In defoliation experiments herbage is cleanly and uniformly removed while actual grazing and browsing typically involves ripping, shredding, tearing, or stripping of the vegetation. Damage resulting from trampling and soil compaction must also be considered. (6) There is evidence which suggests that the recovery of grazed plants is enhanced by the action of growth-promoting substances in the saliva deposited on the wounded plant tissue by insect and vertebrate herbivores (Reardon et al., 1974; Dyer and Bokhari, 1976; Reardon and Merrill, 1978).

All primary defoliation treatments involved the removal of all exposed photosynthetic tissue. In the graminoids, leaves were clipped back to moss level. In the *Eriophorum* treatments three tussocks that were defoliated early in the growing season were covered with opaque plastic (black bag) to prevent photosynthesis. When leaf production ceased, the tussocks were destructively sampled for the stem base and sheath components. The dry weight of these structures was assumed to represent the approximate minimum biomass necessary for tiller growth and maintenance (see Archer and Tieszen, submitted, a, b, for more details). For the shrubs two basic defoliation schemes were imposed: Type I defoliation involved the removal of all current year's production; Type II treatment involved the removal of 1- and 2-yr-old stems in addition to current year's production. For *Ledum*, the evergreen, old leaves were also removed in both treatments. Defoliations on all growth forms were imposed at periodic intervals throughout the growing season. Defoliation regimes initiated on 30 June were designated early spring treatments; those initiated on 15 July, 30 July, and 15 August were designated late spring, summer, and fall, respectively. For chronic treatments regrowth was removed

at 10-d intervals throughout the growing season. Recovery treatments refer to those plants that were chronically defoliated for one growing season and not defoliated at all the subsequent growing season.

Methodology used for determining photosynthetic rate, leaf longevities, and above-ground biomass allocation are given in Johnson and Tieszen (1976).

RESULTS AND DISCUSSION

LEAF GROWTH DYNAMICS AND BIOMASS ALLOCATION

The abruptness and brevity of the arctic growing season places severe restrictions on the timing of plant growth (Figure 1) and limits the amount of time during which even small amounts of high quality forage is available to most herbivores. The plants at Atkasook (70°28'N) have approximately 75 d to initiate current growth, expand and develop photosynthetic tissue, reproduce (either vegetatively or sexually), and translocate nutrients below ground prior to autumn die-back. Differences in seasonal leaf growth dynamics and biomass allocation patterns were observed in the different growth forms and reflect the various strategies employed by arctic plants to fix carbon in the short time allotted.

In the Arctic, graminoids are inactive beneath the winter snow (Tieszen, 1974), but begin to photosynthesize within a few days of melt-off (Tieszen, 1975). The seasonal progression of leaf area accumulation for each of the representative life forms are graphed in Figure 2. By 27 June, *Eriophorum* had exerted over 60% of its normal complement of photosynthetic tissue and *Carex*, the single-shooted graminoid, had exerted 26% of its leaf tissue. Neither shrub possessed current photosynthetic tissue at this point in the growing season. Thus graminoid tillers exploited the early portion of the growing season to a much greater extent than did either of the shrub life forms. This was especially noticeable for *Eriophorum* whose growth form enhances soil warming, decomposition rates, and nutrient availability within the individual tussock. Chapin et al. (1979) observed that *Eriophorum* tussocks became snow free sooner and that intratussock soils thawed faster, reached maximum summer temperature sooner, were 6 to 8°C warmer, and were more thermally stable than soils at comparable depths between tussocks.

In addition to differences in the seasonality of leaf production we noted large differences in patterns of leaf development. Buds on both shrub life forms did not begin expanding until

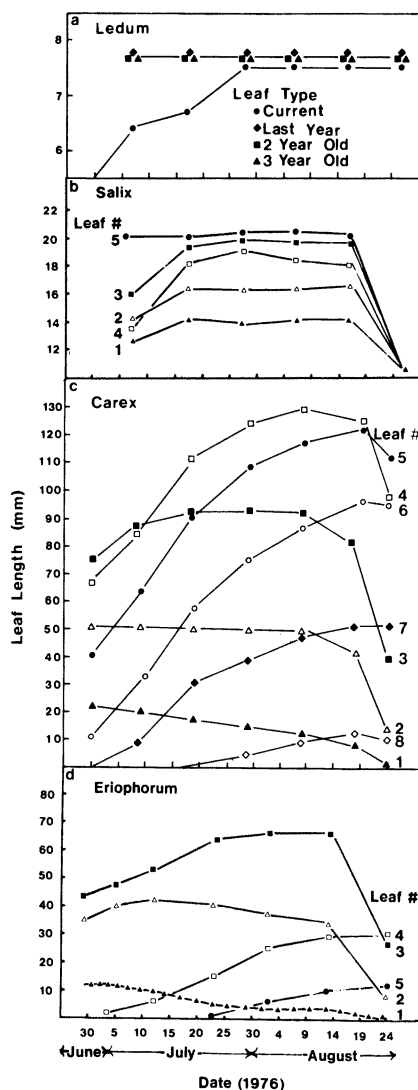


FIGURE 2. Seasonal progression of leaf exertion for each of the principal species in this study. Data were derived from direct growth measurements on marked individuals at Atkasook. Leaf length in each species was highly correlated with leaf area and biomass (Johnson and Tieszen, 1976, with permission of Springer-Verlag; Archer and Tieszen, unpublished).

late June. However, once expansion occurred leaves developed rapidly and concomitantly (Figure 2a, 2b) and by 17 July, within 20 d of emergence, all the leaves from *Salix* buds were fully expanded. The leaves on *Salix* plants typically had an extended maturation phase followed by an abrupt senescence phase. *Ledum*, the evergreen shrub, also exhibited this synchronous pattern of leaf growth. Newly initiated leaves did not, however, attain full development until nearer the end of the growing season. Estimates of leaf mortality suggest that 70% of the leaves initiated on *Ledum* die after two growing seasons and that over 96% die after four growing seasons (Johnson and Tieszen, 1976).

The sequential pattern of leaf exsertion of the graminoids (Figure 2c, 2d) contrasts with the synchronous growth and development of leaves in shrubs. Graminoid leaves exserted late in the growing season became quiescent, then resumed and completed growth the following season. Leaves of *Carex* and *Eriophorum* tillers typically had long growth phases, a short maturation phase, and an extended senescence phase. While both *Carex* and *Eriophorum* initiated some leaves much earlier in the growing season than *Salix* and *Ledum*, neither achieved maximum leaf area until 8 August, for while new leaves were growing, leaves initiated the previous growing season were senescing. Hence, the net increase in biomass was small. In contrast, *Salix* attained maximum leaf area by 17 July, some 20 d sooner than *Carex* and *Eriophorum* (Figure 2).

Allocation of biomass to aboveground tissue also differed markedly among life forms (Figure 3). In both the deciduous and evergreen shrubs 80 to 90% of current aboveground biomass (at peak season) accumulated in the leaf compartment and 10 to 15% accumulated in current stems. In *Eriophorum*, the tussock forming sedge, 96% of the aboveground biomass was contained in leaves. The remaining 4% was invested in reproductive structures. However, in our study area, less than 3% of the *E. vaginatum* tillers flowered (Archer and Tieszen, submitted, a). A given tiller may produce leaves for 3 to 4 yr after which time a terminal inflorescence may be initiated. The tiller then dies (Goodman and Perkins, 1968). *Carex* also allocated nearly 100% of its aboveground biomass to leaf tissue.

Finally, both shrub types committed large portions of biomass to supportive tissue (Fig-

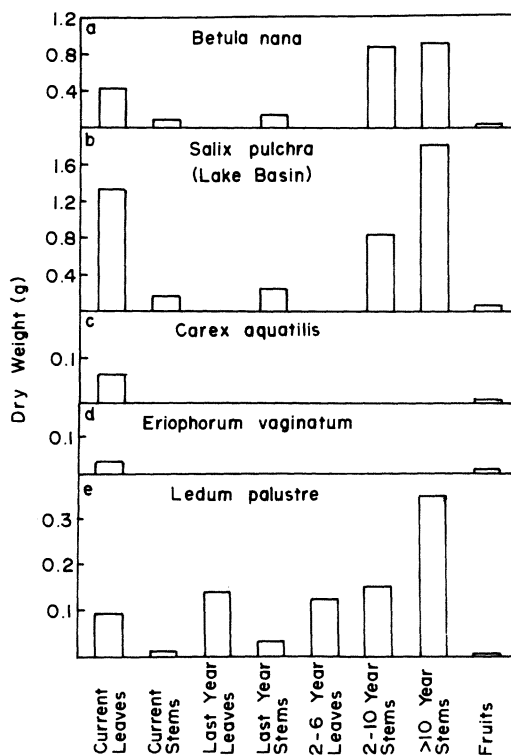


FIGURE 3. Biomass allocation (mean dry weight) for aboveground plant compartments for (a) *Betula nana*, (b) *Salix pulchra*, (c) *Carex aquatilis*, (d) *Eriophorum vaginatum*, and (e) *Ledum palustre*. Average compartment allocations were estimated from a sample of 40 aboveground individuals for *Betula*, *Salix*, and *Ledum* and 50 tillers for *Carex* and *Eriophorum*. Determinations were obtained near peak biomass (21 to 26 July) (Johnson and Tieszen, 1976, with permission of Springer-Verlag; Archer and Tieszen, unpublished).

ure 3). Nearly 84% of the total nonreproductive, aboveground biomass in *Salix* was devoted to stems as compared to 75% in *Ledum*. Neither *Carex* nor *Eriophorum* had any non-photosynthetic tissue to support or maintain.

CARBON ASSIMILATION

Differences in the photosynthetic rates and leaf longevities for representatives of each life form also illustrated different growth strategies. Photosynthetic rates ranged from 5 to 47 mg CO₂ · g dry wt⁻¹ · h⁻¹ for 13 species representing five growth forms (Table 1). Photosynthetic capacities were relatively consistent within a growth form, with deciduous shrubs and single-shooted graminoids generally hav-

TABLE 2
Average duration of different growth phases of leaves of arctic tundra species
as estimated from seasonal progression of dry weight of leaves^a

Species	Length of interval (growing season days)				Leaf longevity	Photosynthetic capacity (mg CO ₂ · g dry wt · h ⁻¹)
	Previous seasons	Current season				
		Growth	Maturation	Senescence		
Graminoids						
<i>Carex aquatilis</i> ^b	25	17	26	17	85	34 ± 3
<i>Eriophorum vaginatum</i>	27	29	24	15	95	27 ± 2
Deciduous shrubs						
<i>Salix pulchra</i>		18	34	12	64	40 ± 3
<i>Betula nana</i>		17	33	11	61	37 ± 4
Evergreen shrubs						
<i>Ledum palustre</i>						
ssp. <i>decumbens</i>	120 ^c		80		200	14 ± 1
<i>Vaccinium vitis-idaea</i>	280 ^c		80		360	6 ± 1

^aFrom Johnson and Tieszen (1976).

^bGrowth data from Tieszen (unpublished).

^cEstimates from leaf mortality data for average leaf.

ing the highest photosynthetic rates, followed by tussock-forming graminoids, forbs, and evergreen shrubs. The high photosynthetic rates observed in deciduous shrubs were, however, offset by relatively short leaf longevities (Table 2). Conversely, the low photosynthetic capacities observed in evergreen shrubs were associated with extended leaf longevities. Presumably evergreen leaves must be retained for more than one growing season in order to provide a positive carbon contribution to the plant. Apparently leaves with high photosynthetic capacity contribute positively to the carbon budget of the plant in only one season. The graminoid growth forms in Table 2 had intermediate photosynthetic rates and also exhibited intermediate leaf longevities.

Thus it appears that among our tundra species photosynthetic capacity is inversely related to leaf longevity. As a result, even though photosynthetic capacity and leaf longevity patterns differed markedly between growth forms, net carbon gain, when considered over the lifespan of a leaf, may be quite similar for these tundra species. *Salix*, with its high photosynthetic rate and synchronous leaf growth exploited the smallest, but most favorable, portion of the arctic growing season. *Ledum*, on the other hand, compensated for its low photosynthetic capacity by exploiting the entire growing season and by

using a leaf for up to three seasons after its exertion (Johnson and Tieszen, 1976). *Carex* and *Eriophorum*, each with photosynthetic rates and leaf longevities intermediate to the deciduous and evergreen shrubs, initiated growth earlier in the growing season and exploited an intermediate proportion of the growing season. This interaction between photosynthetic rates and leaf longevities can even be seen within graminoid growth forms. The fact that *Eriophorum* had exerted over 60% of its current growth biomass by 28 June as compared to only 26% in *Carex* (Figure 2) suggests that the early season growth in *Eriophorum* enables it to compensate for its photosynthetic capacity, which was 20% lower than that of *Carex* (Table 2). Similarly, *Vaccinium*, which had a photosynthetic rate less than half that of *Ledum*, had an average leaf longevity nearly twice as long.

LEAF REPLACEMENT FOLLOWING DEFOLIATION

Recovery from a defoliation event depends upon the reestablishment of a photosynthetic surface. The potential for leaf replacement of a given plant species is a function of and dependent upon the type of leaf-producing unit the plant has evolved. Each *Salix* and *Ledum* shrub was composed of woody stems and leaders that supported many leaf-producing buds. Each *Eriophorum* tussock and *Carex* stand

was composed of one or more rhizome systems that gave rise to leaf-producing tillers.

Shrubs

Buds on *Salix* and *Ledum* bushes were initiated in late June from predictable locations on their stems. By diagrammatically mapping a stem with its associated leaders we recorded the positions of leaf groups and dormant buds. In *Salix* 96% of the buds producing leaf tissue were located on 1-yr-old stems, 3% were initiated from 2-yr-old stems, and about 1% from 3-yr-old stems. The average *Salix* plant, considered in its entirety, initiated growth in less than 20% of its visible buds (an individual plant is defined as all aboveground biomass issuing from a stem which goes below ground). The potential, then, for a defoliated shrub to replace photosynthetic tissue lost to herbivores is great, since a large number of leaf-producing units are available.

For a shrub to replace photosynthetic tissue following a grazing event, however, the mechanism or mechanisms regulating apical dominance of a given stem or leader must be overcome. Bud initiation in *Salix* and *Ledum* was synchronous rather than periodic or sequential. Undisturbed shrubs initiated buds in late June and all buds on the plant producing current stem and leaf tissue had done so by early July. Removing leaf tissue, while leaving stems and buds intact (a simulation of leaf-chewing by some insects and rodents) did not alter this pattern. That is, no additional buds were activated to replace the leaf tissue lost by this type of defoliation. When the terminal 1- and 2-yr-old stems were removed along with current growth, apical dominance of the leader was overcome and buds lower on the stem were activated. Leaf replacement was highly variable, and a minimum of 14 to 21 d usually elapsed before leaf replacement was initiated. Because of the lag time, shrubs defoliated in mid- to late July regenerated photosynthetic tissue too late to recoup the energy investment before the end of the season.

The release of growth of lateral buds was complicated and may have been dependent on environmental history, past growth performance, or nutrient reserves. For example, our defoliation treatments resulted in extensive lateral bud growth in a cool and moist year but did not in a subsequent warmer and drier year. Thus it appears that the release of lateral buds in these shrubs may respond more to

temperature and moisture than to day length or light intensity. Such observations are consistent with those of Laude et al. (1961) and Plumb (1961, 1963). Tinklin and Schwabe (1970), however, found that in *Ribes* shoot tip removal early in the growing season, while new shoots were still elongating, resulted in the outgrowth of several lateral buds. Later in the season, removal of the shoot tips became less and less effective as a means of inducing bud break.

Buds on woody plants may be classified as terminal, axillary, or adventitious (see Berg and Plumb, 1972). Each of these may in turn be classified as short- or long-shoot buds. Long-shoot buds give rise to long shoots whose leaves are separated by distinct internodes and bear lateral buds, some of which develop into more long shoots while others produce short shoots. Internode elongation is essentially lacking in short shoots, and lateral buds on short shoots are either lacking or develop into flowers (Dahl and Hyder, 1977). Terminal buds in *Salix* and *Ledum* were of the long shoot type and were responsible for 96 and 90%, respectively, of the subsequent season's leaf production. Axillary buds were formed at the base of the leaf petiole soon after each leaf expanded. Typically, in *Salix*, five to six leaves were produced per bud initiated (Johnson and Tieszen, 1976; Archer and Tieszen, unpublished); hence five to six axillary buds were generated. On the average about 40% of these axillary buds (typically the two or three most distal on the stem) developed into leaf and stem primordia in the subsequent growing season. The remaining axillary buds retained their position outside the cambium during secondary growth and either remained as visible lateral buds or became buried in the bark (as described by Church and Goodman, 1966, for *Acer*). Those lateral buds buried in the bark have been termed suppressed buds (Kormanik and Brown, 1969) and are apparent only after an anatomical examination of the stem. Adventitious buds, on the other hand, form irregularly in the cambium of older plant parts rather than in leaf axils near an apical meristem (Kozlowski, 1971). All of these bud types played an important, and quite different, role in the resprouting of *Salix* and *Ledum* following defoliation.

Two defoliation treatments, one involving removal of current growth only and the other

involving removal of all biomass back to 3-yr-old stems, elicited quite similar morphological responses in the two life forms. In both *Salix* and *Ledum* lateral buds were released from dormancy following defoliation and new shoot growth was initiated, but only after a highly variable lag time. In both life forms the activated lateral buds were predominantly the short-shoot types. Those few that were of the long-shoot type were weak, and survivorship of the new shoots with next year's potential leaf groups was quite low. Leaves associated with the activated buds were typically small with a much reduced mass and surface area.

In *Salix* the lateral buds most often activated following defoliation were those positioned nearest the point of defoliation. Thus, when only current growth was removed, the lateral buds activated were those on 1- and 2-yr-old stems; when growth was removed back to 3-yr-old stems, the lateral buds on the 3- and 4-yr-old stems were most often activated. *Ledum*, in contrast to *Salix*, initiated nearly 50% of its new shoots from main-stem tissue (stems greater than approximately 5 to 7 yr old) regardless of the type of defoliation treatment. As with *Salix* nearly all new shoots were the short-shoot variety.

While removal of plant parts up to 2 yr old led to the activation of mainly short-shoot, lateral buds, the removal of tissue back to 5- to 7-yr-old stems resulted in the activation of suppressed lateral buds and/or adventitious buds which were buried in the cambium. It is known that stump sprouts may arise from either suppressed lateral buds or adventitious buds (Zimmerman and Brown, 1971). Root sprouts, on the other hand, appear to always arise from adventitious buds (Kozlowski, 1971). While anatomical differences do exist between adventitious and suppressed buds (Dahl and Hyder, 1977), we did not distinguish between them for sprouts arising from the basal portions of defoliated plants. In *Ledum* these activated buds were the short-shoot variety. *Salix*, however, responded by initiating long shoots as well as short shoots. Although we have no quantitative data, our field observations indicate that these basal, long-shoot buds produced current leaf, and especially stem, tissue far in excess of the growth observed in terminal long shoots under normal conditions for one season. The vigorous stems arising from the suppressed buds contained axillary buds, which were both

the long and short shoot variety. Our observations on *Salix pulchra* are similar to those made by Wilson (1970) on other shrub species.

The minimum damage to the plant needed to stimulate these highly productive, long-shoot buds appears to be greater than that imposed by typical browsing activities. Vigorous long shoots may be produced in response to trampling, especially during the winter and early spring when stems are stiff and brittle.

In general *Salix* can readily transform short-shoot buds into long-shoot status when long shoots are removed (Dahl and Hyder, 1977), but this was not a strong tendency in *Salix pulchra* at Atkasook. Most buds activated after long-shoot removal were the short-shoot type; the long-shoot type were weak and generally winter-killed.

The production of short shoots following defoliation (especially late-season defoliation) may be advantageous because they can complete elongation in half the time required by a long shoot (Kozlowski, 1971). This rapid elongation of a short shoot may enable the shrub to exploit a longer portion of the remaining growing season while requiring less carbohydrate and nutrient investment than a long shoot. In addition, Zimmerman and Brown (1971) have shown that downward translocation of photosynthate in many woody plants occurs only after shoot elongation has been completed. Although we have no data regarding root responses to top removal in shrubs, it is possible that the preferential growth of short shoots, with their more rapid completion of elongation, facilitated the reestablishment of a critical root-to-shoot ratio needed to maintain root respiration and nutrient uptake.

Graminoids

Graminoid tillers exerted leaves sequentially and at staggered intervals over the course of the growing season. Leaves grew from the base of the tiller and telescoped upwards until mature (see Youngner, 1972). By exposing less than 100% of the leaf tissue produced throughout the growing season, a smaller investment of nutrients and energy is vulnerable to loss by grazing at any one time. Following defoliation, leaf replacement can be rapid. In fact CO₂ studies in the laboratory with other arctic graminoids indicate that within 3 d of defoliation sufficient leaf area can be restored so that net photosynthesis for

an entire tiller becomes positive (Kingston and Tieszen, unpublished). These observations are similar to those made on temperate, pasture species (Ward and Blaser, 1961; Davidson and Milthorpe, 1965, 1966a, 1966b; Smith, 1975). Whereas removal of or damage to the apical meristematic tissue in graminoids normally results in a cessation of leaf production and death of at least the aboveground portions of a tiller (Hyder, 1972), this was seldom a problem with *Carex* and *Eriophorum* tillers. Because their apical meristems are typically positioned 10 to 15 mm below a layer of moss and soil, these graminoids usually avoid such injuries. The culmless growth habits of each of these sedges insures that, unless they are flowering, the apical meristems will not be elevated above the moss level. Only in years of extreme lemming population densities or heavy trampling by caribou or musk-oxen will the moss and soil cover be sufficiently disturbed to expose the growing points. This strategic location of the growing point, in conjunction with the sequential pattern of leaf exsertion, enables

vegetative *Carex* and *Eriophorum* tillers to continue to produce leaf tissue regardless of the time of season of defoliation.

In summary, the efficiency of the replacement of photosynthetic tissue following a grazing event is ultimately a function of (1) the type of leaf producing unit the plant has evolved and (2) the type of defoliation event, i.e., whether or not the apical meristem is damaged. Leaf replacement is further governed by the frequency, intensity, and timing of the defoliation events and by those abiotic factors that govern growth processes.

SHRUB RESPONSES TO DEFOLIATION

There are several options open to a defoliated shrub with regard to the reestablishment of a new photosynthetic surface: (1) activate a "normal" complement of buds which yield a normal leaf area or biomass, (2) activate more buds than normal with fewer leaves or less leaf tissue per bud, (3) activate fewer buds than normal with more and/or larger leaves per bud, (4) invest less in current stem production and proportionately more in leaf

TABLE 3
Location of new growth (% of activated buds) on Salix pulchra plants following defoliation in early July

Type of defoliation	Stem age						Percentage of plants initiating regrowth
	1 yr	2 yr	3 yr	4 yr	5 yr	> 5 yr	
Type I ^a	57	23	20	0	0	0	60
Type II ^b			43	33	14	10	83
Control (not defoliated)	96	3.3	0.4	0	0	0	

^aRemoval of current leaves and stems on 20 plants.

^bRemoval of current growth plus 1- and 2-yr-old stems on 20 plants.

TABLE 4
Mean (± 1 SE) responses of Salix pulchra following defoliation in early July 1976

Treatment	% buds initiated	Current growth biomass (mg dry wt per leaf group)		
		1976	1977	
		August	June	August
Control	18 (± 1.1) ^a	54.0 (± 0.9) ^a	18.5 (± 0.3) ^a	72.4 (± 2.1) ^a
Type I	13 (± 1.8) ^b	7.2 (± 1.6) ^b	12.6 (± 0.4) ^b	61.0 (± 1.6) ^b
Type II	10 (± 2.9) ^b	5.8 (± 1.1) ^b	11.9 (± 0.2) ^b	59.8 (± 1.4) ^b

^{a,b}Different superscripts indicate significantly different means among treatments in each column (*t*-tests, $p < 0.05$). About 20 plants in each treatment.

production or, in the case of a partially defoliated plant, (5) increase the photosynthetic efficiency and/or extend the longevity of remaining leaves.

Replacement of leaf biomass following defoliation was highly variable in *Salix* and appeared to be greatly influenced by environmental factors. In preliminary experiments concluded in 1976, *Salix* plants recovered 92 and 64% of their current-growth biomass in Type I and Type II treatments (see Methods), respectively. However, in similar treatments at similar points in the growing season in 1977, Type I and Type II defoliated plants recovered only 40 and 20% of their current-growth biomass, respectively. Weather patterns of the two seasons were quite different, the 1976 season being cool and moist and the 1977 season being warmer and drier (Haugen and Brown, 1980, this volume). The ensuing discussion will deal primarily with growth responses from the 1977 growing season for which there is a more substantial and detailed data base.

Defoliated *Salix* plants, regardless of time of season, reinitiated growth from terminal positions on the remaining stems. Following a Type I defoliation in early July, 57% of the buds initiated arose from positions on 1-yr-old stems; 23 and 20% arose from 2- and 3-yr-old stems, respectively. No buds developed on older stem tissue. Forty percent of the plants examined did not initiate any leaf production after defoliation. Following a Type II defoliation 43% of the buds initiated were on 3-yr-old stems; 33 and 14% arose from 4- and 5-yr-old stems, respectively; 10% arose from older stems. Approximately 17% of the Type II plants did not break bud following defoliation (Table 3).

Although the replacement of leaf biomass in *Salix* was highly variable between plants within a treatment and between treatments, some significant differences and trends were noted. Plants subjected to Type I and II defoliations responded similarly (Table 4). In both defoliation treatments a slightly lower percentage of buds initiated growth relative to control plants, and the leaf biomass per bud initiated was substantially lower than that of controls.

Leaf initiation was delayed the following spring in treated plants by up to 20 d (Figure 4). All buds on control plants that were to initiate growth had done so by 17 July. In con-

trast, plants defoliated the previous growing season did not complete leaf initiation until 6 August. The number of leaf groups per plant was comparable in control and defoliated shrubs, but the current growth per plant throughout the growing season was significantly lower in treated plants due to the reduced weight of each leaf group (Table 4). The mean number of leaves produced per bud was 5.0 in both control and recovery plants. However, current stem length decreased from 8.9 mm in controls to 4.1 mm in recovery plants, a reduction of 54%.

In Type I treatments 55% of the 1-yr-old stems died completely, as did the terminal half of an additional 24%. Forty percent of the 2-yr-old stems died completely along with the terminal portions of the remaining 60%. Nineteen percent of the 3-yr-old stems died along with the terminal half of an additional 10%. In nearly every case leaders died back to the location of the first visible bud. In 40% of the leaders this resulted in death back to 3rd yr stems and in 19% to 4th yr stems.

Leaf production the following season was reduced by 47 to 72% in defoliated plants (Table 5). With the exception of the 15 June defoliation there was no difference in leaf production between Type I and Type II defoliation treatments. Generally, those plants defoliated on or after 15 July produced slightly more current-growth biomass the subsequent season than plants defoliated on or before 30 June.

Ledum palustre ssp. *decumbens*, the evergreen shrub, responded even more dramatically to defoliation (Table 6), recovering 10% or less of its current-growth biomass. Plants sub-

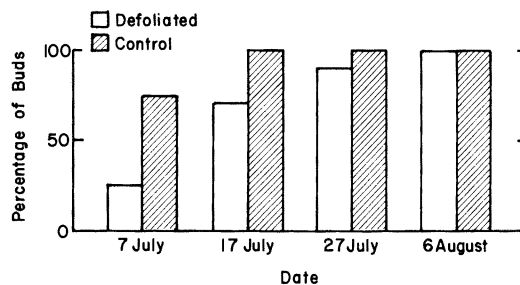


FIGURE 4. Seasonal course of leaf initiation in *Salix pulchra* control plants (untreated) and plants defoliated the previous growing season. Percentage is based on the total number of buds producing leaves by the end of the growing season in 20 plants.

jected to the Type II defoliation produced slightly, but significantly, more leaf biomass than those experiencing a Type I defoliation. In both Type I and Type II treatments, the greatest impacts occurred on plants defoliated prior to 1 July. More than 48% of the leaf groups initiated following defoliation were from buds on the main stem in a Type I defoliation, as compared to 30% in a Type II defoliation, and 11% on undefoliated plants. After the second recovery season this percentage increased to 82 in Type I plants, one plant of the 20 had died, and leaf production in surviving plants remained substantially below that of controls (Table 6).

For *Ledum* the contribution of older leaves to plant growth following defoliation must also be considered. Hadley and Bliss (1964) found that in several ericaceous species, leaves produced in previous growing seasons had negative net photosynthetic rates, and they concluded that old leaves were more important as storage units than as photosynthetic units. However, subsequent work by Johansson and Linder (1975) and Johnson and Tieszen (1976) has shown positive photosynthetic rates in older leaves of several ericaceous species. These positive photosynthetic rates suggest that old leaves may be important in carbon assimilation. Whatever their function, leaves produced in previous years on *Ledum* shrubs were important for the exertion and growth of current leaves and stems. When old leaves were removed and terminal buds left intact, development of that year's activated buds was delayed, and the biomass of the current season's leaves was reduced by 60%. These observations on *Ledum palustre* ssp. *decumbens* agree with those made by Reader (1978) on *L. palustre* ssp. *groenlandicum* in Canada. The loss of old leaves by defoliation altered not only the carbon balance of the plant, by decreasing net carbon assimilation, but also the ability of

TABLE 5
The effect of time of defoliation on mean (± 1 SE) leaf biomass produced the following season for *Salix pulchra*

Date of defoliations (1976)	Dry weight (mg) per leaf group (early July 1977)	
	Type I	Type II
15 June	5.1 (± 0.5) ^a	8.8 (± 1.1) ^{a,b}
30 June	7.2 (± 0.2) ^b	7.2 (± 0.2) ^a
15 July	9.4 (± 0.6) ^c	9.4 (± 0.4) ^b
20 July	8.8 (± 0.3) ^c	9.5 (± 0.3) ^b
15 August	8.6 (± 0.4) ^c	9.9 (± 0.4) ^b
Controls	18.5 (± 0.3) ^d	18.5 (± 0.3) ^c

^{a,b,c,d}Different superscripts indicate significantly different means among treatments in each column (*t*-tests, $p < 0.05$). About 20 plants in each treatment.

Ledum to conserve and cycle nutrients (Thomas and Grigal, 1976; Reader, 1978).

In summary, it appears that none of the hypothesized options for reduction of damage that were listed earlier were employed by arctic shrubs. Generally, a lower percentage of buds was initiated following defoliation. Further, the initiation of these buds was delayed, and the biomass produced from them was substantially lower than that of control plants. Although fewer resources were invested in current stem production there was no apparent or obvious reallocation to leaves. The number of leaves per leaf group remained unchanged following defoliation, and while photosynthetic rates of remaining or replacement leaves were not monitored, no extended rejuvenation or postponement of senescence was observed. Thus both shrub life forms were substantially damaged by defoliation. The effect on carbon balance would be differ-

TABLE 6
Mean (± 1 SE) biomass of current growth in *Ledum palustre* ssp. *decumbens* after one and two seasons of recovery from defoliation

Seasons after initial defoliation (dates measured) ^a	Dry weight (mg) per leaf group		
	Type I	Type II	Controls
One (late August 1976)	2.0 (± 0.2)	3.1 (± 0.5)	31.9 (± 4.2)
Two (late August 1977)	3.2 (± 0.6)		

^aPlants defoliated in early July 1976. About 20 plants in each treatment.

ent for each growth form since their patterns of CO₂ uptake differ (Johnson and Tieszen, 1976; Tieszen et al., in press). Clipping of dwarf evergreen shrubs was most harmful because of their slow replacement of leaves. Although our data did not reflect any strong seasonal trends, Reader (1978) found that for *Ledum palustre* ssp. *groenlandicum* and *Kalmia polifolia* effects were reduced by postponing defoliation treatments from the end of the leaves' first growing season to the middle of their second growing season. Grazing of *Salix* leaves may be especially damaging during early and mid-season because leaf production is synchronized and because new sets of leaves are produced too late in the season to pay for their investment. Birch (*Betula pubescens*), another common arctic deciduous shrub, apparently responds similarly to defoliation and its ability to survive seems to depend upon large reserves gathered during warm years (Kallio and Lehtonen, 1975). While we have no data on root and stem growth, it is likely that defoliation also affects these growth parameters adversely (Kramer and Wetmore, 1943; O'Neil, 1962; Kulman, 1971). Our data indicate, then, that these species are highly intolerant of grazing, especially in the short arctic growing seasons.

GRAMINOID RESPONSES TO DEFOLIATION

Grazing experiments at Barrow, Alaska (Mattheis et al., 1976), showed clearly that *Dupontia fisheri*, a single-shooted arctic graminoid, was quite tolerant of chronic grazing pressure. Its high degree of tolerance resulted from two related factors: (1) an interdependence between tillers which resulted in a flow of nutrients and photosynthate from intact tillers to defoliated tillers via rhizomatous connections and (2) high concentrations and large standing crops of total nonstructural carbohydrates (TNC) which buffer the plant against acute and chronic defoliation (see White, 1973; Trlica and Singh, 1979). In an extension of these preliminary studies we followed leaf growth and tiller biomass following defoliation in *Eriophorum vaginatum* and *Carex aquatilis*. We will summarize here our understanding of *Eriophorum*, the tussock-forming cottongrass of the Arctic.

Figure 5 depicts the general tussock and tiller pattern characteristic of *E. vaginatum*. Although rhizomes are very short, thereby accounting for the tussock form, its basic ana-

tomical configuration is similar to that of other graminoids. A single defoliation, removing leaves to moss level, stimulated leaf production in *Eriophorum* during the season of clipping (Figure 6). Changes in dry weights of tiller components, indicating an expenditure of TNC reserves (Hickman and Pitelka, 1975) suggest that *Eriophorum* relied primarily upon the sheath component for regrowth during the first 10 d following leaf removal. Thereafter, reserves from stem bases were mobilized to supplement sheath reserves (Figure 6). Dry weight losses of nonleaf plant parts reached a maximum at 20 d following defoliation. Storage structures then began to reaccumulate weight, indicating that sufficient leaf tissue had been exerted to establish a positive carbon balance.

Others have also found that light grazing can stimulate production of leaves (McNaughton, 1976). The increased production noted in our experiments could be attributed to canopy effects, for the photosynthetic rates of expanding leaves can increase if the light intensity reaching those leaves increases (Woledge, 1977). Also, a simulation model of physical processes affecting primary production in tundra (Miller and Tieszen, 1972) predicted that periodic reduction of standing dead shoots by grazers would increase plant production.

The accelerated growth of leaf tissue following defoliation (Figure 6) can be attributed to a delayed senescence of older leaves (Archer and Tieszen, submitted, b). Such a strategy would be important in the recovery of lost assimilate following grazing, especially if the decline in photosynthetic rate commonly associated with leaf aging (Leopold, 1961; Jewiss and Woledge, 1967; Ludlow and Wilson, 1971) were delayed or postponed. In other plants defoliation has been shown to prevent the normal decline in photosynthesis associated with leaf age (Maggs, 1964; Hopkinson, 1966; Gifford and Marshall, 1973) and to rejuvenate photosynthesis in senescing leaves to rates comparable to those of recently expanded new leaves (Woolhouse, 1967; Hodgkinson et al., 1972; Hodgkinson, 1974). The preferential growth and maintenance of older leaves might benefit the damaged tiller in several ways: (1) Rejuvenation of old leaves may be more economical than biosynthesis of new leaf material. (2) Maintenance of older, perhaps less palatable leaves, may enable the plant to avoid

and/or minimize the impact of future grazing episodes (Kamstra et al., 1968; Smith and Neales, 1977). (3) Older leaves appear to be the primary source of assimilates for below-ground structures such as roots (Williams, 1964; Wardlaw, 1968) and as such may be instrumental in overcoming the suppression of root extension and nutrient uptake observed in most defoliation studies (Evans, 1972; Bokhari, 1977). (4) Fully expanded leaves have been shown to serve as reservoirs of labile nu-

trients that are important in growth and expansion of younger leaves, especially when nutrient levels are low (Davidson and Milthorpe, 1966a).

Cessation of root growth and substantial decreases in root respiration and nutrient uptake rates following defoliation have been demonstrated in several glasshouse studies (Jameson, 1963; Davidson and Milthorpe, 1966b; Evans, 1972; Bokhari, 1977) and have been interpreted as a consequence of a shift in allo-

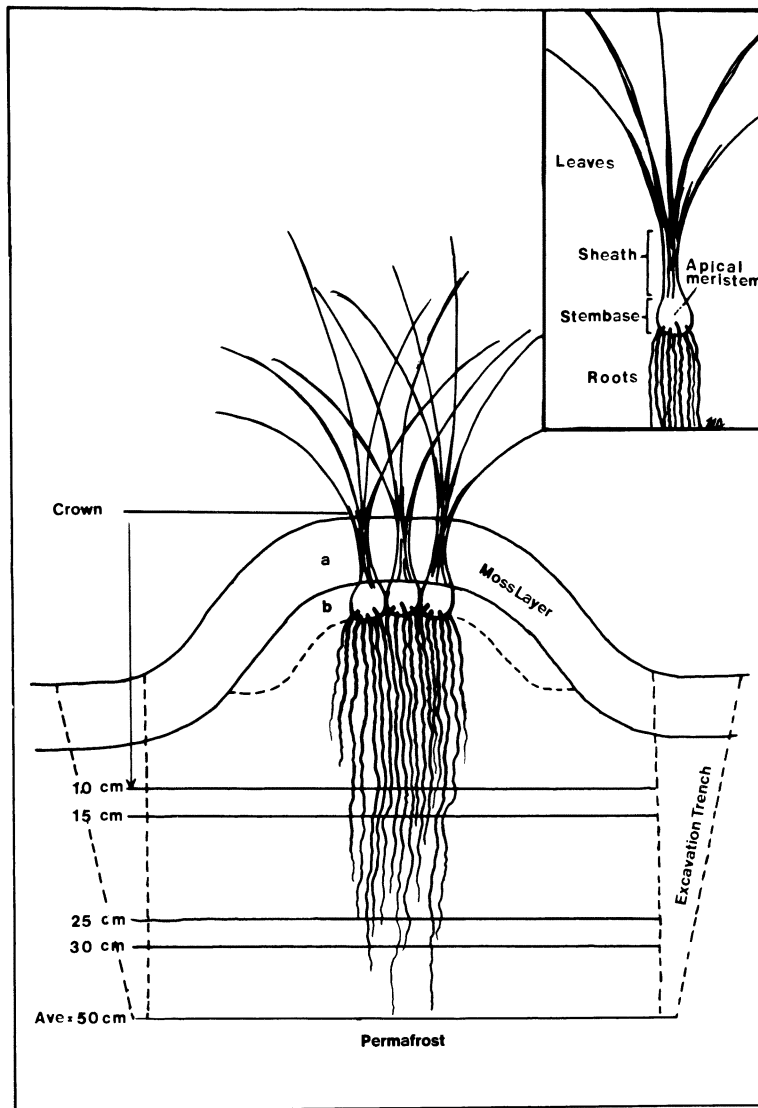


FIGURE 5. Diagrammatic representation of an *Eriophorum vaginatum* tussock and tillers. Apical meristems were protected by a moss layer 8 to 15 mm thick (a). Stem bases formed a nearly continuous layer at the moss-mineral soil interface (b). Depths indicate the regions where numbers of roots were estimated.

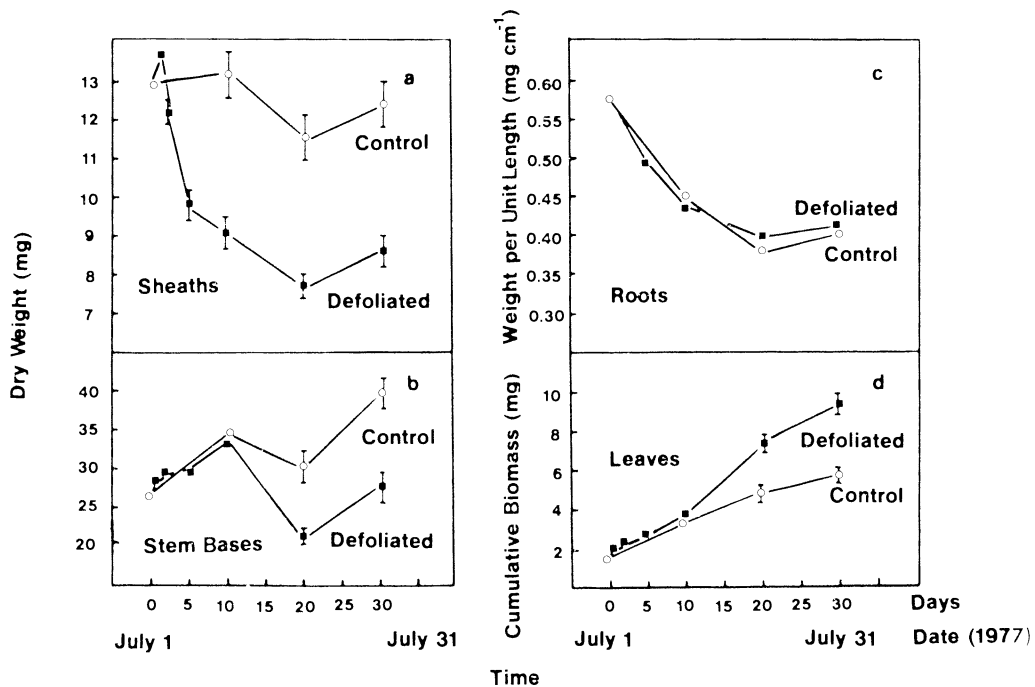


FIGURE 6. Short-term changes in mean ± 1 SE dry weights of stem base, sheath, and leaf compartments and weight per unit length of roots of *Eriophorum* following clipping on 1 July ($N = 80$ for sheaths and stem bases; $N = 50$ for roots; $N = 20$ for leaves).

TABLE 7
Summary of growth form characteristics related to herbivory

Growth form	Photosynthetic rate	Leaf longevity	Probability of being eaten ^a	Principal herbivores	Ability to recover from defoliation	Amount of secondary compounds
Graminoid						
Single-shooted	High	Medium	High	Rodents and	High	Low
Tussock-forming	Medium	Medium	High	ungulates	High	Low
Deciduous Shrub	High	Short	Medium	Ungulates, insects, and rodents	Medium	Medium
Evergreen shrub	Low	Long	Low	None	Low	High
Forbs	Medium	Medium(?)	Medium	Rodents and insects	Medium(?)	Medium

^aProbability based on herbivore preferences.

cation of reserves to shoot growth and restoration of a favorable shoot-to-root ratio. Our results showed that weight per unit length remained the same in *Eriophorum* roots following a single defoliation. These results agree with

the findings of Chapin and Slack (1979) who also observed an increase in weight specific respiration and nutrient uptake in *Eriophorum* roots following top removal. Only after four defoliations, spaced at the 10-d intervals, did

nutrient uptake rates decrease to below control levels. This maintenance and stimulation of root activity is especially important in the Arctic where leaf growth following defoliation depletes nutrient reserves more than carbohydrate reserves (Chapin, 1977).

While the response of *Eriophorum* to a single defoliation was increased leaf production at the expense of belowground structures, multiple defoliation imposed at 10-d intervals for up to two growing seasons resulted in decreased leaf production, further weight loss in storage structures, and a curtailment of root growth. Leaf growth response during the first season of chronic defoliation was similar to that of a single defoliation. During the subsequent growing season, however, leaf length and weight were depressed markedly to 25 to 50% of control values (Figure 7), depending upon the date clipping was initiated. The decline in leaf production was accompanied by substantial weight losses in stem base and sheath components (Figure 8c,d) and a severe curtailment in root initiation and elongation (Figure 9). Overall weight losses continued

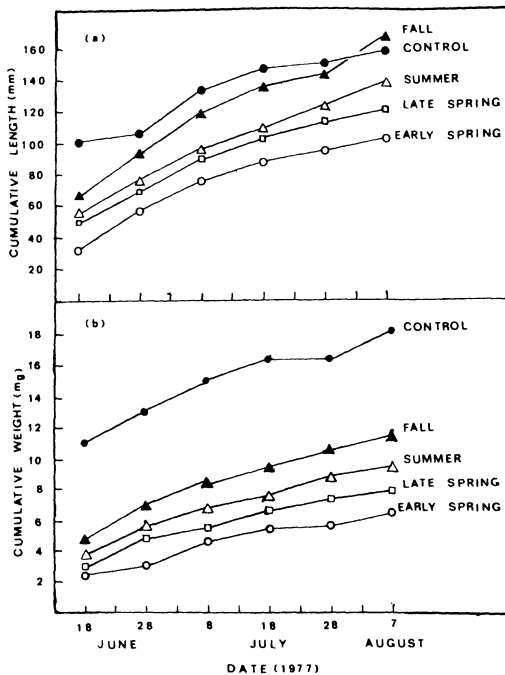


FIGURE 7. Effect of time of initiation of clipping on (a) cumulative leaf length and (b) cumulative leaf weight in *Eriophorum* during the second season of chronic clipping at 10-d intervals ($N = 20$).

until the stem base had lost some 75% of its normal weight in the most severe treatment (black bag). By this time the sheath had died and leaf production ceased. However, even

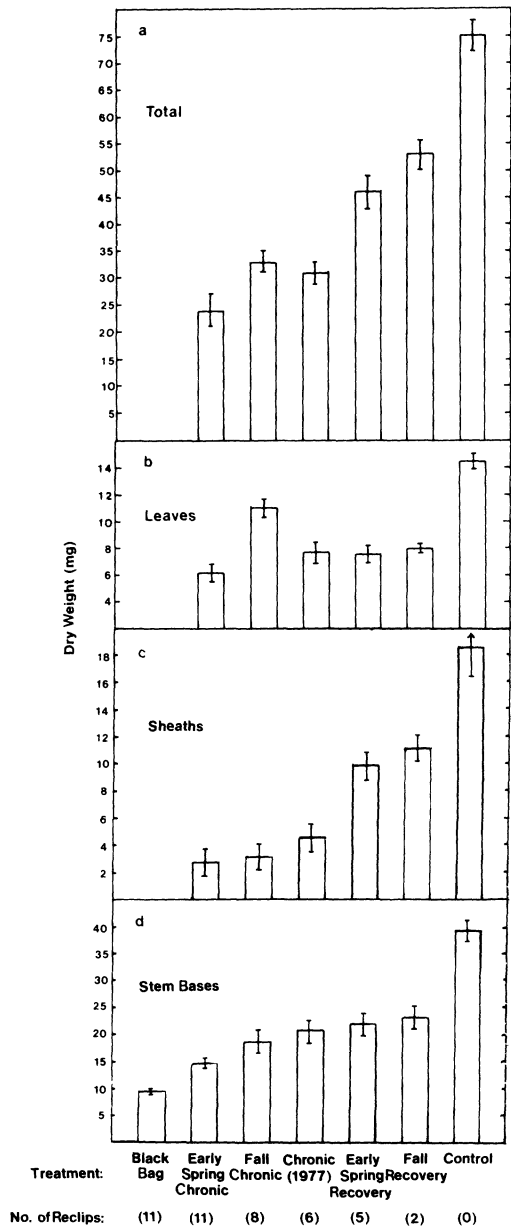


FIGURE 8. Mean biomass ± 1 SE of (a) total tiller (not including roots), (b) leaf, (c) sheath, and (d) stem base compartments of *Eriophorum vaginatum* following various experimental clipping treatments which extended through two growing seasons. See text for details. $N = 20$ for leaf compartment and 80 for sheath and stem base compartments.

after complete defoliation at 10-d intervals for two full growing seasons (11 reclaims) *Eriophorum* stem bases were still 34% above this minimum level. Tillers defoliated for one and one-half and one season were 46 and 52% above this minimum. Note, however, that one full season of recovery was insufficient to restore leaf growth to control levels (Figure 8).

Initiation of vegetatively produced daughter tillers was not significantly depressed by up to 2 yr of chronic defoliation. The weight of each daughter tiller produced was, however, reduced to 25% that of controls. Such low tiller biomass suggests that the success of vegetative reproduction following chronic defoliation might be quite low. Our results also suggest, that under extreme grazing pressure, populations of *E. vaginatum* may experience an indirect loss of sexual reproduction due to lowered plant vigor and a depletion of stored energy and nutrient reserves. In this regard Tikhomirov (1959) and Smirnov and Tokmakova (1971) observed that lemming grazing suppressed flowering in several arctic graminoids. Direct losses of reproductive tissue due to preferential grazing may also occur. Spetzman (1959) and Kelsall (1968) noted that *E. vaginatum* was utilized by caribou, especially during the flowering period (see also White and Trudell, 1980, this volume), and Pearsall (1950) mentioned that deer and sheep graze young flowering shoots of *Eriophorum*. In an environment such as the Arctic, where successful sexual reproduction is already limited, such losses may be significant.

Late-season defoliations appeared to be more detrimental to leaf production in subsequent seasons than did early-season defoliations. For example, the recovery from an early-season treatment was nearly that of the late-season treatment (Figure 8) despite the fact that the plants starting treatment in early spring were clipped five times and the plants

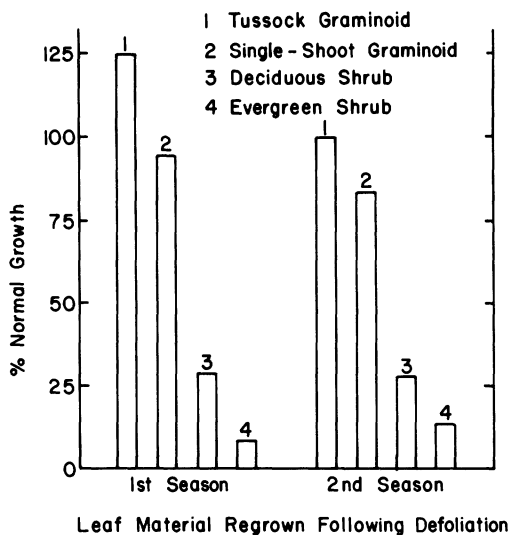


FIGURE 9. Effect of various clipping treatments on mean ± 1 SE (a) number of roots initiated and number of roots extending to depths of (b) 10 and (c) 25 cm in the soil beneath an *Eriophorum* tussock. See text for details. Four tussocks per treatment were excavated for the determinations at 10 and 25 cm; 40 tillers per treatment were examined for root initiation.

treated in the fall were only clipped twice. Late-season defoliations occurred at a time when arctic sun angles and ambient temperatures were decreasing and soil temperatures were at their highest. Decreased light intensity and air temperatures reduce photosynthesis, while higher soil temperatures simultaneously increase respiration of belowground structures. In conjunction with the loss of carbohydrates and nutrients removed with the leaves, which normally would be translocated belowground prior to dieback in the fall (Chapin et al., 1975), such circumstances may lead to tillers entering winter dormancy with reduced carbohydrate and nutrient levels.

COMPARISONS AND CONCLUSIONS

Our results generally support the hypotheses stated in the Introduction. Perhaps the best comparison of the response of different growth forms to defoliation is to compare the amount of leaf tissue produced by intact plants after a single, early season clipping (Figure 10). Leaf replacement was lowest in *Ledum*, the evergreen shrub; highest in *Eriophorum* and *Carex*, the perennial graminoids; and inter-

mediate in *Salix*, the deciduous shrub. The same trends held true for the subsequent season. Neither of the shrubs approached normal foliage production during the second recovery season. Poor replacement of photosynthetic tissue in *Salix* was due largely to a decreased investment in biomass per leaf group or bud rather than to a decrease in the number of buds initiating growth. Although this type of

data was not available for *Ledum*, observations suggested that here too, decreased production was the result of a decrease in biomass per leaf group more than a reduction in the number of leaf groups initiated. Leaf production in *Carex* was nearly normal during the first season (93%) and dropped to 80% of normal during the subsequent season. A nearly 25% increase in leaf production was observed in *Eriophorum* during the first season owing to the preferential growth and maintenance of older leaves, the opening of the normally dense canopy (Archer and Tieszen, submitted, b), and increased root respiration and nutrient uptake following a single defoliation (Chapin and Slack, 1979). During the following growing season foliage production was normal.

A summary of characteristics of the various growth forms and their relationship to herbivory is given in Table 7. The synchronous growth strategy exhibited by shrubs enabled them to exploit more fully the most favorable portion of the arctic growing season. Such a strategy, however, exposes the total season's complement of photosynthetic tissue to loss by grazing. *Ledum*, the evergreen shrub, had the lowest photosynthetic rate (Table 1) of the life forms examined and was evidently dependent upon an extended leaf longevity to secure a positive carbon balance. The retention of leaves for more than one growing season likely requires the synthesis of compounds to protect them from herbivores (Cates and Orians, 1975) and from overwintering stress (Mooney and Dunn, 1970; Small, 1972). Even though these chemicals may represent a considerable expenditure, they enhance the competitive abilities of the plant by reducing loss of photosynthetic tissue to herbivores (Cates, 1975). These factors, in addition to the large consumption of assimilates necessary for year-round maintenance (Penning deVries, 1975), probably result in high growth costs for evergreen leaves and may result in fewer resources available to invest in replacing tissue lost to an herbivore. Jung et al. (1979) have reviewed and described the array of antiherbivore compounds present in arctic growth forms and found that those evergreen shrubs which were unpalatable to all rodents (*Ledum*, *Empetrum*, and *Cassiope*) contained the greatest variety of chemical compounds. *Ledum*, then, appears to have evolved to avoid grazing rather than to tolerate it.

Although Kelsall (1968) makes several ref-

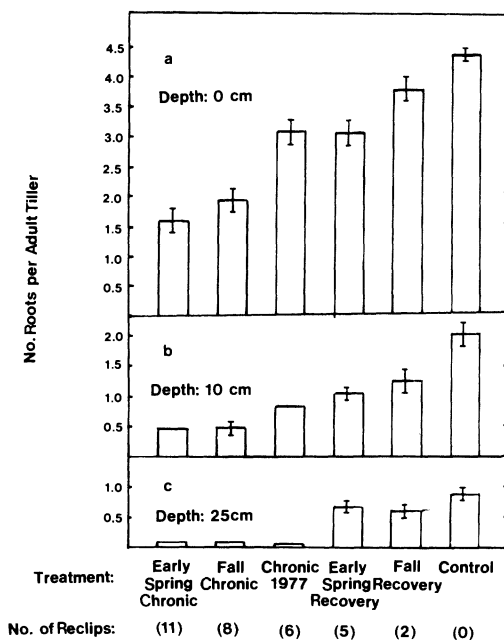


FIGURE 10. Leaf material regrown during the first and second season following a single clipping of 20 plants in late June 1976. (1) *Eriophorum vaginatum*, (2) *Carex aquatilis*, (3) *Salix pulchra*, and (4) *Ledum palustre*.

erences to browsing by caribou and muskox on *Ledum* and other evergreen shrubs, these plants rarely occur in the diets of arctic herbivores near Atkasook (Batzli and Jung, 1980, this volume; Batzli and Sobaski, 1980, this volume; White and Trudell, 1980, this volume; MacLean, pers. comm., 1980). Thomas and Grigal (1976) estimated that the evergreen *Kalmia* lost less than 1.5% of its total leaf area to herbivores. Reader (1978) examined *Ledum palustre* ssp. *groenlandicum* and two other arctic and subarctic ericads and estimated that these plants had lost less than 5% of their biomass to herbivores. He also observed that among the three ericads in his study, the retention time for overwintering leaves depended on their susceptibility to attack by herbivorous insects. Species with the shortest leaf longevity lost more biomass to insect herbivores, but at the same time were least affected by defoliation treatments. Thus, by allocating carbon to support leaf maintenance and preservation, *Ledum* essentially avoids growth problems associated with the

regeneration of leaf tissue following defoliation.

In contrast to the evergreen shrubs, deciduous shrubs had photosynthetic capacities two to four times higher (Table 1). However, these high carbon fixation rates in deciduous shrubs were offset by relatively short leaf longevities (Table 2). Such leaves contribute to the net carbon balance of the plant in only one growing season, but the synchronous pattern of leaf exsertion still exposes the entire season's photosynthetic tissue to potential loss to herbivores. Such a loss of leaf tissue represents not only a loss of photosynthetic input but also substantial amounts of nutrients, especially nitrogen (Chapin, 1980, this volume). *Salix* has apparently sacrificed leaf longevity, avoidance of herbivores, and leaf replacement potential for larger photosynthetic returns. While *Salix* was decidedly more tolerant than *Ledum* to defoliation it was much less so than were the graminoid growth forms. And, while the rate of carbon incorporation was highest in

Salix, it has a much higher probability of being grazed than *Ledum*. *Salix* does, however, have high levels of secondary compounds relative to the graminoid growth forms (Jung et al., 1979).

Patterns of photosynthetic rates and leaf longevities observed in graminoids were intermediate to those of the evergreen and deciduous shrubs. Because of their large nutrient reserves and the telescopic exsertion of leaf tissue from a protected apical meristem, *Carex* and *Eriophorum* were able to respond rapidly to defoliation by replacing the lost tissue. By initiating leaf growth early in the season graminoids were able to exploit an earlier portion of the growing season than were deciduous shrubs. The monocotyledons at Atkasook had the least amount of antiherbivore compounds of all the growth forms (Jung et al., 1979) but compensated for this lack of chemical defense by morphological and physiological mechanisms associated with tolerance to grazing.

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